

## Phylogeny and classification of the Melastomataceae and Memecylaceae

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A systematic analysis of the Melastomataceae, a pantropical family of about 4200–4500 species in c. 166 genera, and their traditional allies, the Memecylaceae, with c. 430 species in six genera, suggests a phylogeny in which there are two major lineages in the Melastomataceae and a clearly distinct Memecylaceae. Melastomataceae have close affinities with Crypteroniaceae and Lythraceae, while Memecylaceae seem closer to Myrtaceae, all of which were considered as possible outgroups, but sister group relationships in this plexus could not be resolved. Based on an analysis of all morphological and anatomical characters useful for higher level grouping in the Melastomataceae and Memecylaceae a cladistic analysis of the evolutionary relationships of the tribes of the Melastomataceae was performed, employing part of the ingroup as outgroup. Using 7 of the 21 characters scored for all genera, the maximum parsimony program PAUP in an exhaustive search found four 8-step trees with a consistency index of 0.86. Because of the limited number of characters used and the uncertain monophyly of some of the tribes, however, all presented phylogenetic hypotheses are weak. A synapomorphy of the Memecylaceae is the presence of a dorsal terpenoid-producing connective gland, a synapomorphy of the Melastomataceae is the perfectly acrodromous leaf venation. Within the Melastomataceae, a basal monophyletic group consists of the Kibessioideae (*Pternandra*) characterized by fiber tracheids, radially and axially included phloem, and median-parietal placentation (placentas along the mid-veins of the locule walls). A second clade, the Melastomatoideae, with libriform fibers and lacking included phloem, and with axile-basal or axillary placentation, comprises the remainder of Melastomataceae and consists of eight reasonably well differentiated tribes, one of them paleotropical (Astronieae), three pantropical (Sonerileae, Melastomeae, and Miconieae), and four neotropical (Meranieae, Microlicieae, Rhexieae, and Blakceae). The Astronieae have several plesiomorphic characters, such as anthers opening by two slits and axile-basal placentation; all other clades have primarily poricidal anthers and consistently axillary placentas. A new subfamilial and tribal classification based on the analysis includes an annotated list of all currently recognized genera with numbers of species, distribution and important synonyms. Significant features of the classification include: the placement of *Pternandra* in a subfamily of its own and the dissolution of the Astronioideae; the merger of three neotropical and paleotropical tribal pairs; and the placement of *Rhexia* in a tribe of its own. Biogeography, fossil history, and hypothesized phylogeny of the Melastomataceae imply an east Gondwanian origin of the family.

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## Introduction and intraordinal relationships

The Melastomataceae Jussieu are a large family of c. 166 genera and 4200–4500 species. Although distributed pantropically, the family has a marked concentration of species in the New World where there are c. 2950 species. About 1275–1550 occur in the Old World, depending on the estimates for the two largest genera, *Medinilla* and *Sonerila*. Melastomataceae are easily recognized among dicots by having leaves with a characteristic acrodromous venation (sensu Hickey 1973) and numerous small, exalbuminous seeds. Melastome stamens are likewise characteristic of the family. They have two locules at maturity (except in *Rhexia*), often a non-fibrous endothecium and poricidal dehiscence, and their connectives lack dorsal glands. Excellent complete descriptions of the family may be found in Gleason (1932), Wurdack & Kral (1982), Whiffin (1990), and Watson & Dallwitz (1991).

Such is the morphological distinctness of the Melastomataceae that there has been very little controversy over their status and circumscription, except for the treatment of *Memecylon* and *Mouriri* and their segregates and *Axinandra* and *Dactylocladus*. The former two have variously been regarded as a separate family, Memecylaceae, or included as a subfamily in the Melastomataceae. Below I argue for the recognition of two families.

*Axinandra* comprises four Asiatic species of trees with glabrous penninerved leaves and few-seeded capsules; closely related is *Dactylocladus stenostachys*, likewise from southeast Asia. *Axinandra* has been seen as lythraceous (e.g., Bentham & Hooker 1867; Lourteig 1965), melastomaceous (Triana 1871; Baillon 1877; Cogniaux 1891; Krasser 1893; Gilg 1897; Bakhuizen 1946/1947), intermediate (Meijer 1972), or as belonging in a separate family together with another Asiatic genus, *Crypteronia* (four species). Apparently *Axinandra*, *Dactylocladus*, and *Crypteronia* share only plesiomorphic characters, such as brochidodromous venation, racemose inflorescences, and stamens with lengthwise dehiscent anthers, and the heterogeneity of the group has been stressed by Johnson & Briggs (1984) and Tobe & Raven (1987a, b). Leaves in *Crypteronia*, but not *Axinandra* and *Dactylocladus*, have stipules, and mainly on account of this but also because of its inflorescences *Crypteronia* has rarely been included in the Melastomataceae (Hallier 1918; Vliet 1981). More often it has been placed in Lythraceae (Bentham & Hooker 1867; Hallier 1911; Lourteig 1965) or a separate family (A. De Candolle 1868), to which were sometimes added the monotypic South African *Rhynchoalix* and the small Central and South American *Alzatea* (A. De Candolle 1868; Beusekom-Osinga & Beusekom 1975). More recently, Johnson & Briggs (1984) and Graham (1984) have argued for recognizing *Rhynchoalix* and *Alzatea* at the family level and for excluding *Axinandra*, *Dactylocladus*, and *Crypteronia* from the Lythraceae. Below it is shown that none of these

groups can go in the Melastomataceae or Memecylaceae. Bremer's (1988) suggestion that Melastomataceae are paraphyletic if the Crypteroniaceae and Memecylaceae are excluded is not supported by my analysis because there is no derived character which would support such a clade and because in many attributes Memecylaceae appear more basal in the Myrtales than Melastomataceae. Hypotheses on Memecylaceae sister group relationships are discussed below in the section on Memecylaceae DC.

Arguments for a close relationship between Crypteroniaceae, Lythraceae, and Melastomataceae are their capsular fruits (replaced by berries in derived clades of Melastomataceae and Lythraceae), pollen morphology (Patel et al. 1984; Nowicke, pers. comm. 1991; S. Graham, in litt. 1992), similar wood anatomy (van Tieghem 1891a, b; Vliet et al. 1981), and the often opposite leaves with marginal nerves. These arguments do not appear strong, and I have therefore considered it best to develop hypotheses on ancestral character states based on evidence from various sources (similar to the approach taken by Johnson & Briggs (1984: 709)) and to root the cladogram using part of the ingroup as outgroup, rather than base my analysis on an uncertain sister group. Neither the Crypteroniaceae nor the Lythraceae (as defined by Graham et al., in press) are distinguished from other myrtalean families by known autapomorphies, and recent cladistic analyses of the Lythraceae based on morphology (Graham et al., in press) and molecular data (Graham, pers. comm.) moreover indicate that Onagraceae too are very close to Lythraceae. Clearly, however, Crypteroniaceae (and Alzateaceae and Rhynchoalycaceae), Melastomataceae, Memecylaceae, and Myrtaceae will have to be appropriately broadly sampled before this plexus can be disentangled.

## History of the classification of the Melastomataceae and Memecylaceae

The history of the classification of the Melastomataceae and Memecylaceae, compared to that of groups of comparable size, is uncomplicated (Tab. 1). However, since internal melastome classification has not been reviewed recently, a summary is necessary to understand more recent developments.

Jussieu (1789) was the first to recognize the Melastomataceae as a natural unit, but it was David Don (1823) who put structure into the family, using mainly placentation and seed characters. Don excluded *Memecylon* and *Mouriri* from the Melastomataceae because they differ from the rest of the family in precisely these characters. *Memecylon* (placed in the Onagraceae by Jussieu!) was first included in the Melastomataceae by Du Petit-Thouars (1811), and *Mouriri* was added by Brown (1818). Shortly thereafter Blume (1826) again excluded *Memecylon* from the Melastomataceae, preferring to treat it as a Myrtaceae, while De Candolle (1828a, b) created a

Tab. 1. Summary of the classifications of Melastomataceae and Memecylaceae. Triana's subfamilies were formalized by Hooker in Bentham & Hooker (1867). Cogniaux's and Krasser's Axinandreae comprise only *Axinandra*, Vliet et al.'s Crypteronieae comprise *Axinandra*, *Dactylocladus*, and *Crypteronia*. Cassebeerieae = Sonerileae, Osbeckieae = Melastomeae, Pternandreae = Kibessieae, Pyxidanthaeae = Blakeeae, Tamoneae = Miconieae.

Triana 1871	Cogniaux 1891	Krasser 1893	Vliet et al. 1981	this paper
<i>Melastomatoideae</i>	<i>Melastomatoideae</i>	<i>Melastomatoideae</i>	<i>Melastomatoideae</i>	<i>Melastomatoideae</i>
Microlicieae	Microlicieae	Tibouchineae	Tibouchineae	Astronieae
Pleromeae	Tibouchineae	Osbeckieae	Sonerileae	Sonerileae
Osbeckieae	Osbeckieae	Rhexieae	Rhexieae	Merianieae
Rhexieae	Rhexieae	Microlicieae	Osbeckieae	Rhexieae
Merianieae	Merianieae	Merianieae	Microlicieae	Melastomeae
Oxyporeae	Oxyporeae	Oxyporeae	Miconieae	Microlicieae
Sonerileae	Sonerileae	Bertolonieae	Merianieae	Miconieae
Bertolonieae	Bertolonieae	Cassebeerieae	Dissochaeteae	Blakeeae
Dissochaeteae	Dissochaeteae	Dissocheteae	Blakeeae	
Miconieae	Miconieae	Tamoneae	Astronieae	
Pyxidanthaeae	Blakeeae	Blakeeae		<i>Kibessioideae</i>
				Kibessieae
<i>Astronioideae</i>	<i>Astronioideae</i>	<i>Astronioideae</i>		
Astronieae	Astronieae	Astronieae		
		Kibessieae		
<i>Memecyloideae</i>	<i>Memecyloideae</i>	<i>Memecyloideae</i>	<i>Memecyloideae</i>	<i>Memecylaceae</i>
Mouririeae	Memecyleae	Memecyleae	Pternandreae	
	Axinandreae	Axinandreae	Memecyleae	
			<i>Crypteronioideae</i>	<i>Crypteroniaceae</i>
			Crypteronieae	

family for the two. Chamisso (1836) once more included them in the Melastomataceae, as did Lindley (1836, 1846), while others (Gardner 1840; Janssonius 1950; Favarger 1952, 1962; Lowry 1976; R. Dahlgren in R. Dahlgren & Thorne 1984 and in G. Dahlgren 1989; Johnson and Briggs 1984; Renner 1989b; Huber 1991) supported the recognition of a distinct family and still others returned to placing *Mouriri* and *Memecylon* in the Myrtaceae (Richard 1845; Grisebach 1864).

In his Quinarian arrangement of the Melastomataceae, De Candolle (1828b) grouped the 68 melastome genera he recognized according to seed type (cochleate with curved embryos vs. straight), degree of fusion between hypanthium and ovary and fruit type, ovary summit (with outgrowths vs. unadorned), and type of anther dehiscence (by one pore, two pores, or by longitudinal slits). From later arrangements, De Candolle's differs most strikingly in its complete disregard of geographic origin.

The next major student of the family, Naudin (1849–1853), emphasized type of placentation and kind and number of seeds, which were used to distinguish five subfamilies (Melastomatoideae, Astronioideae, Kibessioideae, Memecyloideae, and Mouririoidae). Within the Melastomatoideae, Naudin recognized four tribes, Microlicieae, Lasiandreae (more or less today's Melastomeae), Rhexieae, and Miconieae (which include Dissochaetinae, Blakeinae, Merianiinae, and an extremely heterogeneous Sonerilinae).

