



Phylogenetic relationships of the genera of Theaceae based on morphology

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Abstract

This work represents the first phylogenetic analysis of all genera belonging to the plant family Theaceae (*sensu lato*). The study is based on 60 morphological characters derived from herbarium specimens and an extensive literature review of 37 genera (including the outgroup). In contrast to the results from molecular data, Theaceae is here found to consist of one clade in which the recognition of two families or subfamilies would leave Theaceae s.s. paraphyletic. Within that clade, Ternstroemiaceae is supported as monophyletic and includes *Adinandra*, *Anneslea*, *Archboldiodendron*, *Balthasaria*, *Cleyera*, *Eurya*, *Euryodendron*, *Ficalhoa*, *Freziera*, *Symplococarpon*, *Ternstroemia* and *Visnea*. The paraphyletic Theaceae s.s. includes *Apterosperma*, *Camellia*, *Dankia*, *Gordonia*, *Pyrenaria*, *Schima*, and *Stewartia*. Tetrameristaceae (*Pentamerista* and *Tetramerista*) are supported as a monophyletic family, with Pellicieraceae (*Pelliciera*) as sister group, and that clade is sister to the rest of the taxa. Bonnetiaceae (*Archytaea* and *Bonnetia*) and Kielmeyeroideae of the Clusiaceae (*Caraipa*, *Haploclathra*, *Kielmeyera*, *Mahurea*, *Marila*, and *Neotatea*) are also supported as monophyletic. Given the differences between the results obtained from morphological and molecular data, we consider that there is still a need for further research, including combined analyses.

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The family Theaceae (*sensu lato*) represents a good example of a taxonomic group with controversial circumscription and uncertain phylogenetic affinities that requires detailed investigation. This family was previously classified in the order Guttiferales (Bentham and Hooker, 1862; Bessey, 1915) and Parietales (Lawrence, 1951), but more recent classifications place it in the order Theales (e.g., Takhtajan, 1980, 1997; Cronquist, 1981) or Ericales (e.g., Judd et al., 1999, 2002; Stevens, 2001 onwards) (see Table 1).

Theaceae (*sensu* Luna and Villaseñor, 1996; Luna, 1997) consists of 20 genera and 660–760 species. They are shrubs or small to large trees, with alternate spiral to distichous leaves, frequently at the tip of the branches, simple, entire or serrate (usually when young), with setaceous teeth (usually when young), without stipules, frequently evergreen in the tropical species; the flowers

are usually white or pink, solitary or in axillary groups, and frequently showy with strong scent, which makes them highly appreciated by gardeners; the fruit is generally a loculicidal capsule, an indehiscent baccate fruit, or a pome; in some genera the seeds are winged, in others they are covered by a fleshy tissue, and in yet others they are both unwinged and nude; the embryo can have a horseshoe shape or be straight. The best-known species in the family is the tea plant *Camellia sinensis* L. (Record, 1942).

The work of several authors shaped our understanding of Theaceae prior to the advances of large-scale molecular work in the 1990s. Keng (1962), highly influenced by Melchior's (1925) work, produced a very complete generic level monograph using morphology. Using wood anatomy, Record (1942) made a detailed study of the American genera; Liang and Baas (1990, 1991) and Baretta-Kuipers (1976) made more general studies. The work of Kobuski (1935–1963), whose classification was also influenced by that of Melchior (1925), is of particular relevance, because for more than

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Table 1
Different classifications for the family Theaceae

Bentham and Hooker (1862)	Bessey (1915)	Lawrence (1951)	Hutchinson (1973)	Heywood (1979; 1993)	Takhtajan (1980; 1997)	Cronquist (1981)	Young (1982)	Dahlgren (1983)	Thorne (1992)	Judd et al. (1999; 2002)	APG II (2003)
Order Guttiferales	Order Guttiferales	Order Parietales	Order Theales	Order Theales	Order Theales	Order Theales	Order Theales	Order Theales	Order Theales	Order Ericales	Order Ericales
Chlaenaceae	Achariaceae	Suborder Theinae	Actinidiaceae	Dipterocarpaceae	Asteropiaceae	Actinidiaceae	Actinidiaceae	Ancistrocladaceae	Actinidiaceae	Actinidiaceae	Actinidiaceae
Dipterocarpaceae	Bixaceae	Actinidiaceae	Bomeliaceae	Elatinaceae	Bomeliaceae	Caryocaraceae	Aquifoliaceae	Bomeliaceae	Ancistrocladaceae	Balsaminaceae	Balsaminaceae
Elatinaceae	Cariaceae	Caryocaraceae	Caryocaraceae	Guttiferae	Caryocaraceae	Clusiaceae	Cardiopteridaceae	Caryocaraceae	Aquifoliaceae	Clethraceae	Clethraceae
Guttiferae	Caryocaraceae	Dipterocarpaceae	Maregraviaceae	Maregraviaceae	Clusiaceae	Dipterocarpaceae	Clethraceae	Clusiaceae	Asteropiaceae	Cyrtellaceae	Cyrtellaceae
Hypericaceae	Cistaceae	Eucryphiaceae	Ochnaceae	Ochnaceae	Maregraviaceae	Elatinaceae	Cyrtellaceae	Dioncophyllaceae	Bomeliaceae	Ebenaceae	Diapensiaceae
Ternstroemiaceae (incl. Theaceae)	Cochlospermaceae	Guttiferae	Quinaceae	Quinaceae	Maregraviaceae	Maregraviaceae	Icacinaceae	Elatinaceae	Caryocaraceae	Ericaceae	Ebenaceae
	Dipterocarpaceae	(Hypericaceae)	Theaceae (incl. Ternstroemiaceae)	Theaceae (incl. Ternstroemiaceae)	Pellicieraceae	Medusagynaceae	Maregraviaceae	Lecythidaceae	Chrysobalanaceae	Fouquieriaceae	Fouquieriaceae
	Eucryphiaceae	Maregraviaceae			Pentaphyllaceae	Ochnaceae	Ochnothecaceae	Maregraviaceae	Chrysobalanaceae	Lecythidaceae	Lecythidaceae
	Flacourtiaceae	Medusagynaceae			Shadeniaceae	Ochnothecaceae	Pentaphyllaceae	Clusiaceae	Clusiaceae	Myrsinaceae	Halesiaceae
	Guttiferae	Ochnaceae	Theaceae (incl. Ternstroemiaceae)	Theaceae (incl. Ternstroemiaceae)	Stachyuraceae	Paracryphiaceae	Phellinaceae	Nepenthaceae	Cyrtellaceae	Polemoniaceae	Lecythidaceae
	Koerberliniaceae	Quimaceae			Symplocaceae	Pellicieraceae	Sphenostemonaceae	Ochnaceae	Dilleniaceae	Primulaceae	Maregraviaceae
	Malsherberiaceae	Stachyuraceae			Tetrameristaceae	Pentaphyllaceae	Stachyuraceae	Ochnothecaceae	Dioncophyllaceae	Primulaceae	Myrsinaceae
	Maregraviaceae	Theaceae (incl. Ternstroemiaceae)			Theaceae (incl. Ternstroemiaceae)	Quimaceae	Theaceae (incl. Ternstroemiaceae)	Pentaphyllaceae	Elatinaceae	Sapotaceae	Pellicieraceae
	Passifloraceae	Turneraceae			Sarcoalaeniaceae	Sarcoalaeniaceae	Quinaceae	Quinaceae	Lecythidaceae	Styracaceae	Polemoniaceae
	Quimaceae	Violaceae			Sytopetalaceae	Sphaerosetalaceae	Scytotetralaceae	Quinaceae	Elatinaceae	Styracaceae	Polemoniaceae
	Stachyuraceae				Tetrameristaceae	Tetrameristaceae	Stachyuraceae	Medusagynaceae	Maregraviaceae	Syracaceae	Syracaceae
	Theaceae (incl. Ternstroemiaceae)				Theaceae (incl. Ternstroemiaceae)	Theaceae (incl. Ternstroemiaceae)	Theaceae (incl. Ternstroemiaceae)	Nepenthaceae	Medusagynaceae	Theaceae	Sapotaceae
	Turneraceae							Ochnaceae	Ochnaceae	Theophrastaceae	Sarracenaceae
	Violaceae							Oncotheaceae	Paracryphiaceae	Theophrastaceae	Sarracenaceae
								Paracryphiaceae	Pellicieraceae	Symplocaceae	Symplocaceae
								Pellicieraceae	Pentaphyllaceae	Ternstroemiaceae	Symplocaceae
								Phellinaceae	Phellinaceae	Ternstroemiaceae	Ternstroemiaceae
								Quinaceae	Quinaceae	Theaceae	Theaceae
								Sarracenaceae	Sarracenaceae	Theophrastaceae	Theophrastaceae
								Sytopetalaceae	Sytopetalaceae		
								Sphenostemonaceae	Sphenostemonaceae		
								Stachyuraceae	Stachyuraceae		
								Strasburgeriaceae	Strasburgeriaceae		
								Symplocaceae	Symplocaceae		
								Tetrameristaceae	Tetrameristaceae		
								Theaceae (incl. Ternstroemiaceae)	Theaceae (incl. Ternstroemiaceae)		
								Ternstroemiaceae	Ternstroemiaceae		

Table 2
Classification of Theaceae by Keng (1962)

Family THEACEAE	
Subfamily Ternstroemioidae	
Tribe Ternstroemiaceae. <i>Anneslea</i> , <i>Ternstroemia</i>	
Tribe Adinandreae. <i>Adinandra</i> , <i>Archboldiodendron</i> , <i>Cleyera</i> , <i>Eurya</i> , <i>Freziera</i> , <i>Killipiodendron</i> (= <i>Freziera</i> in this work), <i>Melchiora</i> (= <i>Balthasaria</i> in this work), <i>Patascoya</i> (= <i>Freziera</i> in this work), <i>Symplococarpus</i> , <i>Visnea</i>	
Tribe Sladeniaceae. <i>Sladenia</i>	
Subfamily Camellioideae	
Tribe Sturtiidae. <i>Hartia</i> (= <i>Stewartia</i> in this work), <i>Stewartia</i> (= <i>Stewartia</i> in this work)	
Tribe Gordoniaceae	
Subtribe Gordoniinae. <i>Gordonia</i> , <i>Laplacea</i> (= <i>Gordonia</i> in this work)	
Subtribe Schimiinae. <i>Franklinia</i> (= <i>Gordonia</i> in this work), <i>Schima</i>	
Tribe Camellieae	
Subtribe Camellinae. <i>Camellia</i> , <i>Piquetia</i> (= <i>Camellia</i> in this work), <i>Stereocarpus</i> (= <i>Camellia</i> in this work), <i>Yunnanea</i> (= <i>Camellia</i> in this work)	
Subtribe Pyrenariinae. <i>Pyrenaria</i> , <i>Tutcheria</i> (= <i>Pyrenaria</i> in this work)	

three decades he produced detailed studies of many genera from all over the world, in more than 45 publications.

The infrafamilial classification of Theaceae has been controversial. Keng (1962) thought that Theaceae was not clearly defined. He thought it was difficult to find a single character that distinguished it from other families, such as Dilleniaceae, Hypericaceae, and Actinidiaceae. He classified the family into two subfamilies, Ternstroemioidae and Camellioideae (Table 2). For Keng (1962), these two subfamilies constituted the “Grundstock” (Melchior’s word) of the Theaceae. According to him, unilacunar nodes, tricolporate pollen grains and sclereids are common to both subfamilies, but also frequently present in other dicotyledonous families. The most relevant morphological characters that he used to distinguish these two subfamilies are summarized in Table 3. Keng concluded that each one of the

subfamilies has a mixture of “primitive and advanced” characters. The characteristics of certain floral structures (for example, the calyx and corolla differentiation, the number of stamens, and the position of the ovary) made him consider Ternstroemioidae to be the most advanced group, but other floral characteristics, such as the structure of the stamens, and especially the characters of the seed, indicated to him that the Camellioideae was the most advanced group. Wood anatomy studies have also been used to suggest that Camellioideae is the most specialized subfamily.

Cronquist (1981) recognized four subfamilies within Theaceae (Asteropeioidae, Bonnetioideae, Ternstroemioidae, and Theoideae), whereas Takhtajan (1997) recognized three subfamilies (Ternstroemioidae, Theoideae, and Sladenioidae). Molecular studies since the early 1990s have challenged these classifications; Asteropeioidae is classified as a family within the order Caryophyllales (APG II, 2003); Bonnetioideae is classified as a family within the order Malpighiales (Savolainen et al., 2000) or with uncertain position (APG II, 2003); Sladenioidae is considered a family with uncertain position (APG I, 1998) or classified within Ericales, together with Ternstroemiaceae (Savolainen et al., 2000; Anderberg et al., 2002; Bremer et al., 2002; APG II, 2003).

Traditionally, the family has been circumscribed by the following combination of characters, none of them unique to the family Theaceae: (1) alternate leaves (Figs 1B, C), (2) unilacunar nodes, (3) margin of the serrated leaves with “setaceous” teeth (*sensu* Hickey, 1979), (4) sepals and petals with imbricate ptyxis or quincuncial (Figs 1A, C), (5) many stamens (Fig. 1C), and (6) tricolporate or tricolporoidate pollen. The genera are tropical and subtropical in distribution, with 11 found only in East Asia, three exclusively in Africa, two in the Neotropics, three in East Asia and North America, and one, *Ternstroemia*, throughout the tropics and subtropics (Table 4). Five genera have restricted distributions, *Apterosperma* (southern China), *Archboldiodendron* (New Guinea), *Dankia* (Vietnam), *Euryodendron* (southern China), and *Visnea* (Canary Islands).

Table 3
Morphological characters used to distinguish the subfamilies of Theaceae (*sensu* Keng, 1962)

Character	Ternstroemioidae	Camellioideae
Stomata	ranunculaceous (=anomocytic)	gordoniaceous (=paracytic), except for <i>Franklinia</i> and <i>Pyrenaria</i>
Flower size	usually small	usually large and showy
Perianth	calyx and corolla clearly differentiated	calyx and corolla sometimes not clearly differentiated
Fruit	baccate or rarely a pome, reddish to purple when mature	capsular, usually brown or dark brown when mature and frequently pubescent
Pericarp	fleshy, rarely coriaceous (e.g. <i>Ternstroemia</i> , <i>Anneslea</i> and <i>Visnea</i>)	thick or less frequently coriaceous (some species of <i>Camellia</i> and <i>Tutcheria</i>)
Seed	seed cover usually cartilaginous and thin, of 3–10 cells thickness	seed cover thick, except in <i>Schima</i> and <i>Franklinia</i> , where it is corky and relatively thin
Pollen	pollen grains small; exine almost smooth	pollen grains large; exine finely ornamented

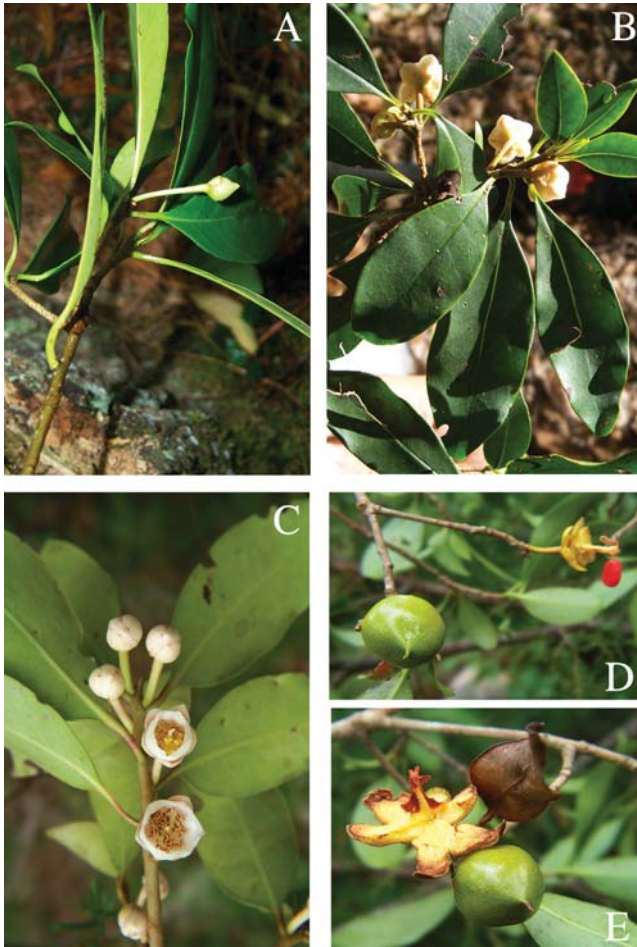


Fig. 1. General morphological features of Theaceae. (A) Flower buds of *Ternstroemia huasteca* B.M. Barthol., Pérez Ortega 39 (FCME); (B) Flowers of *T. sylvatica* Schltdl. et Cham. from behind, O. Alcántara 5505 (FCME); (C) Flowers of *Cleystera theaeoides* (Sw.) Choisy, O. Alcántara 5506 (FCME); (D) Fruits of *T. sylvatica*, O. Alcántara 5505 (FCME); (E) Old flower and fruits of *T. sylvatica*, O. Alcántara 5505 (FCME).

The genus *Camellia* is the largest in the family (Table 4; Chang and Bartholomew, 1984); even so, it is restricted to China and adjacent countries. Southern China is a center of diversity of many genera of Theaceae, and also represents an area of endemism and the main massing of *Camellia* in a pan-biogeographic sense (Luna and Contreras-Medina, 2000). In the Neotropics, most Theaceae *sensu lato* occur in South America, mainly in Colombia, Peru, Bolivia, and in Venezuelan Guyana (Weitzman, 1995). The past distribution of Theaceae *sensu lato* was more extensive, as fossils assignable to several genera are known from Europe, where there are currently no members of this group, and in both East Asia and North America there are fossils of taxa not currently found there (Kvacek and Walther, 1984; Grote and Dilcher, 1989, 1992; Schönenberger and Friis, 2001).

Ternstroemioidae *sensu* Keng (1962) are the most widely distributed. Some genera are found exclusively in East Asia, Africa, or America, but *Ternstroemia* has a more extensive distribution, being found in Asia, Africa, America, and Australia.

The goal of this work is to conduct a cladistic analysis based on morphology in order to better understand the evolution and classification of the members in the family Theaceae, comparing our results to recent DNA cladistic analyses based on more limited sampling. With this we suggest research priorities for this complex and poorly known group, both problematic characters and taxa.

Materials and methods

A complete review of the taxonomic literature for Theaceae was undertaken, which included the original descriptions of genera and species, floristic works at a world-wide level, monographs of genera, and any other work with information about morphology and biology of the taxa.

Table 4
Distribution and approximate number of species (parentheses) of the genera of Theaceae

East Asia–Malesia	Africa	America	E Asia–America	E. Asia–America, Africa, Australia
<i>Adinandra</i> (76)	<i>Balthasaria</i> (3)	<i>Freziera</i> (58)	<i>Cleystera</i> (17)	<i>Ternstroemia</i> (110–160)
<i>Anneslea</i> (2–3)	<i>Visnea</i> (1)	<i>Symplococarpon</i> (1)	<i>Gordonia</i> (70)	
<i>Archboldiodendron</i> (1)	<i>Ficalhoa</i> (1)		<i>Stewartia</i> (8)	
<i>Camellia</i> (200)				
<i>Eurya</i> (80–140)				
<i>Pyrenaria</i> (30)				
<i>Schima</i> (1)				
<i>Apterosperma</i> (1)				
<i>Dankia</i> (1)				
<i>Euryodendron</i> (1)				
<i>Sladenia</i> (2)				

Our personal observations included a thorough review of herbarium material from the National Herbarium of Mexico, Instituto de Biología, UNAM (MEXU); Royal Botanical Gardens of Kew (K); Natural History Museum Herbarium, London (BM); Harvard University Herbaria, Cambridge, Massachusetts (A, B, ECON, GH); Missouri Botanical Garden, St Louis, Missouri (MO); the New York Botanical Garden, Bronx, New York (NY); and the United States National Herbarium, Smithsonian Institution, Washington, DC (US). A representative exemplar sampling for the species was used, including at least four specimens per species, and especially the types, when available. We tried to sample as many species per genus as possible (Appendix 1). Emphasis was placed on macromorphological characters.

Taxon sampling

After reviewing herbarium material and literature, we established the following criteria to select the terminals to be included in our analysis:

1. We followed the generic circumscription adopted by Luna and Villaseñor (1996), summarized in Appendix 2.

2. We included all genera that were classified in Theaceae by at least one of the following authors: Cronquist (1981); Luna and Villaseñor (1996); Takhtajan (1997); Prince and Parks (2001); or Stevens (2001 onwards). We chose Cronquist (1981) and Takhtajan (1997), because they are the traditional classifications most commonly used; Luna and Villaseñor (1996), because they offered the last review of Theaceae *sensu lato*; Prince and Parks (2001), because they provided the most comprehensive DNA phylogenetic analysis of Theaceae s.s.; and Stevens (2001 onwards), because he offered one of the most comprehensive classification of seed plants based on DNA phylogenetic analyses (Table 5).

3. We included representative genera that were at some point classified as part of Theaceae and that are now considered, at least by one of the mentioned authors, to belong in other families within the same order, Theales/Ericales (Table 5).

4. We included the genus *Cornus* L., because according to DNA phylogenetic analysis (e.g., Bremer et al., 2002; APG II, 2003) it shares a most common recent ancestor with Ericales, which is different from the one of Malpighiales, an order in which many of the genera formerly placed in Theaceae are classified according to this type of data.

5. We used the genus *Physena*, a Caryophyllales, as the functional outgroup to root the tree, because this order is certainly an outgroup of the clades that include Malpighiales and Theales, and because the genus *Asteropeia* was placed in this order by Savolainen et al. (2000).

Considering the synonymy, our sampling consisted, aside from the functional outgroup (*Physena*), of the following 36 genera: *Actinidia*, *Adinandra*, *Anneslea* (including *Paranneslea*), *Apterosperma*, *Archboldiodendron*, *Archytaea* (including *Ploiarium*), *Asteropeia*, *Balthasaria*, *Bonnetia*, *Camellia*, *Caraipa*, *Cleyera*, *Cornus*, *Dankia*, *Eurya* (including *Ternstroemiopsis*), *Euryodendron*, *Ficalhoa*, *Freziera* (including *Patascocya* and *Killipiodendron*), *Gordonia* (including *Franklinia* and *Laplacea*), *Haploclathra*, *Kielmeyera*, *Marcgravia*, *Mahurea*, *Marila*, *Neotatea*, *Pelliciera*, *Pentamerista*, *Pentaphylax*, *Pyrenaria* (including *Tutcheria*), *Schima*, *Sladenia*, *Stewartia* (including *Hartia*), *Symplococarpon*, *Tetramerista*, *Ternstroemia*, and *Visnea*.

To facilitate discussion, the genera will be grouped *a priori* and preliminarily as follows:

1. Clusiaceae subfamily Kielmeyeroideae (6): *Caraipa*, *Haploclathra*, *Kielmeyera*, *Mahurea*, *Marila*, and *Neotatea*.

2. Theaceae:

- a. Theaceae s.s. (7): *Apterosperma*, *Camellia*, *Dankia*, *Gordonia* (including *Franklinia* and *Laplacea*), *Pyrenaria* (including *Tutcheria*), *Schima*, and *Stewartia* (including *Hartia*).

- b. Ternstroemiaceae (13): *Adinandra*, *Anneslea* (including *Paranneslea*), *Archboldiodendron*, *Balthasaria*, *Cleyera*, *Eurya* (including *Ternstroemiopsis*), *Euryodendron*, *Ficalhoa*, *Freziera* (including *Patascocya* and *Killipiodendron*), *Sladenia*, *Symplococarpon*, *Ternstroemia*, and *Visnea*.

3. Bonnetiaceae (2): *Archytaea* (including *Ploiarium*) and *Bonnetia*.

4. Tetrameristaceae (2): *Pentamerista* and *Tetramerista*.

5. Actinidiaceae (1): *Actinidia*.

6. Asteropeiaceae (1): *Asteropeia*.

7. Cornaceae (1): *Cornus*.

8. Marcgraviaceae (1): *Marcgravia*.

9. Pellicieraceae (1): *Pelliciera*.

10. Pentaphylacaceae (1): *Pentaphylax*.

11. Physenaceae (1): *Physena*.

Data analyses

A data matrix of 37 taxa and 60 characters (Table 6) was constructed using WinClada (Nixon, 2002). We included five problematic continuous characters that were analyzed using descriptive statistics to define character states. These characters were corolla length, number of stamens, pollen size, number of ovules per loculus, and seed length. For these characters we constructed graphs (not shown) including all available measurements at the species level. Based on these graphs we defined intervals, trying to avoid overlapping. These intervals were used to construct a second set of graphs (figures shown under the corresponding characters) in

Table 5

Genera included in Theaceae by different authors (de Candolle, 1824; Don, 1831; Spach, 1835; Endlicher, 1843; Bentham and Hooker, 1862; Baillon, 1872; von Szyszlowicz, 1895; Melchior, 1925) and their recent classifications. In bold are those that were not included in this study

Genus	Classification according to Luna and Villaseñor (1996) = included in Theaceae	ORDER and family according to Cronquist (1981)	ORDER and family according to Takhtajan (1997)	ORDER and family according to Stevens (2001 onwards)
<i>Actinidia</i> Lindl.	Actinidiaceae	THEALES Actinidiaceae	ACTINIDIALES Actinidiaceae	ERICALES Actinidiaceae
<i>Adinandra</i> Jack	=	–	THEALES Theaceae	ERICALES Pentaphylacaceae
Anneslea Wall.	=	THEALES Theaceae	THEALES Theaceae	ERICALES Pentaphylacaceae
<i>Anthodiscus</i> G. Mey.	Caryocaraceae	THEALES Caryocaraceae	THEALES Caryocaraceae	MALPIGHIALES Caryocaraceae
<i>Apatelia</i> DC.	= <i>Saurauia</i>	–	–	–
<i>Apterosperma</i> H.T. Chang	=	–	–	ERICALES Theaceae
<i>Archboldiodendron</i> Kobuski	=	–	THEALES Theaceae	–
<i>Archytaea</i> Mart.	Bonnetiaceae	–	HYPERICALES Bonnetiaceae	MALPIGHIALES Bonnetiaceae
<i>Asteropeia</i> Thouars	Asteropeiaceae	THEALES Theaceae	THEALES Asteropeiaceae	–
<i>Balthasaria</i> Verdc.	=	–	THEALES Theaceae	ERICALES Pentaphylacaceae
<i>Blumea</i> G. Don	= <i>Saurauia</i>	–	–	–
<i>Bonnetia</i> Mart.	Bonnetiaceae	THEALES Theaceae	HYPERICALES Bonnetiaceae	MALPIGHIALES Bonnetiaceae
<i>Camellia</i> L.	=	THEALES Theaceae	THEALES Theaceae	ERICALES Theaceae
<i>Caraipe</i> Aubl.	Clusiaceae	–	HYPERICALES Clusiaceae	–
<i>Caryocar</i> L.	Caryocaraceae	THEALES Caryocaraceae	THEALES Caryocaraceae	MALPIGHIALES Caryocaraceae
<i>Cespedezia</i> Ruiz & Pav.	Ochnaceae	–	OCHNALES Sauvagesiaceae	–
<i>Clematoclethra</i> Maxim.	Actinidiaceae	THEALES Actinidiaceae	ACTINIDIALES Actinidiaceae	ERICALES Actinidaceae
<i>Cleyera</i> Thunb.	=	–	THEALES Theaceae	ERICALES Pentaphylacaceae
<i>Cochlospermum</i> Kunth	Bixaceae or Cochlospermaceae	VIOLALES Bixaceae	CISTALES Cochlospermaceae	MALVALES Bixaceae
<i>Dankia</i> Gagnep.	=	–	–	–
<i>Dicalyx</i> Poir.	<i>Symplocos</i> Jacq. Symplocaceae	–	–	–
<i>Eroteum</i> Sw.	= <i>Freziera</i>	–	–	–
<i>Eurya</i> Thunb.	=	THEALES Theaceae	THEALES Theaceae	ERICALES Pentaphylacaceae
<i>Euryanthe</i> Cham. & Schldl.	= <i>Amoreuxia</i> Moc. & Sessé Cochlospermaceae	–	–	–
<i>Euryodendron</i> H. T. Chang	=	–	–	–
<i>Ficalhoa</i> Hiern	=	–	–	ERICALES Sladeniaceae
<i>Franklinia</i> Marshall	= <i>Gordonia</i>	THEALES Theaceae	THEALES Theaceae	ERICALES Theaceae
<i>Freziera</i> Willd.	=	–	THEALES Theaceae	ERICALES Pentaphylacaceae
<i>Geeria</i> Blume	= <i>Eurya</i>	–	–	–
<i>Godoya</i> Ruiz & Pav.	Ochnaceae	–	OCHNALES Sauvagesiaceae	MALPIGHIALES Ochnaceae
<i>Gordonia</i> J. Ellis	=	–	THEALES Theaceae	ERICALES Theaceae
<i>Haemocharis</i> Salisb.	= <i>Gordonia</i>	–	–	–

Table 5
(continued)