Triana's system, published in 1865 and slightly modified in 1871, is the one in use today (Cogniaux 1891; Krasser 1893; Melchior 1964; Hutchinson 1973; Bremer

1983, 1988; Takhtajan 1983; Cronquist 1988; Thorne 1992). Triana, a native Colombian with extensive knowledge of the family in the field, worked in London and Paris and thus had access to all important collections then available. Geographic isolation played a paramount role in his understanding of the family; differing from his predecessors, he rigorously separated Old and New World genera, recognizing the new groups thus formed at the tribal level. In order to key out the resulting new tribes Triana (1865, and following him all later workers) had to rely on characters such as number of floral parts, connective appendages, and geography (the Dissochaeteae are distinguished from the Miconieae and the Tibouchineae from the Osbeckieae by the first of each pair being paleo-, the second neotropical). At the subfamilial level, on the other hand, Triana merged Naudin's Astronioideae and Kibessioideae, recognizing only three major taxa: Memecyloideae, Astronioideae, and Melastomatoideae (formalized by J. D. Hooker in Bentham & Hooker 1867).

Severe discrepancies between the distribution of wood anatomical characters and Triana's classification were first pointed out by van Tieghem (1891a) who studied the wood of most of the genera recognized by Triana and concluded (1) that wood anatomy did not support the merging of Astronioideae and Kibessioideae, and (2) that wood anatomy did not support those of Triana's tribes that were based solely on connective configuration. Groupings based on seed morphology, on the other hand, were supported by wood anatomy.

A total of 489 genera have been proposed in the fam-

Tab. 2. Classification of the Melastomataceae and Memecylaceae, with the genera assigned to subfamily and tribe according to the new scheme. Generic synonymizations made in recent monographic and floristic literature are indicated but no new ones are suggested, except in the cases of *Tigridiopalma* C. Chen, *Tylanthera* C. Hansen, and *Vietsenia* C. Hansen. See text for perceived generic relationships. Numbers in parentheses give the total species for a genus; species numbers and geographic range data are mainly from herbarium surveys and recent revisions and floras as cited; only the most general indication of the geographic range is given. Melastomataceae total: c. 166 genera, 4200–4500 species. Memecylaceae total: 6 genera, 430 species.

## Memecylaceae DC.

- Lijndenia* Zoll. & Moritz (10) – W Malesia, Java, Ceylon (3), Madagascar (6), West Africa (1); Bremer (1982)  
*Memecylon* L. (incl. *Klaineastrum* Pierre ex A. Chev.) (300) – Asia and Oceania, Africa (70), Madagascar (78); Bremer (1979, 1983); Maxwell (1980b)  
*Mouriri* Aubl. (81) – tropical America, most diverse in Brazil; Morley (1976, 1985, 1989)  
*Spathandra* Guill. & Perr. (2) – W Africa; Jacques-Félix (1978b, 1985)  
*Votomita* Aubl. (8) – eastern Amazonia (Brazil, French Guiana); Morley (1963, 1985, 1989)  
*Warneckea* Gilg (33) – Africa (24), Madagascar (9); Jacques-Félix (1978b, 1985)

## Melastomataceae Jussieu

### Subfamily Kibessioideae Naudin (1849)

#### Tribe Kibessieae Krasser (1893)

- Pternandra* W. Jack (incl. *Kibessia* DC., *Ewyckia* Bl., *Macroplicis* Bl., *Rectomitria* Bl.) (15) – SE Asia, Malaysia; Maxwell (1981).

### Subfamily Melastomatoideae Naudin (1849)

#### Tribe Astronieae Triana (1865)

- Maxwell & Veldkamp (1990a, b)  
*Astrocalyx* Merrill (1) – Philippines  
*Astronia* Blume (59) – Malay archipelago  
*Astronidium* A. Gray (incl. *Naudiniella* Krasser) (67) – Malay archipelago  
*Beccarianthus* Cogniaux in Boerlage (incl. *Bamleria* Lauterb. & K. Schum. and *Everettia* Merr.) (22) – Malay archipelago

#### Tribe Sonerileae Triana (1865)

- A. *Oxyspora* Alliance  
*Anerincleistus* P. W. Korthals (incl. *Pomatostoma* Stapf, *Creaghiella* Stapf, *Oritrephes* Ridley, *Plagiopetalum* Rehder (Hansen 1988a), *Phaulanthus* Ridley, *Perilimnastes* Ridley, *Krassera* O. Schwartz) (30) – India and Malesian region; Maxwell (1989)  
*Barthea* J. D. Hooker (1) – China, Taiwan, Vietnam; Hansen (1980b)  
*Blastus* Loureiro (12) – Assam, China to Vietnam, Malay archipelago; Hansen (1982)  
*Bredia* Blume (incl. *Tashiroea* Matsum.) (13) – China, Japan, Formosa  
*Driessenia* P. W. Korthals (incl. *Triuranthera* Backh. and *Vietsenia* C. Hansen (Hansen 1984)) (18) – Vietnam, Borneo, Sumatra, Java; Hansen (1985b)  
*Neodriessenia* Nayar (6) – Borneo; Hansen (1985a)  
*Ochthocharis* Blume (incl. *Phaeoneuron* Gilg) (7) – Asia (5); Africa (2); Hansen & Wickens (1981)  
*Oxyspora* DC. (incl. *Allomorpha* Bl., *Campimia* Ridley (Hansen 1988c), *Cyphotheca* Diels (Hansen 1990a), *Styrophyton* Hu, and *Tayloriophyton* Nayar) (65) – India, China, Malay Peninsula, Sumatra, Melanesia (Fidschi Is.); Maxwell (1982)  
*Poikilogyne* E. G. Baker (incl. *Dicerospermum* Bakh. f. and *Scrobicularia* Mansf.) (21) – SE Asia  
*Poilannammia* C. Hansen (4) – Vietnam; Hansen (1987a)  
*Sporoxeia* W. W. Smith (4) – upper Burma, China  
*Stussenia* C. Hansen (based on *Blastus membranifolius* Li = *Neodriessenia membranifolia* (Nayar) C. Hansen, 1980) (1) – Vietnam; Hansen (1980a, 1985c)

#### B. *Sonerila*–*Bertolonia*–*Gravesia* Alliance

- Amphiblemma* Naudin (13) – tropical West Africa; Jacques-Félix (1974a)  
*Aschistanthera* C. Hansen (1) – Vietnam; Hansen (1987b), probably identical with *Phyllagathis*  
*Bertolonia* Raddi (18) – SE Brazil, 1 sp. in Venezuela; Baumgratz (1989–1990)  
*Boyania* Wurdack (1) – Guyana  
*Brittenia* Cogniaux (1) – Borneo (Sarawak); Hansen (1985d)  
*Calvoa* J. D. Hooker (19) – tropical Africa; close to *Gravesia*  
*Centradenia* G. Don (4) – Mexico to coastal Colombia; placed here following Almeda (1977 and in press)  
*Centradeniastrum* Cogniaux (2) – northern Andes (Almeda 1977)  
*Cinnobotrys* Gilg (incl. *Gravesiella* A. & R. Fernandes, *Haplophyllaphorus* A. & R. Fernandes, and *Primularia* Brenan) (6) – tropical Africa; Jacques-Félix (1975)  
*Cyanandrium* Stapf (5) – Borneo  
*Dicellandra* J. D. Hooker (2) – tropical West Africa; Jacques-Félix (1974b)  
*Diplarpea* Triana (1) – Ecuador, Colombia  
*Enaulophyton* Steenis (1) – Malaysia  
*Feliciadamia* Bullock (1) – Africa (Guinea); nomenclatural substitute for *Adamia* Jacques-Félix (1951)  
*Fordiophyton* Stapf (incl. *Stapfiophyton* Li) (8) – China, Indochina  
*Gravesia* Naudin (incl. *Veprecella* Naud., *Phornothamnus* Bak., *Urotheca* Gilg, *Petalonema* Gilg, *Orthogoneuron* Gilg, *Neopetalonema* Brenan) (100) – Madagascar (95), Africa (5)  
*Kerriothyrsus* C. Hansen (1) – Laos; Hansen (1988b), probably identical with *Phyllagathis*  
*Macrocentrum* J. D. Hooker (21) – N South America, reaching Brazil  
*Maguireanthus* Wurdack (1) – Guyana; Wurdack (1964a)  
*Monolena* Triana (10) – Guatemala to Amazonia  
*Opisthocentra* J. D. Hooker (1) – Colombia, Venezuela to N Brazil (Rio Negro)  
*Phyllagathis* Blume (incl. *Tigridiopalma* C. Chen and *Tylanthera* C. Hansen (1990b)) (30) – southern China to Thailand, Sumatra and Borneo  
*Preussiella* Gilg (2) – tropical West Africa (Cameroun, Gabon); Jacques-Félix (1977b)  
*Salpinga* Martius ex DC. (incl. *Saccolena* Gleason) (8) – N South America  
*Sarcopyramis* Wallich (1) – Nepal, China, Taiwan, Thailand, Malay archipelago; Hansen (1979)  
*Scorpiothyrsus* Hui-Lin Li (6) – China; very close to *Phyllagathis*  
*Sonerila* Roxburgh (100–175) – tropical Asia; Lundin (1983)  
*Tateanthus* Gleason (1) – Venezuela  
*Triolena* Naudin (incl. *Diolena* Naudin) (22) – Mexico to Amazonia  
*Tryssophyton* Wurdack (1) – Guyana; Wurdack (1964a)
- #### Tribe Merianieae Triana (1865)
- Adelobotrys* DC. (25) – Mexico and Jamaica to Brazil and Bolivia  
*Axinaea* Ruiz & Pavon (30) – Costa Rica to Bolivia; close to *Meriania*; Eves (1936)  
*Behuria* Chamisso (10) – SE Brazil  
*Benevidesia* Saldanha & Cogniaux (2) – SE Brazil (Bahia)  
*Bisglaziovia* Cogniaux (1) – SE Brazil (Bahia)  
*Centronia* D. Don (15) – Panama to Peru and Brazil, Guayana  
*Dolichoura* Brade (1) – SE Brazil (Espírito Santo)  
*Graffenrieda* A. P. DC. (incl. *Calyptrella* Naud. and *Ptilanthus* Gleason) (44) – Central and S. America to Bolivia; West Indies

*Huberia* A. P. DC. (6) – SE Brazil, 1 sp. in the Andes  
*Meriania* O. Swartz (74) – Central and S. America to Bolivia; West Indies  
*Merianthera* Kuhlmann (3) – SE Brazil  
*Neblinantha* Wurdack (1) – Venezuela to NW Brazil (Cerro de la Neblina)  
*Ochtheophilus* Wurdack (1) – Venezuela  
*Pachyloma* A. P. DC. (incl. *Urodesmium* Naudin) (6) – Colombia, Venezuela, Guyana, N Brazil  
*Phainantha* Gleason (4) – Guayana  
*Tessmannianthus* Markgraf (7) – Colombia, Ecuador, and Peru; Wurdack (1989); Almeda (1989b, 1990b)

#### Tribe Rhexieae DC. (1828)

*Rhexia* L. (13) – North America, concentrated in SE coastal plain; Kral and Bostick (1969)

#### Tribe Microlicieae Naudin (1849)

*Bucquetia* A. P. DC. (3) – Northern Andes  
*Cambessedesia* DC. (incl. *Pyramia* Cham.) (21) – south-central Brazil; Martins (1984)  
*Castratella* Naudin (2) – Colombia, Venezuela; a high-altitude *Tibouchina*  
*Chaetostoma* DC. (12) – south-central Brazil; very close to *Microlicia*  
*Eriocnema* Naudin (1) – south-central Brazil  
*Lavoisiera* DC. (46) – south-central Brazil  
*Lithobium* Bongard (1) – south-central Brazil  
*Microlicia* D. Don (100) – south-central Brazil, a few species in Guayana, Peru, and Bolivia  
*Rhynchanthera* DC. (15) – most diverse in SE Brazil, but extending to Mexico; Renner (1990)  
*Stenodon* Naudin (1) – Brazil (Bahia)  
*Trembleya* DC. (11) – south-central Brazil

#### Tribe Melastomeae (Osbeckieae DC. (1828))

Paleotropical genera  
*Amphorocalyx* J. G. Baker (5) – Madagascar; close to *Dionycha*  
*Antherotoma* (Naudin) J. D. Hooker (2) – Africa (2), Madagascar (1)  
*Caillietia* Jacques-Félix (1) – Africa (Guinea)  
*Dichaetanthera* Endlicher (incl. *Sakersia* Hook. f. and *Barbayastrum* Cogn.) (30) – Madagascar (23), Africa (7)  
*Dinophora* Benthham (1) – tropical West Africa (Sierra Leone to Angola)  
*Dionycha* Naudin (3) – Madagascar; Perrier de la Bâthie (1951)  
*Dionychastrum* A. Fernandes & R. Fernandes (1) – Africa (Tanzania)  
*Dissotis* Benthham (incl. *Podocaelia* (Bth.) A. & R. Fernandes) (140) – Africa (120), Madagascar (20); close to *Osbeckia*  
*Guyonia* Naudin (1–2) – tropical West Africa; close to *Osbeckia*  
*Heterotis* Benthham (14) – tropical West Africa; close to *Osbeckia*; Jacques-Félix (1981b)  
*Melastoma* L. (50) – Asia; 1 sp. introduced in Madagascar  
*Melastomastrum* Naudin (6) – tropical West Africa; close to *Osbeckia*; Jacques-Félix (1974)  
*Nerophila* Naudin (1) – Africa (Senegal); perhaps a *Chaetolepis* (Wurdack, pers. comm. 1985)  
*Osbeckia* L. (incl. *Rousseauxia* DC.; Jacques-Félix (1973)) (50) – Asia ( $\pm$  30); Australia; Africa (5), Madagascar (13); Hansen (1977)  
*Otanthera* Blume (incl. *Lachnopus* Blume) (3) – China to the Philippines and Australia; very close to *Melastoma*  
*Pseudosbeckia* A. & R. Fernandes (1) – Africa (Mozambique); close to *Osbeckia*  
*Tristemma* A. L. Jussieu (incl. *Tetraphyllaster* Gilg) (14) – Africa; 1 sp. in Madagascar and the Mascarene Islands; close to *Osbeckia*; Jacques-Félix (1976)

#### Neotropical genera

*Acanthella* J. D. Hooker (2) – Venezuela, Colombia, Brazil (Rio Negro)

*Aciotis* D. Don (30) – Mexico, Lesser Antilles, Brazil and Bolivia  
*Acisanthera* P. Browne (17) – Venezuela, Guianas, Brazil to Paraguay  
*Appendicularia* A. P. DC. (1) – Guianas and northeastern Brazil  
*Arthrostemma* Pavon ex D. Don (7) – from Mexico and the West Indies to Bolivia (absent from Brazil)  
*Brachyotum* (A. P. DC.) Triana (58) – Colombia to Argentina; Wurdack (1953)  
*Chaetolepis* (A. P. DC.) Miquel (10) – Colombia, Venezuela, West Indies, N Brazil  
*Comolia* A. P. DC. (22) – tropical South America, most diverse in Brazil  
*Comoliopsis* Wurdack (1) – Venezuela (Cerro de la Neblina)  
*Desmoscelis* Naudin (1) – Venezuela to Brazil and Bolivia (savannas)  
*Ernestia* A. P. DC. (incl. *Brachypremna* Gleason and *Pseudornerstia* (Cogn.) Krasser) (16) – Andes and upper Amazon basin, Guianas, Brazil  
*Fritzschia* Chamisso (1) – south-central Brazil  
*Heterocentron* W. J. Hooker & G. A. Walker Arnold (27) – Mexico and Central America; Whiffin (1972)  
*Loricalepis* Brade (1) – Brazil (upper Rio Negro)  
*Macairea* A. P. DC. (incl. *Siphanthropsis* Brade) (22) – most diverse in Guayana, also Colombia, Brazil, and Bolivia; Renner (1989a)  
*Mallophyton* Wurdack (1) – Venezuela (Chimantá Mt.); Wurdack (1964a)  
*Marcetia* A. P. DC. (27) – Venezuela, Guayana, Colombia, Brazil; Martins (1989)  
*Microlepis* (A. P. DC.) Miquel (4) – south-central Brazil  
*Monochaetum* (A. P. DC.) Naudin (45) – Mexico to Peru and Venezuela; Almeda (1978)  
*Nepsera* Naudin (1) – Central America, West Indies, to central Brazil  
*Pilocosta* Almeda & Whiffin (4) – Costa Rica to Ecuador; Almeda and Whiffin (1980); close to *Tibouchina*  
*Poteranthera* Bongard (2) – Brazil, Venezuela; Wurdack (1963)  
*Pterogastra* Naudin (2) – northern South American savannas; Renner (in press)  
*Pterolepis* (A. P. DC.) Miquel (14) Mexico and West Indies to Paraguay; Renner (in press)  
*Sandermania* Gleason (1) – Venezuela, Brazil, Peru; Renner (1987)  
*Schwackaea* Cogniaux (1) – Mexico to Colombia; Renner (in press)  
*Siphanthera* Pohl ex DC. (incl. *Meisneria* DC. and *Farringtonia* Gleason) (16) – Colombia, Venezuela, Brazil, Bolivia  
*Svitramia* Chamisso (2) – Brazil (Bahia, Minas Gerais)  
*Tibouchina* Aublet (incl. *Purpurella* Naudin and *Itatiaia* Ule) (240) – Mexico, West Indies to northern Argentina  
*Tibouchinopsis* Markgraf (2) – Brazil (Bahia)

#### Tribe Miconieae DC. (1828)

Paleotropical genera; see especially Maxwell (1980a, 1983)  
*Boerlagea* Cogniaux (1) – Borneo  
*Catanthera* F. V. Mueller (incl. *Hederella* Stapf and *Phyllapophysis* Mansfeld) (16) – Malesian region (New Guinea, Borneo, Sumatra)  
*Creochiton* Blume (incl. *Eisocrochiton* Quisumb. & Merrill and *Anplectrella* Furtado) (9) – New Guinea, Java, Philippines  
*Diplectria* (Blume) H. G. L. Reichenbach (incl. *Anplectrum* A. Gray, *Backeria* Bakh.) (8) – Burma, Indo-China, Malesian region; Veldkamp et al. (1978); *Diplectria* will be treated as synonymous with *Dissochaeta* in the Flora of Thailand (Renner, ms)  
*Dissochaeta* Blume (incl. *Omphalopus* Naudin, *Dalenia* Korth., and *Neodissochaeta* Bakh. f.) (22) – India, Malesian region  
*Kendrickia* J. D. Hooker (1) – South India, Ceylon  
*Macrolenes* Naudin ex Miquel (11) – Malay Peninsula, Philippines

*Medinilla* Gaudichaud-Beaupré (incl. *Hypenanthus* Bl., *Carionia* Naudin, *Medinillopsis* Cogn., *Cephalomedinilla* Merr.) (200–400) – Madagascar (70), Africa (2), SE Asia (85); Maxwell (1978), Regalado (1990), Whiffin (1990)  
*Pachycentria* Blume (10) – SE Asia; Maxwell (1978)  
*Plethiandra* J. D. Hooker (9) – Borneo, Malay Peninsula  
*Pogonantha* Blume (1) – Malay Peninsula, Philippines, Malay archipelago; Maxwell (1978)  
*Pseudodissochaeta* Nayar (6) – Assam to Indo-China

#### Neotropical genera

*Alloneuron* Pilger (7) – Andes  
*Allomaieta* Gleason (1) – Colombia  
*Anaectocalyx* Triana (3) – Venezuela (Miconieae)  
*Bellucia* Necker ex Rafinesque (7) – tropical America; Renner (1989a); incl. in *Loreya* by Judd (1989)  
*Calycogonium* A. P. DC. (incl. *Mommsenia* Urban & Ekman) (31) – Greater Antilles  
*Catocoryne* J. D. Hooker (1) – Colombia  
*Chalybea* Naudin (1) – Colombia  
*Charianthus* D. Don (5) – West Indies, Jamaica (1), Lesser Antilles; polyphyletic fide Judd (1989), see also Judd & Skean (1991)  
*Clidemia* D. Don (incl. *Heterotrichum* DC.) (120) – Mexico to Peru; axillary-flowered species excl. as *Sagraea* by Judd (1989)  
*Conostegia* D. Don (43) – Mexico to Peru, reaching the West Indies and Brazil  
*Cyphostyla* Gleason (2) – Colombia  
*Henriettea* A. P. DC. (12) – Amazon basin, esp. Brazil  
*Henriettella* Naudin (51) – West Indies and Guatemala to Bolivia and Brazil; should probably be included in *Henriettea*; Judd (1989)  
*Huilaea* Wurdack (4) – Colombia; close to *Chalybea*  
*Killipia* Gleason (4) – Colombia, Ecuador  
*Kirkbridea* Wurdack (2) – Colombia; Wurdack (1976)  
*Leandra* Raddi (incl. *Tschudya* DC., *Oxymeris* DC., *Clidemias-*

*trum* Naud., *Platycentrum* Naudin) (175) – Mexico to Argentina, absent in the West Indies, most diverse in southeastern Brazil  
*Llewelynia* Pittier (1) – Venezuela (coastal mts.); should be incl. in *Henriettea*; Judd (1989)  
*Loreya* A. P. DC. (incl. *Heteroneuron* Hook. f.) (13) – Central America to Brazil and Bolivia; Renner (1989a)  
*Maieta* Aublet (3) – Amazon basin (esp. Colombia, Venezuela, Brazil)  
*Mecranium* J. D. Hooker (incl. *Ekmaniocharis* Urban) (23) – Greater Antilles; Skean (1993)  
*Miconia* Ruiz & Pavon (incl. *Copedesma* Gleason, *Pachydesmia* Gleason, and *Icaria* Macbr.) (1000) – throughout tropical America  
*Myriaspora* A. P. DC. (1) – Guyana and Amazon basin; incl. in *Loreya* by Judd (1989)  
*Myrmidone* C. F. P. Martius (incl. *Hormocalyx* Gleason) (2) – Colombia, Guyana, Venezuela, Brazil (Amazon basin); incl. in *Clidemia* by Judd (1989)  
*Necranium* Britton (1) – Trinidad and Venezuela  
*Ossaea* A. P. DC. (incl. *Octopleura* Griseb. and *Diclemia* Naudin) (91) – West Indies and Mexico to Brazil; likely polyphyletic and dismembered by Judd (1989) into *Pentossaea* Judd and *Sagraea* DC.; see also Judd & Skean (1991)  
*Pachyanthus* A. Richard (16) – West Indies and Cuba  
*Pleiochiton* Naudin ex A. Gray (7) – southeastern Brazil; scarcely distinguishable from *Leandra* (Wurdack 1962) and incl. in that genus by Judd & Skean (1991).  
*Tetrazygia* L. C. Richard ex A. P. DC. (incl. *Tetrazygiopsis* Borhidi) (21) – Antilles and Guayana  
*Tococa* Aublet (incl. *Micropysca* Naudin) (54) – Mexico to Brazil and Bolivia; West Indies (Tobago)

#### Tribe Blakeaceae Hook. in Benth. & Hook. (1867)

*Blakea* P. Browne (incl. *Pyxidanthus* Naudin) (100) – Mexico and West Indies to Bolivia; Almeda (1990a)  
*Topobea* Aublet (62) – Mexico to Amazonia, absent in the West Indies

ily, 90 of these since Cogniaux (1891); only about 166, however, are currently recognized (Tab. 2). The Cyphostyleae (Gleason 1929) and Feliciadamieae (Jacques-Félix, in litt. 1991) are the only tribes that have been added to the 13 recognized traditionally. On the other hand, several workers have suggested merging the Sonerileae and Bertolonieae (J. D. Hooker in Benth & Hooker 1867; Gleason 1932; Bakhuizen 1946–1947; Wurdack 1964a), and J. D. Hooker (in Benth & Hooker 1867) and Wurdack (in a letter to J. Hutchinson of 8 September 1969) among others also doubted the distinctness of the Tibouchineae and Melastomeae as traditionally conceived.