Genus	Classification according to Luna and Villaseñor (1996) = included in Theaceae	ORDER and family according to Cronquist (1981)	ORDER and family according to Takhtajan (1997)	ORDER and family according to Stevens (2001 onwards)
<i>Haploclathra</i> Benth.	Clusiaceae	–	–	–
<i>Hartia</i> Dunn	= <i>Stewartia</i>	–	–	= <i>Stewartia</i>
<i>Kielmeyera</i> Mart.	Clusiaceae	THEALES ? Theaceae	HYPERICALES Clusiaceae	MALPIGHIALES Clusiaceae
<i>Killipiodendron</i> Kobuski	= <i>Freziera</i>	–	–	–
<i>Laplacea</i> Kunth	= <i>Gordonia</i>	THEALES Theaceae	THEALES Theaceae	ERICALES Theaceae
<i>Lettsomia</i> Ruiz & Pav.	= <i>Freziera</i>	–	–	–
<i>Leucoxydon</i> G. Don	= <i>Diospyros</i> L.	–	–	–
<i>Mahurea</i> Aubl.	Clusiaceae	–	HYPERICALES Clusiaceae	–
<i>Malachodendron</i> J. Mitch.	= <i>Stewartia</i>	–	–	–
<i>Marcgravia</i> L.	Marcgraviaceae	THEALES Marcgraviaceae	THEALES Marcgraviaceae	ERICALES Marcgraviaceae
<i>Marila</i> Sw.	Clusiaceae	–	–	MALPIGHIALES Clusiaceae
<i>Melchiora</i> Kobuski	= <i>Baltasaria</i>	–	–	–
<i>Medusagyne</i> Baker	Medusagynaceae	THEALES Medusagynaceae	MEDUSAGYNALES Medusagynaceae	MALPIGHIALES Medusagynaceae
<i>Microsemma</i> Labill.	<i>Lethedon</i> Spreng.	–	THYMELAEALES Thymelaeaceae	MALVALES Thymelaeaceae
<i>Mountnorrisia</i> Szyszyl.	= <i>Ameslea</i>	–	–	–
<i>Neotatea</i> Maguire	Clusiaceae	THEALES ? Theaceae	–	–
<i>Norantea</i> Aubl.	Marcgraviaceae	THEALES Marcgraviaceae	THEALES Marcgraviaceae	ERICALES Marcgraviaceae
<i>Omphalocarpum</i> P. Beauv.	Sapotaceae	–	–	–
<i>Paranneslea</i> Gagnep.	= <i>Ameslea</i>	–	–	–
<i>Patascocya</i> Urb.	= <i>Freziera</i>	–	–	–
<i>Pelliciera</i> Planch. & Triana	Pellicieraceae	THEALES Pellicieraceae	THEALES Pellicieraceae	ERICALES Pellicieraceae
<i>Pentaphylax</i> Gardner & Champ.	Pentaphylacaceae	THEALES Pentaphylacaceae	THEALES Pentaphylacaceae	ERICALES Pentaphylacaceae
<i>Piquetia</i> Hallier f.	= <i>Camellia</i>	THEALES Theaceae	–	–
<i>Ploiarium</i> Korth.	= <i>Archytaea</i>	THEALES Theaceae	HYPERICALES Bonnetiaceae	MALVALES Thymelaeaceae
<i>Poecilandra</i> Tul.	= Ochnaceae	–	OCHNALES Sauvagesiaceae	–
<i>Poeciloneuron</i> Bedd.	Clusiaceae	–	HYPERICALES Clusiaceae	–
<i>Polyspora</i> Sweet	= <i>Gordonia</i>	–	–	ERICALES Theaceae
<i>Pyrenaria</i> Blume	=	–	THEALES Theaceae	ERICALES Theaceae
<i>Reinwardtia</i> Korth.	= <i>Ternstroemia</i>	–	LINALES Linaceae	–
<i>Quiina</i> Aubl.	Clusiaceae	THEALES Quiinaceae	OCHNALES Quiinaceae	MALPIGHIALES Quiinaceae
<i>Ruyschia</i> Jacq.	Marcgraviaceae	THEALES Marcgraviaceae	THEALES Marcgraviaceae	ERICALES Marcgraviaceae
<i>Saurauia</i> Willd.	Actinidiaceae	THEALES Actinidiaceae	ACTINIDIALES Actinidiaceae	ERICALES Actinidiaceae
<i>Schima</i> Reinw. ex Blume	=	–	THEALES Theaceae	ERICALES Theaceae
<i>Sladenia</i> Kurz	=	THEALES Theaceae	THEALES Theaceae	ERICALES Sladeniaceae

Table 5
(continued)

Genus	Classification according to Luna and Villaseñor (1996) = included in Theaceae	ORDER and family according to Cronquist (1981)	ORDER and family according to Takhtajan (1997)	ORDER and family according to Stevens (2001 onwards)
<i>Stachyurus</i> Siebold & Zucc.	Stachyuraceae	VIOLALES Stachyuraceae	THEALES Stachyuraceae	CROSSOSOMATALES Stachyuraceae
<i>Stereocarpus</i> Hallier	= <i>Camellia</i>	–	–	–
<i>Stewartia</i> L.	=	–	THEALES Theaceae	ERICALES Theaceae
<i>Symplococarpon</i> Airy Shaw	=	–	THEALES Theaceae	ERICALES Pentaphylacaceae
<i>Taonabo</i> Aubl.	= <i>Ternstroemia</i>	–	–	–
<i>Ternstroemia</i> Mutis ex L.f.	=	THEALES Theaceae	THEALES Theaceae	ERICALES Pentaphylacaceae
<i>Ternstroemiopsis</i> Urb.	= <i>Eurya</i>	–	–	–
<i>Tetramerista</i> Miq.	Tetrameristaceae	THEALES Tetrameristaceae	THEALES Tetrameristaceae	ERICALES Tetrameristaceae
<i>Thea</i> L.	= <i>Camellia</i>	= <i>Camellia</i>	= <i>Camellia</i>	–
<i>Tremanthera</i> P. & K.	= <i>Saurauia</i>	THEALES Actinidiaceae	–	–
<i>Tutcheria</i> Dunn.	= <i>Pyrenaria</i>	–	THEALES Theaceae	–
<i>Ventenatia</i> P. Beauv.	= <i>Oncoba</i> Forssk. Flacourtiaceae	–	–	–
<i>Visnea</i> L.f.	=	THEALES Theaceae	THEALES Theaceae	ERICALES Pentaphylacaceae
<i>Wickstroemia</i> Schrad.	= <i>Gordonia</i>	–	–	–
<i>Yunnanea</i> Hu	= <i>Camellia</i>	–	–	–

which all available information was grouped within the defined intervals to show the distribution of character states. Finally, we plotted the information at generic level and traced the character states to define the corresponding coding for the characters in the cladistic matrix (figures shown under the corresponding characters). We coded the character states for each genus according to the values falling within the standard deviation in the generic plots. When available, we also considered for the matrix coding reports without precise values, because that allowed us to place them within a range, even if they were not used to construct the plots; these cases are mentioned under the discussion of the characters.

Parsimony tree searches were conducted using Nona (Goloboff, 1999). A total of 10 000 random addition sequences (seeds) were submitted to TBR holding 50 trees. These were conducted in sets of 1000 seeds followed by a more extensive TBR holding 50 000 trees (10 times: h/50 mu*1000 h50 000 max*). All most parsimonious trees (MPTs) found were collected, and ambiguously supported branches were collapsed. Identical trees were then removed and a consensus was calculated using the option “Nelsen” in WinClada (Nixon, 2002).

Any potential ambiguity in the placement of taxa was evaluated using the option “ambiguity filter” under terminals in WinClada (Nixon, 2002). This option highlights the taxa that have the selected level of ambiguity. Taxa with more than 20% ambiguity were

sequentially removed, and the resulting matrices were analyzed in the same way as the complete matrix. The topology of the resulting consensus trees was visually compared to assess the effect of removing ambiguous taxa in the topology of the consensus of the MPTs.

A simple sequential character removal analysis (Davis et al., 1993) was conducted as implemented in WinClada (Nixon, 2002), with TBR set to 100 replications holding 20 trees, followed by more extensive TBR holding 5000 for each of the matrices resulting from the sequential elimination of a character (60 times: h/20 mu*100 h5000 max* nel). The resulting 60 consensus trees were compared visually to assess the relevance of each character in the topology of the MPTs consensus.

A Jackknife analysis was conducted as implemented in WinClada (Nixon, 2002), re-sampling 1000 times with TBR set to 100 replications holding 20 trees, followed by more extensive TBR holding 5000 trees, and saving the consensus for each re-sampled matrix (1000 times: h/20 mu*100 h5000 max* nel).

Bremer support (Bremer, 1994) was calculated using the option “BS 5” of Nona (Goloboff, 1999) on 10 000 trees held in memory.

Only unambiguously optimized characters present in all the MPTs (those that did not change their branch support when they were optimized as acctran or deltran) were mapped onto the consensus tree using the option “apo” of Nona (Goloboff, 1999).

Table 6

Data matrix including 37 taxa and 60 characters. ? = missing data; - = inapplicable data; A = 0 and 1; B = 1 and 2; C = 0, and 2; D = 0, 1, and 2; E = 0, 2, and 3; F = 1 and 3; G = 0 and 4; H = 0, 2, 3, and 4; I = 2 and 4; J = 2 and 3; K = 0 and 3. Acronyms next to genera represent family or subfamily (capitals), in Theaceae they are followed by tribe and, when existing, subtribe (lower case) following Keng (1962). Families outside Theaceae follow Stevens (2001 onwards).

	5	10	15	20	25	30	35	40	45	50	55	60
<i>Physena</i> PHY	10000100?00?0?11000020110-1001-A0100001?20?001111021--00?0??											
<i>Actinidia</i> ACT	B001AA211100C0110AA02011A1000011B01AA01?0??0A2001010-1011A10											
<i>Adinandra</i> TER-Adi	100011CA21011011011AA0A11011B-10111A10A01100100A2B0A011-00100A1											
<i>Anneslea</i> TER-Ter	100011CA210110110011210111-001111100011001?101100112--010101											
<i>Aptosperma</i> THE	10?011C1210?1??100102?0A1A-001110100001???0111??01011-0?0010											
<i>Archboldiodendron</i> TER-Adi	100011C021011011A010110111-A01111100011???012??1011-001?011											
<i>Archytaea</i> BON	A1A000C0210101010010A101AB210100B00A000100?00200A0000-AA0010											
<i>Asteropeia</i> AST	10?001000101A??100102A00002001100100001120?00100A0011-00?01?											
<i>Balthasaria</i> TER-Adi	100011C0210110?1AA10210112-10111A100011001?012??00A??000?011											
<i>Bonnetia</i> BON	A11000C0010101010010DA01ABB10100B0A0001100?0021AA00A0-A0?010											
<i>Camellia</i> CAM-Cam-Cam	100011EA21011001AA10DA011B-A0111A1A00A11A010A100A0011-000000											
<i>Caraipa</i> KIE	111001001110B101A000200A010001002010020A00?0A10000010-100001											
<i>Cleyera</i> TER-Adi	100011C1210110111A1021011A-10111A10101100100A2B0A011-A000011											
<i>Cornus</i> COR	F0?01020DA00101AAAA020AACD00AD00111001101?2A00AA031--0110A?											
<i>Dankia</i>	10?0?0?0?0?0?10?10010200111-0011?B100001???011??10011-??0??											
<i>Eurya</i> TER-Adi	100011EA21011011AA10B11110-1011101000110A100A1B01011-0000011											
<i>Eurydendron</i>	10?01?G0210??0?10110210110-101110101011???012??0011-00?01?											
<i>Ficalhoa</i> SLA	10001?H02111A0?101102101000001110000100011?012??10011-00?010											
<i>Freziera</i> TER-Adi	10A01AC021011A111A10D2111A-0011AA100011001?0A2?00111-0000011											
<i>Gordonia</i> CAM-Gor-Gor	100011CA2101A0A1AA10B1A11B-0011AB0100A110010AB00AA0A1-100000											
<i>Haploclathra</i> KIE	110001001010B1000002000B0001001000000A00?0A00000000-100000											
<i>Kielmeyera</i> KIE	110001100010A1010000B01002000100B0100C010A?0020000000-110000											
<i>Mahurea</i> KIE	1110A1002010100100002000010001002000020100?0020000000-010010											
<i>Marcgravia</i> MAR	B011A1I0AA01A031AA0AD00001A00112A1A10010A1?002000101A-001A1?											
<i>Marila</i> KIE	1110A1202A10D000000A200A0D0001A0B000A20A00?0A20000000-010010											
<i>Neotatea</i> KIE	01?0A1C0201010010000A00002100100B000021100?0020000000-100010											
<i>Pelliciera</i> PEL	00?10?20?00100210010A10113-010100100011101?0001?0023--00?10?											
<i>Pentamerista</i> TET	A0?100J01?010?110A10A101001010100100001000?000K?0010-001?0A0											
<i>Pentaphylax</i> PEN	10001?212?000?0100A0200A00100010010?1010A1?001A10A011-10?001											
<i>Pyrenaria</i> CAM-Cam-Pyr	100011E0210110A10A10210111-A01112110001A0010110010AAA1000000											
<i>Schima</i> CAM-Gor-Sch	100011EA2101A0010A1021011B-A0111B10000110010111001011-100001											
<i>Sladenia</i> TER-Sla	10001?E02101101101102001000001110101101001?0010001000-10?010											
<i>Stewartia</i> CAM-Stu	100011E1210110010A10220112-A0111B0100011001011?0A0011-A10000											
<i>Symplocarpon</i> TER-Adi	100011??0110111A10210110-10111A100011001?1A1?01012--0000A1											
<i>Ternstroemia</i> TER-Ter	100011CA210110110A11B1A11A-A0111B1000A10010001A0A011-A0101A1											
<i>Tetramerista</i> TET	10?100J01?010?110A10A101001010100100001100?000K?0010-001?000											
<i>Visnea</i> TER-Adi	100011C121011011A010200110-101110100011001?11B?01012--010011											

The final tree figures are metafile trees saved in WinClada (Nixon, 2002) and edited in PowerPoint and Photoshop 6.0.

Results and discussion

Characters and character states

The following set of 60 characters was derived largely from external morphology; other characters are derived from wood anatomy, palynology, and organic compounds.

1. Life form: (0) pachycaul; (1) leptocaul; (2) lianas; (3) herbaceous. The first three states of this character are represented by plants that have some type of secondary growth in the aerial portions. Pachycaul plants develop

a buttress in contrast to leptocaul (trees or shrubs), which do not have a buttress; lianas require external support. These features are related to biomechanical factors that are genetically controlled. Most of the taxa included in this analysis are leptocaul represented by shrubs or more commonly medium size trees, although some species can reach 30 m. The genera of Clusiaceae are leptocaul, except for the *Neotatea* species, which are pachycauls. The genus *Pelliciera* is also pachycaul. Most species in *Bonnetia sensu lato* (including the possible “genera” *Neblinaria*, *Acopanea*, and *Neogleasonia*) are pachycauls, but there are some leptocauls; *Archytaea* and *Pentamerista* are also polymorphic, including leptocauls and pachycauls. Both *Actinidia* and *Marcgravia* are polymorphic including leptocauls and lianas. According to the literature, *Ternstroemia* includes herbaceous and climbing forms, but in the examined

specimens these life forms were not found and therefore this taxon was coded as leptocaul. Herbaceous forms are only present in *Cornus*, which also includes leptocaul species.

2. Xanthones: (0) absent; (1) present. The only taxa that produce a wide range of xanthones are Bonnetiaceae and Kielmeyeroideae (Clusiaceae).

3. Siphonostele in petiole: (0) absent; (1) present. Siphonostele is only present in *Marcgravia* (Schofield, 1968), *Bonnetia*, some Clusiaceae (Kielmeyeroideae), *Mahurea*, *Marila*, and *Caraipa* (Stevens, unpubl. manuscript), and in some species of *Archytaea* (Stevens, unpubl. manuscript) and *Freziera* (Weitzman, 1987a), which were coded as polymorphic. The absence of a siphonostele is here considered a homologous condition, because all the taxa that lack it have an open arch (Schofield, 1968). In addition to the arcuate stele reported by Schofield (1968), P. Stevens (pers. comm.) mentioned that *Ficalhoa* and *Sladenia* also have it, and Metcalfe and Chalk (1972) reported it for *Pentaphylax*. There is no information on this character for *Apterosperma*, *Asteropeia*, *Cornus*, *Dankia*, *Euryodendron*, *Neotatea*, *Pelliciera*, or Tetrameristaceae.

4. Raphides in ray cells: (0) absent; (1) present. The presence of these specialized cells of the parenchyma has only been reported for *Actinidia*, *Marcgravia*, *Pelliciera*, *Pentamerista*, and *Tetramerista* (Metcalfe and Chalk, 1972).

5. Vessel perforation plates of the wood: (0) simple; (1) scalariform. Vestal (1937), Record (1942) and Liang and Baas (1991) reported scalariform perforation plates for Ternstroemiaceae and Theaceae s.s. This type of perforation is also present in *Cornus* (Ocegueda, 1998), and *Pentaphylax* (Watson and Dallwitz, 1992). Liang and Baas (1991) say that the wood anatomy of Kielmeyeroideae (Clusiaceae) and Bonnetiaceae is very similar, and different from that of Theaceae, mainly due to the existence of simple perforations and paratracheal unilateral parenchyma. In *Asteropeia*, *Pelliciera*, *Physena*, and Tetrameristaceae the perforation plates are simple (Maguire et al., 1972; Miller and Dickison, 1992). In addition to scalariform perforation plates, simple perforation plates were also present in some species of *Actinidia* and *Marcgravia* (Metcalfe and Chalk, 1972); *Mahurea*, *Marila*, and *Neotatea* are also polymorphic (Stevens, unpubl. manuscript). There is no information for *Dankia*.

6. Nodal structure: (0) trilacunar; (1) unilacunar. Most of the taxa have unilacunar nodes; only Bonnetiaceae and Tetrameristaceae (Maguire et al., 1972) have a trilacunar nodal structure. Nevertheless, Weitzman (1987a) found that several species of *Freziera*, e.g., *F. guatemalensis* (Donn. Sm.) Kobuski, *F. canescens* Humb. & Bonpl., and *F. angulosa* Tul., among others, have trilacunar nodes, in which two of the traces are smaller than the other. This author warns that “trilac-

unar” nodes in *Freziera* can be considered only as grossly similar to trilacunar nodes found in other angiosperm families, in which the three traces leave the stele at the same level and are commonly of the same size. Schofield (1968) reported unilacunar nodes for Bonnetiaceae and Clusiaceae; also Vestal (1937) recorded unilacunar nodes for Bonnetiaceae (included within his Theaceae). On the contrary, Stevens (unpubl. manuscript) and Weitzman (pers. comm.) recorded trilacunar nodes in all Bonnetiaceae. In this work we consider the nodes in Bonnetiaceae to be trilacunar. We found no information for *Pelliciera* and *Pentaphylax*.

7. Axial parenchyma types: (0) scanty paratracheal; (1) banded; (2) diffuse apotracheal; (3) diffuse in aggregates; (4) vasicentric. Most of the species are polymorphic, with different combinations of the states. In *Marcgravia*, two authors (Vestal, 1937; Metcalfe and Chalk, 1972) reported different character states, and both are included in the analysis. The most common polymorphism implies scanty paratracheal and diffuse apotracheal parenchyma (Baretta-Kuipers, 1976; Liang and Baas, 1990, 1991). However, Theaceae s.s. also has diffuse aggregate parenchyma; *Euryodendron* and *Ficalhoa* also have vasicentric parenchyma. Liang and Baas (1991) reported banded axial parenchyma in *Kielmeyera*, while *Tetramerista* and *Pentamerista* have a diffuse apotracheal and in aggregates axial parenchyma (Maguire et al., 1972; Liang and Baas, 1991). There is no information for *Symplococarpon* and *Dankia*. The character was coded as unordered.

8. Spiral thickenings on the vessel walls: (0) absent; (1) present. Most of the taxa do not have spiral thickenings on the vessel walls. They are present only in *Actinidia*, *Apterosperma*, *Cleyera*, *Pentaphylax*, *Stewartia*, and *Visnea* (Liang and Baas, 1991; Vestal, 1937). The thickenings are restricted to the tips of the vessel members or associated with pit apertures in these taxa. In other genera they may or may not be present depending on the species, as in *Adinandra*, *Anneslea*, *Eurya*, and *Ternstroemia*; these genera were scored as polymorphic. There is no information for *Dankia* and *Symplococarpon*.

9. Vessel member length: (0) medium (between 800 and 1000 μm); (1) long (between 1300 and 1500 μm); (2) very long (more than 1500 μm). Baretta-Kuipers (1976), following the standard terms of the IAWA (1937), classified the length of the vessel members in four categories, including, in addition to those used here, a small one. Most of the taxa have very long vessel members (Metcalfe and Chalk, 1972; Baretta-Kuipers, 1976). The vessels of *Caraipa*, *Haploclathra* (Clusiaceae) and Tetrameristaceae are long and those of *Asteropeia*, Bonnetiaceae and *Kielmeyera* (Clusiaceae) are medium size (Baretta-Kuipers, 1976; Maguire et al., 1972). It is important to mention that this character is complex and the codification could change with more sampling and

different statistical tests to define the ranges. For instance, according to Liang and Baas (1990) the average length of the vessel members in Ternstroemiaceae and Theaceae s.s. varies from 660 to 1980 μm . In this work, nevertheless, we followed Baretta-Kuipers (1976), because Liang and Baas did not provide specific measurements for the genera. On the other hand, there are some cases for which there are no specific measurements; therefore we coded the relative measures as reported: *Actinidia* as long (Vestal, 1937); *Marcgravia* as medium to large (Metcalf and Chalk, 1972); and *Pentaphylax* as very long (Metcalf and Chalk, 1972). It would be desirable to later verify the coding for these taxa. Because it is possible to postulate a logical successive transformation in size as a primary homology hypothesis (*sensu* De Pinna, 1991), this character was coded as additive.

10. Fiber types: (0) libriform tracheids; (1) fiber tracheids. Most taxa have fiber tracheids with distinctly bordered pits (Vestal, 1937; Baretta-Kuipers, 1976). Libriform tracheids are consistently present only in *Haploclathra*, *Kiellmeyera*, *Mahurea*, *Neotatea*, *Pelliciera*, and *Physena*. Other genera (i.e., *Cornus*, *Marcgravia*, and *Marila*) have fibres or libriform tracheids within the same genus (Baretta-Kuipers, 1976; Vestal, 1937; Ocegueda, 1998). Stevens (unpubl. manuscript) considered that it is not easy to make a clear distinction between the two types of fibres, and unfortunately there is infra-taxon variation, but this may be true only within Clusiaceae. There is no information on this character for *Dankia*, *Pentaphylax*, *Symplococarpon*, or Tetrameristaceae.

11. Exudate production: (0) absent; (1) present. Most taxa do not produce exudates. In Clusiaceae, esquizogonic secretory receptacles, commonly in the form of canals, exist typically in all the species, although they can also be found in cavities. The alternative name of the first family is Guttiferae, which according to Stevens (unpubl. manuscript, 2003) emphasizes that exudate production was considered a characteristic of the group by A.L. de Jussieu (1789). According to Robson (1961), the genus *Ficalhoa* produces some type of exudate in the bark.

12. Sclerenchymatous idioblasts: (0) absent; (1) present. Most taxa present idioblasts. Schofield (1968) maintained that “Idioblasts are a well-known feature of Theaceae, as are glands of the Guttiferae”. The same author argued that there is much diversity in the sizes and forms of these structures, and their existence can serve as a diagnostic characteristic, not only among the families of Guttiferales, but for many other families. In this respect, Keng (1962) maintained that one of the only anatomical characters that Theaceae shares is the presence of sclereids in almost all parts of the plant. Metcalfe and Chalk (1972) supported this idea, maintaining that the sclerenchymatous idioblasts in the

parenchymatous tissues of the leaf, as well as in the cortex and pith, are especially characteristic of the family. These authors classified them in several types according to form, size and position. In *Stewartia* they were found only in the pedicel (Keng, 1962; Metcalfe and Chalk, 1972). Robson (1961) found them in *Ficalhoa*, but these are less specialized than those of typical Theaceae. Idioblasts are also found in Bonnetiaceae, providing evidence for why so many authors believe these genera should be included in Theaceae (e.g., Kobuski, 1950; Schofield, 1968). They are also present in *Asteropeia* (Watson and Dallwitz, 1992), *Pelliciera*, and Tetrameristaceae (Metcalf and Chalk, 1972). Keng (1962) reported them as “almost absent” in *Sladenia*, and therefore we coded this genus as having them. These structures are absent in *Actinidia*, *Cornus*, *Kiellmeyeroideae* (Clusiaceae), and *Pentaphylax*. Information is lacking for *Apterosperma*, *Dankia*, *Euryodendron*, and *Physena*.

13. Indumentum: (0) glabrous plants; (1) with unicellular trichomes; (2) with multicellular trichomes. Most taxa have unicellular trichomes. Trichomes are characteristic of Theaceae, whereas they fall off in many genera when the plant is mature and can only be seen in the young stems. Nevertheless, there are genera that are recognized in the adult state by their great quantity, as in the case of *Archboldiodendron*, with silky copper-colored trichomes that cover the vegetative parts and flowers almost totally (Fig. 2), in a characteristic manner. Keng (1962) considered that there are three main types of trichomes in this group: (1) the most common, a unicellular type, with thickened walls, which is present for example in *Tutcheria* (within *Pyrenaria* in this work); (2) a much less common fasciculated type with unicellular rays; it has only been observed in some species of *Gordonia*, *Ternstroemiopsis* (in *Eurya* in this work),



Fig. 2. Leaves of *Archboldiodendron merrillianum* Kobuski showing the copper-colored unicellular trichomes, *P. van Royen* 30138 (K). (A) leaf bud; (B) Abaxial view of a mature leaf.

Franklinia alatahama (in *Gordonia*) and in *Laplacea grandis* Brandege (also in *Gordonia*); (3) a third type is also unicellular, but differs in that it is thin-walled, with a high degree of curling and two to three times longer than the first; this is characteristic of *Melchiora schliebennii* (in *Balthasaria*). Although these distinctions could have potential for cladistic analyses, the coding cannot be extended to other species with hairs. Therefore, we consider all the variation reported by Keng (1962) to be unicellular trichomes. Unicellular trichomes are also registered for *Caraipa*, *Cornus*, *Haploclathra*, *Mahurea*, and *Neotatea*. In *Cornus*, the trichomes are branched into two arms. Bonnetiaceae, *Pelliciera*, *Pentaphylax*, *Physena*, and Tetrameristaceae are glabrous. This character is polymorphic for *Actinidia*, *Asteropeia*, *Caraipa*, *Ficalhoa*, *Gordonia*, *Haploclathra*, *Kiellmeyera*, *Marcgravia*, *Marila*, and *Schima*. This character was coded as additive, because the presence/absence of trichomes by itself represents a hypothesis of homology that could have equally been coded as an additional character (additive binary coding).

14. Colleters: (0) absent; (1) present. Most of the taxa lack colleters; these finger-shaped secretory structures have not been reported for the genera studied (Thomas, 1991). The last author cited the existence of these structures in Ternstroemiaceae but he only recorded them in the petiole of *Saurauja*, which he classified in this family. Weitzman (1987a) was the first to observe colleters in Theaceae (in *Freziera*); these structures are triangular, flat and red to black, and are frequently present between the stem and the base of each leaf. They can be solitary or in groups, but usually they are arranged in a line decreasing in size toward the center of the leaf base. These structures are present in Bonnetiaceae and in Kiellmeyeroideae considered here, except for *Marila* and *Neotatea* (Stevens, unpubl. manuscript). In *Mahurea exstipulata* Berth. the same author found a form of paired stipuliform structures that possibly represent modified colleters. We coded the genus as lacking colleters, because this is the only species in the genus in which this structure has been observed, and it is inconclusive that it corresponds to colleters. Tabor (1911) registers colleter glands in the shape of mallets in the axils of the leaves of *Archytaea*. We did not find these structures in *Actinidia*, *Cornus*, *Marcgravia*, or *Pelliciera*. There is no information for *Apterosperma*, *Asteropeia*, *Pentaphylax*, *Physena*, or Tetrameristaceae.

15. Stomata type: (0) paracytic (stomata with one or more subsidiary cells on each side and parallel to the greater axis of the pore and of the guard cells; Beauvisage, 1920); (1) anomocytic (irregular-celled stomata, characterized by lacking subsidiary cells; Keng, 1962); (2) encyclocytic (stomata surrounded by five concentric subsidiary cells; Cronquist, 1981); (3) staurocytic (four subsidiary cells oriented in a crossed position to the pore; Fryens-Claessens and Van

Cotthem, 1973). Most taxa have either paracytic or anomocytic stomata, but many species of *Pyrenaria* and *Franklinia alatahama* (*Gordonia* in this work) have both types (Keng, 1962). The same author reported that there are two basic stomata types in Theaceae, ranunculaceous (= anomocytic), and an “intermediate” form between anomocytic and paracytic (called by him “gordoniaceous”), characterized by the presence of obliquely situated subsidiary cells; we coded this form as paracytic. Keng (1962) also observed that Ternstroemiaceae (his Ternstroemioidae) have anomocytic stomata and Theaceae s.s. (his Camellioideae) paracytic. *Actinidia*, *Cornus*, Tetrameristaceae, and *Physena* also have anomocytic stomata (Metcalfe and Chalk, 1972; Watson and Dallwitz, 1992), whereas Bonnetiaceae, the revised genera of Clusiaceae, and *Pentaphylax*, have paracytic stomata (Watson and Dallwitz, 1992). According to Cronquist (1981) in *Pelliciera* the stomata are encyclocytic. According to Watson and Dallwitz (1992) and Fryens-Claessens and Van Cotthem (1973), *Marcgravia* has staurocytic stomata. We lack information on the stomata of *Apterosperma*, *Balthasaria*, *Dankia*, *Euryodendron*, and *Ficalhoa*. This character was coded as nonadditive.

16. Leaf position: (0) opposite; (1) alternate. Most sampled taxa have alternate leaves (Figs 1B, C); only *Marila* and *Haploclathra* have opposite leaves (Fig. 3D). Stevens (pers. comm.) suggested that some genera of Clusiaceae (e.g., *Caraipa*, *Kiellmeyera*, and *Mahurea*) were included within Theaceae, because of the alternate leaves. This author also mentioned that the genera with punctate alternate leaves might show a relationship between Clusiaceae and Bonnetiaceae-Theaceae.

17. Leaf arrangement: (0) spiral; (1) distichous. Leaf arrangement is independent of their relative position with respect to the nodes; both alternate or opposite leaves can be spiral or distichous (there are no decussate leaves in the sampled taxa). Most sampled taxa have a spiral leaf arrangement. However, spiral and distichous leaf arrangements can be present in the same genus, e.g., *Adinandra*, *Archboldiodendron*, *Balthasaria*, *Caraipa*, *Cornus*, *Camellia*, *Eurya*, *Gordonia*, *Marcgravia*, and *Visnea*. These taxa were coded as polymorphic. Weitzman (1987a) claimed that distichous leaves are a shared characteristic of the Freziereae tribe (Ternstroemiaceae); nevertheless, specimens have been found belonging to that tribe with leaves in a spiral arrangement, as in *Adinandra*, *Archboldiodendron* (Barker, 1980), *Balthasaria*, *Euryodendron* (Chang, 1963), and *Visnea*. Distichous leaf arrangement appears to be constant only in *Cleyera*, *Freziera*, and *Symplocarpon*.

18. Leaf consistency: (0) coriaceous; (1) membranaceous to chartaceous. Most genera have a coriaceous leaf consistency, although many of them have species with membranaceous to chartaceous leaves (*Actinidia*, *Adinandra*, *Balthasaria*, *Camellia*, *Cleyera*, *Cornus*,

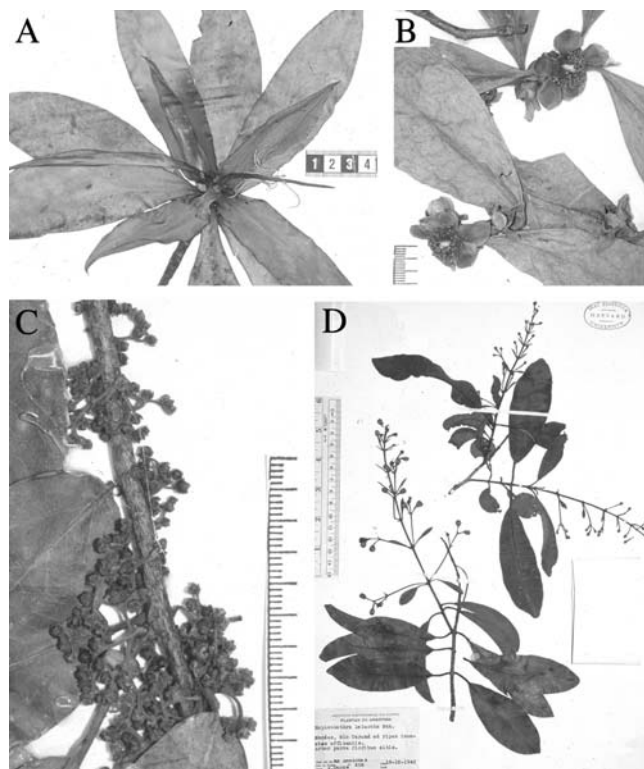


Fig. 3. Different aspects of representative genera included in the analysis. (A) *Pelliciera rhizophorae* Planch. et Triana, *H.P. Fuchs & L. Zanella* 21841 (K); (B) *Pyrenaria garretiana* Craib, *A.F.G. Kerr* 5128 (BM); (C) *Ficalhoa laurifolia* Hiern, *A. Schmitz* 4921 (BM); (D) *Haploclathra leiantha* (Benth.) Benth., *A. Ducke* 656 (GH).

Eurya, *Freziera*, *Gordonia*, *Marcgravia*, *Pyrenaria*, *Schima*, *Stewartia*, *Symplococarpon*, Tetrameristaceae, and *Ternstroemia*). Only *Euryodendron*, *Sladenia*, and *Ficalhoa* have consistently membranaceous to chartaceous leaves.

19. Leaf margin: (0) entire; (1) serrate. Most of the taxa have serrate leaf margins. Many times these serrations end in marginal setae, in the form of a small mucro, in Theaceae. Hickey (1979) named this tooth, which also occurs in Ochnaceae, as setaceous. Bonnetiaceae also have serrate leaves with marginal setae, but in most cases they can only be observed in the leaf buds. Tabor (1911) suggested that the teeth of *Archytaea alternifolia* Szyszyl. (Bonnetiaceae) are ephemeral structures that mature quickly, dry and disappear. Stevens (unpubl. manuscript) suggested that the typical “theaceous” setae are intimately associated with the vascular tissue (as in *Archytaea*), but in the case of other Bonnetiaceae, such as *Neblinaria celiae* Maguire, *Neogleasonia wurdackii* Maguire (in *Bonnetia* in this work) and *Bonnetia sessilis*, the associated veins are absent. Tabor (1911) claimed that the teeth of *Archytaea* are in fact hydathodes, a very special type that lets water pass through by intercellular spaces and not by pores. These functions are only carried out in the very young leaves (buds). In several species of *Camellia*, similar teeth to those of *Archytaea* have been observed (Tabor, 1911), but apparently the function is different, because in *Camellia* they are apparently functional not only in the leaf buds, but also in the mature leaves. In *Pelliciera* the young leaves have “teeth”, possibly homologous to those of other Theaceae. Kobuski (1951a) named this leaf margin as glandular-denticulated. In a herbarium specimen, *M. S. Hayes* 76 (K), the field notes mentioned that the leaves of *Pelliciera* have “...very curious teeth, which seem to be articulated with it [the blade] (in fact these little teeth seem quite like minute leaflets)” (Fig. 4). Collins et al. (1977) claimed that the leaf margin of *Pelliciera* has a series of small glands that give the leaf a serrate appearance. As the leaf ages, these “glands”, once green and secretory, dry, and therefore

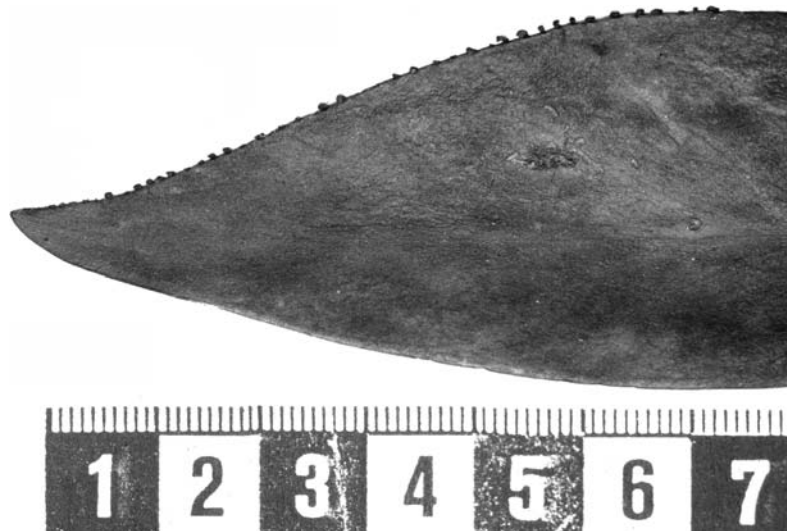


Fig. 4. Leaf margin of *Pelliciera rhizophorae* Planch. et Triana, *M.S. Hayes* 76 (K).

they cannot be seen in the old leaves, probably as a result of being detached mechanically by the wind, rain, or other agents. The function of these “glands” is not known with certainty, but the presence of fluid droplets along the leaf margin with a salty flavor (pers. obs.) suggests that they might operate as salt secretory glands, which would be appropriate for the habitat of these plants. Despite the fact that a serrate margin may have different phylogenetic origins, all taxa with this condition are recorded as the same. Entire margins are consistently present only in *Adinandra*, *Kiellmeyeroideae* (Clusiaceae), and *Marcgravia*.

20. Punctate leaves: (0) absent; (1) present. Most taxa do not have punctate leaves, that is, the lamina is covered by points or very small depressions. Only *Anneslea* and *Ternstroemia* consistently have punctate leaves. Some species of *Adinandra* (Kobuski, 1947), *Marila* (Stevens, unpubl. manuscript) and *Marcgravia* (De Roon, 1970) also have punctate leaves; these taxa were coded as polymorphic.

21. Petiole: (0) absent; (1) inconspicuous; (2) conspicuous. Most genera have conspicuous petioles, such as *Actinidia*, *Anneslea*, *Apterosperma*, *Asteropeia*, *Balthasaria*, *Cleyera*, *Cornus*, *Dankia*, *Euryodendron*, *Ficalhoa*, *Pentaphylax*, *Physena*, *Pyrenaria*, *Schima*, *Sladenia*, *Stewartia*, *Symplococarpon*, *Visnea*, and the revised Clusiaceae (Fig. 3D) (except for most of *Neotatea* and *Kiellmeyera*). Different combinations of polymorphisms are also frequently observed. The leaves of Theaceae usually have a well-developed petiole, although in some species they are inconspicuous, as they are in some species of *Adinandra*, *Archboldiodendron* (Fig. 2A), and *Eurya*, or even absent, as in *Freziera*. Several species of Bonnetiaceae have sessile leaves, although in some they are either very short or conspicuous. Tetrameristaceae, *Neotatea* and *Pelliciera* (Fig. 3A) have sessile or subsessile leaves. This character was coded as additive, because the presence/absence of pedicel by itself represents a hypothesis of homology that could have equally been coded as an additional character (additive binary coding).

22. Decurrent base of the leaf lamina: (0) absent; (1) slender; (2) expanded into a “wing”. The majority of the genera have a slender decurrent leaf lamina base, although in different degrees. That is the case in *Adinandra*, *Anneslea*, *Archboldiodendron*, *Archytaea* (Maguire et al., 1972), *Balthasaria*, *Cleyera*, *Eurya*, *Euryodendron*, *Ficalhoa*, *Gordonia*, *Pelliciera* (Metcalf and Chalk, 1950), *Pyrenaria*, *Schima*, *Symplococarpon*, *Ternstroemia*, and Tetrameristaceae (Maguire et al., 1972). Kobuski (1949) defines the base of the leaf in *Laplacea* (= *Gordonia*) as “tapering at the base into a short petiole”, which we consider to be a slender decurrent base. According to Kobuski (1941b) and Weitzman (1987a), all the species of *Freziera*, when present, have “winged” petioles by a continuation of

the leaf lamina to the base of the petiole, which we interpret as an extreme condition of decurrent base. This condition distinguishes *Freziera* from *Eurya* according to Kobuski (1941b). Spongberg (1974) observed that the petioles of all the species of *Stewartia* are also winged or inflated. The genera *Asteropeia*, *Camellia* and *Bonnetia* (Maguire et al., 1972) are polymorphic. All genera with species lacking petioles, for which this character would have to be coded as inapplicable (–), also have species with subsessile to long petiolated leaves; the condition for the present character was coded from the species with petioles. This character was coded as additive, because the presence/absence of decurrent bases by itself represents a hypothesis of homology that could have been coded as an additional character (additive binary coding). This character needs to be checked for *Apterosperma*, which was coded with question marks.

23. Unisexual flowers: (0) absent; (1) present. Most of the genera only have bisexual flowers, but some have unisexual flowers with different sex distributions. Species of *Actinidia* can be monoecious or dioecious (Watson and Dallwitz, 1992); *Eurya japonica* Thunb. can be monoecious, gynodioecious or dioecious (Murata et al., 1991), and we extrapolate the presence of unisexual flowers to the genus; *Freziera* is gynodioecious (Weitzman, 1987a,b); *Kiellmeyera* is andromonoecious, with hermaphroditic terminal flowers and staminate lateral ones. In other genera, some species have only hermaphroditic flowers but other have unisexual flowers, i.e., these genera are polymorphic. Some species of *Gordonia* are gynodioecious. Species of *Ternstroemia* can be dioecious, andromonoecious or androdioecious (Kobuski, 1961; Barker, 1980). For example, *T. philippinensis* Merrill var. *philippinensis* is dioecious, and *T. urdanatensis* (Elmer) Kobuski is androdioecious; in the latter the hermaphroditic flower has well developed stamens but they are very reduced in number (Kobuski, 1961). Most of the species of *Cornus* have hermaphroditic flowers but a few are dioecious (e.g., *C. volkensii* Harms, Watson and Dallwitz, 1992).

24. Inflorescence/flower position: (0) terminal; (1) axillary. Most of the genera have axillary inflorescences or flowers. The position of the flowers and/or inflorescences in Theaceae is always axillary, but Chang (1976) mentioned that they could also be terminal in *Apterosperma*. Because we could not verify this for lack of material, we coded this genus as polymorphic, but we believe this condition needs to be verified, because *Apterosperma* may well be just axillary. *Anneslea* and some species of *Schima* and *Camellia* have been reported as being terminal, but the flower was always adjacent to a terminal meristem and therefore we coded them as axillary. Only in *Asteropeia*, *Marcgravia* and the Clusiaceae included herein is the inflorescence always terminal, except for *Marila* and *Caraipa*, where both character states are present.

25. Flower arrangement: (0) in inflorescences; (1) solitary. The flowers of most Theaceae are solitary (Figs 1A and 3B); this condition is not always evident at first sight. In some cases the flowers appear to occur in groups of two or three, resembling fascicles, but the flowers are not born at exactly the same point. In these cases, the internodes are short and the flowers are close together and at the same time, the leaves that support them could either not develop or drop, making the flowers appear to be grouped in small racemes. Chang (1976) mentioned that the flowers are disposed in racemes in *Aptosperma*. Although we did not see herbarium material of this taxon, we believe the author's figure shows solitary flowers, as in the rest of Theaceae. Also in *Schima* (Bloembergen, 1952), some species of *Stewartia*, and less frequently some species of *Camellia*, which have solitary flowers, have been reported as having inflorescences. *Sladenia* and *Ficalhoa* are the only

genera within Theaceae where the flowers are borne in cymose inflorescences (Fig. 3C). Outside Theaceae, only *Pelliciera* has solitary flowers (Fig. 3A). The flowers in *Asteropeia* (Schatz et al., 1999), Clusiaceae (Fig. 3D), *Cornus*, *Marcgravia*, *Pentaphylax*, *Physena* and Tetramistaceae are always grouped in inflorescences. Both flower arrangements are present in *Actinidia* and Bonnetiaceae. The genus *Acopanea* (included within *Bonnetia* in this study) has a flagelliform inflorescence according to Stevens (unpubl. manuscript).

26. Corolla size: (0) up to 0.7 cm; (1) 0.7–2 cm; (2) 2–5 cm; (3) more than 5 cm. To define the states for this character we plotted information for 289 accessions corresponding to 33 genera. We summarize this information in two graphs, one corresponding to the generic characterization and the other to the character state distribution (Fig. 5). Keng (1962) used flower size as one criterion to distinguish his Ternstroemiodeae (here

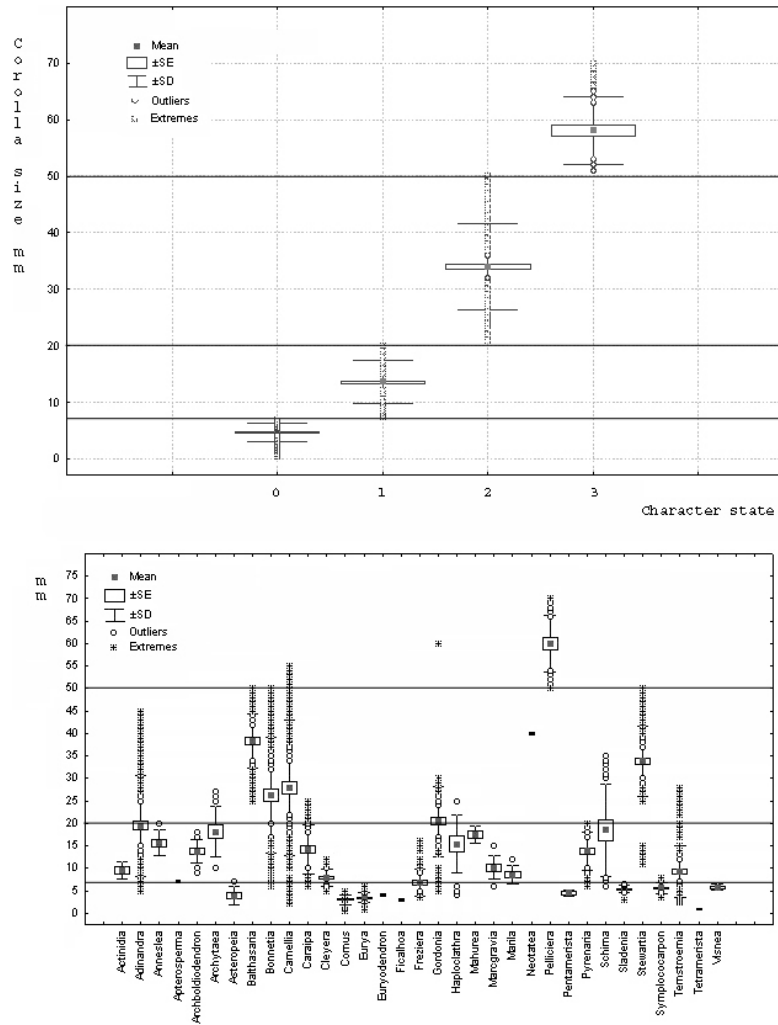


Fig. 5. Corolla size: character state distribution at species level, based on 289 accessions (above); generic variation (below).

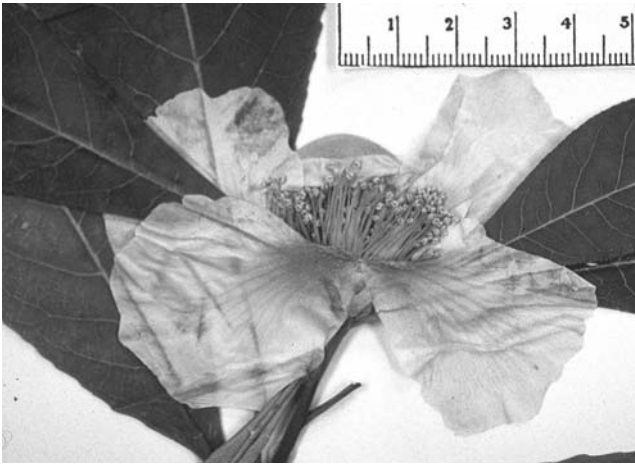


Fig. 6. Flower of *Franklinia alatamaha* Marshall, G.P. DeWolf & P. Bruns 2188 (BM).

Ternstroemiaceae) with less than 2 cm, from his Camellioideae (here Theaceae s.s.) with more than 2 cm (Fig. 6). In our taxon sample, we observed that the ranks suggested by Keng (1962) could also be applied to most of the genera; the finest subdivision allows one to establish more precise homology assessments, even though several genera have subset-polymorphisms. For instance, *Asteropeia* (Schatz et al. 1999), *Eurya*, *Euryodendron*, *Ficalhoa*, *Pentamerista*, *Pentaphylax*, *Sladenia*, *Symplococarpon*, *Tetramerista*, and *Visnea* have corollas of less than 7 mm; *Actinidia*, *Anneslea*, *Archboldiodendron*, *Caraipa*, *Dankia*, *Mahurea*, *Marcgravia*, and *Pyrenaria* have corollas between 7 mm and 2 cm; *Balthasaria*, *Kiellmeyera*, *Neotatea*, and *Stewartia* have corollas between 2 and 5 cm; in *Pelliciera* the corollas are more than 5 cm in size. Some genera are polymorphic, as in *Adinandra*, in which the corolla size ranges from 5 mm to 4.5 cm; *Archytaea*, ranging from 1 to 2.7 cm; *Bonnetia*, from 0.5 to 5 cm; *Camellia*, from 0.2 to 5.5 cm; *Cleyera*, 0.5–1.2 cm; *Freziera*, from 0.3 to 1.6 cm; *Gordonia* from 0.5 to 3 cm; *Haploclathra*, from 0.4 to 2.5 cm; most of the species in *Marila* have large corollas of more than 2 cm (Stevens, pers. comm.) but some have small ones (6–12 mm); *Schima*, from 0.5 to 3.5 cm; and *Ternstroemia*, from 0.2 to 2.9 cm. Most species of *Cornus* (Ocegueda, 1998) have corollas of less than 6 mm, but some species have corollas more than 2 cm. The corolla is 7 mm long in *Apterosperma*, which is the size that was used to distinguish states 0 and 1; this genus was coded as subset-polymorphic, given our inability to unambiguously assign it to one of the states. *Physena* is coded as inapplicable, because it lacks a corolla. Although it is true that all Theaceae s.s. have medium to large flowers, and almost all Ternstroemiaceae have small flowers, exceptions to Keng's (1962) generalization occur in *Anneslea*, *Apterosperma*, and *Balthasaria*, the latter with the extreme petal variation,

up to 4.5 cm long. This character was coded as additive on the basis that there is a logical progression in character states.

27. Inflorescence type: (0) cymose; (1) racemose; (2) paniculate. All taxa with solitary flowers, such as most Theaceae and *Pelliciera* (Fig. 3A), were coded as inapplicable (–). *Bonnetia*, with solitary flowers and inflorescences was coded from the species that have inflorescences (panicules). Clusiaceae (except *Neotatea*) (Fig. 3D), *Ficalhoa* (Fig. 3C) and *Sladenia* have cymes. The inflorescences are racemose in *Neotatea*, *Pentaphylax*, *Physena*, and Tetrameristaceae; *Asteropeia* has panicles; *Cornus* (cymose, racemose, and paniculate) and *Marcgravia* (cymose and racemose) are polymorphic. This character was coded as nonadditive.

28. Apical eglandular sepal projection: (0) absent; (1) present. Most taxa lack an apical eglandular sepal projection. This structure is present in many Ternstroemiaceae (except in *Anneslea*, *Apterosperma*, *Ficalhoa*, *Freziera*, and *Sladenia*) and Bonnetiaceae, and can be present or not (polymorphic) in Theaceae s.s. (except *Dankia* and *Gordonia*, where they are always absent). These projections can be better observed when the sepals are very young. They are over 2 mm long, or they can be inconspicuous, fugaceous and overlooked (Stevens, unpubl. manuscript). Weitzman (1987a) mentioned that the sepals of Frezieraee (*Eurya*, *Adinandra*, *Archboldiodendron*, *Cleyera*, *Symplococarpon*, *Balthasaria*, and *Visnea*) end in a setae, except for those of *Freziera*. The structure is similar to the setaceous teeth of the margins of the leaves; Stevens (unpubl. manuscript) claimed that the presence of these projections in taxa such as *Ploiarium* (included within *Archytaea* here) is directly related to the marginal setae of the lamina. These projections are not homologous to the erose or even fimbriate sepals margins of *Hypericum* (Clusiaceae), structures that commonly end in a gland.

29. Glands in the sepals: (0) absent; (1) present. Glands resembling pores or openings, on the adaxial surface of the sepals, are present in *Pelliciera* (Maguire et al., 1972; Cronquist, 1981). These structures apparently correspond in form, function and position to those found in Tetrameristaceae, which were therefore coded as the same. These glands are present only in the sepals and are not considered the same as those in Clusiaceae, which are schizogenous secretory cavities.

30. Number of sepals/petals versus number of stamens: (0) equal; (1) less than stamens. Even though the number of floral parts is variable within the sampled taxa, most taxa in this study have more stamens than petals. Nevertheless, *Actinidia*, *Pelliciera*, *Pentaphylax*, and Tetrameristaceae have equal number of petals and stamens. This character is polymorphic for *Cornus* (less, equal or more sepals/petals than stamens).

31. Corolla aestivation: (0) contorted; (1) imbricate. Most taxa have imbricate corolla aestivation. Petals in

Theaceae, as well as the sepals, are quincuncial (a particular type of imbricate aestivation). The petal aestivation is consistently contorted only in Bonnetiaceae and Clusiaceae (except *Marila*); Stevens (unpubl. manuscript) is revising *Bonnetia*, *Neogleasonia* (in *Bonnetia* here), and *Neotatea* and has claimed that the aestivation is contorted, as opposed to Robson (1981), who previously reported it as imbricate; in this work we coded them as contorted. The genus *Marila* has some species with contorted aestivation and others with imbricate aestivation; *Cornus* is also polymorphic with contorted, imbricated or valvated corollas. *Physena* lacks petals, so we coded it as inapplicable.

32. Petal connation: (0) free; (1) basally; (2) distally. Most of the taxa have petals which are either free or connate at the base to varying degrees. Apparently all the genera have basally connate petals in Theaceae, although they can also be free (polymorphic) in *Gordonia* and *Freziera*. In *Balthasaria*, *Cleyera*, *Euryodendron* (Tien-lu and Bartholomew, 2003), *Pyrenaria*, and *Symplocarpon* they are only slightly connate at the very base; Shui et al. (2002) suggested that *Sladenia* has basally connate petals, Robson (1961) reported gamopetalous flowers in *Ficalhoa* and we observed that the petals are only basally connate. Spongberg (1974) mentioned that *Schima* has petals connate at the base, forming a very shallow tube. Outside Theaceae only *Actinidia* has basally connate petals. *Marcgravia* is characterized by its distally connate petals, which form a deciduous calyptra. The remaining genera have free petals (Kearns et al., 1998; Stevens, unpubl. manuscript). We have no information on *Dankia*.

33. Stamen number: (0) less than 30 (Figs 3B and 6), (1) 30–70, (2) more than 70. One of the characters that has served to relate Bonnetiaceae and Clusiaceae to Theaceae and Ochnaceae is the number of stamens. In defining the states for this character we plotted information for 171 accessions corresponding to 27 genera. We summarize this information in two graphs, one corresponding to the generic characterization and the other to the character state distribution at the species level (Fig. 7). This number is variable in Theaceae, although as a rule the group is characterized by having a high number. Keng (1962) mentioned that Ternstroemiaceae (Ternstroemiaceae here) has fewer stamens (less than 30), except for *Adinandra* (up to 60), compared to Camellioideae (Theaceae s.s. here) which usually has over 40. In the herbarium material we found more exceptions to Keng's generalization; *Archboldiodendron* has 30–60 stamens, *Balthasaria* 15–35, *Symplocarpon* 20–40, and *Anneslea* 30–40. Genera of Ternstroemiaceae with fewer stamens are *Eurya* 5–15, *Euryodendron* 15, *Ficalhoa* 15, *Freziera* 6–42 (Weitzman, 1987a), *Sladenia* 10, and *Visnea* 12–21. *Ternstroemia* is reported to have 20–250 stamens (Kobuski, 1963; Keng, 1978; Barker, 1980), but we have not seen material with more than

60 stamens. Chang (1976) described *Apterosperma* as having 22–24 stamens, an unusual number for a member of the Camellioideae (here Theaceae s.s.), where he placed the genus. In *Actinidia* there are more than 30 stamens, but because we lack precise information, we coded it as a subset-polymorphism with states 1 and 2; *Asteropeia* has 10–15, Bonnetiaceae and Clusiaceae always have over 30, *Cornus* has 4–5, *Marcgravia* 7–50, *Pelliciera* 5, *Physena* 8–25, there are 5 in *Pentaphylax*, and 4 or 5 in Tetrameristaceae (depending on the genus). This character was coded as additive on the basis that there is a logical progression in character states.

34. Stamen arrangement: (0) in fascicles; (1) in series. Most taxa have stamens arranged in series. Stevens (unpubl. manuscript) maintained that it has often been assumed that the androecium of Bonnetiaceae and Clusiaceae is basically fasciculate, and that the stamens are developed in five groups that are born opposed to the petals. In addition to these families, fasciculate stamens are present in *Actinidia* (Cronquist, 1981), *Gordonia* (Keng, 1972), and *Ficalhoa* (Robson, 1961). Erbar (1986) reported that the primordia of the individual stamens in *Stewartia pseudocamellia* Maxim originate centrifugally in five fascicles, which we extrapolated to the entire genus. Robson (1961) observed that fasciculate stamens are present in several species of *Eurya* and in *Adinandra*; this affirmation seems to be incorrect based on our herbarium revision, therefore we coded these genera as having stamens in series. In Theaceae (except *Gordonia*, *Ficalhoa*, and *Stewartia*) the stamens are in series (whorls) that vary from 1 to 6 (Kobuski, 1947, 1949, 1952a,b, 1956; Keng, 1962; Chang and Bartholomew, 1984). In general, the large number of stamens in these groups can obscure their disposition, and therefore with more anatomical studies the codification for this character could change.

35. Anther attachment to the filament: (0) basifixed; (1) dorsifixed. Most taxa have basifixed anther attachment. Keng (1962) stated that Ternstroemiaceae (here Ternstroemiaceae) can be separated from Camellioideae (here Theaceae s.s.) by anther attachment; the anthers are basifixed in Ternstroemiaceae and versatile in Theaceae s.s. The more common condition in Theaceae is to have basifixed anther attachment; dorsifixed anthers only occur in *Gordonia*, *Pyrenaria*, *Stewartia* and most species of *Camellia* (Chang, 1981; Chang and Bartholomew, 1984), which was coded as polymorphic. Furthermore, Bloembergen (1952) mentioned that *Schima* has basifixed anthers, which we have confirmed, although Keng (1950, 1972) reported versatile anthers for this same genus. The anthers in *Archytaea* are basifixed and in *Bonnetia* they can be either basifixed or dorsifixed; they are usually basifixed in Kielmeyerioideae (Clusiaceae), although they are dorsifixed in *Caraipa* and *Kielmeyera*. This character is polymorphic in *Marcgravia*.