## The status and relationships of the Memecylaceae DC.

The six genera of Memecylaceae form a morphologically homogeneous group, and Naudin's (1849–1853) suggestion to recognize two subfamilies, the paleotropical Memecyloideae and the neotropical Mouririoidae, based on differences in placentation and seed number was never taken up. It is assumed that the present range of the family represents the remnant of a once continuous

Gondwanian distribution. *Memecylon* today comprises about 300 species in Asia (Maxwell 1980b; Bremer 1979, 1982, 1983), 70 in Africa (Jacques-Félix, in litt. 1991) and 78 in Madagascar (Jacques-Félix 1984, 1985). Very close to *Memecylon* are *Warneckea* with 33 species in Africa and Madagascar (Jacques-Félix 1978a, b, 1985), *Lijndenia* with three species in southeast Asia, six in Madagascar and one in West Africa (Bremer 1982; Jacques-Félix 1985), and *Spathandra* with two species in Africa (Jacques-Félix 1978a, b, 1985 and in litt. 1991). The two neotropical genera, *Mouriri* with 81 species (Morley 1953, 1976, 1985, 1989) and *Votomita* with eight species (Morley 1963, 1985, 1989), are very close to each other and should perhaps be merged.

Memecylaceae and Melastomataceae share no apomorphic states and differ in all but a few basic myrtalean features such as intraxylary phloem, diplostemonous flowers, and presence of a well developed floral tube. Characters that disagree in the two families are listed in Tab. 3, and the states found in Memecylaceae are discussed below; the respective states in Melastomataceae are discussed in the next section and not repeated here.

Memecylaceae have 1-locular ovaries with a free central placenta or 2–5-locular ovaries with central-basal, basal, or in ten species of *Mouriri* and four of *Votomita* axillary placentation (Morley 1953). Up to 18 ovules

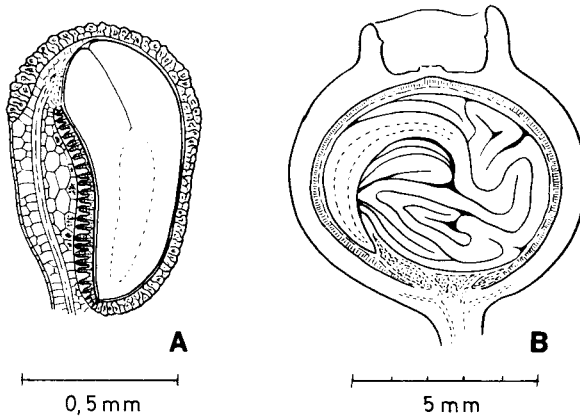


Fig. 1. A. Seed of Melastomataceae. – B. Seed of Memecylaceae.

have been recorded in *Memecylon* and up to 16 per locule in *Mouriri* (*M. trunciflora*; Morley 1976), but usually only one or two of them develop into a large subglobose seed (Fig. 1), containing an embryo with well developed cotyledons that are either rolled or wrinkled (in *Memecylon*; Jacques-Félix 1977a; Bremer 1981) or thick and fleshy (*Mouriri* and *Memecylon rivulare*). Germination in Memecylaceae is cryptocotylar, with the testa being raised above the soil and enclosing the cotyledons (Duke 1969; Vogel 1980; Burt 1991; pers. obs.). The seeds store starch.

Memecylaceae flowers have antepetalous ovary loc-

ules in the species in which this has been investigated (Morley, in litt.) and often radially thickened endothecium cells (Eyde & Teeri 1967), the plesiomorphic condition in the order although not necessarily in the family (Morley 1953: 252). The anthers open by two longitudinal slits in *Memecylon* and its segregates and by two short, drop-shaped slits in most species of *Mouriri*. Functionally the latter are equivalent to pores: *Mouriri* but not *Memecylon* flowers are buzz-pollinated by pollen collecting bees. A few species of *Mouriri* and *Votomita* that do not have thickened endothecium cells or any detectable endothecium still have anthers that dehisce longitudinally (Morley 1953, 1976). Assuming an ancestral condition which combined a thickened endothecium with a longicidal mode of dehiscence (as represented in *Memecylon*), the problem becomes the sequence of character build-up during the evolution of the family for the buzz pollination syndrome (i.e., poricidal dehiscence and loss of an endothecium).

Dorsally the connective carries a concave gland covered by a viscuous liquid that at various times was thought to be nectar or floral oil, but probably is neither. The role of the clearly terpenoid glandular products in pollination is unclear (Renner 1989b).

*Memecylon* and *Mouriri* have large sclereids that are associated with the terminations of the veins (Foster 1946; Morley 1976; Rao et al. 1980, 1983; Rao & Jacques-Félix 1978); *Memecylon* stands out in the possession of globular silica bodies in the epidermis (Baas 1981). Stomata in Memecylaceae are paracytic (Mentink & Baas 1992). The wood has fibre-tracheids and axially

Tab. 3. Differences between Memecylaceae and Melastomataceae.

	Memecylaceae	Melastomataceae
Anther connective	with a terpenoid-producing gland	lacking glands
Endothecium	fibrous	not fibrous
Anther dehiscence	longicidal, slits sometimes short and functioning as pores ( <i>Mouriri</i> )	poricidal, rarely longicidal; the pores developing in an epidermis-free region
Placentation	axillary, axile-basal, basal or free central ( <i>Memecylon</i> )	axillary, axile-basal, or parietal ( <i>Pternandra</i> )
Locules	opposite the petals	opposite the sepals except in <i>Pternandra</i> and <i>Rhexia</i>
Seeds	few, large and with thick or convolute cotyledons with fibrous exotegmen	numerous, small, and with short cotyledons without fibrous exotegmen
Germination	cryptocotylar	phanerocotylar
Leaf venation	brochidodromous	acrodromous
Stomata	paracytic	anomocytic, polocytic, cyclocytic
Leaf sclereids	large	absent
Indumentum	usually glabrous	usually with hairs and/or emergences
Ant and mite domatia	absent	common in Miconieae
Wood	with fibre-tracheids and interxylary phloem	with libriform fibers and lacking interxylary phloem except in <i>Pternandra</i>
Growth form	trees and shrubs	shrubs, treelets, herbs, climbers

included (interxylary) phloem and vessel-ray pits that are small with vested borders.

Chemical differences between the Memecylaceae and Melastomataceae include the frequent occurrence of acylated anthocyanins in the latter, whereas so far only non-acylated anthocyanins have been found in the Memecylaceae (Lowry 1976; but only two species of *Memecylon* have been investigated), and Favarger (1952, 1962) noted a difference in the colour of the root tips between the two families, Melastomataceae but not Memecylaceae containing anthocyanin in the root tips.

Based on pentamery and the more primitive forms of placentation occurring only in the New World, Morley (1953 and pers. comm.) suggested that *Mouriri* is closer to the ancestral condition than *Memecylon*. This is supported by cotyledon morphology, which in *Memecylon* and *Spathandra* appears more derived than in *Mouriri*. Anther dehiscence, on the other hand, appears plesiomorphic in *Memecylon* and relatives.

The closest affinities of the Memecylaceae, in my opinion, lie with Myrtaceae, but I know of few potential synapomorphies uniting these groups. These are the terpenoid-containing connective glands, in Myrtales found only in Myrtaceae and Memecylaceae (but erroneously scored as absent in the latter by Johnson & Briggs (1984)), and the few large starch-containing seeds. Further light on the relationships of both families will probably only be shed by new kinds of data. Other myrtalean families, such as the Crypteroniaceae and Lythraceae, appear more distantly related to the Memecylaceae because of their capsular fruits, numerous small seeds with minute embryos, and lack of axially included phloem.

## Melastomataceae characters: variation and polarization

The purpose of this section is to pull together all information relevant to solving infrafamilial relationships in the family and, for the subset of characters found phylogenetically informative, to discuss polarization. Unless otherwise indicated, the circumscription of the higher taxa is that proposed in the Phylogenetic analysis below and shown in Tab. 2.

### Germination

Germination is phanerocotylar, the eophylls being decussate with the cotyledons, but seedlings of only relatively few species have been studied (Ziegler 1925; Favarger 1952, 1962; Gadella et al. 1969; Rao & Chin 1972).

### Vegetative architecture

Melastomataceae exhibit a diversity of growth habits, including herbs, shrubs, treelets, and trees to 30–45 m

high; the latter are concentrated in the Merianieae and Miconieae (*Alloneuron*, *Loreya*, *Miconia*, *Tessmannianthus*). Root climbers are quite common in the Miconieae (*Catanthera*, *Clidemia*, *Dissochaeta* s. l., *Kendrickia*, *Leandra* (incl. *Pleiochiton*), *Macrolenes*, *Medinilla*, a few *Miconia*) but occur also in the Astronieae (a few species of *Astronia*), and Merianieae (*Adelobotrys*, *Phainantha*). Several non-climbing species of Blakeeae and Miconieae (e.g., *Medinilla* spp., *Pogonanthera*, *Pachycentria*) are capable of growing as facultative epiphytes, and many herbaceous species, especially of Sonerileae, grow low on trunks or on fallen logs (Renner 1986 for a survey).

Forty-four genera are largely or entirely herbaceous, but although this is about a quarter of the total number of genera, only relatively few species are involved, the shrubby groups comprising by far the majority of all species. Herbaceous species are concentrated in the Melastomeae and Sonerileae, of which 19 and 20 genera, respectively, include herbs. Many sonerilean herbs are acaulescent with basal rosettes of large, somewhat turgescent leaves. Tuber formation occurs in *Cinnibotrys*, *Heterotis*, *Monolena*, and *Phyllagathis*.

The question as to the ancestral growth habit in Melastomataceae can be answered by looking at closely related families, such as Lythraceae, Crypteroniaceae, and Myrtaceae all of which are basically ligneous. Although growth form was among the characters surveyed for all genera, I have not included it among the characters used in the phylogenetic analysis because it proved too variable.

### Reproductive architecture

The variety of inflorescences in the Melastomataceae corresponds to the size of the family but shows less diversity than, for example, the Myrtaceae (Johnson & Briggs 1984). Inflorescences are determinate thyrsoid ramification systems (Mora Osejo 1966; Cremers 1986; Weberling 1988). Uniparous (scorpioid) cymes are particularly frequent in the Sonerileae, but occur scattered in other groups. Single terminal flowers are rare, occurring mainly in the fruticose and herbaceous groups (Sonerileae, Melastomeae); they are the result of reduction and suppression as has been shown in various genera (Wurdack 1953; Almeda 1978; Cremers 1986). Cauli- and ramiflory is most frequent in the Miconieae and is a derived feature.