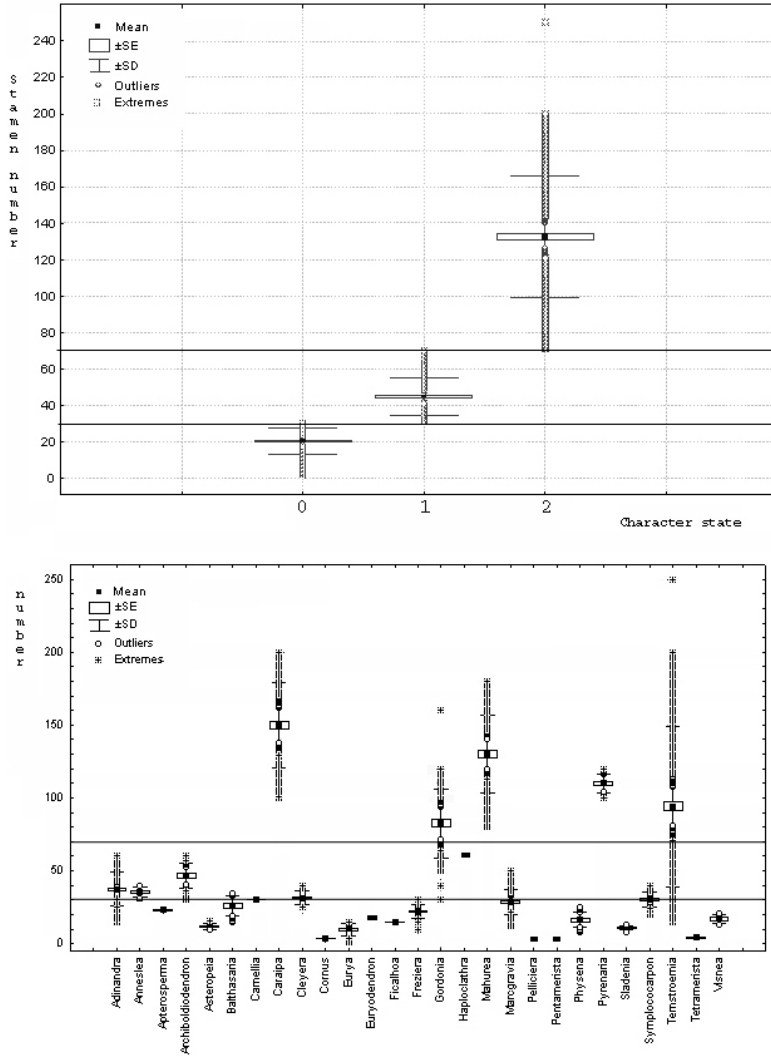


Fig. 7. Stamen number: character state distribution at species level, based on 171 accessions (above); generic variation (below).

36. Anther surface: (0) glabrous; (1) pilose or hispid. Most taxa have a glabrous anther surface. Pilose or hispid anthers only occur in *Cleyera*, *Cornus*, *Euryodendron*, *Marcgravia*, *Sladenia* and some species of *Actinidia*, *Adinandra* and *Archytaea* (coded as polymorphic). We have no information for *Pentaphylax*.

37. Anther dehiscence: (0) longitudinal slits; (1) apical pores. In most of the taxa, dehiscence is carried out through longitudinal slits. Dehiscence through apical pores only occurs in *Ficalhoa*, *Sladenia* and some species of *Actinidia* and *Marila* (Stevens, unpubl. manuscript). There is some controversy in the literature. For example, Kobuski (1941a) claimed that *Cleyera* anthers dehisce through longitudinal slits and Robson (1961) maintained that this genus has dehiscence through apical pores; a review of herbarium material showed that this genus always dehisces through longitudinal slits. Robson (1961) reported that in *Ficalhoa* the anthers

start to dehisce through apical pores which develop later into a longitudinal slit. We did not observe material with longitudinal slits and therefore coded this genus as only having apical pores. Some drawings of *Freziera* and *Symplococarpon* denote apical pores. Our observations, nevertheless, corroborate the reports by Weitzman (1987a) that the anthers of *Freziera* dehisce through longitudinal slits. The herbarium material of *Symplococarpon* showed longitudinal slits that begin to open at the top. This could correspond to what Robson (1961) described for *Ficalhoa*, but in the case of *Symplococarpon*, because the anther ultimately dehisces through a longitudinal slit, we coded it as having this character state, not pores.

38. Extension of connective in the stamens: (0) absent; (1) present as a protrusion; (2) present forming a gland. Most taxa lack an extension of the connective. Keng (1962) claimed that the presence of a connective

extending in a short protrusion is characteristic of Ternstroemiaceae (here Ternstroemiaceae); we corroborated this, but such a connective is also present in some species of *Camellia* and *Gordonia* (Theaceae s.s.), which we coded as polymorphic. This character is also present in *Pelliciera*. The connective is broad and forms a small gland in Kielmeyeroideae (except *Haploclathra*), although this only occurs in some species of *Kielmeyera* (Lleras, 1972; Stevens, unpubl. manuscript). This character was coded as additive, because the presence/absence of the extension of the connective by itself represents a hypothesis of homology that could have equally been coded as an additional character (additive binary coding).

39. Stamen persistence: (0) persistent when fruiting; (1) deciduous. In most taxa the stamens do not persist in the fruit, except for *Archytaea*, *Ficalhoa* and Kielmeyeroideae (Clusiaceae), where the calyx is also persistent.

40. Pollen grain size: (0) small (polar axis less than 30 μm); (1) large (polar axis 30 μm or more). Palynological studies within the group are scattered and difficult to compare given the use of different methodological tools and terminology. We coded this character as provisional, because there is important information that needs to be considered in future research. Nevertheless, we found information for 114 accessions corresponding to 27 genera. We summarize this information in two graphs, one corresponding to the generic characterization and the other to the character state distribution at the species level (Fig. 8). Keng (1962) observed that the pollen grains are small in Ternstroemiaceae (either of the two axes of the grain, including the exine, less than 20 μm , except for *Melchiora schliebenii* Kobuski [= *Balthasaria* in this work] and *Visnea*, in which the axis measures close to 29 μm), and larger in Theaceae s.s. (either of the two axes over

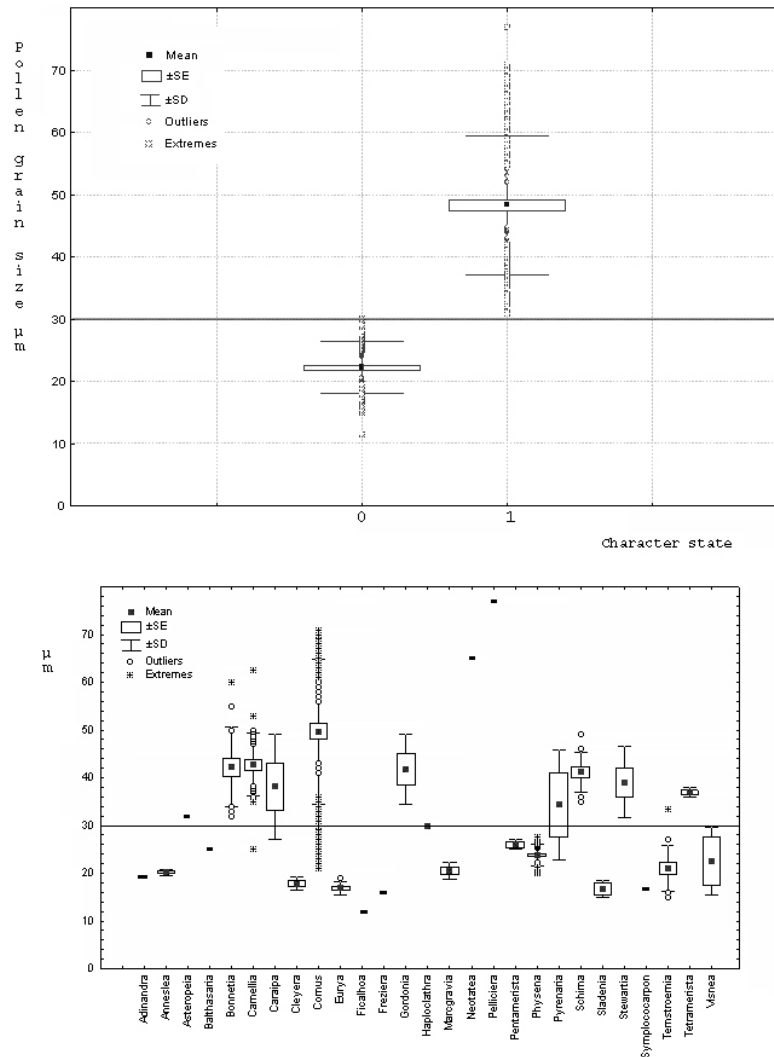


Fig. 8. Pollen grain size: character state distribution at species level, based on 114 accessions (above); generic variation (below).

30 μm). Except for *Asteropeia* and some species of *Marila*, outside Theaceae most pollen grains are larger than 30 μm , although they are variable in size. Maguire et al. (1972) recorded, for example, that the pollen grains of several species of *Bonnetia* are about 40–50 μm long; Seetharam (1985) examined other species of *Bonnetia*, and claimed that they vary between 32 and 34 μm . Considerable variation in size can apparently be present in the same species. For instance, *Nebelinaria celiae* (= *Bonnetia* in this study) has reports of approximately 55 μm (Maguire et al., 1972) as well as between 32 and 42 μm (Seetharam, 1985). The pollen of *Pentaphylax* is 14–28.5 μm (Stevens, 2001 onwards). We found no information for *Actinidia*, *Apterosperma*, *Archboldiodendron*, *Dankia*, and *Euryodendron*.

41. Pollen grain aperture: (0) tricolporate; (1) tricolporoidate. Most genera have tricolporate pollen grain apertures. According to Lee (1987), Ternstroemiaceae (here Ternstroemiaceae) has tricolporate pollen grains and Theaceae (here Theaceae s.s.) has tricolporoidate pollen grains. However, Zavada and Wei (1993) described the 20 species of *Camellia* that they studied as having tricolporate pollen grains. Therefore, we coded this genus as polymorphic. Huang (1972) reported tricolporate pollen grains for *Adinandra*, *Anneslea*, *Camellia*, *Cleyera*, *Gordonia*, *Pyrenaria*, *Schima*, and *Ternstroemia*. These observations for *Camellia*, *Gordonia*, *Pyrenaria*, and *Schima* also contradict Lee's (1987) generalization, but Lee provided no specific information for these genera (except *Camellia*), and therefore we coded them as having tricolporate grains. Tricolporate grains have also been reported for Bonnetiaceae, Clusiaceae, *Cornus* (Stafford and Heath, 1991), *Freziera* (Weitzman, 1987a), *Pelliciera* (Fuchs, 1970), *Sladenia* (Wei et al., 1999), and Tetrameristaceae (Erdtman, 1952). Tricolporoidate pollen grains have been reported for *Ficalhoa* (Robson, 1961). Tricolporate to tricolporoidate pollen grains have been reported for *Eurya* (Erdtman, 1952; Keng, 1962), and *Marcgravia* (Alvarado and Palacios-Chávez, 1987; Watson and Dallwitz, 1992), which were coded as subset-polymorphic. Even though Wei et al. (1999) recorded only tricolporate pollen for *Pentaphylax*, we coded this genus as subset-polymorphic, because Watson and Dallwitz (1992) and Wei et al. (1999) also reported the presence of tricolporoidate pollen grains. Erdtman (1952) and Watson and Dallwitz (1992) reported tricolporoidate pollen grains for *Asteropeia*, but a recent specialized study by Morton et al. (1997) recorded tricolporate pollen grains for this genus and for *Physena*. Given the focus of Morton et al.'s research, we used their report to code both genera. We lack information for *Apterosperma*, *Archboldiodendron*, *Dankia*, and *Euryodendron*.

42. Supratectal ornamentation pattern of the exine: (0) very evident; (1) smooth or with little ornamentation. As in the previous character, the comparison of exine

ornamentation among the taxa included in this analysis can be problematic. We have simplified the different conditions in two character states, but further detailed studies could result in more precise homology hypotheses. Very evident ornamentation is here considered as the condition in which evident bacula, spicules, spinules, thorns, or verrucae are developed; by way of contrast, smooth or little ornamentation is here considered as the condition in which smooth, psilate, prickly or finely granulate to rugulate surfaces are present. Most taxa have either an evident exine ornamentation pattern or smooth to little ornamentation. An exception is the genus *Kielmeyera*, which is variable from smooth to verrucose (Barth, 1980), and which was coded as polymorphic. Keng (1962) observed that the exine of the pollen grains seen with an optical microscope is almost smooth in Ternstroemiaceae (here Ternstroemiaceae) and heavy granular or rugose in Camellioideae (here Theaceae s.s.). Erdtman (1952) reported baculate ornamentations for *Camellia*. Weitzman (1987a), using a scanning electronic microscope, observed that the pollen exine of *Freziera* can be granulate or rugulate to almost psilate, as has already been reported. In other genera of Ternstroemiaceae the pollen grains have rugose to prickly exine, as in *Adinandra*, *Eurya*, *Cleyera*, and *Symplocarpon*. Huang (1972) reported granular ornamentations for *Adinandra*, *Anneslea*, and *Cleyera*, and scabrate processes for *Gordonia* and *Schima*. Personal observations confirmed the finely granular ornamentation in the Mexican taxa of *Cleyera* and *Ternstroemia*. Pollen grain ornamentation in Ternstroemiaceae is indeed much less evident than it is in Theaceae s.s. Pollen grains are psilate in *Pentaphylax* (Watson and Dallwitz, 1992). The grains are almost smooth in *Pelliciera* (Fuchs, 1970). We found no supratectal ornamentations in *Marcgravia*, looking at the SEM pictures presented by Alvarado and Palacios-Chávez (1987). Pollen grains are slightly granulated in *Cornus* (Ocegueda, 1998). Pollen grains are spinulate to thorny in *Asteropeia* (Morton et al., 1997). Pollen grains are echinate, spinulate, or sometimes baculate in *Physena* (Dickison and Miller, 1993; Morton et al., 1997). Bonnetiaceae, Clusiaceae and Tetrameristaceae have a conspicuous ornamentation (Maguire et al., 1972; Seetharam, 1985). We have no information on *Actinidia*, *Apterosperma*, *Archboldiodendron*, *Dankia*, and *Euryodendron*.

43. Pseudopollen grains in connective. (0) absent; (1) present. Tsou (1997) reported the presence of a special kind of pseudopollen, formed at the connective, in *Apterosperma*, *Camellia*, *Gordonia*, *Pyrenaria*, *Schima*, and *Stewartia*, which is characterized by containing large vacuoles and a marginally situated nucleus. This type of pseudopollen is not present in *Cleyera*, *Ternstroemia*, and *Adinandra*, and Tsou considered it is unique in Theaceae s.s. (her Camellioideae) among all

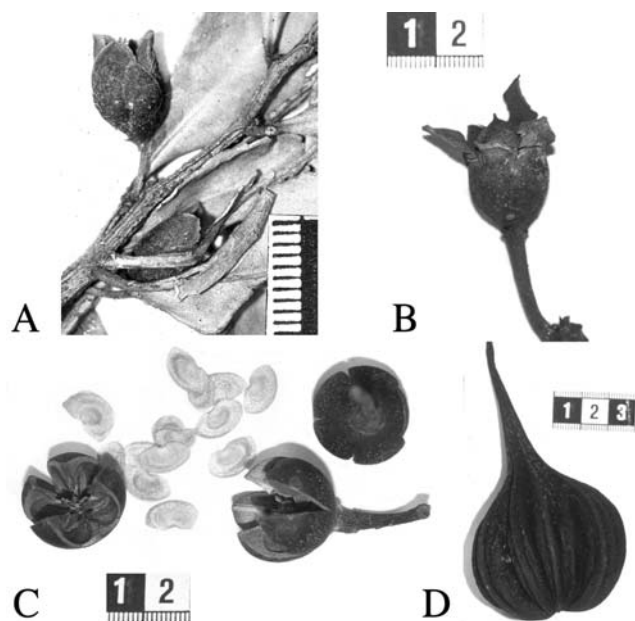


Fig. 9. Fruits of representative genera included in the analysis. (A) *Visnea mocanera* L.f., R.T. Lowe s.n. (BM); (B) *Anneslea crassipes* Choisy, H. Griffiths 741 (K); (C) *Schima wallichii* Choisy, A. Henry 9215B (K); (D) *Pelliciera rhizophorae* Planch. et Triana, S. Hayes 76 (K).

Angiosperms. Because the recognition of this type of pseudopollen requires very oriented studies, we decided to be cautious in the extrapolation of its absence in all Angiosperms other than in Theaceae s.s. Therefore, we coded the character as question mark in all the taxa that were not examined by Tsou.

44. Ovary position: (0) superior; (1) semi-inferior (Fig. 9B). In general, the ovary is superior. Nevertheless, there are three genera within Ternstroemiaceae, *Anneslea*, *Symplocarpon*, and *Visnea*, which have the ovary partially immersed in the receptacular tissue. These have been referred to in the literature as half-inferior to inferior ovaries (Keng, 1962). Although Weitzman (pers. comm.) considered that the position of the ovary in *Visnea* with respect to that of *Anneslea* and *Symplocarpon* was not necessarily homologous, the floral pattern and vascularization in these three cases is essentially the same (Keng, 1962), and we therefore considered the differences in ovary position among the three genera as representing different degrees of a common trend. Therefore, we coded all of them as having the same character state (semi-inferior ovary position). *Cornus* has inferior ovary (Ocegueda, 1998).

45. Ovary surface: (0) glabrous; (1) with trichomes. Most taxa have glabrous ovary surfaces. Keng (1962) mentioned that the ovary in Camellioideae (here Theaceae s.s.) is pubescent, whereas in Ternstroemiaceae (here Ternstroemiaceae) it is glabrous. This is generally only true for Theaceae s.s., where in *Pyrenaria* the entire

ovary is hispid, in *Schima* the ovary is pubescent at the base, and in *Dankia* and *Stewartia* it is completely pubescent. Nevertheless, *Camellia* and *Gordonia* have some species with glabrous ovaries, and both were therefore coded as polymorphic. The generalization of Keng (1962) for Ternstroemiaceae is not supported by our observations. We consider only *Anneslea*, *Sladenia* (Shui et al., 2002) and *Ternstroemia* to have glabrous ovaries; *Euryodendron*, some species of *Freziera* (Weitzman, 1987a) and *Visnea* are pubescent only at the apex; *Adinandra*, *Cleyera*, *Eurya*, and *Symplocarpon* are polymorphic; the rest of the genera have trichomes in the entire ovary surface. The ovary is glabrous in *Asteropeia*, Bonnetiaceae, *Marcgravia*, Tetrameristaceae, *Pelliciera*, *Pentaphylax* and *Physena*; this condition also prevails in Kielmeyeroideae (Clusiaceae), although some species of *Caraipa*, *Haploclathra* and *Marila* are pubescent (genera coded as polymorphic). *Cornus* is also polymorphic.

46. Ovules per locus: (0) one; (1) up to 8; (2) more than 8. To define the states for this character we plotted information for 106 accessions corresponding to 24 genera. We summarize this information in two graphs, one corresponding to the generic characterization and the other to the character state distribution at the species level (Fig. 10). We coded as state 0 only the genera that consistently have a single viable ovule per locus. Some taxa have one to less than eight viable ovules per locus. We coded this condition as different from the previous case, because the number is never consistently one. The number of ovules per locus varies from few to many in Theaceae. The most frequent number of ovules per locus is either up to 8 or larger than 8 at the species level (Fig. 10B). There is an inversely proportional relationship between the size of the seeds and their number—the larger the size of the seeds, the smaller the number. There are few ovules per locus in Theaceae s.s., except for some species of *Gordonia*, which was coded as subset-polymorphic. For example, *Camellia* has 4–6 ovules, *Schima* 2–6, *Stewartia* 1–4, and *Pyrenaria* 2–7. In contrast, the genera of Ternstroemiaceae commonly have more ovules per locus. For example, *Adinandra* has up to 100 ovules per locus, although *Euryodendron* has only 12 ovules, *Visnea* more than one and less than 20, while some species of *Freziera* (Weitzman, 1987a) have only three ovules per locus. Interestingly, it is common that species with a large number of stamens have few ovules per locus and smaller seeds. In Bonnetiaceae and Kielmeyeroideae (Clusiaceae) they always have many ovules/locus, except for *Caraipa* (2–3) and *Haploclathra* (1 ovule) (Stevens, pers. comm.). In *Marcgravia* they are many ovules per locus, c. 50–100 (De Roon, 1970); in *Actinidia* 15–50 (Dunn, 1911; Watson and Dallwitz, 1992); in *Asteropeia* 2–6 (Morton et al., 1997); in

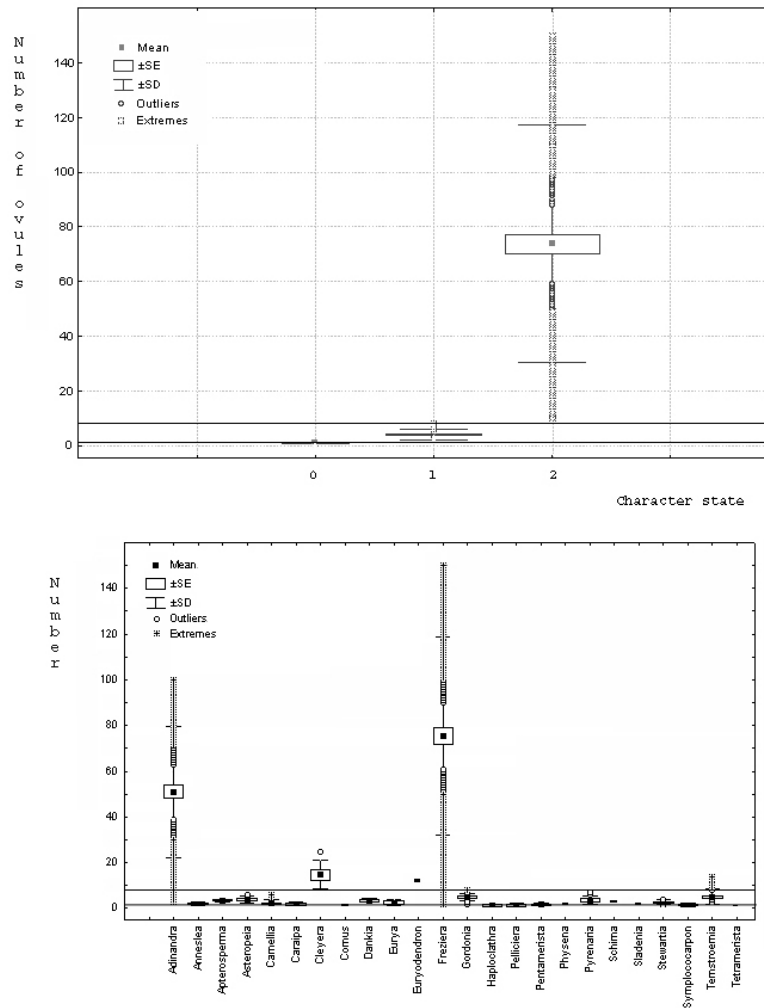


Fig. 10. Number of ovules per locus: character state distribution at species level, based on 106 accessions (above); generic variation (below).

Pentaphylax and *Physena* 2 (Watson and Dallwitz, 1992; Morton et al., 1997); and in *Pelliciera* and Tetrameristaceae only one ovule per locus (Maguire et al., 1972).

47. Ovule position: (0) anatropous; (1) campylotropous; (2) amphitropous; (3) epitropous. This character appears to be of phylogenetic importance and we used it, even though there is no information for many of the genera included here. Most genera have anatropous ovule position; campylotropous ovules are present in *Anneslea*, *Bonnetia*, *Pelliciera*, *Physena*, and *Schima*. According to Tsou (1995), Ternstroemiaceae is characterized by amphitropous ovules, but this has only been confirmed for *Adinandra*, *Cleyera*, and *Eurya*, which can also have campylotropous ovules (and therefore coded as subset-polymorphic). Watson and Dallwitz (1992) registered anatropous and epitropous ovules for Tetrameristaceae. We have no information for *Apterosperma*,

Archboldiodendron, *Balthasaria*, *Dankia*, *Euryodendron*, *Ficalhoa*, *Freziera*, *Stewartia*, *Symplococarpon*, or *Visnea*.

48. Nucellar development: (0) tenuinucellate; (1) crassinucellate. Tenuinucellate ovules are those in which the archesporial cell develops directly into the megaspore mother cell, while crassinucellate is here restricted to those ovules in which the archeosporial cell cuts off a primary parietal cell (Davis, 1966). The embryology of many genera has not been examined carefully, and thus this character should be viewed as provisional. Most taxa examined (Davis, 1966; Prakash and Lau, 1976; Johri et al., 1992; Stevens, unpubl. manuscript; Tsou, 1995, 1997; Yang and Ming, 1995) have tenuinucellate ovules. Crassinucellate ovules are only consistently present in *Pentaphylax* and *Physena* (Johri et al., 1992; Dickison and Miller, 1993). *Cornus* has both, depending on the species (Murrell, 1992, 1993). We have no



Fig. 11. Gynoecium of *Archboldiodendron merrillianum* Kobuski showing free styles, P. van Royen 30138 (BM).

information for *Apterosperma*, *Archboldiodendron*, *Balthasaria*, *Dankia*, *Ficalhoa*, *Pelliciera*, *Sladenia*, *Symplocarpon*, or Tetrameristaceae.

49. Number of styles: (0) one; (1) more than one. Most taxa have a single style. Style number varies from one to five in Theaceae, being 5–7 only in *Archboldiodendron* (Fig. 11). Kilmeyeroideae (Clusiaceae), Tetrameristaceae, *Marcgravia*, *Pelliciera*, and *Pentaphylax* have a single style; *Physena* has two styles and *Asteropeia* has one or three (Morton et al., 1997); in Bonnetiaceae there is one to several; in *Cornus* 1–4; and in *Actinidia* 5–16.

50. Number of stigmas with respect to the number of styles: (0) equal; (1) larger. When the gynoecium has more than one style, the number of stigmas is the same; nevertheless, in the genera with a single style, the stigmas can be divided or not, having one or more stigmas. *Anneslea*, *Apterosperma*, *Freziera*, *Marcgravia*, *Schima*, and *Sladenia* have a single style and more than one stigma; *Pentaphylax* and the species of *Gordonia* with a single style can have one to several stigmas (Keng, 1980a; Watson and Dallwitz, 1992).

51. Fruit type: (0) capsular (Fig. 6C); (1) baccate (Figs 1D and E)/pome (Figs 6A and B); (2) nut (Fig. 6D); (3) drupe. This character is problematic, because there are no anatomical studies that reveal the nature of the fruits and there are species that have fruits intermediate between capsules and berry fruits. Most sampled taxa, nevertheless, undoubtedly have capsular

fruits. Keng (1962) considered the genera of Ternstroemiaceae (here Ternstroemiaceae) with superior ovary to have baccate fruit (*Adinandra*, *Euryodendron*, *Freziera*, and *Ternstroemia*) and in those with semi-inferior ovary there is a fruit similar to a pome (*Anneslea*, *Symplocarpon*, and *Visnea*). Because the definition of pome in these taxa is largely dependent on the inferior ovary, rather than anatomical features, and given that we have already coded a character for the ovary position, we are coding the pomes as a variation of baccate fruits. Both *Cleyera* and *Eurya* (Ternstroemiaceae) were originally described as having capsules (Thunberg, 1783); nevertheless, a careful examination of both dry and fresh material shows that the fruit is baccate. In *Archboldiodendron* the fruit is baccate, although in herbarium specimen annotations it is referred as a drupe. Kobuski (1956) called *Melchiora* (= *Balthasaria*) capsular; unfortunately, we have been unable to verify this; such fruit would be unusual for Ternstroemiaceae, to which this genus belongs; to be cautious we coded this taxon as having a subset-polymorphism. Species of Theaceae s.s. have dehiscent capsules, except for some species of *Pyrenaria*. In this genus a woody or coriaceous pericarp tend to be succulent and the fruits remain indehiscent; in other species, fruits have a dense, thin or cartilaginous pericarp and tend to be dehiscent (Keng, 1980b). “Indehiscent drupaceous fruits” better corresponds to baccate fruits, and we coded this genus as subset-polymorphic. The fruit is a capsule in *Asteropeia* (Perrier de la Bathie, 1950), Bonnetiaceae, *Ficalhoa*, Kilmeyeroideae (Clusiaceae), *Marcgravia*, *Pentaphylax*, and *Sladenia*. The fruit is baccate in *Actinidia* and Tetrameristaceae. The fruit is a drupe (Ocegueda, 1998) in *Cornus*. The fruit of *Pelliciera* is unique among the studied genera. It is a spongy, not fleshy, large indehiscent fruit bearing a single seed. We have called this fruit a type of nut. We also consider that *Physena* has a nut, because the fruit in this genus is dry, indehiscent, thick-walled, somewhat inflated, one seeded (Dickison and Miller, 1993; Morton et al., 1997).

52. Fruit shape: (0) narrowly ellipsoid; (1) spheroid (Fig. 9C); (2) obpyriform (Fig. 9B); (3) turbinate (Fig. 9D). With some exceptions, the fruit is usually more or less spheroid in Theaceae; the fruit of the genera with semi-inferior ovary are obpyriform (*Visnea*, *Symplocarpon*, *Anneslea*); in *Sladenia* it is narrowly ellipsoid; in the case of certain species of *Gordonia* and *Pyrenaria* the capsules can be narrowly ellipsoid (these genera were coded as subset-polymorphic). The fruit is narrowly ellipsoid in *Actinidia*, *Archytaea*, some species of *Bonnetia*, Kilmeyeroideae (Clusiaceae), except *Caraipa*, and Tetrameristaceae. In *Asteropeia*, *Caraipa*, *Cornus*, *Marcgravia*, *Neogleasonia* (*Bonnetia* in this work), *Pentaphylax*, and *Physena* the fruit are spheroid. *Pelliciera* is the only genus with turbinate fruit.