The systematic usefulness of inflorescence architecture in Melastomataceae appears limited to low taxonomic levels, but several generic realignments in Miconieae based on inflorescence position (terminal vs. lateral) have been proposed by Judd (1986a, 1989) and Judd & Slean (1991). A recent attempt at interpreting the distribution of different inflorescence types on the background of the traditional system (Sell & Cremers 1987) suffers from a misrepresentation of that system. Thus it is said that the



Memecyleae, Blakeeae, and Miconieae are the most primitive tribes in the family, certainly not the orthodox view (cf. History of the classification of Melastomataceae and Memecylaceae).

### Wood anatomy

The distribution of wood-anatomical characters in the family is very important (Tieghem 1891a, b; Janssonius 1914; Metcalfe & Chalk 1950; Vliet et al. 1981) and provides one of the major reasons for breaking up the Astronioideae sensu Triana (1871) and Cogniaux (1891). Typical Melastomataceae wood has libriform fibers, often large and simple vessel-ray pits, fiber dimorphism, libriform septate and non-septate fibers, and grouped vessels. Most members of Triana's Astronioideae (*Astronia*, *Astronidium*, *Astrocalyx*, and *Beccarianthus*) have this kind of wood; *Pternandra*, however, has fiber tracheids and axially and radially included phloem.

I have used one wood anatomical character in the phylogenetic analysis, namely fiber type, fiber tracheids being generally considered plesiomorphic in the Myrtales and in the angiosperms as a whole, libriform fibers as derived.

### Leaf morphology and anatomy

Extensive summaries of the pioneer studies of Pflaum (1897), Palézieu (1899), and Gottschall (1900) on melastome leaf morphology and anatomy may be found in Solereder (1899 & 1908) and Metcalfe and Chalk (1950; the latter is difficult to use because of the numerous synonymous generic names and the insufficient distinction in the summary statements of Memecylaceae and Melastomataceae). A recent complete survey is that of Mentink & Baas (1992).

Melastomataceae leaves are entire or dentate and decussate and typically have a petiole. The primary lateral vascular bundles run parallel to the leaf margin from the base to the apex. This type of venation is rare in the angiosperms (Hickey 1973) and nowhere as persistent as in the Melastomataceae. A few isolated genera and species, notably *Centradenia*, *Sonerila*, and some Miconieae (e.g., *Loreya arborescens*, *Macairea rufescens*; Renner 1989a) have imperfectly acrodromous or penninerved leaves, and it would be interesting to know the developmental mechanisms behind such switches.

A feature of the ground tissue that may have taxonomic significance is the presence or absence of diverse calcium oxalate crystals (raphides, styloids, druses, and crystal sand). Thus, Baas (1981) suggested that one or two parallel lines of specialization are exemplified in the Astronieae and Miconieae where the crystal complement in the leaves has come to consist exclusively of styloids, and Judd (1986b) has shown that within the Miconieae, crystal type is sometimes useful at the generic level.

Anisophylly is common in the Sonerileae sensu lato and Miconieae, less so in the Kibessieae, Astronieae, Merianieae, Microlicieae, Melastomeae, and Rhexieae. (Sonerileae: *Anerinckleistus*, *Barthea*, *Blastus*, *Bredia*, *Driessenia*, *Neodriessenia*, *Stussenia*, *Amphiblemma*, *Calvoa*, *Cinnobotrys*, *Fordiophyton*; *Phyllagathis* (incl. *Tylanthera*), *Sarcopyramis*, *Sonerila*; *Bertolonia*, *Centradenia*, *Diplarpea*, *Macrocentrum*, *Monolena*, *Triolena*; Merianieae: *Phainantha*; Miconieae: *Allomaieta*, *Catanthera*, *Clidemia*, *Maieta*, *Medinilla*, *Myrmidone*, *Tococa*; Blakeeae: *Blakea*, *Topobea*). Sometimes alternate leaves on a stem are reduced or caducous so that phyllotaxy appears alternate (species of *Blakea*, *Catanthera*, *Centradenia*, *Cinnobotrys*, *Clidemia*, and *Macrocentrum*), and in *Phainantha* all leaves on one side of the stem are replaced by climbing roots.

Ant domatia in melastomes are confined to the Miconieae (*Allomaieta*, *Clidemia*, *Conostegia*, *Henriettella*, *Maieta*, *Myrmidone*, *Ossaea*, *Tococa*) and Blakeeae and are typically situated in leaf bases, though hollow stems occupied by ants occur in *Blakea*, *Miconia*, *Tococa*, and *Topobea*. In the Old World, leaf domatia are rare (but are found in *Medinilla disparitifolia*), their ecological function being taken by root domatia (*Pachycentria*, *Pogonanthera*). Mite domatia have so far been reported from Miconieae, Blakeeae, and Sonerileae (Schnell 1963; Almeida 1989a, 1990a; Baumgratz 1989–1990).

### Epidermal features

Stomatal types in Melastomataceae are extremely varied; especially frequent are the following kinds: anomocytic (neighbouring cells not different from guard cells), polycytic (guard cells incompletely surrounded by a single subsidiary cell), diacytic (stoma enclosed by a pair of subsidiary cells whose common wall is at right angles to the guard cells), and tetracytic (stomate surrounded by four subsidiary cells, two lateral and two polar), but other types and intermediate kinds also occur (Mentink & Baas 1992). Anomocytic stomata are the basic type in the Myrtales (Baas 1981; R. Dahlgren & Thorne 1984: 636; Keating 1984: 816), but it is difficult to polarize stomatal types. The epidermis may be glabrous or possess an elaborate indumentum of glandular, stellate, or simple hairs and emergences (Wurdack 1986; Mentink & Baas 1992), and the cuticle may carry waxy ornamentations (illustrations: Wurdack 1986, Renner 1989a). With the exception of the conspicuous trichomes that characterize the leaves and floral tubes of many Melastomeae (the "tibouchinoid hairs" of Wurdack 1986), few major groupings are evident from epidermal features. An example are the Astronieae, which are characterized by non-glandular peltate scales, mainly anomocytic stomata, a 1–3-layered hypodermis, and a complex vascular pattern (Mentink & Baas 1992). Some of these features also occur scattered in the Miconieae. The Kibessieae, according to Mentink and Baas, are clearly distinct from the Astronieae, and

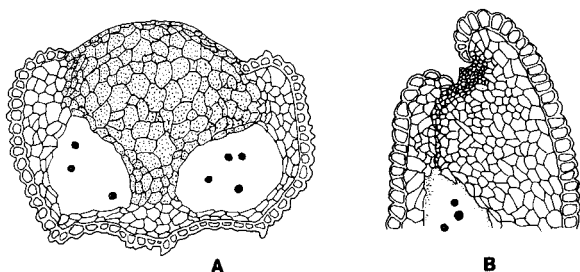


Fig. 2. Melastomatoideae pore opening mechanism. – A. Cross section through mature anther. – B. Longitudinal section. The pore develops in an epidermis-free region via the desiccation of exposed mesophyll.

characterized by anomo-cyclocytic and paracytic stomata (stoma accompanied on either side by one or more subsidiary cells parallel to the long axis of the pore and guard cells), druses, the absence of non-glandular peltate scales and of a hypodermis, and the occurrence of a simple vascular pattern in midrib and petiole. The remainder of the family is heterogeneous in leaf anatomy (Mentink & Baas 1992). In Sonerileae s.l. polocytic stomata are generally present, and in the Blakeeae anomocytic ones.

## Floral morphology and anatomy

### General considerations

The floral features most useful for higher level systematics in melastomes are placentation, configuration of the ovary apex, and staminal morphology. These are discussed in turn below. Much has been made of the number of floral parts, for example, by Triana (1865, 1871), but this feature is usually too variable for generic grouping (Wurdack 1964a; Renner 1989a). Petal aestivation is right-contorted and petal venation is imperfectly acrodromous.

### The androecium

Flowers in the family are actinomorphic, often with zygomorphic androecia, and are usually diplostemonous, with the inner set of stamens usually smaller than the outer one. The opposite is the case in *Monochaetum* (Almeda 1978) and *Dissochaeta* (incl. *Diplectria*) where due to ontogenetic displacements the stamens in the outermost ring are placed in front of the petals, the smaller in front of the sepals (obdiplostemony). In some other species the inner whorl is more or less rudimentary, with the antepetalous stamens either staminodial or lacking entirely (haplostemony). Immature anthers are tetrasporangiate and dithecal; mature anthers are generally bisporangiate with the exception of *Rhexia* where they are unisporangiate, one of numerous autapomorphies of that genus. In a few genera the anthers open by two longitudinal slits (*Pterandra* and the four genera of *Astroniaeae*). In the vast

majority of genera, however, they are 1-pored, 2-pored or, rarely, 4-pored (some *Miconia*). A few *Miconieae* (some species of *Charianthus*, *Mecranium*, and *Miconia* sect. *Chaenantha*) have anthers with rimose pores or slits, apparently a secondary development from poricidal opening (Wurdack, pers. comm.; Judd, in litt. 1992). The 2-pored condition occurs scattered in the *Merianieae* (*Tessmannianthus*), *Sonerileae* (*Scorpiothyrus*, *Sonerila*), *Miconieae* (*Bellucia*, *Chalybea*, *Huilaea*, *Loreya*, *Mecranium*, *Medinilla*, *Miconia*), and *Blakeeae* (*Blakea*, *Topobea*), and is variable within certain genera (e.g., *Loreya*) which comprise 1- and 2-pored species. The lack of the usual fibrous thickenings of the radial endothecium cell walls is correlated with a special mode of anther opening in *Melastomataceae* (Fig. 2): the pores develop in an epidermis-free region via the desiccation of exposed mesophyll (Ziegler 1925; Eyde & Teeri 1967). In other myrtalean families the irregular shrinkage of the endothecium cells during anther dehydration leads to the rupture of the wall (e.g., in *Memecylon*: Eyde & Teeri 1967). In the cladistic analysis, anthers that still have a functional endothecium and open along their entire length were scored as the ancestral condition.

Melastome connectives are of striking plasticity, but two major types may be discerned (Triana 1871: plates 1–5): one with dorsal connective spurs and basally unprolonged connectives, the other with a basal-ventrally prolonged connective for which the term pedoconnective was introduced by Jacques-Félix (1953: 977; 1981a). The criterion I have used for scoring a taxon as having pedoconnectives was that in the affirmative case the connectives of the largest stamens found are curved so that a knee is formed between connective and filament. Because other myrtalean families do not have such geniculate connectives or appendages, in the cladistic analysis an unprolonged and dorsally unappendaged connective was assumed to be the ancestral condition.

### The gynoecium

Ovary locules in *Melastomataceae* are antesepalous except in *Pterandra* and *Rhexia* where they are antepetalous. An important character provided by the gynoecium is its perigyny or epigyny. The degree of adnation between ovary wall and hypanthium, however, is not always easy to discern in herbarium material (Eyde & Teeri 1967) and is not correlated with either the hypanthium or ovary wall becoming fleshy in fruit (see below: fruit characters).

The ovary apex in capsular-fruited melastomes is often crowned by bristles, scales, or lobes around the style that persist into the fruit stage and sometimes play a role in seed dispersal (Weber 1987; Stone & Weber 1988). Such ovary outgrowths are especially common in the *Sonerileae* s. s. and *Melastomeae* and may characterize these lineages but their homology is unclear. I consider ovaries with unadorned tops plesiomorphic.