53. Capsule dehiscence: (0) septicidal; (1) loculicidal. This character is coded only for capsular fruits, because by definition the other types of fruits are indehiscent and if we coded them as such we would be weighting this condition. Therefore, taxa with berries, drupes, pomes, or nuts are coded as inapplicable (–). For *Pyrenaria*, which can have baccate or capsular fruits, we coded this character using the species with capsular fruits. Species with capsular fruits commonly open either through the septa or through the locules. Nevertheless, in *Marcgravia* the fruits dehisce loculicidally and septifragally from the base (De Roon, 1970); this genus was coded as polymorphic. The Theaceae with capsules are usually loculicidal. Although some species of *Pyrenaria* indeed have loculicidal capsules, according to Keng (1980b), other species can have septicidal capsules, unusual for Theaceae s.s.; considering Keng's report, we coded this genus as polymorphic. Bonnetiaceae and Kielmeyeroideae (Clusiaceae) have septicidal capsules, though in *Caraipa* and *Haploclathra* they are septifragal; *Asteropeia* has loculicidal capsules (Perrier de la Bathie, 1950). We have no information for the species of *Balthasaria* with capsular fruit.

54. Exocarp texture of the baccate fruits: (0) fleshy; (1) dry. This character is coded only for taxa with baccate fruits, the rest were coded as non-applicable (–). The baccate fruits are typical of Ternstroemiaceae; nevertheless, the texture of these fruits varies. Most of the genera have a fleshy exocarp, but in some species of *Cleyera* and *Ternstroemia* the exocarp of the fruits can be dry. The species of *Pyrenaria* with baccate fruits have a dry pericarp. *Actinidia* also has dry exocarp. Tetrameristaceae has baccate fruits apparently with fleshy exocarp.

55. Wing in the seeds: (0) absent; (1) present. Most taxa lack winged seeds. In Theaceae, winged seeds are present in *Gordonia*, *Schima*, *Sladenia* and in some species of *Stewartia* (coded as polymorphic). Outside Theaceae, wings are present in *Pentaphylax* (Tien-lu and Bartholomew, 2003) and in Kielmeyeroideae (Clusiaceae), except in *Mahurea* and *Marila*. In Bonnetiaceae Stevens (unpubl. manuscript) has observed very small wings in several species of *Bonnetia* and in *Ploiarium* (*Archytaea* in this study) therefore we coded both genera as polymorphic. We have no information for *Dankia*.

56. Endosperm in the seed: (0) absent/very scarce; (1) abundant. Most taxa do not have or have very scarce endosperm. All genera in Theaceae s.s. lack or have scarce endosperm, except *Stewartia*. The absence of endosperm in the group had already been noted by Bentham (1861; as Gordonieae). Endosperm is abundant in the seed in *Actinidia*, *Adinandra*, *Anneslea*, *Archboldiodendron*, *Cornus*, *Ternstroemia*, Tetrameristaceae (Maguire et al., 1972), and *Visnea*. In *Sladenia* there is no endosperm and in *Ficalhoa* there is little.

Clusiaceae is usually described as lacking endosperm, however, it occurs in *Marila*, *Mahurea* and *Kielmeyera* (Stevens, unpubl. manuscript). Endosperm has been recorded in *Ploiarium alternifolium* Melch. (*Archytaea* in this work) (Corner, 1976), but other species of *Archytaea* lack endosperm, hence we coded this genus as polymorphic. The condition for *Apterosperma*, *Dankia*, and *Euryodendron* is unknown.

57. Endosperm development: (0) nuclear; (1) cellular. There is only scattered information for this character, but it has been traditionally considered valuable in plant systematics. The embryology of many genera has not been examined, and this character should be viewed as provisional. Most of the genera with reports have nuclear endosperm development (Corner, 1976; Prakash and Lau, 1976; Johri et al., 1992; Tsou, 1995, 1997). Only *Actinidia*, *Cornus*, and *Marcgravia* have cellular endosperm development (Corner, 1976; Johri et al., 1992). We have no information for *Archboldiodendron*, *Asteropeia*, *Balthasaria*, *Bonnetia*, *Dankia*, *Euryodendron*, *Ficalhoa*, *Pelliciera*, *Physena*, *Pentaphylax*, *Sladenia*, and *Tetrameristaceae*.

58. Fleshy structure that more or less envelops the seed: (0) absent; (1) present. Fleshy tissues surrounding the seeds can have different origins (e.g., aril versus sarcotesta). To distinguish them, anatomical and ontogenetic studies need to be carried out. In the studied taxa, there are species with seeds more or less enveloped by fleshy tissues for which no such studies have been carried out. In order to consider the presence of fleshy tissues in the seed, we have decided to code this character even though we are aware that the structures may not be homologous. We hope that our analysis will provide a first hypothesis for the homology assessment of these structures that can be later tested with careful anatomical and/or ontogenetic research. Fleshy structures surrounding the seeds are present in *Actinidia*, *Anneslea*, *Pelliciera*, *Ternstroemia*, and possibly *Marcgravia*. Kobuski reported for *Anneslea* (Kobuski, 1952a) and *Ternstroemia* (Kobuski, 1942a,b, 1943) the presence of an aril, but Corner (1976) indicated that the nature of the fleshy tissue in both genera corresponds to a sarcotesta. In the seed of *Pelliciera*, Kobuski (1951a) maintained that frequently there is "a pasty cover in undefined quantity" that we have interpreted as a fleshy tissue of unidentified origin. *Actinidia chinensis* Planch. appears to have an aril, but *A. polygama* Franch. et Sav. is reported as exarillate; we coded this genus as subpolymorphic (Corner, 1976). There are contradicting reports for the genus *Marcgravia*, which need to be corroborated. In this genus, seeds have been described as exarillate, with a slightly multilayered, possibly lignified, testa (Corner, 1976), but also as arillate with a red testa (Johri et al., 1992). We decided to provisionally code this taxon as polymorphic, considering presence and lack of a fleshy tissue.

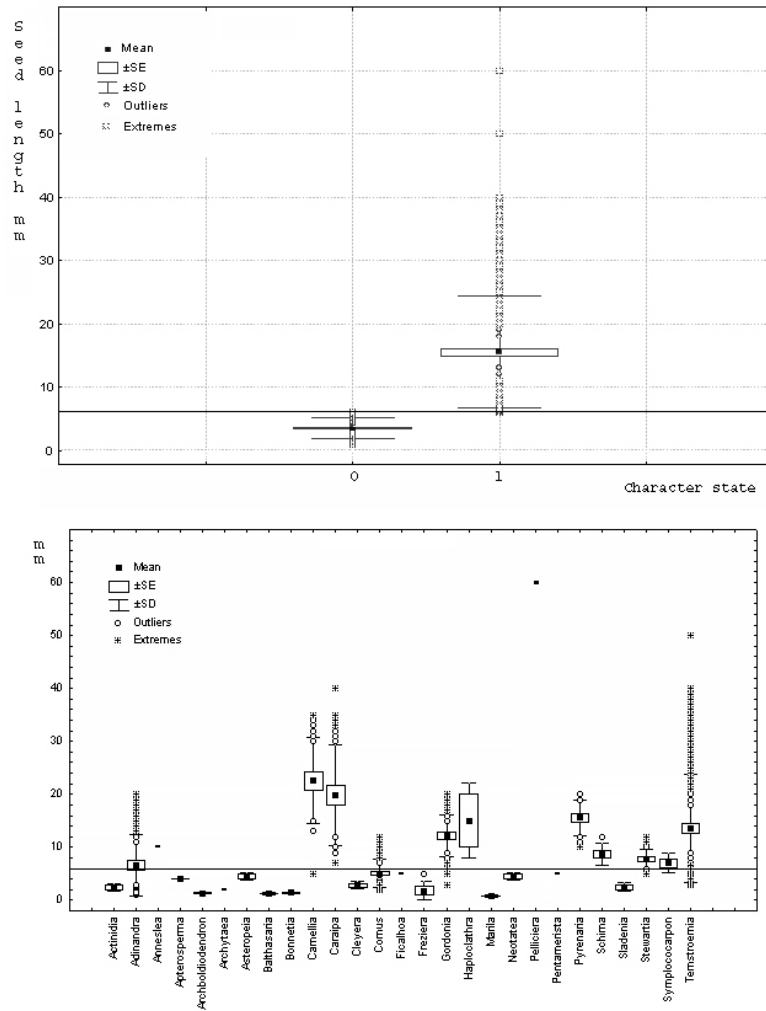


Fig. 12. Seed length: character state distribution at species level, based on 145 accessions (above); generic variation (below).

59. Seed length: (0) large (over 6–7 mm); (1) small (under 6 mm). To define the states of this character we plotted information for 145 accessions corresponding to 27 genera. We summarize this information in two graphs, one corresponding to the generic characterization and the other to the character state distribution (Fig. 12). Most taxa have seeds less than 6 mm long. The seeds are generally large in Theaceae s.s., except for *Apterostroma*, and some species of *Camellia* and *Gordonia*. In contrast, Ternstroemiaceae has small seeds, except for *Symplococarpon*, which has seeds that can measure over 6 mm. Stevens (pers. comm.) claimed that many Kilmeyeroideae have very large seeds (over 6 mm), except for *Mahurea* and *Marila*. The seeds of *Pelliciera*, *Pentaphylax* (Tien-lu & Bartholomew, 2003) and *Tetramerista* (Maguire et al., 1972) measure more than 6 mm. Small seeds occur in *Actinidia* (2–3 mm), *Asteropelta* (4–5 mm), *Bonnetiaceae* (1–2 mm), *Marcgravia*, and *Sladenia* (1–3 mm). *Cornus* has drupaceous fruits and

the endocarp can house more than one seed; in some species, the endocarp can be larger than 6 mm, but even then the seeds are less than 6 mm. We have no information for *Dankia* and *Physena*.

60. Embryo position: (0) straight; (1) curved. Reports of this character are conflicting for some genera, in which case we use the last record reported for the genus. This is the case for *Ficalhoa*, whose embryo was cited by Robson (1961) as curved, but APG II (2003) cited it as straight. Most Theaceae s.s. have a straight embryo, while most Ternstroemiaceae have curved embryos. Exceptions to this are *Schima*, with a curved embryo (Bloembergen, 1952; Corner, 1976), and *Ficalhoa* and *Sladenia*, with straight embryos (Kobuski, 1951b; APG II, 2003; Tien-lu & Bartholomew, 2003). Most Kilmeyeroideae (*Clusiaceae*) have fusiform embryos (Stevens, 2001 onwards), coded as straight, except for *Caraipa* (Kubitzki et al., 1978); *Bonnetiaceae* has straight embryos (Corner, 1976; Stevens, 2001 onwards);

Tetrameristaceae has erect embryos (Maguire et al., 1972), coded as straight; *Actinidia* has straight embryos (Dunn, 1911); *Pentaphylax* has curved embryos (AP GII, 2003; Tien-lu & Bartholomew, 2003). We have no information for *Asteropeia*, *Cornus*, *Dankia*, *Euryodendron*, *Marcgravia*, *Pelliciera*, or *Physena*.

Matrix

This is the first time that all genera of Theaceae have been incorporated into a cladistic analysis. The resulting matrix (Table 6) contains a total of 139 cells (6%) with missing values, 61 cells (2%) with inapplicable values and 247 (11%) with subset and full polymorphisms. Full ambiguity (missing, inapplicable and full-polymorphic data) is mostly randomly distributed, i.e., not concentrated in a particular character or taxon. The genera with the most ambiguous cells were *Dankia* (38.3%), *Cornus* (33.3%), *Euryodendron* (26.6%), *Actinidia* and

Apterosperma (23.3%), *Marcgravia* (20%), *Freziera* and *Camellia* (16.6%), and *Bonnetia*, *Gordonia*, and *Ternstroemia* (15%). There are few collections and little available information on *Apterosperma*, *Dankia*, and *Euryodendron*, therefore these genera have several missing values, while *Actinidia*, *Camellia*, *Cornus*, *Freziera*, *Gordonia*, *Marcgravia*, and *Ternstroemia* have many species and/or are very diverse, and therefore have several polymorphic characters.

Trees

The parsimony analysis resulted in 45 equally most parsimonious trees (MPTs) of 219 steps (minimum = 78; maximum = 501), a consistency index (CI) of 0.35 and retention index (RI) of 0.66. The consensus tree (Fig. 13) shows some correlation at the family and subfamily level with traditional classifications (e.g., Keng, 1962; Cronquist, 1981; Takhtajan, 1997) and

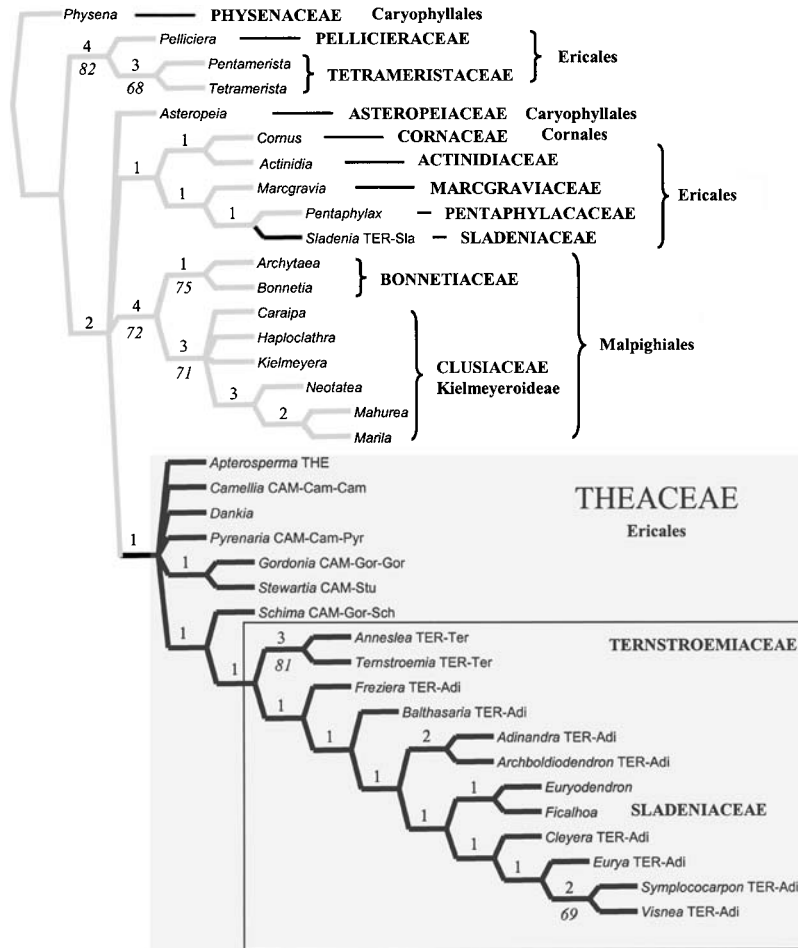


Fig. 13. Consensus tree of the 45 equally most parsimonious trees (MPTs L = 219; CI = 0.35; RI = 0.66). Numbers below branches indicate Jackknife support; numbers above branches indicate Bremer support. Dark lines correspond to Theaceae. Acronyms next to genera in Theaceae represent subfamily (capitals), tribe and, when existing, subtribe (lower case) classification following Keng (1962). Family and order outside Theaceae follow Stevens (2001 onwards).

molecular analyses (e.g., Stevens, 2001 onwards; Anderberg et al., 2002). In all MPTs, Bonnetiaceae, Kilmeyeroideae (Clusiaceae), and Tetrameristaceae were monophyletic. Theaceae consists of one clade in which the recognition of two families or subfamilies would leave Theaceae s.s. paraphyletic.

Subfamily rank for Theaceae s.s. (Camellioideae) and Ternstroemiaceae (Ternstroemioidae) has been independently supported by embryological evidence (Tsou, 1995); the width of the integuments, 6–7 cells in Camellioideae and 3 in Ternstroemioidae; the embryo sac formation (Yang and Ming, 1995), *Allium*-type in *Camellia*, *Polygonum*-type in *Pyrenaria* and Ternstroemioidae; the epidermis of the ovule, normal in Camellioideae and tanniniferous in Ternstroemioidae; and the hypostase, present in Camellioideae, absent in Ternstroemioidae. Family rank for Theaceae s.s. and Ternstroemiaceae is supported by molecular evidence (Prince and Parks, 2001; Stevens, 2001; onwards;

Anderberg et al., 2002). These studies, nevertheless, have only included representatives of Theaceae. Based on our results, the recognition of two taxa would not reflect a natural classification, because Theaceae s.s. is not supported as monophyletic. However, Ternstroemiaceae is supported as a monophyletic taxon, including *Adinandra*, *Anneslea*, *Archboldiodendron*, *Balthasaria*, *Cleyera*, *Eurya*, *Euryodendron*, *Ficalhoa*, *Freziera*, *Symplococarpum*, *Ternstroemia*, and *Visnea*. The hypothetical paraphyletic Theaceae s.s. includes *Apterosperma*, *Camellia*, *Dankia*, *Gordonia*, *Pyrenaria*, *Schima*, and *Stewartia*.

The analysis of the characters that unambiguously support the branches in all the MPTs, and which are here mapped on to the consensus (Fig. 14), shows that most of the major clades are supported by a unique combination of characters that, with a few exceptions, also includes synapomorphic character states. This is not the case for Theaceae, because the clade in all MPTs



Fig. 14. Consensus tree of the 45 equally most parsimonious trees (MPTs L = 219; CI = 0.35; RI = 0.66) showing the character states that can be unambiguously optimize in all the MPTs. Numbers above dots indicate the character and below dots the character state. Apomorphic states are shown in black dots and homoplastic states in white dots. Dark lines correspond to Theaceae. Acronyms next to genera (capitals) represent family or subfamily classification; for Theaceae, acronyms in lower case indicate the classification at tribe level and, when existing, subtribe, following Keng (1962).

is only unambiguously supported by the presence of solitary flowers (with a regression in *Ficalhoa*), a condition also consistently present only in *Pelliciera*.

Pellicieraceae and Tetrameristaceae are grouped in a clade sister to the rest of the taxa, and supported by the synapomorphy of presence of glands in the sepals (29/1; $ci = 1$), and a unique combination of homoplastic character states, the presence of raphides (4/1; $ci = 0.33$), inconspicuous petioles (21/1; $ci = 0.25$), equal number of petals and stamens (30/1; $ci = 0.33$), and one ovule per loculus (46/0; $ci = 0.20$). Baretta-Kuipers (1976) suggested that the wood of *Pelliciera* is very different to that of Theaceae, mainly in having simple perforations and raphides, and is similar to that of Tetrameristaceae (*Tetramerista* and *Pentamerista*); our cladistic analysis supports this association. This relationship also corroborates the results based on the DNA evidence of Soltis et al. (2000), Savolainen et al. (2000), and Stevens (2001 onwards), which questioned the hypothesis of Weitzman (1995), that *Pelliciera* could represent a highly specialized Theaceae. Maguire et al. (1972) suggested that *Pelliciera* could be “a radially adaptive product of either *Tetramerista* or *Pentamerista* or, more reasonably, of their common or related forebears”; in our results *Pelliciera* shares an earliest common ancestor with both genera. Both *Pelliciera* and Tetrameristaceae were found to be within Ericales according to molecular data, but in all cases the clade is sister to the rest of the order. In our analysis, the clade is sister to a clade that includes (*sensu* molecular data) *Asteropeia*, Cornales, Ericales, and Malpighiales, supported by the presence of fiber tracheids (10/1; $ci = 0.33$) and capsular fruits (51/0; $ci = 0.5$). This result questions either the position of these taxa within Ericales, or the circumscription of the orders, which could be an artifact of the sampling in the molecular analyses, but it could also be an artifact of our sampling, which is limited to Ericales.

The clade that includes *Asteropeia*, Cornales, Ericales, and Malpighiales forms a polytomy in the consensus that reflects conflict regarding the relationship between *Asteropeia* and three other clades. The small longitude of the corolla (26/0; $ci = 0.30$) and the tricolpate pollen grains (41/2; $ci = 0.66$) distinguish *Asteropeia* from the other three clades. *Asteropeia* was first placed as an anomalous genus within Samydeaceae (Bentham and Hooker, 1862: = Salicaceae). It was later doubtfully transferred to Bixaceae-Callantiaceae (Baillon, 1872), and then to Theaceae-Asteropeiiae by von Szyszylowicz (1895). Based on anatomical data, Baretta-Kuipers (1976) suggested that this genus was closely related to Bonnetiaceae. Our results do not support the inclusion of this genus within either Theaceae or Bonnetiaceae. Reveal and Hoogland (1990) validated the family Asteropeiaceae as accommodating this genus, a proposal that was accepted by the APG (1998, 2003),

including the family within Caryophyllales, not being immediately related to any of the orders in which the other families just mentioned are placed. According to molecular evidence (Savolainen et al., 2000; Stevens, 2001 onwards), *Asteropeia* is sister to *Physena* (Caryophyllales). In order to test this, we used *Physena* as the functional outgroup, and our analysis does not corroborate this hypothesis. In our results, *Asteropeia* is more closely related to Malpighiales-Ericales-Cornales than it is to Caryophyllales.

In the polytomy, one of the clades is formed by Bonnetiaceae and Kielmeyeroideae (Clusiaceae), and it shares the following synapomorphic character states: presence of xanthones (2/1; $ci = 1$) and contorted corollas (31/0; $ci = 1$), in addition to the homoplastic characters: stamens arranged in fascicles (34/0; $ci = 0.25$), narrowly ellipsoid fruit (52/0; $ci = 0.37$), and septicidal capsules (53/0; $ci = 0.5$). Within this clade, Kielmeyeroideae is supported by a unique combination of character states (11/1; 12/0, 19/0). Clusiaceae was classified by Soltis et al. (2000) within Malpighiales, and Bonnetiaceae was classified within the same order by Savolainen et al. (2000). Our results show a relatively close relationship between these two families, but the sampling is too poor to say more.

Another clade in the polytomy is formed by representatives of Ericales and *Cornus*. This clade is supported by the homoplastic pubescent anther (36/1; $ci = 0.33$) and smooth pollen surface (42/1; $ci = 0.33$). There are two noticeable facts related to this clade, the placement of *Cornus*, nested within Ericales and sister to *Actinidia*, and the embedded clade formed by *Marcgravia*, *Pentaphylax*, and *Sladenia*.

According to DNA phylogenetic analyses (e.g., Savolainen et al., 2000; Anderberg et al., 2002; Bremer et al., 2002; APG II, 2003), *Cornus* shares a most common recent ancestor with Ericales, but does not belong in the group. The placement of *Cornus* within Ericales may be caused by a sampling artifact in our analysis, because we only used this genus as representative of the order Cornales.

With even more controversy, the genus *Sladenia* was described within Theaceae (Kurz, 1873), but was soon transferred to Dilleniaceae (Gilg, 1893). Later, Gilg and Wedermann (in Kobuski, 1951b) included it in the segregate family, Actinidiaceae. In the same year, Hallier (1924) transferred *Sladenia* to Linaceae, although this position was never accepted. Metcalfe and Chalk (1950) returned it to Theaceae based on their anatomical studies, considering it as an anomalous genus within the family. Using pollen morphology, Wodehouse (in Kobuski, 1951b) related *Sladenia* with *Ternstroemia*. Record (1942) using anatomical evidence, related it to *Eurya*. Keng (1962) and Kobuski (1951b) classified this genus in a monotypic tribe or subtribe, respectively (Sladenieae or Sladeniinae) within

Ternstroemioidae, separating it because of its dichasial cymes, few stamens, elongated filaments, and pilose anthers. In 1965, Airy-Shaw described the family Sladeniaceae to place the genus. More recently, Shui et al. (2002) described a second species of *Sladenia*, classifying it within Sladeniaceae, which was considered as a family *incertae sedis* by APG (1998, 2003), but placed within Ericales by Savolainen et al. (2000). Stevens (2001 onwards) retained the family Sladeniaceae including *Sladenia* and *Ficalhoa*. Our analysis supports the exclusion of *Sladenia* from Theaceae, a sister relationship with *Pentaphylax*, and a distant relation of both to *Ficalhoa*.

Based on DNA evidence, Stevens (2001 onwards) reduced Ternstroemiaceae to Pentaphylacaceae, the latest as sister to Sladeniaceae. Recent DNA studies suggest that *Ficalhoa* and *Sladenia* are sister taxa, sharing a recent common ancestor with Ternstroemiaceae-Pentaphylacaceae (Anderberg et al., 2002). Our analysis supports the sister relationship of *Sladenia* and *Pentaphylax*, both having very long vessel members (9/2; *ci* = 0.33), corolla less than 7 mm (26/0; *ci* = 0.3), anthers dehiscence by apical pores (37/1; *ci* = 0.5), and winged seeds (55/1; *ci* = 0.16), but place these genera as sister to *Marcgravia* according to the presence of small pollen grains (40/0; *ci* = 0.33). In molecular analyses (Morton et al., 1996; Savolainen et al., 2000; Soltis et al., 2000; Stevens, 2001 onwards; Anderberg et al., 2002), *Marcgravia* appears closely related to *Pelliciera* and Tetrameristaceae. This relationship is morphologically supported by the presence of raphides, which in our analysis appears as an homoplastic condition.

The last clade in the polytomy corresponds to Theaceae, supported by having solitary flowers (25/1; *ci* = 0.33). This clade, nevertheless, has low support values (either Jackknife or Bremer support) in our analysis (Fig. 13).

Within the Theaceae there is a large basal polytomy that reflects the ambiguous position of *Apterosperma*, *Dankia*, *Camellia*, *Pyrenaria* and *Gordonia-Stewartia*.

Apterosperma is a poorly known monotypic genus described by Chang (1976), who considered it to be closely related to *Camellia*, but it has also been suggested to be a synonym of *Schima* (Liang and Baas, 1990). Tsou (1997) considered *Apterosperma* as a valid genus belonging in Theaceae s.s., because of the presence of pseudopollen. Our analysis supports the distinction of *Apterosperma* and *Schima* and a close relationship with other Theaceae s.s.

Dankia is a monotypic genus that was described as part of Flacourtiaceae (Gagnepain, 1939) and later considered to be a synonym of *Camellia* (Phamhoang, 1991). Our analysis suggests that *Dankia* is a distinct taxon from *Camellia*.

Within Theaceae, there are several characters that support the monophyly of Ternstroemiaceae, the synapomorphic condition of lacking pseudopollen (43/0; *ci* = 1), the homoplastic presence of a small protrusion as an extension of the anther connective (38/1; *ci* = 0.28), pollen grains of less than 30 μm (40/0; *ci* = 0.33), a smooth pollen surface (42/1; *ci* = 0.33); and baccate fruits (51/1; *ci* = 0.5). *Schima* is sister to Ternstroemiaceae, a relationship supported by the curved embryo (60/1; *ci* = 0.25). Anderberg et al. (2002) presented a monophyletic Theaceae s.s., with *Schima* as sister to all other members of the clade. Prince and Parks (2001) and Tsou (1997) considered *Schima* to be sister to *Gordonia*. In our analysis, *Gordonia* and *Stewartia* are sister taxa, a relationship supported by the stamens arranged in fascicles (34/0; *ci* = 0.25).

Ternstroemiaceae

A clade containing *Anneslea* and *Ternstroemia* is sister to the rest of Ternstroemiaceae. The close relationship between *Anneslea* and *Ternstroemia*, which was suggested both by Keng (1962), placing them in the same tribe (Ternstroemiaceae), and by Kobuski (1952a). This clade is supported by the unique combination of punctate leaves (20/1; *ci* = 1), glabrous ovary (45/0; *ci* = 0.5), abundant seed endosperm (56/1; *ci* = 0.12), and seeds surrounded by a fleshy tissue (58/1; *ci* = 0.5).

Next in a grade is *Freziera*, which was suggested to be related to *Eurya* and *Cleyera* (Kobuski, 1937, 1941a), a relationship not supported by our analysis. Next in a grade is *Balthasaria*, earlier suggested as a close relative of *Adinandra* (Kobuski, 1956, 1957), which in our analysis forms a clade with *Archboldiodendron*. Previously, Kobuski (1947) had suggested a close relationship between *Adinandra* and *Archboldiodendron*, which is indeed supported by our analysis, the two of them having inconspicuous petioles (21/1; *ci* = 0.25) and abundant endosperm (56/1; *ci* = 0.12). The terminal portion of the grade is formed by two clades, one including *Euryodendron* and *Ficalhoa*, the other including *Cleyera*, *Eurya*, *Symplocarpon*, and *Visnea*.

When Chang (1963) described the genus *Euryodendron*, he considered it to be intimately related to *Eurya* and *Cleyera*. When *Ficalhoa* was described by Hiern (1898), he placed it within Ericaceae due to the presence of poricidal anthers and the small and numerous seeds produced in loculicidal capsules; it was later included in Sapotaceae (Airy-Shaw, 1965). More recently, Robson (1961) transferred this genus to a new tribe (Ficalhoeae) within Theaceae, even though this genus has “atypical latex” in the bark and dichasial cymes. The relationship of *Ficalhoa* and *Euryodendron* in our analysis is supported by the membranous to chartaceous leaf consistency (18/1; *ci* = 0.5).

Robson (1961) considered *Ficalhoa* to be related to *Cleyera*, *Eurya*, and *Freziera*, while Airy-Shaw (1939) suggested that *Symplococarpon* is related to *Cleyera* and *Freziera*; in our analysis *Cleyera* is sister to *Eurya*, *Symplococarpon* and *Visnea*, the last two forming a monophyletic group supported by a semi-inferior ovary (44/1; $ci = 0.66$). The four genera are grouped by the spiral thickenings of the vessel walls (8/1; $ci = 0.2$).

Taxon ambiguity and tree resolution

When the taxa with the greatest amount of ambiguity were removed, interesting results were obtained. When removing *Dankia*, which has a similar number of missing cells as an average fossil (Nixon, 1996), the topology of the consensus (15 MPTs; $L = 220$; $ci = 0.35$; $RI = 0.66$) remains identical, as in the analysis that includes all taxa (Fig. 15a). In contrast, when *Cornus* (33.3% of cells with full ambiguity) is removed (20 MPTs; $L = 220$; $ci = 0.35$; $RI = 0.66$), the resolution is almost completely lost within Ericales (except *Pelliciera* and Tetrameristaceae that remain in their original position), while *Asteropeia* appears as sister to Malpighiales (Fig. 15b). On the contrary, when *Euryodendron* (26.6% of cells with full ambiguity) is removed, only three most parsimonious trees are obtained ($L = 217$; $ci = 0.35$; $RI = 0.66$) and the consensus is considerably well resolved (Fig. 15c). In this consensus, *Asteropeia* appears again as sister to Malpighiales; *Cornus*, as supported by molecular data, is sister to Ericales (except *Pelliciera* and *Tetramerista*, which remain in the original position); *Marcgravia*, *Pentaphylax*, *Sladenia*, *Ficalhoa*, and *Apterosperma* form a grade basal to Theaceae; Theaceae s.s. is monophyletic, with *Actinidia* nested within the clade; and Ternstroemiaceae is again supported as monophyletic, without changes with respect to the original analysis. The main clades persist when *Apterosperma* (23.3% of cells with full ambiguity) is removed (27 MPTs; $L = 218$; $ci = 0.35$; $RI = 0.66$), but resolution among them is gained (Fig. 15d), with *Asteropeia* as sister to *Cornus*–Ericales (except *Pelliciera* and *Tetramerista*, which remain in the original position and Theaceae), and Malpighiales sister to Theaceae. In this analysis the relationships within Theaceae remain the same as in the original analysis. When *Actinidia* (23.3% of cells with full ambiguity, same number as in *Apterosperma*) is removed (99 MPTs; $L = 209$; $ci = 0.37$; $RI = 0.67$) resolution is almost completely lost (Fig. 15e). Finally, when *Marcgravia* (20% of cells with full ambiguity) is removed (83 MPTs; $L = 212$; $ci = 0.36$; $RI = 0.68$), *Cornus* and *Pentaphylax* becomes sister to *Pelliciera* and *Tetramerista*, which remained in the original position, and resolution was lost within the Theaceae clade, which also includes *Actinidia* (Fig. 15f).

We support the idea that all available information should be included in a cladistic analysis, even though it may be incomplete, and that the hypotheses that result from that analysis should be considered as the most corroborated and therefore the best at the time (Kluge and Wolf, 1993; Nixon and Carpenter, 1996). Nevertheless, as was previously noted (Nixon, 1996), the more ambiguity coded for a taxon, the weaker the parsimony test. Therefore, we recommend that the results of our analysis should be taken with caution until more information (taxa and characters) is acquired and the hypothesis is independently corroborated.

Our results show that ambiguity can produce the same results, either when it is caused by a lack of information (poorly known taxa) or when it is caused by polymorphism (highly diverse taxa). With these results, we suggest that a future research program should consider as priority the gathering of more information about the poorly known genera, such as *Apterosperma*, *Dankia*, and *Euryodendron*. Moreover, we consider that it is important to test the monophyly of some of the genera using species as terminals. The amount of polymorphism and the dramatic changes in resolution produced when some genera are removed from the analysis may indicate potential circumscription problems, and we therefore consider the revision of these taxa in a phylogenetic context as a high priority. Genera in need of a revision in a phylogenetic context are *Actinidia*, *Camellia*, *Cleyera*, *Eurya*, *Gordonia*, *Marcgravia*, and *Ternstroemia*. The case of *Freziera* is notable, because this genus was recently carefully reviewed, although its monophyly was not tested in a phylogenetic context.

Characters and tree resolution

The analysis of character removal (Davis et al., 1993) is used here as a way of identifying characters that affect tree topology, allowing us to detect the existence of potentially problematic characters, and the need to review the primary homology assessments (*sensu* De Pinna, 1991) by doing more careful anatomical, developmental, or morphological research.

In this test, 28 characters can be removed without affecting the topology of the consensus (1–2, 4–5, 11, 14, 16, 19–21, 23–25, 29–32, 37, 39, 41, 43–44, 48, 51–54, and 58); removing character 6 (nodal structure) only collapses the Bonnetiaceae clade; removing character 17 (leaf arrangement) only collapses the *Euryodendron*–*Ficalhoa* clade; removing character 34 (stamen arrangement) only collapses the *Gordonia*–*Stewartia* clade; and removing character 60 (embryo position) only collapses *Schima* as sister to Ternstroemiaceae. The removal of the other 28 characters produces different results, including decreases and increases in resolution.

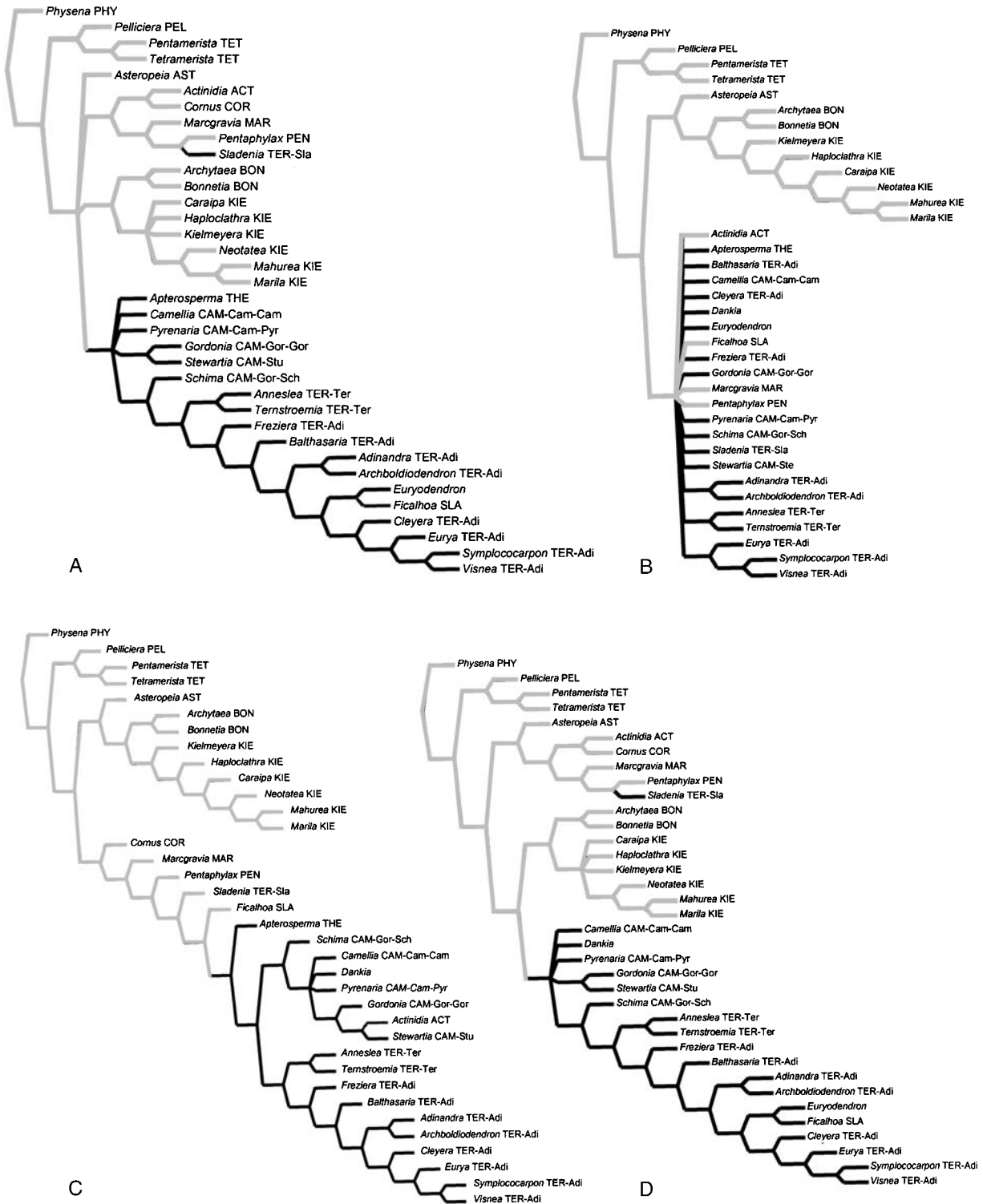


Fig. 15. Consensus trees of the equally most parsimonious trees resulting from sequential removal of seven genera with relatively high ambiguity proportions (20% or more). (A) Consensus when *Dankia* (15 MPTs; L = 220; CI = 0.35; RI = 0.66) is removed; (B) Consensus when *Cornus* is removed (20 MPTs; L = 220; CI = 0.35; RI = 0.66); (C) Consensus when *Euryodendron* (3MPTs; L = 217; CI = 0.35; RI = 0.66) is removed; (D) Consensus when *Apterosperma* is removed (27 MPTs; L = 218; CI = 0.35; RI = 0.66). (E) Consensus when *Actinidia* is removed (99 MPTs; L = 209; CI = 0.37; RI = 0.67). (F) Consensus when *Marcgravia* is removed (83 MPTs; L = 212; CI = 0.36; RI = 0.68). Dark lines correspond to Theaceae. Acronyms next to genera (capitals) represent family or subfamily classification; for Theaceae, acronyms in lower case indicate the classification at tribe level and, when existing, subtribe, following Keng (1962).

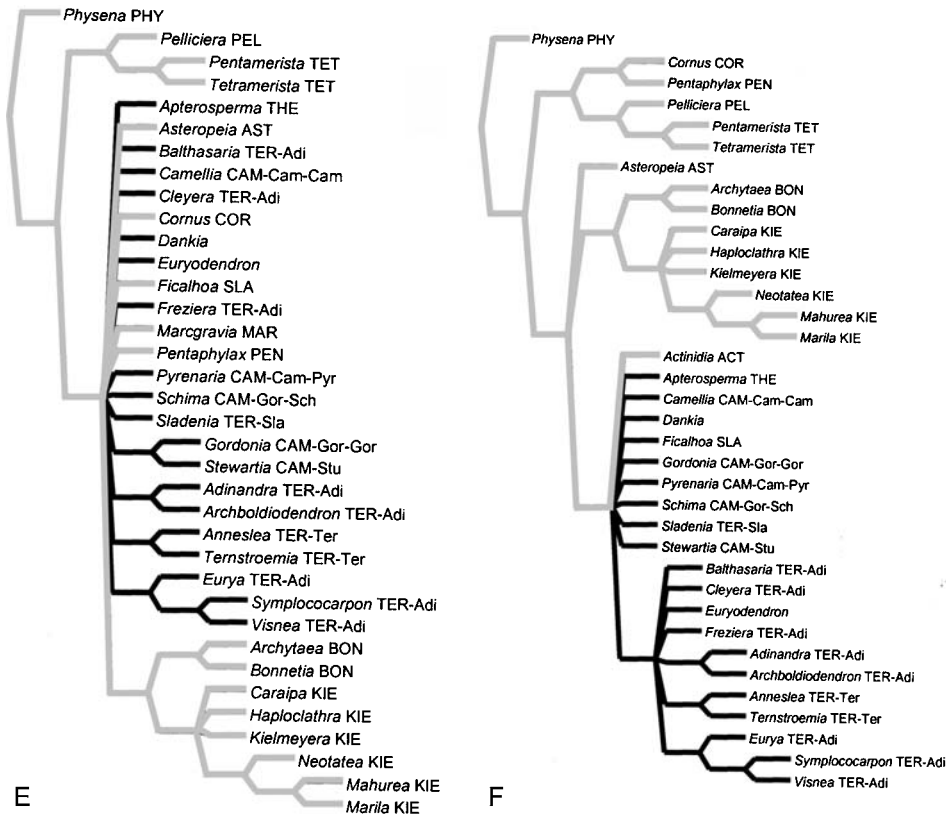


Fig. 15. (continued)

Twenty-one characters are fundamental to maintaining a reasonable resolution of the trees; if one of them is removed, the tree collapses almost entirely. These are character 7 (axial parenchyma types), 8 (spiral thickenings of the vessel walls), 9 (vessel member length), 12 (sclerenchymatous idioblasts), 13 (indumentum), 18 (leaf consistency), 22 (decurrent base of the leaf lamina), 26 (corolla size), 33 (stamen number), 35 (anther attachment to the filament), 36 (anther surface), 40 (pollen grain size), 42 (pollen surface), 45 (ovary surface), 46 (ovules per loculus), 47 (ovule position), 49 (number of styles), 50 (number of stigmas), 55 (wing in the seed), 56 (endosperm), and 59 (seed length). Most of these characters are not problematic, reflecting the existence of relative support for the clade containing Theaceae. Nevertheless, some of them are problematic, such as characters 7 (axial parenchyma types), 8 (spiral thickenings of the vessel walls), 9 (vessel member length), 42 (pollen surface), and 47 (ovule position), which have scattered information, and whose coding may vary as more data are gathered and as standard terminology is used among different study groups. We again encourage the sampling in wood anatomical studies to be improved. With respect to the pollen surface, there are only scattered studies that do not consider many taxa at once. Again, comparative

palynological studies within the group are promising and highly encouraged. For character 22 (decurrent base of the leaf lamina), the presence of a decurrent base can be confused with sessile leaves and it would therefore be desirable to check this character with fresh material and to use standardized terminology. Characters 13 (indumentum) and 55 (wing in the seed), as currently used, may include non-homologous conditions in the same character states (Stevens, unpubl. manuscript). To define more precisely any potentially homologous character states, ultrastructure and development studies are again encouraged. For characters 26 (corolla size), 33 (stamen number), 40 (pollen grain size), 46 (ovules per loculus), and 59 (seed length), we used descriptive statistics to define the character states. As more information is gathered, more specific statistical tests can be done, but we do not expect major changes with respect to our current definitions.

The removal of seven characters only partially affects the resolution of the consensus. These are character 3 (siphonostele in petiole), 10 (fiber type), 15 (stomata type), 27 (inflorescence type), 28 (apical eglandular sepal projection), 38 (extension of the connective), and 57 (endosperm development). When one of these characters is removed, the relationships among the main clades are resolved; for example, *Asteropeia* becomes

sister to Malpighiales (removing characters 15 or 28) or to Theaceae (removing character 10). Alternatively, some main clades are collapsed; for example, the clade *Pelliciera*–Tetrameristaceae is no longer sister to the rest of the taxa and *Cornus*–Ericales (except Theaceae) is collapsed when characters 10, 15 or 27 are removed.

Character evolution

In this section we will discuss a few characters for which different authors have postulated “evolutionary trends”, or some of which require a revision of the primary homology assessment (*sensu* De Pinna, 1991) using different tools.

According to Schofield (1968), the unilacunar node structure (6) in Theaceae was derived from a trilacunar one by the fusion of lateral and median traces. Our analysis does not support this idea, because in all cases trilacunar nodal structures appear to be derived from unilacunar ones (at least for independent origins).

Baretta-Kuipers (1976) claimed that very long vessels are more derived than short ones (9). Our analysis shows two different tendencies in length vessel evolution. It appears that the plesiomorphic condition is to have long vessels that have increased multiple times (in Theaceae, within Kielmeyeroideae and in *Pentaphylax-Sladeria*) and also independently decreased multiple times (in Bonnetiaceae, *Asteropeia*, and *Kielmeyera*). In other words, there is no progressive change from small to very large or vice versa.

Baretta-Kuipers (1976) claimed that fiber tracheids are plesiomorphic to libriform tracheids (10). Our results show that the evolution of this character is more complex, due to homoplasy ($ci = 0.33$). The plesiomorphic condition seems to be libriform tracheids, which evolved into fiber tracheids with several reversals.

Exudate production (11) has two independent origins in our phylogenetic hypotheses. It would be interesting to chemically study the exudate in *Ficalhoa*, the only genus within Theaceae that is reported to produce it. One indication that the exudate in *Ficalhoa* and Clusiaceae is not homologous is given by the location of the exudate system, which in *Ficalhoa* occurs only in the bark.

The presence of sclereids (12) has been considered a diagnostic feature of Theaceae (Schofield, 1968; Metcalfe and Chalk, 1972). Schofield (1968) included members of Bonnetiaceae within Theaceae, because of the presence of sclereids. Keng (1962), nevertheless, noted that although this is constant within the ingroup, sclereids are also present in other genera outside the family (e.g., *Tetramerista* and *Pelliciera*). He considered the diagnostic condition of Theaceae to be the presence of sclereids in combination with the lack of raphides, which are present in Tetrameristaceae and *Pelliciera*, a combination that also occurs in Marcgraviaceae

(De Roon, 1967). Our results do not support Schofield’s (1968) classification, and show that the presence of sclereids can be interpreted as plesiomorphic. Although the presence of sclereids has been corroborated as a diagnostic feature of several taxa of Theaceae, detailed studies describing their morphology have only been done for *Camellia* (Foster, 1944; Barua and Wight, 1959; Boyd et al., 1982). Possibly the detailed description of the sclereids in other taxa could potentially provide more informative characters for future phylogenetic analyses. On the other hand, in our sampling, the presence of raphides (4) can be interpreted as a derived condition, *contra* Gibbs (1958), who interpreted its presence as primitive. Raphides have several independent origins; according to our analysis, they unite Tetrameristaceae–Pellicieraceae and have two other independent origins in Actinidiaceae and Marcgraviaceae. According to molecular evidence (Stevens, 2001 onwards) they may have at least two independent origins, once in the common ancestor of Balsaminaceae–Marcgraviaceae–Pellicieraceae–Tetrameristaceae and another in Actinidiaceae.

Our results regarding the evolution of indumentum (13) show that the ancestral condition of glabrous plants is reacquired independently in several lineages, but the presence of unicellular trichomes has a single origin. Given our results, one would interpret the unicellular trichomes present in Clusiaceae as homologous to those present in Theaceae. Keng (1962) considered that within Theaceae there are three different basic unicellular trichome types. Two were based on differences in the thickness of the cell walls, while in *Franklinia alatamaha* Marshall (= *Gordonia*) the hairs are fasciculate (Keng, 1962). Our results do not support this conclusion, and suggest that the different thicknesses of the cell walls could have evolved from homologous unicellular trichomes. It is possible that the ultrastructure of the trichomes could shed light on the homology assessments, so more detailed studies, such as that of Anderson (1983) for *Gordonia lasianthus* (L.) Ellis, are needed to clarify possible indumentum evolution.

Reproductive biology

The presence of hermaphroditic or unisexual flowers (23) is interesting, because it is related to reproductive biology strategies. Our analysis shows that the presence of unisexual flowers has evolved independently several times. Genera with unisexual flowers represent different degrees of evolution of dioecism (see discussion of the character).

The presence of inflorescences or solitary flowers, character 25 (flower arrangement), is obviously related to different reproductive strategies. Our analysis allows us to postulate that solitary flowers represent a derived condition resulting from the reduction of inflorescences,

showing at least four independent origins (in *Pelliciera*, in Theaceae, in some species of *Actinidia* and in some Bonnetiaceae). Based on our hypothesis, the presence of inflorescences in *Ficalhoa* has to be interpreted as a derived condition (regression) within Theaceae. This character by itself then does not support the inclusion of *Ficalhoa* within Theaceae. Another character related to reproductive biology that supports the exclusion of *Ficalhoa* from Theaceae is the anther dehiscence type (37). This genus, together with *Pentaphylax*, *Sladenia*, and some species of *Actinidia* and *Marila*, has poricidal anthers instead of longitudinal slits. Poricidal anther dehiscence has been associated with buzz pollination in other groups (e.g., *Senna*, *Solanum*, Ochnaceae, etc.); Bittrich et al. (1993) presented evidence of buzz pollination for *Archytaea* and two species of *Ternstroemia* that have longitudinal anther slits, by female bees of *Aucochloropsis*, *Bombus*, *Euglossa*, *Melipona*, and *Xylocopa*. Pollen in the *Ternstroemia* species studied by Bittrich et al. (1993) is small and dry.

Small pollen grains (40) resulted in our analysis as a derived condition with at least six independent origins (in *Pentamerista*, in *Marcgravia-Pentaphylax-Sladenia*, in Ternstroemiaceae, within *Pyrenaria*, and at least twice within Kiehmeyeroideae). Ternstroemiaceae is characterized by having almost smooth pollen surfaces, which in our analysis is a derived character state (42), also independently originating in *Pelliciera*, in the most recent common ancestor of *Actinidia-Cornus-Marcgravia-Pentaphylax-Sladenia*, and in some species of *Kiehmeyera*. Also related to pollination biology is the anther attachment to the filament (35); in our analysis, dorsifixed anthers are interpreted as having at least six independent origins, this supports Keng's (1962) interpretation of versatile anthers (a type of dorsifixed anthers) as more evolved than the basifixed ones. The presence of trichomes on the anther (36) is also homoplastic, with at least five independent origins. According to Keng (1962), the biological meaning of these structures is unknown, but is probably related to the pollination mechanism. Keng (1962) noted that the extension of the connective tissue in the anthers (38) has been interpreted in two different and contradictory ways. On the one hand, Parkin (1951, in Keng, 1962) suggested that it is an ancestral condition and can be compared to a Bennettitalean microsporophyll; on the other hand, Canright (1952, in Keng, 1962) stated that this projection is the first of the six trends of specialization in stamens within Magnoliaceae. Our results show that the absence of an extension of the connective tissue in the anthers is the plesiomorphic condition that derived at least four times independently into eglandular extensions and at least once into glandular protrusions (within Kiehmeyeroideae). Here we show an apparent phylogenetically promising connection of several characters related to pollination biology, but an integrative

interpretation of pollination evolutionary biology in the group requires field observations in most of the genera.

Melchior (1925), Airy-Shaw (1939), and Kobuski (1952a) considered the presence of a semi-inferior ovary (44) as convergent, evolving from three different lineages. Nevertheless, this interpretation is mostly based on the fact that the three genera have a disjunct distribution, being totally isolated one from another. Our analysis supports the idea of a convergent origin, but it postulates only two independent origins, one in *Anneslea* and another in *Symplocarpon-Visnea*.

Seed dispersal

Characters related to seed dispersal are interesting, but at this moment can only be discussed at the level of syndromes, because there have been very few field observations. Seed dispersal syndromes include fruit type and seed morphology. Taking into account fruit and seed characters, we can broadly define at least two dispersal syndromes: animals and wind.

In the case of the fruits, there are two types (51) that can be associated with animal dispersion syndromes. That which was here called pome (derived from semi-inferior ovaries) is homoplastic, with two independent origins. The pomes of *Anneslea* seem to have originated independently to those of *Symplocarpon* and *Visnea*. There is a report of bird dispersal for *Symplocarpon* (Wheelwright et al., 1984). In contrast, given the weight of the seeds of *Anneslea fragrans* Wall., FAO (1975) considered that they could be wind dispersed.

Another fruit type associated with animal dispersal is the baccate fruit: fleshy and normally brightly colored. According to our results, baccate fruit has evolved three times independently, in *Actinidia*, Tetrameristaceae and Ternstroemiaceae. The texture of the exocarp (54) is fleshy, except for some species of *Ternstroemia* and *Cleyera*. The origin of fleshy baccate fruits is ambiguous in our analysis; it can be interpreted as a single plesiomorphic origin or alternatively as an ancestral condition, changing to dry and regressing to fleshy within Ternstroemiaceae. There is only one anatomical study (Keng, 1962) for fruits in two genera of Theaceae (*Cleyera* and *Camellia*), and there are important differences between the dry baccate fruits and the capsular fruits, respectively. Furthermore, although the exocarp in the dry ripening baccate fruits of *Cleyera* is thick and has sclereids, the cells of the outer layers contain purplish pigments and the seeds are embedded in a pulp (I. Luna, pers. obs.) formed by the enlarged placental region (Keng, 1962); then animal dispersal is possible. Indeed, the baccate fruits of *Tetramerista glabra* Miq. are one of the most important elements in the diet of Orang-utans (see <http://www.brookfieldzoo.org/pagegen/inc/ACvansch.pdf>).

Drupaceous fruits (present in *Cornus*), also associated with animal dispersal, in our analysis appear to be derived either from baccate or capsular fruits (ambiguous optimization).

The presence of capsular fruits, on the contrary, is not associated with animal dispersal syndrome at the level of the fruit. In our analysis, capsular fruits appear to have two origins, the first derived from a nut type and the second as a result of a reversal, derived from a baccate type within Ternstroemiaceae, which normally has fleshy fruits; capsular fruits occur in *Ficalhoa*. In the case of capsular fruits, the liberated seeds can be winged or un-winged. The presence/absence of a wing in the seed (55) is related to wind dispersal syndrome, and in our analysis it is a highly homoplastic character ($ci = 0.2$). In our analysis, winged seeds seem to have originated at least four times. Stevens (unpubl. manuscript) pointed out that in different taxa the nature of the wing seems to be very different; the degree of wing development can be associated with different dispersal agents. For example, Kubitzki (1989) reported water dispersal in *Haploclathra*, which has narrowed wings in the seeds, while Troup (1975) and FAO (1975) reported air-dispersed seeds in *Schima wallichii* Choisy.

Fleshy tissue surrounding the seeds (58), in the bird dispersion syndrome, are consistently present in three genera, which have three different fruit types, *Anneslea* with a pome (accessory fleshy fruit), *Pelliciera* with a nut (spongy fruit), and *Ternstroemia* with a fleshy or dry baccate fruit. Although the fleshy tissue has been considered as equivalent in the three genera (Kobuski, 1951a; Keng, 1962, among others), our results show two independently derived origins ($ci = 0.5$), one in *Pelliciera* and the other in *Anneslea-Ternstroemia*. Corner (1976) described the fleshy tissue of *Anneslea* and *Ternstroemia* as a sarcotesta; in these genera the tissue is fleshy and orange or red. In *Pelliciera*, the tissue described as “buff-colored and with mealy texture” (Kobuski, 1951a), could correspond to an aril. There are reports for *Pelliciera* that the fruit is water dispersed (Kobuski, 1951a), but nothing has been said regarding the function of the fleshy tissue. In contrast, we have observed, in the cloud forest of Hidalgo, birds feeding on the red sarcotestas of *Ternstroemia huasteca* Barthol. and *T. sylvatica* Schldl. & Cham., and there is also a report of bird dispersal in *T. gymnanthera* Sprague (Corlett, 1996). All these observations support the results of our analysis, that the fleshy tissue in *Pelliciera* is not homologous to that present in *Anneslea-Ternstroemia*. Some species of *Actinidia* and *Marcgravia* also have seeds surrounded by a fleshy tissue. According to our analysis, these have an independent origin. In *Actinidia polygama* Franch & Sav., and *A. chinensis* Planch., the seeds are surrounded by a white pulpy aril (Corner, 1976).

As in the case of other characters, anatomical studies of the fruit and seed types are fundamental in re-evaluating our hypotheses of primary homology (*sensu* De Pinna, 1991).

Future research

Several of the polymorphisms in our matrix that introduce ambiguity in particular terminals are caused by the use of genera as terminals. Although it would be more desirable to use species as terminals, that is not possible due to the lack of material and comparative studies. If species had been considered as terminals, polymorphic terminals would have been substantially reduced and some characters that we had to exclude, because they were not informative, could become potentially informative.

Examples of this are the leaf persistency (deciduous versus persistent) and number of perianth parts. The leaves in Theaceae are usually persistent, as are the leaves of *Actinidia*, *Asteropeia*, Bonnetiaceae, Clusiaceae, *Cornus*, *Marcgravia*, *Pelliciera*, and Tetrameristaceae. Nevertheless, several species of *Stewartia*, *Cleyera*, and *Camellia* have deciduous leaves. Spongberg (1974) classified the species of *Stewartia* according to whether they are evergreen or deciduous, e.g., the species of *Hartia* (included in *Stewartia* in this work) are evergreen and those of *Stewartia*, deciduous.

In the case of perianth parts, the genera that include species with more or fewer than five sepals/petals also have species with five sepals/petals. The base number of sepals in Theaceae is five, though there can be six in *Archboldiodendron*, *Pyrenaria*, *Schima*, and *Stewartia*, five to seven in *Ternstroemia* and five to many (due mainly to horticulture influence) in *Camellia*. The only genus in which a smaller number is registered is *Gordonia*, with species with three to five sepals. The number of sepals in *Asteropeia*, Bonnetiaceae, Clusiaceae, and *Pelliciera* is always five; in *Pentamerista* (Tetrameristaceae) and in *Tetramerista* there are five and four, respectively.

Palynological characters were included in the analysis with caution. Palynological terminology is not always consistent among authors (Socorro Lozano, Instituto de Geología, UNAM, pers. comm.), and because observations can also vary, it would be convenient to come to an agreement over terms and to do new comparative studies at this level. For example, in the literature, measurements and descriptions of pollen grains of the same species vary significantly.