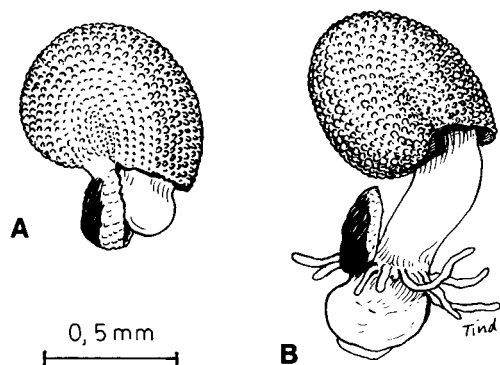


Fig. 3. Melastomeae seed. – A. The emerging radicle pushes the operculum from the micropyle. – B. Germination.

### Placentation

There are axillary, axile-basal, and median-parietal placentas, and this is one of the most useful characters for phylogenetic reconstruction because the three types appear to have become fixed early in the phylogeny of the family. Median-parietal placentation is only found in *Pternandra* (incl. *Kibessia*) and ontogenetically results from the strong expansion of the ovary bottom which pushes initially axillary placentae onto the walls of the ovary (Schumann 1887). Basal placentas are found in the Astronieae, where they are large and may ascend into the locules (Schumann 1887; Maxwell & Veldkamp 1990a, b). Axillary placentas characterize the remainder of the family. Although there is some variation within this last type (the placentas may fill out the entire locule space, be restricted to the central part of the ovary column, or may be stalked), it appears that axillary placentation arose only once in ancestral Melastomataceae. Based on Schumann's ontogenetic study and by comparison with closely related groups, especially the Crypteroniaceae and Lythraceae, a plastic axile-basal or axile placentation appears to be the plesiomorphic condition.

### The fruit

About 2150–2350 species in 41 genera have berries, 2000–2200 in 125 capsules. Fleshy fruit walls arose several times, correlated with dispersal by animals, mainly birds, and even closely related species, such as *Melastoma sanguineum* and *M. malabathricum* or *Pternandra echinata* and *P. coerulescens*, may differ in seed dispersal and fruit morphology (further examples are found in *Otanthera* and *Aciotis*). While the capsule of the first species in these pairs opens loculicidally to release wind-dispersed seeds, the second species are animal dispersed. In *M. malabathricum* this is achieved by the dry exocarp tearing open irregularly to expose dark red, fleshy placentae in which the seeds remain embedded until eaten by a bird; in *P. coerulescens* the hypanthium but not the ovary

wall becomes fleshy and there is no pulp surrounding the seeds. Conflicting information on fruit type is often given by collectors on herbarium labels and in floras and monographs (Bakhuizen 1946–1947; Maxwell 1981), and great care must be taken to ascertain the primitive condition in each case. Dry capsules from epigynous ovaries are found in the Merianieae (*Merianthera*, *Tateanthus*), Sonerileae (*Feliciadamia*), Melastomeae (*Dinophora*), Rhexieae (*Rhexia*), and Miconieae (*Alloneuron*, *Allomaieta*, *Cyphostyla*), and fleshy capsules from perigynous ovaries have evolved repeatedly in the Melastomeae. Further critical examination of fruit attributes in the family is a matter of high priority, and may reveal the phylogenetic affinities of some unusual genera, such as *Kendrickia* or *Alloneuron* and its allies.

Because in Crypteroniaceae and Lythraceae dry capsules are plesiomorphic and because completely inferior ovaries are generally considered more derived than perigynous ones, in the cladistic analysis fleshy fruits from inferior ovaries and with seeds embedded in pulp were scored as apomorphic.

### Ovules, embryos, and seeds

Embryological studies in Melastomataceae, including ovule ontogeny, megagametogenesis, and embryogeny, have been conducted in 20 genera (Hofmeister 1858; Ruys 1924; Ziegler 1925; Mauritzon 1939; Subramanyam 1942, 1944, 1946, 1948, 1951a, b; Crété 1956, 1957, 1960a, b; Iconomidis 1958; Etheridge & Herr 1968), representing all tribes except the Astronieae, Merianieae, and Blakeeae. The functioning megaspore develops into the *Polygonum* type megagametophyte. The ovules are anatropous except in *Rhexia* where they are atropous (Etheridge & Herr 1968; Schmid 1984) and bitegmic, with both integuments contributing to the micropyle (resulting in a more or less Z-shaped micropyle). A micropyle formed by both integuments is common in the Myrtales, as are the mature exalbuminous seeds characteristic of all Melastomataceae.

Seeds are of three major types: straight with a smooth or tubulate surface, straight with a foveolate surface, or cochleate (campylotropous; Fig. 3) with a tubulate surface (Don 1823; Cogniaux 1891; SEMs: Whiffin & Tomb 1972; Renner 1989a; C. Hansen's numerous unpublished SEMs of the seeds of Asiatic species are available for study in the herbarium in Copenhagen). Campylotropy becomes manifest rather late during the ontogeny of the ovules, and only the mature seeds are fully campylotropous (Bouman & Boesewinkel 1991). Such seeds with a distinctly convex antiraphal side and the micropyle situated close to the chalaza are found in Melastomeae and *Rhexia*. The adaptive advantage of campylotropy, as discussed by Bouman and Boesewinkel, may be that it enables seeds to contain embryos twice as long as the seed itself, giving better opportunities for the early establishment of the seedling.

Tab. 4. Character coding for Melastomataceae cladistic analyses; see text for discussion of additional characters and rationale for polarizations.

1. Libriform fibers: 0 = absent; 1 = present
2. Anther dehiscence: 0 = by two slits; 1 = by one or two pores
3. Pedoconnective: 0 = absent; 1 = present
4. Dorsal connective appendages: 0 = absent; 1 = present
5. Ovary crowned by outgrowths: 0 = absent; 1 = present
6. True berries: 0 = absent; 1 = present
7. Consistently axillary placentation: 0 = absent; 1 = present

### Nectar production and pollination biology

A summary of pollination in melastomes, including a survey of the relevant older literature, is available (Renner 1989b). The vast majority of the total species offer pollen as a reward and are pollinated by bees that use thoracic vibrations which are transmitted to the anthers to collect the pollen. Nectar production is rare in Melastomataceae, but occurs in 70–80 neotropical species belonging to *Blakea*, *Axinaea*, *Meriania*, *Centronia*, *Brachyotum*, *Tibouchina*, *Chalybea* and *Huilaea*, *Charianthus*, *Mecranium*, and *Miconia* (references in Renner 1989b).

Melastome nectaries lack histologically differentiated nectariferous tissue and may be located on the filaments near the insertion of the connective, at the filament insertion into the hypanthium, or at the petal tips (*Medinilla magnifica*; *Tococa guianensis*; Tobe et al. 1989; Rutschhauser, pers. comm. 1991). According to Tobe and collaborators (Stein & Tobe 1989; Tobe et al. 1989) they are unique in Myrtales and perhaps among angiosperms as a whole. Nectar secretion so far is known only from New World Melastomeae, Meranieae, Miconieae, and Blakeeae, but the status of knowledge in this area and the unstructured nature of melastome nectaries make it impossible so far to use the presence of nectar secretion as a systematic character.

### Pollen morphology

Based on the limited number of studies, c. 110 species in 30 genera (Patel et al. 1984; Renner 1989a; Skean, in press; Nowicke, unpubl.; Almeda, unpubl.; Hansen, unpubl.), there exists little variation in pollen morphology. The pollen is small, tricolporate, radially symmetrical, and isopolar; occasionally grains may have 4, 5 or more colpi, and some grains are dicolporate or heteropolar. Faint to distinct pseudocolpi (or subsidiary colpi, in the terminology of Patel et al. (1984)) are usually present. The surface sculpture is smooth and striate or rugulate or rugulate-verrucate. Polyads and tetrads are known from *Tococa spadaciflora* and *Miconia melanotricha* (Patel et al. 1984; Skvarla, pers. comm.).

Contrary to earlier statements, mature pollen of Melastomataceae contains two, not three cells (Tobe & Raven 1984).

### Karyology

Almeda & Chuang (1992) have recently summarized karyological work in the family (mainly by Favarger 1952, 1962, and Solt & Wurdack 1980) and based on this and their own work have suggested a base-number of  $n=17$  for the neotropical Miconieae. Polyploidy is frequent in the family.

### Chemistry

Relevant data may be found in Hegnauer (1990), and some references were provided above (The status and relationships of Memecylaceae DC.) to chemical traits distinguishing Memecylaceae and Melastomataceae. Chemical characters that would underline the naturalness of certain intrafamilial groups have not yet been found.

### Phylogenetic analysis

The following 21 characters were analyzed in representatives of all genera of Melastomataceae and Memecylaceae using herbarium material (studied during visits to BK, BKF, BM, C, E, K, L, and US) and literature (cited above and in Tab. 2) and in a few cases fresh material: growth form, leaf venation, presence and degree of anisophylly, presence and type of domatia, inflorescence position and architecture, floral bracts (presence, shape, whether persistent), calyx type (whether persistent) and shape, flower sex (hermaphrodite or unisexual), mery, stamen number, mode of anther dehiscence, presence and degree of stamen dimorphism, presence and type of connective appendages, presence of a pedoconnective, configuration of the ovary apex, ovary locule number, placentation type, ovule number, fruit type, fruit cross section, and seed shape. Only seven of these (Tab. 4) were used in the cladistic analyses because they were known for each genus, sufficiently invariable at the level of investigation, and of reasonably likely homology; all autapomorphies were deleted from the data matrix. The analyses were performed using the program PAUP ver-

Tab. 5. Data matrix for the Melastomataceae. The Kibessieae are outgroup for the remainder of the Melastomataceae.

Melastomataceae character states	
Kibessieae	00 00 000
Astronieae	10 00 000
Sonerieae	11 00 101
Meranieae	11 01 001
Microlicieae	11 10 001
Melastomeae	11 10 101
Rhexieae	11 01 001
Miconieae	11 00 011
Blakeeae	11 00 011