Several other characters might be included from the analysis, but the available information is too scattered and in some cases misinterpreted. Examples of these are the ovary placentation and embryological data. In the first case, the interpretation of placentation within Theaceae is confused. Keng (1962) provided a detailed

description of the placentation in *Cleyera*, classifying it as possibly a “falsely axile”, because the lower portion of the ovary is divided into three locules, while the upper portion has a single chamber. Among different taxa, one can see different kinds/degrees of carpel fusion (in Keng’s examples, *Stewartia ovata* (Cav.) Weath., *Hartia sinensis* Dunn., and *Gordonia chrysandra* Cowan). These characteristics indicate that the placentation type reported in the literature could depend on which portion of the ovary was sectioned, which is not normally specified. There is confusion regarding the origin of the placentation type in Theaceae that cannot be resolved until careful floral anatomical studies are carried out and are evaluated/interpreted in a phylogenetic context.

Embryological data promise to generate potentially informative characters. Nevertheless, only very recently has there been an interest in careful embryological studies in the group, and only for very few species. There are three studies of anther and ovule development for some species of *Adinandra*, *Camellia*, *Cleyera*, *Eurya*, *Franklinia* (= *Gordonia*), *Pyrenaria*, and *Schima* (Tsou, 1995, 1997; Yang and Ming, 1995). These studies show differences among the genera and between the four species of Theaceae s.s. and the three of Ternstroemiaceae. For example, the embryo sac development is *Polygonum*-type in all genera except for *Camellia*, in which it is *Allium*-type (Tsou, 1995). On the other hand, pseudopollen production was found in all genera of Theaceae s.s. and is absent in Ternstroemiaceae (in Tsou, 1997), but there are no detailed studies outside Theaceae. However, the inclusion of such information in the data matrix would currently result in a great amount of missing data.

Chemotaxonomic research could be extremely interesting, but again the information is too scattered to be included in a cladistic analysis. Several genera in Theaceae are known for their medicinal uses; many of the species that have been chemically investigated in *Camellia* (e.g., Chang and Bartholomew, 1984) and *Ternstroemia* (unpublished data) contain alkaloids. The nature of these alkaloids varies and hence seems to have potential for phylogenetic analysis. *Camellia* is known to have theine in addition to other medicinally important compounds, i.e., steroids (Itoh et al., 1981) and triglycerids (Liao et al., 1987). Syrup produced from *Visnea* was traditionally added to food and medicines in the Canary Islands (Keng, 1962). The bark of *Schima* is ground and mixed with ashes to poison fishes in South-western Asia (Bloembergen, 1952). In Mexico, species of *Ternstroemia* (commonly and commercially known as “té de tila” or “star tila”, Fig. 16) are used in folk and experimental medicine as hypnotics, anticonvulsants (as in epilepsy) and sedatives, in some cases with similar effects to diazepam (Aguilar-Santamaría and Tortoriello, 1996; Molina et al., 1999; Nsour et al., 2000).



Fig. 16. Flowers of *Ternstroemia sylvatica* Schldtl. et Cham. used in Mexican folk medicine to elaborate “Té de Tila”, a sedative and antianxiolytic infusion.

Other characters that have only been studied in a few species are growth and germination patterns, as well as chromosome numbers. In addition to some general data (Keng, 1962), aspects of growth and germination have only been studied for genera such as *Schima* (Boojh and Ramakrishnan, 1982, 1983). With respect to chromosome numbers, the scattered information shows much variation that is difficult to interpret and incorporate into cladistic analyses. In *Camellia*, the reports vary from $n = 15$ to $2n = 120$, with frequent polyploidy, especially in cultivated plants (Bezbaruah, 1971; Kondo, 1977; Li and Liang, 1990). Other than *Camellia*, reports varying from $n = 15$ or 18 (e.g., *Schima wallichii* Choisy; Goldblatt, 1981) to $n = 42$ (e.g., *Adinandra griffithii* Dyer; Goldblatt, 1981) are known from only about 20 species.

As more information is gathered for the group, we can aim to combine morphological and molecular data, ideally at the species level, which will result in better-supported phylogenetic hypotheses.

Conclusions

This work shows that previous classifications, mainly those of the 19th century and the beginning of the 20th century, grouped the members of Theaceae by superficial similarity (total morphological similarity), in particular by emphasizing the importance of having alternate leaves and multiple stamens. Apparently for this reason, distantly related genera have been included in Theaceae, such as members of Kiehmeyeroideae (Clusiaceae) and Bonnetiaceae *sensu* Stevens (unpubl. manuscript). More specialized studies (e.g., DNA, wood anatomy, embryology, palynology) suggest the segregation of genera previously placed in Theaceae into several families and even orders. The results of our analysis

provide evidence that Bonnetiaceae (*Bonnetia* and *Archytaea*) and Kielmeyeroideae–Clusiaceae (*Kielmeyera*, *Mahurea*, *Marila*, *Neotatea*, *Haploclathra*, and *Caraipa*) form a clade outside Theaceae. The members of these two taxa produce xanthones, a character that is not present in any of the genera in Theaceae. In our analysis, Tetrameristaceae (*Pentamerista* and *Tetramerista*) with *Pelliciera* (Pellicieraceae) are sister to Ericales–Cornales and Malpighiales, while *Asteropeia* appears to be more closely related to other Ericales than it is to Caryophyllales.

The result of our cladistic analysis indicates that Theaceae could be recognized as a single family, with Theaceae s.s. paraphyletic to Ternstroemiaceae. On the contrary, both DNA and embryological evidence, suggest that familial rank might be best, as was earlier proposed (e.g., de Candolle, 1824; Spach, 1835; Airy-Shaw, 1939; Willis, 1973; among others). In our analysis, Ternstroemiaceae includes *Adinandra*, *Anneslea*, *Archboldiodendron*, *Balthasaria*, *Cleyera*, *Eurya*, *Euryodendron*, *Ficalhoa*, *Freziera*, *Symplococarpon*, *Ternstroemia*, and *Visnea*. The paraphyletic Theaceae s.s. includes *Apterosperma*, *Camellia*, *Dankia*, *Gordonia*, *Pyrenaria*, *Schima*, and *Stewartia*.

Research of microstructural characters to extend the analysis of the relationships among the genera of Theaceae is necessary. Unfortunately, several of these characters could not be included in this analysis, because they are known for only a few species.

Given the relatively low proportion of characters to the number of terminals and the relatively low ci values, it is not surprising that only few clades in the consensus have relatively high support values (Jackknife and/or Bremer support). This indicates the need for continued morphological research. Nevertheless, our analysis represents to date the most comprehensive study of phylogenetic relationships within Theaceae. With this study we have not only advanced the systematics of Theaceae, but also prioritized future areas of research, of taxa that need revising and comparative characters that need more extensive study, in order to attain a better understanding of the systematics of this poorly understood family.

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Appendix 1

List of representative exemplars consulted

- Acopanea ahogadoi** Steyermark. VENEZUELA: J.A. Steyermark 9023 (NY, PARATYPE); J.A. Steyermark, J.L. Luteyn & O. Huber 129924 (NY, ISOTYPE); O. Huber et al. 10109 (US).
- Actinidia arguta** (Siebold et Zucc.) Planch. ex Miq. JAPAN: K. Okamoto SN. (MEXU); K. Yonekura 5708 (MEXU); M. Maruyama SN. (MEXU).
- Actinidia callosa** Lindl. CHINA: Sino-America Guizhou Botanical expedition 1883 (MEXU).
- Actinidia coriacea** Dunn. CHINA: Sino-America Guizhou Botanical expedition 202 (MEXU).
- Actinidia deliciosa** (A. Chev.) C.F. Liang & Ferguson. CHINA: D.E. Boufford et al. 24864 (MEXU).
- Actinidia fulvicoma** Hance var. **lanata** (Hemsl.) C. F. Liang. CHINA: L. Lin-bo 0791 (MEXU);
- Actinidia kolomikta** (Rupr. & Maxim.) Maxim. JAPAN: K. Okamoto SN. (MEXU); Y. Ito 7178 (MEXU); USSR T.S. Elias & D. Murray 11060 (MEXU).
- Actinidia latifolia** (Gardn. et Champ.) Merr. CHINA: K.L. Shi 13044 (MEXU); L. Li-bo 0792 (MEXU).
- Actinidia polygama** (Sieb. et Zucc.) Planch. ex Maxim. JAPAN: H. Kubota SN. (MEXU); K. Okamoto SN. (MEXU); T. Yokoyama SN. (MEXU); Y. Saiki & K. S. Lee 4443 (MEXU).

Adinandra acutifolia Hand.-Mazz. CHINA: C.S. Fan et al. 516 (BM); A.N. Steward et al. 149 (BM).

Adinandra bockiana E. Ritz. CHINA: A.N. Steward et al. 964 (BM).

Adinandra cordifolia Ridley. SARAWAK: Ilias Paie S. 26183 (NY).

Adinandra manni Olw. ISLAND OF ST. THOMAS: A.G. Mann. 11–1861 (K); CONGO and CAMERUN: G. Thormé 38 (K).

Adinandra millettii Benth. et Hook.f. K.L. Shi 13087 (MEXU).

Anneslea crassipes Choisy. MALAYSIA: Foxworthy 12207 (BM); Cuming 2347 (BM); A.L. Wray Jr. 1109 (BM); H.C. Robinson, 06–1913 (BM); signature 3294, 06–1892 (BM); without collector 622, 02–1890 (BM); L. Wray et al. 5322 (BM); H. Griffiths 741 (K); Scortechini 408b (BM).

Anneslea fragrans Wall. CHINA: Tsang 22227 (BM); G. Forrest 24001 (BM); G.D. Tao 21166 (MEXU); A. Henry 11591B (BM); E.D. Merrill 12238 (BM); S.K. Lau 4777 (BM); BURMA: F. Kingdon-Ward 21767 (BM); INDIA: R.H. Beddome 438 (BM); J.C. Prazer 05–1888 (BM); B. Khan 301 (BM); Abdul Huk 01–1891 (BM); J.C. Prazer 17 (BM); Capt. F. Kingdon-Ward 11195 (BM); INDOCHINA, SIAM: A.F.G. Kerr 509 (BM); 3259 (BM); 3307 (BM); A.F.G. Kerr 5259 (BM); A.F.G. Kerr 10388 (BM); Jao s/n (BM); Dr C.C. Housseus 216 (BM); Harmand 212 (BM). THAILAND: J.F. Maxwell 87–1598 (MEXU).

Archboldiodendron calocericeum Kobuski ssp. **kaindinsis**. PAPUA NEW GUINEA: B. Verdcourt et al. 5108 (K); D.B. Foreman LAE60354 (K); G. Laerivita LAE70590 (K); K. Kerenga et al. LAE74379 (K); E.H. Henty NGF 49171 (K, ISOTYPE) G. Laerivita LAE 70588 (K).

Archboldiodendron calocericeum ssp. **merrillianum** (Kobuski) W.R. Barker. NEW GUINEA: R. Pullen 5399 (K); L.A. Craven et al. 1382 (K); C.E. Carr 15091 (K); J. Croft et al. NGF 34962 (K, TYPE); L.J. Brass 4863 (K); A. Vinas et al. LAE59439 (K); R. Schlechter 19810 (K); R. Archbold 4863 (K, HOLOTYPE).

Archboldiodendron merrillianum Kobuski. PAPUA NEW GUINEA: P. van Royen NGF 30138 (BM).

Archboldiodendron sp. NEW GUINEA: H. Streimann et al. NGF39100 (K).

Archytaea multiflora Benth. BRITISH GUIANA: R.S. Cowan 1723 (NY); B.A. Whilton 223 (NY).

Asteropeia sphaerocarpa Baker. MADAGASCAR: Baron 3401 (K).

Balthasaria schliebenii (Melchior) Verdc. AFRICA: M. Reekmans 6421 (K).

Balthasaria schliebenii (Melchior) Verdc. var. **intermedia** (Boutique & Troupin) Verdcourt. AFRICA: M. Reekmans 3146 (K); M. Reekmans 1005 (K);

D. Bridson 184 (K); G. Bouxin 266 (K); R. Christiansen 1536 (K); G. Troupin 2590 (K).

Bonnetia neblinae Maguire. VENEZUELA: Maguire, Wurdack & Maguire 42100 (NY, HOLOTYPE).

Bonnetia paniculata Spruce ex. Benth. BRAZIL: C. Farney 2104 & E.F. Batista (K). PERU: S. Knapp et al. 8524 (MEXU).

Bonnetia roraimae Benth. VENEZUELA: B. Maguire 33421 (NY).

Bonnetia sessilis Benth. GUYANA: B. Maguire & C.K. Maguire 65550 (K).

Bonnetia tepuiensis Kobuski & Steyermark. VENEZUELA: J.A. Steyermark 60871 (NY) (ISOTYPE).

Bonnetia tristyla Gleason. VENEZUELA: B. Maguire, Cowan and Wurdack 30665 (NY).

Bonnetia wurdackii Maguire. VENEZUELA: J.J. Wurdack 34181 (NY, HOLOTYPE).

Camellia acutissima H.T. Chang. CHINA: Luo Lin-bo 0797 (MEXU).

Camellia caudata Wall. CHINA: K.L. Shi 13062 (MEXU).

Camellia cuspidata (Kochs) Bean. CHINA: Sino-American Guizhou Botanical Expedition 524 (MEXU).

Camellia japonica JAPAN: L.H. Kanai et al. 10252 (MEXU); K. Okamoto 1173 (MEXU).

Camellia japonica L. var. **macrocarpa** Masamune. JAPAN: M. Togasi 1481 (MEXU).

Camellia oleifera Abel. CHINA: Sino-American Guizhou Botanical Expedition no. 1423 (MEXU).

Camellia piquetiana (Pierre) Sealy. INDOCHINA: L. Pierre 1708 (K, ISOTYPE), M.E. Poilane 23790 (K).

Camellia pitardii Cohen-Stuart var. **pitardii**. CHINA: D.E. Boufford & B. Bartholomew 24323 (MEXU); Sino-American Guizhou Botanical Expedition no. 1420 (MEXU).

Camellia rosthorniana Hand.-Mazz. CHINA: K.L. Shi 12975 (MEXU).

Camellia rusticana Honda. JAPAN: M. Togasi 7129 (MEXU); M. Togasi 1696 (MEXU); M. Togasi 1697 (MEXU); M. Togasi 1591 (MEXU).

Camellia sinensis (L.) O. Kunze var. **assamica** (Masters) H.T. Chang. THAILAND: J.F. Maxwell 88–875 (MEXU).

Caraipa densiflora Mart. BRAZIL: G.T. Prance 12172 (NY). COLOMBIA: F. Restrepo 516 (NY); BOLIVIA: A. Cruz 62 (NY).

Caraipa guianensis Aublet. COSTA RICA: R. Liesner 1855 (MEXU).

Cleyera albopunctata (Griseb.) Krug & Urb. PUERTO RICO: R.A. Howard 16820 (MEXU); R.A. Howard & L.I. Nevling 15961 (MEXU).

Cleyera cernua (Tul.) Kobuski. MEXICO: E. Hernández X, & P. Segalen 335 (MEXU); C. Jurgensen 604, no. 155309 (ISOTYPE PHOTOGRAPH).

- Cleyera integrifolia** (Benth) Choisy. MEXICO: Matuda 30667 (MEXU); E. Lyonnet 2843 (MEXU); E. Matuda 32032 (MEXU); X. Madrigal 3083 (MEXU); C.G. Pringle 6957 (MEXU); F. Miranda 9042 (MEXU).
- Cleyera japonica** Thunb. JAPAN: N. Maruyama & K. Okamoto 1619 (MEXU); JAPAN: H. Kanai 6851 (MEXU); CHINA: Sino-American Guizhou Botanical Expedition 2153 (MEXU).
- Cleyera japonica** Thunb. var. **wallichiana** D.C. Sealy. NEPAL: Grey-Wilson & Phillips 114 (K).
- Cleyera ochracea** D.C. UPPER BURMA: F.M. Buchanan 174 (NY).
- Cleyera theaeoides** (Sw.) Choisy. MEXICO: F. Ventura 8163 (MEXU); F. Salazar s/n (MEXU); R. Cedillo & D. Lorence 909 (MEXU); M. Cházaro 292727 (MEXU); E. Matuda 5135 (MEXU). COSTA RICA: G. Davidse et al. 26157 (MEXU); GUATEMALA: A.J. Sharp 45125 (MEXU); L.O. Williams & A. Molina 11126 (MEXU).
- Cleyera velutina** B.M. Barthol. MEXICO: E. Martínez et al. 3911 (MEXU).
- Cornus alternifolia** L. f. CANADA: P. Louis-Marie SN (MEXU); USA: J.R. Boxeman et al. 9097 (MEXU); M.G. Zola B. & M. Cházaro B. 00979 (MEXU); M. Nee 14521-b (MEXU); S.A. Thompson & Jay H. Nishida 2333 (MEXU).
- Cornus amomum** Mill. USA: F.H. Utech 84–341 (MEXU); M. Nee 14527-a (MEXU); M. Nee et al. 43627 (MEXU); V. E. McNeilus 95–595 (MEXU).
- Cornus asperifolia** Michaux USA: M. Nee 4758 (MEXU); S.W. Leonard & A.E. Redford 1687 (MEXU); V.E. McNeilus 95–343 (MEXU); CANADA: Fr. Allyre S.C. 756 (MEXU).
- Cornus disciflora** Moc. & Sessé ex DC. COSTA RICA: W. A. Harber & E. Bello C. 2078 (MEXU);
- Cornus drummondii** C. A. Meyer. USA: D. S. Carrell & C. L. Lundell 18817 (MEXU); H.S. Taylor 5926 (MEXU); P. Keiran 332 (MEXU); V.E. McNeilus 90–932 (MEXU).
- Dankia** sp. VIETNAM: M.E. Polaine s/n (K).
- Eurya asimensis** Masanume. JAPAN: M. Furuse 1758 (MEXU).
- Eurya emarginata** Makino. JAPAN: M. Togasi 1451 (MEXU).
- Eurya groffii** Merr. CHINA: G.D. Tao 21617 (MEXU); Cui Jing Yun 12665 (MEXU); J.H. Zhang et al. 11070 (MEXU).
- Eurya huiana** Kobuski. CHINA: Sino-American Guizhou Botanical Expedition 1653 (MEXU).
- Eurya japonica** Thunberg. JAPAN: N. Maruyama & K. Okamoto 1618 (MEXU)
- Eurya loquaiana** Dunn. CHINA: K.L. Shi 13008 (MEXU); Sino-American Guizhou Botanical Expedition 1873 (MEXU).
- Eurya muricata** Dunn. CHINA: Li Zhen-yu et al. 5 (MEXU).
- Eurya nitida** Korth. CHINA: K.L. Shi 13107 (MEXU).
- Eurya symplocina** Bl. CHINA: G. Forrest 25334 (K); G. Forrest 9423 (K).
- Ficalhoa laurifolia** Hiern. CONGO: A. Leonard 5119 (K); M. Reekmans 5038 (MEXU); A. Leonard 3997 (K); R. Pielot 2073 (K); A. Schmitz 4921 (K).
- Franklinia alatamaha** Marshall. UNITED STATES: Herb. Forsyth 1835 (K); Mr Saul (K); G.P. DeWolf & P. Bruns 2188 (K); G. Nicholson 09–1889 (K); S.L. Rilsey 156 (K); S.L. Rilsey 182 (K); without collector 7267 (K); Torr. & Gray (K); G.P. Delelotl & P. Bruns 2188 (NY).
- Freziera calophylla** Triana & Planch. PANAMA: L. Forero et al. 16907 (MEXU); A. Gentry & S. Mori 14141 (MEXU).
- Freziera candicans** Tul. MEXICO: D.E. Breedlove 40424 (MEXU). COSTA RICA: W.C. Burger & M. Burger 7672 (MEXU); Haber 545 (MEXU). PANAMA: S. Mori & J. Kallunki 5699 (MEXU); T.B. Croat 66176 (MEXU).
- Freziera canescens** Humb. & Bonpl. ECUADOR: V. Zak & J. Jaramillo 3521 (MEXU); J. Morán et al. 97 (MEXU); G. Tipaz 28 (MEXU).
- Freziera chrysophylla** Bonpl. ECUADOR: W. Palacios & D. Rubio 7189 (MEXU).
- Freziera friedrichsthaliana** (Szyszyl.) Kobuski. COSTA RICA: G. Herrera 1496 (MEXU).
- Freziera grisebachii** Krug & Urban. MEXICO: G. Martínez 504 (MEXU); P. Vera et al. 242 (MEXU). VENEZUELA: J.A. Steyermark & G. Davidse 116958 (MEXU).
- Freziera guatemalensis** (Donn.-Sm.) Kobuski. GUATEMALA: A. Campos 3885 (MEXU); E. Contreras 100968 (MEXU). MEXICO: M. Ishiki et al. 1609 (MEXU); D.E. Breedlove 19895 (MEXU). HONDURAS: D. Mejía 398 (MEXU); O. Téllez & M. Martínez 8687 (MEXU).
- Freziera hieronymi** Kobuski. PANAMA: M. Nee & J.D. Dwyer 9205 (MEXU).
- Freziera lanata** (Ruiz López & Pavón) Tul. PERU: D. N. Smith & A. Pretel 8029 (MEXU).
- Freziera macrophylla** Tul. MEXICO: E. Matuda 5388 (MEXU).
- Freziera nervosa** Bonpl. ECUADOR: J. Jaramillo & V. Zak 8064 (MEXU).
- Freziera reticulata** Humb. & Bonpl. ECUADOR: W. Palacios & E. Freire 5297 (MEXU); W. Palacios & H. van der Werff 3701 (MEXU).
- Freziera** sp. (**Eurya guatemalensis** Donn. Sm.). HONDURAS: T.G. Yuncker et al. 6161 (NY).
- Freziera** sp. MEXICO: F. Miranda 9187 (MEXU).
- Freziera steyermarkii** Kobuski. VENEZUELA: A.L. Bernardi 5879 (MEXU).

Freziera tomentosa (Ruiz López & Pavón) Tul. PERU: D.N. Smith & A. Pretel 8002 (MEXU); V. Zac 1335 (MEXU). ECUADOR: J. Jaramillo & V. Zak 8152 (MEXU).

Freziera uncinata Weitzman. BOLIVIA: J.C. Solomon 18199 (MEXU).

Freziera undulata (Sw.) Willd. DOMINICA: D. Nicolson 4143 (MEXU).

Freziera undulata (Sw.) Willd. var. **elegans** (Tul.) Krug & Urb. DOMINICA: R.L. Wilbur 8181 (MEXU); D.C. Wasshausen & E.S. Ayensu 408 (MEXU).

Freziera undulata (Sw.) Willd. var. **undulata**. DOMINICA: R.L. Wilbur et al. 8177 (MEXU).

Freziera verrucosa (Hieron.) Kobuski. COLOMBIA: R. Callejas et al. 6494 (MEXU). ECUADOR: C.E. Cerón & C. Iguago 5686 (MEXU); V. Zak 1185 (MEXU); V. Zak 1172 (MEXU); B.A. Stein et al. 2679 (MEXU).

Gordonia brandegei H. Keng. MEXICO: J. Chavelas et al. ES-4121 (MEXU); Comisión de Dioscóreas 4635 (MEXU); A. Gómez-Pompa s/n (MEXU); T. Wendt et al. 5285 (MEXU); H. Hernández 189 (MEXU). HONDURAS: H. Thomas et al. 465 (MEXU); D. Hazlett 3108 (MEXU). COSTA RICA: T.B. Croat 26603 (MEXU); W.A. Haber et al. 5278 (MEXU).

Gordonia fruticosa (Schrader) H. Keng. PANAMA: G. de Nevers et al. 8362 (MEXU); BRAZIL: Reitz & Plein 7096 (NY).

Gordonia lasianthus (L.) Ellis. UNITED STATES: B. Hansen & G. Robinson 100000 (MEXU); L.J. Dorr et al. 2466 (MEXU); B. Hansen & G. Robinson 10257 (MEXU); S.W. Leonard & A.E. Radford 1695 (MEXU); S.A. Thompson et al. 2705 (MEXU).

Gordonia luzonica Vidal. PHILIPPINES: A. Loher 92 (K); Com. S. Vidal (K, TYPE).

Gordonia obtusa Wall. INDIA: C.E. Ridsdale 57 (MEXU).

Gordonia planchonii H. Keng. PERU: R. Vázquez & N. Jaramillo 3981 (MEXU).

GUATEMALA: M. Quej SN (MEXU); HONDURAS: P. House 1172 (MEXU); D. Mejía 17 (MEXU);

Haploclathra leiantha (Benth.) Benth. BRAZIL: R. Schomburgk 935 (NY, ISOTYPE); H. Ducke 656 (GH); H. Ducke 23451 (US).

Haploclathra paniculata (Martius) Benth. var. **paniculata**. BRAZIL: Ducke 29043 (NY).

Hartia microsepala Merr. & Metcalf. CHINA: W.T. Tsang 21252 (K).

Hartia sinensis Dunn. = **Stewartia pteropetiolata** H. T. Chang. CHINA: A. Henry 10465 A (K).

Hartia sinensis Dunn. CHINA: G. Forrest 8063 (K). K.L. Shi 13057 (MEXU).

Kielmeyera albopunctata Saddi. BRAZIL: T.S. Santos 2588 (NY).

Kielmeyera apparicana Saddi. BRAZIL: G. Hatschbach 40823 (MEXU).

Kielmeyera coriacea Mart. BOLIVIA: A. Fuentes 1453 (MEXU).

Laplacea brenesii Standl. COSTA RICA: A. Brenes 6215 (NY).

Laplacea costarricensis. PUERTO RICO: J. Urban 1896 (MEXU).

Laplacea fruticosa (Schrader) Kobuski. COSTA RICA: A. Carvajal 252 (MEXU).

Laplacea grandis T.S. Brandegee. MEXICO: H. Hernández 2309 (MEXU); H. Hernández 2612 (MEXU).

Laplacea hematoxylon (Sw.) G. Don. JAMAICA: G.R. Proctor 27787 (MEXU).

Laplacea semiserrata (Nees) Cambessedes. FRENCH GUYANA: Wachenheim 47 (NY).

Mahurea casiquiarensis Spruce. VENEZUELA: R. Spruce 1161 (NY).

Mahurea extipulata Benth. BRITISH GUIANA: Schomburgk 280 (K).

Mahurea tomentosa Ducke. BRAZIL: A. Ducke 23779 (NY).

Marcgravia affinis Hemsl. COLOMBIA: E. Forero et al. 5944 (MEXU); COSTA RICA: L.O. Williams & A. Molina R. 19703 (MEXU); A. Carvajal 362 (MEXU); T.B. Croat 68135 (MEXU); L.D. Gómez et al. 20904 (MEXU); R. Liesner & E. Judziewicz 14704 (MEXU); R.W. Lent 3742 (MEXU); ECUADOR: James L. Luteyn & María Lebron-Luteyn 5819 (MEXU); PANAMA: T. Antonio 2183 (MEXU); G. McPherson 7040 (MEXU); K.J. Sytsma 1875 (MEXU); G. McPherson 11116 (MEXU); B. Hammel 2345 (MEXU).

Marcgravia atropunctata de Roon. ECUADOR: Dodson et al. 14631 (MEXU); PANAMA: B. Hammel 2263 (MEXU); G. McPherson 8657 (MEXU); A. Gentry 3623 (MEXU); K. J. Sytsma 4037 (MEXU).

Marcgravia brownei (Triana & Planch.) Krug & Urb. COSTA RICA: J. Gómez-Laurito et al. SN (MEXU); A. Carvajal 354 (MEXU); G. Herrera Ch et al. 544 (MEXU); HONDURAS: H. Thomas & D. Mejía 524 (MEXU); H. Thomas 386 (MEXU); MEXICO: A. Méndez Girón (A. Shilom T) 8890 (MEXU); D.E. Breedlove & B.T. Keller 49328 (MEXU); E. Martínez S. 18145 (MEXU); H. Mejía E. & A. Luna G. 940 (MEXU); F. Miranda 9184 (MEXU).

Marcgravia caudata Triana & Planch. COLOMBIA: E. Forero et al. 7526 (MEXU); E. Forero et al. 6662 (MEXU).

Marcgravia coriacea Vahl. VENEZUELA: J.A. Steyermark et al. 114714 (MEXU).

Marcgravia crenata Poepp. ex Wittm. BRAZIL: G.T. Prance et al. 7287 (MEXU); PERU: P.J. Barbour 5722 (MEXU); R. Vasquez et al. 17955 (MEXU); V. Huashikat 156 (MEXU).