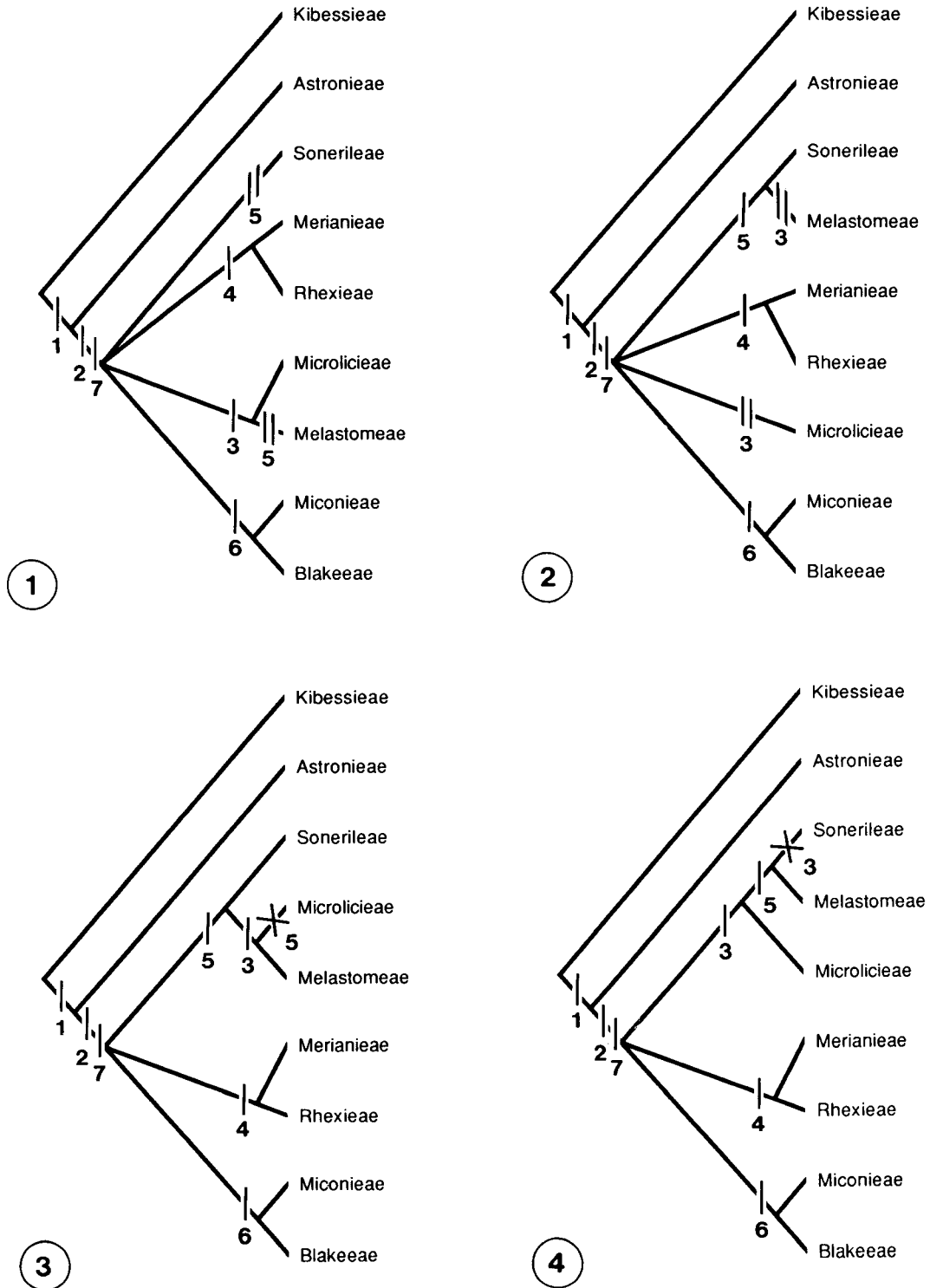


Fig. 4. 1–4. Topologies of the four equally parsimonious trees generated by PAUP in an exhaustive search with Kibessieae as functional outgroup; length = 8; C.I. (excluding uninformative characters) = 0.86. Characters: 1. libriform fibers; 2. anther dehiscence by pores; 3. pedoconnective; 4. dorsal connective appendages; 5. ovary crowned; 6. true berries; 7. consistently axillary placentation; single lines = synapomorphies, double lines = homoplasies, × = losses (reversals). See Tab. 4 and text for character states and explanation of characters. Tree 1: preferred hypothesis.

sion 3.0s (Swofford 1991) on a Macintosh PC, and the characters were polarized as discussed in the preceding section and as shown in Tab. 4. The Kibessieae was used to root the cladogram because they retain the ancestral condition in all characters employed in the analysis (cf. data matrix, Tab. 5).

The units accepted as monophyletic and employed in the analysis are those appearing as headings in the following discussion; they are formally recognized at the tribal level to conform as much as possible with taxonomic tradition in the family. Their composition may be found in Tab. 2 in which all genera currently recognized in the family are assigned to tribe. Since the discussion that follows incorporates much information presented in Melastomataceae characters: variation and polarization, references to morphological studies will not be repeated but may be found above under the respective character type.

An exhaustive search using the data matrix shown in Tab. 5 yielded four equally parsimonious 8-step trees with a consistency index of 0.86 (excluding uninformative characters). The alternative topologies shown in Fig. 4 assume homoplasy (including losses) for either pedoconnectives, dorsal connective appendages, or ovary crowns. Tree 1, hypothesizing the independent evolution of ovary crowns in Melastomeae and Sonerileae s. s., was selected as the preferred hypothesis because this seems intuitively likely (compare discussion of this character under Gynoecium). Less likely seem a parallel evolution of pedoconnectives in Melastomeae and Microlicieae (tree 2) or a loss of ovary crowns in Microlicieae (tree 3). Tree 4, which assumes a loss of pedoconnectives in Sonerileae, is contradicted by the present distribution of Sonerileae, Melastomeae, and Microlicieae (see below). Additional evidence from characters not used in the formal analysis as well as distribution data will be considered in the further discussion of the preferred cladogram.

### Kibessieae

The Kibessieae, comprising only *Pternandra* (incl. *Kibessia*) with 15 species in southeast Asia (Maxwell 1981), are rich in autapomorphies, such as median-parietal placentation, antepetalous ovary locules, and radially included phloem, but share no derived traits with the remainder of the Melastomataceae other than the acrodromous venation, the synapomorphy of the family. As is apparent from the data matrix (Tab. 5) Kibessieae are here regarded as the sister taxon to all other tribes and, following Naudin (1849–1953), formally recognized as a subfamily (Tab. 2). In wood anatomy, *Pternandra* stands out in having axially (in addition to radially) included phloem and fiber tracheids, and it has therefore been proposed as a link between the Melastomataceae and Memecylaceae (Thorne in R. Dahlgren & Thorne 1984: 677). Interxylary phloem, however, is common in alliances with intraxylary phloem such as the Myrtales (Met-

calfe & Chalk 1983, quoting Solereder) and may be present or absent even within single genera, viz. *Strychnos* (Baas, in litt.) and the roots of *Lythrum salicaria* (Metcalfe & Chalk 1950). An independent origin of the axially included phloem in Memecylaceae and *Pternandra* is supported by the fact that vessel ray pits in *Pternandra* are simple (like those of other Melastomataceae) whereas Memecylaceae have half-bordered pits. Radially included phloem, on the other hand, while not known from Memecylaceae has been found in other Melastomataceae (*Medinilla*).

### Astronieae

This paleotropical group of four genera (Maxwell & Veldkamp 1990a, b) is macromorphologically, leaf anatomically, and biogeographically very homogeneous. *Astronia* with 59 and *Astronidium* with 67 species differ from one another mainly in stigma and placenta shape and the smaller *Beccarianthus* (22 species) is separated on calyx and capsule morphology. The monotypic *Astrocalyx*, finally, is simply a pleiostemonous *Astronia*. Astronieae share several plesiomorphic character states, such as a woody habit, dry capsules with cuneate or linear seeds, basal or axile-basal placentation, longicidal anther opening, and a complex vascular pattern in the midrib (Mentink & Baas 1992), but seem to lack an autapomorphy. A synapomorphic trait joining them with the Melastomatoideae is the possession of libriform fibers (van Tieghem 1891a; Vliet 1981).

### Sonerileae

The Sonerileae s. l. occur mainly in Southeast Asia and Madagascar, whereas they have few species in the neotropics; they may comprise 560–600 species in 40 genera. The clade is heterogeneous, and the synapomorphic character accepted in the cladistic analysis as characterizing it, namely the apically crowned ovaries, is only found in two-thirds of the genera. I have recognized two provisional alliances within the Sonerileae s. l. (Tab. 2), the *Oxyspora–Anerinacleistus* alliance and the *Sonerila–Bertolonia–Gravesia* group, but the distinction between the two is weak, and for example *Bredia* and *Driessenia* could go in both (compare Tieghem 1891a; Cogniaux 1891; Diels 1932; Hansen 1985b). The first alliance comprises mainly shrubs with terminal or axillary, umbellate, fasciculate, or thyrsoid paniculate cymes (scorpioid in some *Neodriessenia*) and 8- or 10-ribbed, occasionally tetragonal (*Bredia*) capsules. The second consists mainly of herbs with often uniparous (scorpioid) inflorescences, more rarely with paniculate cymes or flower clusters and typically 3- or 4-angular capsules. The core of the first group is made up of *Oxyspora*, *Anerinacleistus*, *Poilarnammia*, *Bredia*, *Barthea*, *Driessenia*, *Neodriessenia*, *Blastus*, and *Stussenia*. The second group in Asia com-

prises *Sonerila*, *Sarcopyramis*, and *Phyllagathis* (incl. *Tigridopalma*) and the satellites *Scorpiothyrsus*, *Aschistanthera*, and *Kerriothyrsus* plus a few small or monotypic genera (Tab. 2).

Most Sonerileae are herbaceous plants of shady habitats, often with a basal whorl of large, somewhat turgescenscent leaves, sometimes with tubers. As in many herbaceous melastomes, there is a pronounced tendency to reductions in the androecium, with the inner set of stamens becoming staminodial. Old World Sonerileae usually have isomerous flowers whereas New World ones typically are anisomerous (5-merous androecia with 3-locular ovaries). Exceptions are the neotropical *Tryssophyton*, which is isomerous (Wurdack 1964a: 156) and the paleotropical *Calvoa*, which is anisomerous.

Most Asiatic Sonerileae belong to the taxonomically very poorly understood genus *Sonerila*, while the majority of African and Madagascan Sonerileae belongs to *Gravesia* and its close relatives *Amphiblemma* and *Calvoa*. More isolated are the small or monotypic *Cincinnotrys*, *Dicellandra*, *Preussia*, and *Feliciadamia*, the last recently elevated to tribal status (Jacques-Félix, in litt. 1991) because of its capsular fruits that develop from an epigynous ovary. This condition, however, has evolved repeatedly in the family (see Melastomataceae characters: variation and polarization), and on its own does not have much significance. The neotropical Sonerileae, finally, consist of a core made up by *Bertonia*, *Macrocentrum*, *Monolena*, *Salpinga*, *Triolena*, and *Diplarpea* and some phenetically more isolated groups, such as *Maguireanthus*, *Opisthocentra*, *Tateanthus*, and *Boyania* (Wurdack 1964a, Solt & Wurdack 1980). Almeda (1977 and in press) has suggested that *Centradenia*, *Centradeniastrum*, and a new central American genus too are soneriloid, mainly because of their pyramidal seeds.

Two relatively strong characters support a clade consisting of the Sonerileae and all following tribes (Fig. 4), namely fixed axillary placentation and poricidal anthers. By contrast, the Sonerileae themselves, whether in the strict sense (excluding the *Oxyspora*-*Anerincleistus* alliance) or in the broad sense accepted here, are a poorly defined group. Ontogenetic studies of sonerilean fruits are planned.

## Merianieae

This clade, the core of which is made up by *Axinaea*, *Meriania*, *Centronia*, *Graffenrieda*, *Adelobotrys*, and *Phainantha*, consists almost entirely of treelets, shrubs, or woody climbers with dry capsules, leathery leaves and rather large flowers with dorsally thickened and variously spurred stamens without pedoconnectives. It may comprise 16 genera and c. 220 species. A number of small southeastern Brazilian shrubs (*Behuria*, *Benevidesia*, *Merianthera*, *Dolichoura*, *Huberia*, and *Bisglaziovina*), the Orinoco-Rio Negro savanna genus *Pachyloma*, and the Andean *Tessmannianthus* are added to this core

mainly on account of their stamens and seeds. The seeds of *Pachyloma*, however, are unlike those of all other Merianieae. In some of these genera the dorsal connective appendages are present in the larger stamens only and moreover are bifid and curved so that they appear like ventral appendages (compare illustrations of *Tessmannianthus* in Wurdack 1989, and Almeda 1989b, 1990b). More difficult to place are the monotypic, probably ancient Guayana groups *Neblinanthera* (Wurdack 1964a) and *Ochthephilus* (Wurdack 1972). *Ochthephilus* differs from all other Merianieae in being herbaceous.

## Rhexieae

In the preferred cladogram (Fig. 4.1.) *Rhexia* appears as the sister group to Merianieae on the basis of shared stamen characters (dorsally thickened connectives, lack of pedoconnectives), but the evidence is weak. *Rhexia* is the only genus of Melastomataceae with an entirely North American distribution and rich in autapomorphies, such as atropous ovules, capsules from completely inferior ovaries, locules in front of the petals instead of alternating with them, and mature unilocular anthers. The cochleate seeds found in most but not all species of *Rhexia* develop from atropous ovules and therefore must have originated independently from the cochleate seeds of Melastomeae, which develop from anatropous ovules. *Pachyloma*, placed next to *Rhexia* by Triana and Cogniaux, shares no derived characters with that genus and is here regarded as merianiean.