- Marcgravia guatemalensis** Standl. COSTA RICA: L.O. Williams et al. 28663 (MEXU); GUATEMALA: E. Contreras 4755 (MEXU); MEXICO: E. Martínez S. 6964 (MEXU).
- Marcgravia longifolia** Macbr. PERU: J.J. Pipoly et al. 12627 (MEXU); T.B. Croat 19023 (MEXU).
- Marcgravia macrophylla** (Wittm.) Gilg. BRAZIL: G.T. Prance et al. 7522 (MEXU).
- Marcgravia membranacea** Standl. COSTA RICA: R. Robles & A. Chacón 2714 (MEXU); Sánchez-Zamora 405 (MEXU); A. Moreno 68 (MEXU); L.D. Gómez et al. 21017 (MEXU); R. Liesner 14303 (MEXU); PANAMA: K.J. Sytsma 3953 (MEXU); B. Hammel 2596 (MEXU); J.P. Folsom & R. Page 5959 (MEXU); H.W. Churchill et al. 4575 (MEXU); J.P. Folsom & L. Collins 6472 (MEXU); G. McPherson 8093 (MEXU).
- Marcgravia mexicana** Gilg. COSTA RICA: O. Téllez et al. 5383 (MEXU); W.A. Haber 1300 (MEXU); MEXICO: R. Cedillo T. 2900 (MEXU); J.I. Calzada 1174 (MEXU); A. Torres R. & A. Campos V. 24 (MEXU); T. Wendt et al. 3732 (MEXU); F. Vázquez B. & D. Hernández 67 (MEXU); M. Souza 3569 (MEXU); R.V. Ortega O. 1160 (MEXU); G. Ibarra M et al. 4048 (MEXU); F. Ventura A. 20223 (MEXU); S. Sinaca C. 1138 (MEXU).
- Marcgravia nephentoides** Seeman. BELIZE: P.H. Gentle 3337 (MEXU); COSTA RICA: G. Herrera 2074 (MEXU); R. Liesner 1839 (MEXU); GUATEMALA: E. Contreras 3442 (MEXU); HONDURAS: R. Evans 1605 (MEXU); MEXICO: J. Rivera H et al. 1411 (MEXU); C.H. Perino 3196 (MEXU); T. Wendt et al. 3069 (MEXU); NICARAGUA: P.P. Moreno 19205 (MEXU).
- Marcgravia nervosa** Triana & Planch. COLOMBIA: E. Forero et al. 7571 (MEXU); PANAMA: K.J. Sytsma & L. Anderson 4605 (MEXU).
- Marcgravia panamensis** S. Dressler. PANAMA: A. Knapp et al. 4712 (MEXU); G. McPherson 7417 (MEXU); G. de Nevers & H. Herrera 4359 (MEXU); K. J. Sytsma 1919 (MEXU).
- Marcgravia parviflora** Rich. ex Wittm. BRAZIL: B.V. Rabelo et al. 3706 (MEXU); C.A. Cid et al. 1668 (MEXU); G.T. Prance & T.D. Pennington 1952 (MEXU); J. Pruski D. et al. 3287 (MEXU);
- Marcgravia pittieri** Gilg. COSTA RICA: A. Estrada & J. Solano 1811 (MEXU); PANAMA: G. de Nevers & H. Herrera 4226 (MEXU).
- Marcgravia polyantha** Delp. BRAZIL: J.M. Silva et al. 1978 (MEXU).
- Marcgravia purpurea** Bailey I.W. PERU: R. Vasquez et al. 13827 (MEXU).
- Marcgravia rectiflora** Triana & Planch. GUATEMALA: E. Contreras 9426 (MEXU); M. Véliz et al. MV12305 (MEXU); PERU: J.J. Pipoly R. et al. 12372 (MEXU); MEXICO: J. I. Calzada 05131 (MEXU).
- Marcgravia schippii** Standl. PANAMA: B. Hammel et al. 16398 (MEXU).
- Marcgravia sintenisii** Urb. PUERTO RICO: D. Atha & T.A. Zanoni 896 (MEXU); R.A. Howard 16813 (MEXU).
- Marcgravia stonei** Utley. MEXICO: F. Miranda 1116 (MEXU); B.P. Reko 4140 (MEXU); M. Cházaro B. 1253 (MEXU); A. García et al. 3040 (MEXU); R. Torres C. & L. Cortes 10220 (MEXU);
- Marcgravia struena** Macbr. PERU: R. Vasquez & N. Jaramillo 11737 (MEXU); D. Smith & W. Brack E. 2934 (MEXU).
- Marcgravia trinitatis** Presl. BRAZIL: C.A. Cid F et al. 8205 (MEXU); G.T. Prance & T.D. Pennington 1940 (MEXU).
- Marcgravia umbellata** L. DOMINICA: D.H. Nicolson 1838 (MEXU); G.L. Webster 13238 (MEXU); MEXICO: A. De Avila 736 (MEXU); A. Benítez P. 2449 (MEXU); B. Hallberg 880 (MEXU); C. Gutiérrez B. 3536 (MEXU); E. Guizar N. & A. Niembro 398 (MEXU); F. Boutin & F. Brandt 2895 (MEXU); F. Miranda 3623 (MEXU); F. González-Medrano et al. 3390 (MEXU); G.B. Hinton 25184 (MEXU); G. Ibarra C. 235 (MEXU); H. Rubio 292 (MEXU); H.S. Gentry 2117 (MEXU); J. Ballin et al. 11 (MEXU); J. Freeland & I. Spetzman 85 (MEXU); J.N. Rosen 2371 (MEXU); J. Rzedowski 18271 (MEXU); J. L. López G. 241 (MEXU); M. Heat & A. Long AM1 (MEXU); R.A. Bye Jr. 5864 (MEXU); R.E. González & S. Aguilar 661 (MEXU); S.D. Koch & I. Sánchez V. 7913 (MEXU); PANAMA: G. McPherson 9268 (MEXU).
- Marila geminata** Cuatr. COLOMBIA: A. Gentry et al. 59585 (MEXU).
- Marila laxiflora** Rusby. COLOMBIA: J. Cuatrecasas 16483 (NY).
- Marila racemosa** Sw. DOMINICA: C. Whitefoord 7202 (MEXU).
- Marila spiciformis** McDearman & McDaniel. PERU: Hutchinson & Wright 3705 (MO, NY, ISOTYPES).
- Melchiora schliebenii** Kobuski var. **glabra**. TANGANYICA: J.E.A. Procter 183 (K, ISOTYPE); A. Leonard 5055 (K).
- Melchiora schliebenii** Kobuski var. **greenwayi**. AFRICA: Greenway 6556 (K, HOLOTYPE).
- Melchiora schliebenii** Kobuski var. **intermedia**. TANGANYIKA: P.J. Greeway et al. 8740 (K). CONGO: A. Leonard 3438 (K); A. Leonard 2316 (K); Michelson 742 (K, ISOTYPE). RWANDA: H. Renier 247 (K). UGANDA: W.J. Eggeling 3274 (K).
- Melchiora schliebenii** Kobuski var. **schliebenii**. TANGANYICA: R.B. Drummond et al. 1766 (K); H.J. Schlieben 3175 (K, ISOTYPE).
- Melchiora schliebenii** Kobuski. TANZANIA: H.J. Schliebe 3175 (717) (K).
- Neblinaria celiae** Maguire. VENEZUELA: B. Maguire, J.J. Wurdack & C.K. Maguire 42139 (NY, HOLOTYPE).

Neogleasonia multinervia Maguire. VENEZUELA: B. Maguire 33329 (NY, HOLOTYPE).

Neogleasonia wurdackii Maguire. VENEZUELA: J.A. Steyermark & J.J. Wurdack 1053 (NY, HOLOTYPE); J.A. Steyermark & J.J. Wurdack 629 (NY).

Neotatea colombiana Maguire. COLOMBIA: R.E. Schultes & I. Cabrera 15040 (NY).

Neotatea longifolia (Gleason) Maguire. VENEZUELA: G.H.H. Tate 537 (NY, HOLOTYPE); Cowan & Wurdack 31113 (NY); Maguire & Maguire 29117 (NY).

Neotatea neblinae Maguire. VENEZUELA: Maguire et al. 37002 (NY); Maguire et al. 37290 (NY). P. Osorio H. 132 (MEXU); D.H. Lorence et al. 4357 (MEXU); E. Ramirez G. 743 (MEXU); M. Souza et al. 4402 (MEXU).

Paranneslea donairensis Gagnep. VIETNAM: M.E. Polaine 294 (K).

Parapyrenaria hainnanensis H.T. Chang. CHINA: K.S. Chow et al. 78443 (K).

Pelliciera rhizophorae Planch. & Triana. PANAMA: B. Hammell 1979 (MEXU); COLOMBIA: J.L. Zarucchi & H. Cuadros 3971 (MEXU); M.S. Hayes 76 (K); H.P. Fuchs & L. Zanella 21841 (K).

Pentamerista neotropica Maguire. VENEZUELA: B. Maguire et al. 36680 (NY, HOLOTYPE); B. Maguire et al. 41486 (US) (PARATYPE).

Ploiarium alternifolium (Vahl.) Melchior. BORNEO: Rajuyap A. 316 (NY). SARAWAK: J.L. Panero 6276 (MEXU).

Pyrenaria acuminata Planch. SUMATRA: H. Forbes 2191 (K). MALAYSIA: King's collector 8714 (K); Holinberg 725 (K); King's collector (K); C. Cartis 2321 (K). SINGAPORE: Cumings 2423 (K); Ridley 4798 (K).

Pyrenaria attenuata Seem. INDIA: Wallich 1451 (K); Wallich 1457 (K).

Pyrenaria barringtoniaefolia Seem. INDIA: Government of India 1895 (K); Dr King's collector 1890 (K); C.B. Clarke 07-04- 1885 (K).

Pyrenaria cameliflora Kurz. INDOCHINA: A.F.G. Kerr 1102 (K).

Pyrenaria cameliiflora Kurz. SIAM: A.F.G. Kerr 10016 (K); A.F.G. Kerr 702 (K); Rabil 346 (K).

Pyrenaria garretiana Craib. SIAM: Put 3853 (K); A.F.G. Kerr 5181 (K, ISOTYPE). INDOCHINA: A.F.G. Kerr 1102 (K).

Pyrenaria kainstleri King. BORNEO: Elmer 21377 (K).

Pyrenaria kunstleri King. MALAYSIA: H.N. Ridley 13537 (K).

Pyrenaria lanceolata. MALAYSIA: H.F. Hance s/n (K).

Pyrenaria lasiocarpa Korth. SUMATRA: H.C. Robinson et al. 186 (K). MALAYSIA: H.O. Forbes 1081 (K).

Schima wallichii Choisy. THAILAND: J.F. Maxwell 88–98 (MEXU); J.F. Maxwell 89–142 (MEXU). CHINA: Lui Jung Yun 22771 bi (MEXU); A. Henry 9215 B (K).

Sladenia celastrifolia Kurz. INDOCHINA: A.F.G. Kerr 5367 (BM). BURMA: J.H. Lace 6252 (NY). CHINA: A. Henry 11884 A (K).

Stewartia malachodendron L. UNITED STATES: R.D. Thomas 119715 (MEXU); D.S. Correll et al. 29632 (MEXU).

Stewartia ovata (Cav.) Weatherby. UNITED STATES: W.B. Fox 5500 (MEXU); S.W. Leonard & D.B. Russ 2554 (MEXU).

Stewartia pseudo-camellia Maxim. JAPAN: S. Togasi 1774 (MEXU).

Stewartia pteropetiolata W.C. Cheng. CHINA: Y. Tsiang 12994 (K); A. Henry 10465A # 1898 (K).

Stewartia rubiginosa H.T. Chang. var. **glabra** Yan. CHINA: Li Zhen-yu et al. 388 (K).

Stewartia sinensis Rehder. CHINA: H. Reed 6166 (K); A. Henry Reed 1889 (K); R.C. Ching 3006 (K) (SINTYPE of *S. gemmata*); P.H. Wilson 2148 (K, ISOTYPE).

Stuartia pentagyna L'Hér. UNITED STATES: Bentham Trusters 3918 (K).

Symplococarpon airishawanum Kobuski. MEXICO: G.B. Hinton 3081 (K, ISOTYPE).

Symplococarpon brenesii Kobuski. COSTA RICA: A. Gentry & B. Haber 48729 (MEXU).

Symplococarpon purpusii (Brandege) Kobuski. MEXICO: E. Matuda 696 (MEXU). E. Matuda 5169 (MEXU); F. Miranda 6967 (MEXU); S. Moreno 167 (MEXU); X. Madrigal 2532 (MEXU); E. Matuda 5480 (MEXU); F. Miranda 6234 (MEXU); D.E. Breedlove & R.F. Thorne 21106 (MEXU); J.R. Calzada 593 (MEXU); J. Vázquez 86a (MEXU); A. Delgado et al. 156 (MEXU); G.B. Hinton 3678 (NY).

Ternstroemia brasiliensis Camb. BRAZIL: G. Hatschbach 82 (MEXU); G. Hatschbach 1989 (MEXU).

Ternstroemia cf. toquian F. Villar. PHILIPPINES: C.E. Ridsdale 1223 (MEXU).

Ternstroemia circumscissilis Kobuski. BOLIVIA: B.A. Krukoff 11065 (NY, TYPE).

Ternstroemia dentisepala Bartholomew. MEXICO: D.E. Breedlove & F. Almeda 45631 (MEXU).

Ternstroemia gymnanthera (Wight et Arn.) Sprague. JAPAN: J.L. Gressitt 612 (BM); H. Kanai 10556 (MEXU). CHINA: B. Bartholomew et al. 115 (BM); J.F. Rock 25197 (BM); Taquet (BM); G. Forrest 12047 (BM); W.T. Tsang 22580 (BM); S.K. Lau 4455 (BM); B. Bartholomew et al. 914 (BM); H.D. McLaren 150 (BM).

Ternstroemia hartii Kr. & Urb. JAMAICA: G.R. Proctor 29969 (MEXU).

Ternstroemia hemsleyi Hochr. MEXICO: D. Robledo 101 (MEXU); G.L. Webster et al. 17263 (MEXU); R.E. Schultes & B.P. Reko 462 (MEXU); T. MacDougall SN (MEXU).

Ternstroemia heptasepala Krug & Urb. PUERTO RICO: T.G. Hartley 13323 (MEXU).

Ternstroemia huasteca Bartholomew. MEXICO: R. Hernández et al. 6107 (MEXU); F. Miranda 32526 (MEXU); L. Vela & X. Madrigal 251 (MEXU); A.J. Sharp 46198 (MEXU).

Ternstroemia impressa Lundell. MEXICO: D.E. Breedlove 24727 (MEXU); D.E. Breedlove & A.R. Smith 313757 (MEXU); D.E. Breedlove & R.F. Thorne 30994 (MEXU); D.E. Breedlove & R.F. Thorne 31177 (MEXU).

Ternstroemia japonica Thunb. CHINA: E.E. Maire 1715 (BM); E.E. Maire 1593 (BM); G. Forrest (BM); E.D. Merrill 04-06-1924 (BM); F.A. McClure 9522 (BM); E.H. Wilson 9568 (BM); Herb. Mus. Brit. 41 (BM); Hupeh 3301 (BM); H.F. Hance 099 (BM); F.B. Forbes 39 (BM); J. Lamont 46 (BM); H.D. McLaren 202c (BM); McLaren 239c (BM); A. Henry 12108a,b & c (BM); Lamont 46 (BM); C.B. Clarke 40311 (BM); Maximowicz 1862 (BM). JAPAN: Thunberg 224 (BM, TYPE); Fortune 1861 (BM); U. Faurie 3822 (BM); E.H. Wilson 7143 (BM); Maximowicz (BM).

Ternstroemia japonica Thunb. var. **wightii** Dyer. CHINA: G. Forrest 11059 (BM); G. Forrest 11895 (BM); G. Forrest 11429 (BM); E.H. Wilson 2219 (BM).

Ternstroemia jelskii (Szyszyl.) Melchior. PERU: S. Knapp et al. 8521 (MEXU).

Ternstroemia klugiana Kobuski. PERU: R. Vázquez et al. 5991 (MEXU); R. Vázquez et al. 2806 (MEXU).

Ternstroemia kwangtungensis Merr. CHINA: K.L. Shi 13143 (MEXU); W.T. Tsang 22679 (BM); W.T. Tsang 21179 (BM); A.N. Steward et al. 845 (BM); A.N. Steward et al. 1086 (BM); C.S. Fan et al. 319 (BM); A.N. Steward et al. 336 (BM).

Ternstroemia lineata DC. ssp. **chalicophila** (Loes) B.M. Barthol. MEXICO: E.J. Alexander 1132 (MEXU); J.L. Luteyn & M. Lebron-Luteyn 11640 (MEXU); T.F. Daniel & B. Bartholomew 5021 (MEXU).

Ternstroemia lineata DC. ssp. **lineata**. MEXICO: R. MacVaugh 11769 (MEXU); E. Matuda et al. 30743 (MEXU); G.B. Hinton 646 (MEXU); S.K. Koch & J. García 7646 (MEXU); F. Boutin & F. Brandt 2539 (MEXU); G. & S. Davidse 9833 (MEXU); A. Campos 3337 (MEXU).

Ternstroemia oocarpa (Rose) Melchior. MEXICO: D.E. Breedlove 11215 (MEXU); D.E. Breedlove 32883 (MEXU); F. Miranda 2654 (MEXU); J. Rzedowski 31119 (MEXU).

Ternstroemia peduncularis DC. DOMINICA: W.L. Stearn & D. Wasshausen 2459 (MEXU); DOMINICAN REPUBLIC, HISPANIOLA: A.H. Liogier 13460 (MEXU).

Ternstroemia penduliflora Kobuski. PERU: R. Vázquez & N. Jaramillo 5261 (MEXU); C. Díaz & N. Jaramillo 286 (MEXU); T.B. Croat 18681 (MEXU).

Ternstroemia pringlei (Rose) Standley. MEXICO: L. Torres & P.S. Sáenz 161 (MEXU); MEXICO: Rodríguez et al. 50 (MEXU); J. Santos Martínez 2043 (MEXU); A. Díaz & A. Vargas 164 (MEXU).

Ternstroemia pseudoverticillata Merr. & Chun. CHINA: F.C. How 73574 (BM).

Ternstroemia punctata (Aubl.) Sw. BRAZIL: A. Gentry & J. Ramos 12941 (MEXU).

Ternstroemia seemanii Triana & Planch. MEXICO: J.I. Calzada 01027 (MEXU); F. Menendez 177 (MEXU); L. Gutiérrez Carvajal 345 (MEXU); A. Gómez-Pompa 381 (MEXU); J. Chavelas et al. ES-2923 (MEXU); A.D.L. Orozco 239 (MEXU); P.H. Gentle 2480 (MEXU); E. Contreras 6517 (MEXU).

Ternstroemia sp. BRAZIL: A. Gentry 12951 (MEXU); CHINA: Lamont (BM).

Ternstroemia stahlia Krug & Urb. PUERTO RICO: A. Liogier 9741 (MEXU).

Ternstroemia sylvatica Schldl. & Cham. MEXICO: M. Willians & E. Krista 47 (MEXU); P. Tenorio & C. Romero 535 (MEXU); H. Narave & M. Cházaro 31 (MEXU); G. Castillo 459 (MEXU); R.V. Ortega 0–517 (MEXU).

Ternstroemia tepezapote Schldl. & Cham. MEXICO: G. Guevara 35 (MEXU).

Ternstroemiopsis sp. (**Eurya sandwichensis** A. Gray). HAWAII: T. Flynn et al. 2658 (K).

Tetramerista sp. MALAYSIA: O.D. Wilde et al. 20554 (US).

Thea sinensis L. JAPAN: M. Togasi 1251 (MEXU).

Tutcheria microcarpa Dunn. CHINA: C. Ford 610 (NY); W.T. Tsang 20410 (NY).

Visnea mocanera L.f. CANARY ISLANDS: G. Abandon 145 (BM); without collector and date (BM); R. Bourgeau 110 (BM); Lamothe 1804 (BM); Bouchet 1812 (BM); R.T. Lowe (BM) R.P. Murray s.n. (BM); Herb. R.T. Lowe 114 (BM); R.P. Murray 10-05-1899 (BM); Herb. R.T. Lowe 148 (BM); D. Brandwell et al. 3303 (BM); Berthelot 1827 (BM); Fr. Mapen 1778 (BM, TYPE); R.T. Lowe 221 (K); E. Bourgeau 1274 (K).

Appendix 2. Genera synonyms used in this work

1. *Adinandra* Jack, *Malayan Misc.* 2(7): 49. 1822.
Sarosantha Korth. in Temminck, *Verh. Natuurl. Gesch. Ned. Overz. Bezitt, Bot. Kruidk.* 103. 1840.

2. *Anneslea* Wall., *Pl. Asiat. Rar.* 1: 5, t. 5. 1829 [1830], *Annesleia* Spach in Orbigny, *Dict. University Hist. Nat.* 1: 546. 1840, *orth. mut.*; *Annesleya* Post & O. Kuntze, *Lex.* 32. 1903, *orth. mut.*; *nom. cons.-non-Anneslia* Salisb. 1807 (Fabaceae).

- Richtera* Rchb., Deutsche Bot. Herbarienbuch (Nom.) 208. 1841.
- Callosmia* C. Presl, Abh. Königl. Böhm. Ges. Wiss. ser. 5, 3: 533. 1845.
- Daydonia* Britten, J. Bot. 26: 11. 1888.
- Mountnorrisia* Szyszyl. in Engler & Prantl, Nat. Pflanzenfam. 3(6): 189. 1895.
- Paranneslea* Gagnep., Bull. Soc. Bot. France 95: 29. 1948.
3. *Apterosperma* H.T. Chang, Acta Sci. Nat. University Sunyatseni 2: 91. 1976.
4. *Archboldiodendron* Kobuski, J. Arnold Arbor. 21: 140. 1940.
- Adinandra* Jack sect. *Eleutherostyla* Melch. in Engler & Prantl, Nat. Pflanzenfam. ed. 2. 21: 145. 1924.
5. *Balthasaria* Verdc., Kew Bull. 23: 469. 1969.
- Adinandra* Jack sect. *Eleutherandra* Szyszyl. in Engler & Prantl, Natur. Pflanzenfam. 3(6): 189. 1895.
- Adinandropsis* Pitt-Schenkel, J. Ecol. 26: 80. 1938, nom. nud.
- Melchiora* Kobuski, J. Arnold Arbor. 37: 154. 1956, non-*Melchioria* Penzig & Saccardo 1969 (Fungi: Sphaeriales).
6. *Camellia* L., Sp. Pl. 698. 1753.
- Thea* L., Sp. Pl. 515. 1753.
- Tsubaki* Adans., Fam. Pl. 2: 399. 1763.
- Tsia* Adans., Fam. Pl. 2: 450. 1763.
- Calpandria* Blume, Bijdr. 178. 1825.
- Theaphylla* Raf., Medical Fl. 2: 267. 1830.
- Sasanqua* Nees in Siebold, Nippon 4: 13. 1833–4.
- Theaphylla* Raf., Fl. Tell. 1: 17. 1837, orth. mut.
- Kemelia* Raf., Sylva Tell. 139. 1838.
- Demitus* Raf., Sylva Tell. 139. 1838.
- Drupifera* Raf., Sylva Tell. 140. 1838.
- Piquetia* Hallier f., Beih. Bot. Centralbl. 39(2): 162. 1921.
- Stereocarpus* Hallier f., Beih. Bot. Centralbl. 39(2): 162. 1921.
- Camelliastrum* Nakai, J. Jap. Bot. 16: 699. 1940.
- Theopsis* Nakai, J. Jap. Bot. 16: 704. 1940.
- Yunnanea* Hu, Acta Phytotax. Sin. 5: 282. 1956.
- Glyptocarpa* Hu, Acta Phytotax. Sin. 10: 25. 1965.
7. *Cleyera* Thunb., Nova Genera Pl. 68. 1783, nom. cons., non-*Cleyera* Adans., 1763 (Loganiaceae).
- Tristylium* Turcz., Bull. Soc. Imp. Naturalistes Moscou 31(1): 247. 1858.
- Cleyera* Szyszyl. in Engler & Prantl, Natur. Pflanzenfam. 3(6): 189. 1895.
- Eurya* Szyszyl. in Engler & Prantl, Natur. Pflanzenfam. 3(6): 189. 1895.
- Eurya* subg. *Cleyera* (Thunb.) Melch. in Engler & Prantl, Nat. Pflanzenfam. ed. 2. 21: 147. 1924.
- Sakakia* Nakai, Fl. Sylv. Koreana 17: 76. 1928.
8. *Dankia* Gagnep. in Humbert, Suppl. Fl. Gén. Indo-Chine 1: 198. 1939.
9. *Eurya* Thunb., Nova Genera Pl. 67. 1783.
- Geeria* Blume, Bijdr. 124. 1825.
- Ternstroemiopsis* Urb., Ber. Deutsch. Bot. Ges. 14: 49. 1896.
- Pseudoeurya* Yamam., J. Soc. Trop. Agric. 5: 351. 1933.
10. *Euryodendron* H.T. Chang, Acta Sci. Nat. University Sunyatseni 4: 129. 1963.
- Lishichenia* H.T. Chang, Sunyatsenia 1: 6, 23, 31. 1962, nom. nud.
11. *Ficalhoa* Hiern, J. Bot. 36: 329. 1898.
12. *Freziera* Willd., Sp. Pl. 2(2): 1179. 1799, *Fresiera* Mirb. Nouv. Bull. Sci. Soc. Philom. Paris 1813: 381. 1813, orth. mut.; nom. cons.
- Lettsomia* Ruiz & Pav., Fl. Peruv. Prodr. 4: 77. 1784, non-*Lettsomia* Roxb. 1814 (Convolvulaceae).
- Eroteum* Sw., Prodr. 5: 85. 1788.
- Patascocya* Urb., Ber. Deutsch. Bot. Ges. 14: 283. 1896.
- Eurya* subg. *Freziera* Melch. in Engler & Prantl, Nat. Pflanzenfam. ed. 2. 21: 148. 1924.
- Killipiodendron* Kobuski, J. Arnold Arbor. 23: 231. 1942.
13. *Gordonia* J. Ellis, Philos. Trans. 60: 520, t. 11. 1771, *Gordona* Cothen., Disp. 26. 1790, orth. mut.; nom. cons.
- Lasianthus* Adans., Fam. Pl. 2: 398. 1763, non-*Lasianthus* Jack 1823 (Rubiaceae).
- Franklinia* Marshall, Arb. Amer. 48. 1785; *Franklina* J.F. Gmel., Syst. Nat. 2: 775. 1791, orth. mut.
- Michauxia* Salisb., Prodr. Stirp. 386. 1796, non-*Michauxia* L'Her. 1788 (Campanulaceae).
- Lacathea* Salisb., Parad. Lond. 56, t. 56. 1805.
- Wikstroemia* Schrad. in Gotting, Gel. Anz. 71: 710. 1821.
- Lindleya* Nees, Flora 4: 299. 1821, non-*Lindleya* Kunth 1824 (Rosaceae).
- Laplacea* Kunth, in H.B.K., Nova Genera et Sp. 5: 161. 1822 [folio], 207. 1882 [quarto].
- Haemocharis* Salisb. ex Mart. & Zucc., Nova Genera Sp. 1: 106. 1826 [1824].
- Polyspora* Sweet ex G. Don, General Hist. 1: 564, 574. 1831.
- Antheischima* Korth. in Temminck, Verh. Natuurl. Gesch. Ned. Overz. Bezitt, Bot. Kruidk. 137. 1842; *Antheishma* Hassk., Flora 30: 661. 1847, orth. mut.; *Antheischima* Benth. in Bentham & Hooker, General 1: 186. 1862, orth. mut.
- Closaschima* Korth. in Temminck, Verh. Natuurl. Gesch. Ned. Overz. Bezitt, Bot. Kruidk. 137. 1842.
- Carria* Gardner, Calcuta J. Nat. Hist. 7: 6. 1846.
- Dipterosperma* Griff., Notul. Pl. Asiat. 4: 564. 1854, non-*Dipterosperma* Hassk. 1842 (Bignoniaceae).
- Nabiasodendron* Pit., Actes Soc. Linn. Bordeaux 57: 54. 1902.
- Nesogordonia* Baill. Bull. Mesn. Soc. Linn. Paris 555. 1886.

14. *Pyrenaria* Blume, Bijdr. 1119. 1827.
Eusynaxis Griff., Notul. Pl. Asiat. 4: 560, t. 603.
 1854.
Tutcheria Dunn, J. Bot. 46: 324. 1908.
Sinopyrenaria Hu, Acta Phytotax. Sin. 5: 281. 1956.
Parapyrenaria H.T. Chang, Acta Phytotax. Sin. 8:
 287. 1963.
 15. *Schima* Reinw. ex Blume, Cat. Buitenzorg 80. 1823.
 16. *Sladenia* Kurz, J. Bot. 11: 194. 1873.
 17. *Stewartia* L., Sp. Pl. 698. 1753; *Stuartia* L'Hér.,
 Stirp. 153. 1789 ("1785"), *orth. mut.*; *Stewartia* Cothen.,
 Disp. 26. 1790, *orth. mut.*
Malachodendron J. Mitch., Diss. Brev. Bot. Zool.
 38. 1769; *Malachodendrum* Juss., General 275. 1789,
orth. mut.
Cavanilla Salisb., Prodr. Stirp. 385. 1796, *-non*-J.F.
 Gmelin 1791 (Sterculiaceae-Byttneriaceae).
Hartia Dunn, Hooker's Icon. Pl. 2727. 1902.
 18. *Symplococarpon* Airy Shaw, Hookers' Icon. Pl. 34:
 3342. 1937.
 19. *Ternstroemia* Mutis ex L. f, Suppl. 39: 264. 1782,
nom. cons.
Taonabo Aubl., Hist. Pl. Guiane 569. 1775;
Tonabea Juss., General Pl. 262. 1789, *orth. mut.*
Dupinia Scop., Introd. 195. 1777.
Hoferia Scop., Introd. 194. 1777.
Amphania Banks 1821.
Reinwardtia Korth. in Temminck, Verh. Natuurl.
 Gesch. Ned. Overz. Bezitt. 101. 1840.
Llanosia Blanco, Fl. Filip. ed. 2. 319. 1845.
Erythrochiton Griff., Proc. Linn. Soc. London 1:
 282. 1846, *-non*-Nees et Mart., 1823 (Rutaceae).
Voelckeria Klotzsch & H. Karst. ex Endl.,
 General suppl. 5: 66. 1850.
Mokofua O. Kuntze, Rev. General 1: 63. 1891.
Mofokf Sprague 1923.
Adinandrella Exell, J. Bot. 65 (Suppl. 1): 30. 1927.
Mokof Adans., Fam. Pl. 2: 501, 1763.
 20. *Visnea* L. f., Suppl. 36: 251. 1782.
Mocanera Juss., General Pl. 318. 1789, *-non*-*Moca-*
nera Blanco 1837.