## Melastomeae

A huge well-defined clade (c. 850 species in 47 genera) the members of which share the following synapomorphies: cochleate seeds, stamens with pedoconnectives, and ovaries typically crowned by persistent trichomes. Melastomeae are mainly annual or perennial herbs, subshrubs, or shrubs, rarely treelets. Inflorescences are terminal paniculate or rarely glomerulate cymes; occasionally they are few-flowered and axillary or consist of solitary flowers. Flowers are usually diplostemonous with unequal stamens, or one whorl is staminodial or lacking (some species of *Tibouchina*, *Monochaetum*, *Acisanthera*, *Siphanthera*, and *Poteranthera*). The capsules of neotropical representatives are dry and have wind-dispersed seeds, those of some paleotropical species tear open to expose fleshy placentae (cf. Melastomataceae characters: variation and polarization) or have true berries (*Melastoma orientale*). The adaptive significance of this and also of the campylotropous seeds has already been discussed (Melastomataceae characters: variation and polarization). Unusual are the flattened and broadly winged seeds of *Acanthella*, and the placement of this genus is therefore uncertain. Indumentum complexity in the family reaches its pinnacle in the Melastomeae (Wurdack

1986), and there are striking parallelisms in hypanthium indumentum in, for example, *Osbeckia*, *Dissotis*, and *Pterolepis* from Asia, Africa, and South America, respectively.

*Monochaetum*, traditionally placed in the Rhexieae (Triana 1871; Cogniaux 1891), belongs in the Melastomeae on account of its campylotropous seeds (Almeda 1978), setose ovary apex, wood anatomy (ter Welle & Koek-Noorman 1981), and chromosome number (Almeda & Chuang 1992).

### Microlicieae

*Microlicia*, *Chaetostoma*, *Lavoisiera*, *Rhynchanthera*, *Trembleya*, and *Cambessedesia* form a cohesive assemblage centered in south-central Brazilian savannas. Autapomorphic characters are the straight, sometimes slightly winged seeds with a usually foveolate surface (SEMs: Whiffin & Tomb 1972; Renner 1990) and shrubby, often microphyllous habit. A synapomorphy with Melastomeae is the presence of pedoconnectives (Fig. 4).

Problematic is *Bucquetia*, an Andean group of three species placed variously in Microlicieae (Triana 1871; Cogniaux 1891), Melastomeae-Tibouchineae (Baillon 1877; van Tieghem 1891a; Krasser 1893), and Merianieae (Wurdack 1980). Wood-anatomically it is anomalous in any of these alliances because of the mainly procumbent ray cells (ter Welle & Koek-Noorman 1981: 372). The seeds are pyramidal, the ovary apex glabrous or setose, and the stamens simple. *Bucquetia* is here placed in the Microlicieae because that is where it seems to disagree least.

The monotypic genera *Castratella*, *Eriocnema*, and *Lithobium* differ from other Microlicieae in being herbaceous and *Lithobium* in addition by having 3-merous flowers. Indeed, Baillon (1877) and Krasser (1893) held *Eriocnema* to be soneriloid (bertolonioid).

### Miconieae

The Miconieae comprise c. 2200 species in 38 genera mostly of shrubs, trees, and treelets and are distinguished by epigynous ovaries that usually develop into baccate fruits typically dispersed by birds. In some Old World Miconieae, such as *Dissochaeta*, *Medinilla*, and *Macrolenes*, the fusion of ovary and hypanthium is incomplete because there are deep pockets in the tissue between the ovary wall and receptacle, corresponding to the bud positions of the stamens; and in some New World genera the hypanthium and ovary wall do not become fleshy in fruit (*Allomaieta*, *Alloneuron*, *Cyphostyla*). *Kendrickia*, a woody climber, traditionally placed in the Oxysporeae because of its dry fruit, is here placed in the Miconieae because it appears closely related to *Medinilla* in habit and floral morphology. The Andean genera *Allomaieta*, *Alloneuron*, and *Cyphostyla* (with together ten species)

were proposed by Gleason (1929) to form the tribe Cyphostyleae, which he thought characterized by capsules developing from inferior ovaries, haplostemonous androecia, and calyptrate calyces. However, and as pointed out by Gleason, each of these features has developed repeatedly in the family (capsules from inferior ovaries in Melastomeae, Merianieae, Rhexieae, and Sonerileae, haplostemonous androecia in Melastomeae, Microlicieae, and Miconieae, and calyptras in Astronieae, Blakeeae, Kibessieae, Merianieae, and Miconieae), and it is particularly in the Miconieae that these derived characters abound (viz. haplostemony in *Dissochaeta* p.p. (incl. *Omphalopus*), and *Miconia* p.p.; pleiostemony in some *Clidemia*, *Conostegia*, *Llewelynina*, *Miconia*, and *Plethiandra*; calyptras in *Bellucia*, *Centronia*, *Conostegia*, *Llewelynina*, *Mecranium*, *Myriasporea*, and some *Tococa*; for miconiean genera with ant and mite domatia, nectar secretion, or woody climbers compare the section on Melastomataceae characters).

### Blakeeae

*Blakea* and *Topobea*, two extremely close taxa (Gleason 1945; Wurdack 1957; Almeda 1990a), are traditionally separated from the Miconieae because of their persistent floral bracts, axillary flowers, and conspicuously cross-venulate leaves with often very numerous, strictly parallel lateral veins. They share baccate fruits with seeds embedded in pulp with Miconieae (Fig. 4), and are also closest to Miconieae in wood anatomy (Koek-Noorman et al. 1979). Possibly therefore Miconieae become paraphyletic by ranking Blakeeae at the tribal level. On the other hand, little is gained at present by including this distinct clade in the already huge Miconieae.

## A new classification of the Melastomataceae

The arrangement proposed in Tab. 2 and for which the rationale has been presented above differs from the traditional one (Cogniaux 1891) as follows: (1) the Memecylaceae are removed from the Melastomataceae, (2) *Pternandra* is placed in a subfamily of its own, (3) the Astronioideae are abolished, (4) three neotropical and paleotropical tribal pairs are merged (Bertolonieae with Sonerileae-Oxysporeae, Tibouchineae with Melastomeae, and Miconieae with Dissochaeteae), (5) the Cyphostyleae are submerged in the Miconieae, and (6) *Rhexia* is placed in a tribe of its own. As pointed out in the historical review of melastome classification, most of these changes have also been suggested by other workers or present a return to pre-Triana classificatory schemes.



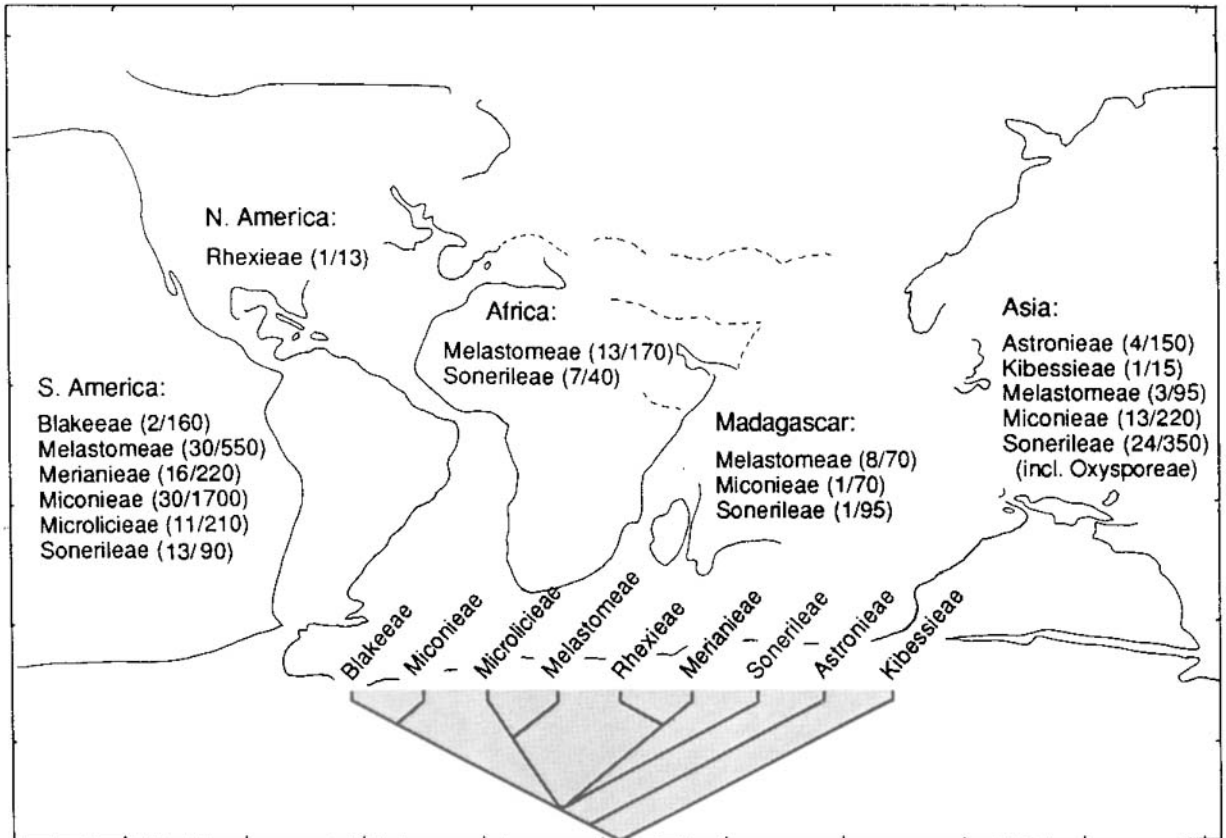


Fig. 5. Preferred phylogenetic hypothesis and present day distribution of Melastomataceae superposed on a Late Cretaceous (80 m.y.b.p.) reconstruction to indicate continental locations during initial tribal diversification. Figures in brackets indicate the number of genera/species in the different areas.

## Geographical distribution and fossil evidence

The geographic distribution of all genera is given in Tab. 2, and these data will now be used, together with the fossil record and the hypothesized phylogeny (Fig. 4), to develop a broad picture of the evolutionary history of the family.

The acrodromous venation emerges as the single most important character of Melastomataceae, acquired before the poricidal mode of anther dehiscence. Based on wood anatomy there are two major groups, Kibessioideae and Melastomatoideae, and they are supported by placentation characters: median-parietal placentas are typical of Kibessioideae and axillary ones of Melastomatoideae including Astronieae (since the axile-basal placentation of the latter ontogenetically derives from axillary placentas). The fossil record of the Melastomataceae has recently been reviewed (Pingen & Collinson, in press). There is one tentatively acceptable pollen fossil from the Paleocene of Colombia (Hammen & García de Mutis 1966), which would be the oldest record of the family; Miocene

and Pliocene pollen has been reported from Costa Rica and Panama (A. Graham 1987, 1991). Unfortunately melastome pollen is of a general type, similar to pollen of several other myrtalean families, and may be difficult to assign with certainty (Patel et al. 1984). Macrofossils, however, clearly show that the Melastomataceae were present by the early Tertiary. Thus, there are Eocene leaves from Colombia (Huertas 1977), Brazil (Duarte 1956), North America (Hickey 1977), and Borneo (Geyler 1887), and an Upper Miocene leaf has been reported from Sumatra (Kräusel 1929). The most interesting record in terms of the biogeographic history of the family is an Antarctic leaf from Tertiary deposits on Seymour Island (Dusén 1908). Although a critical modern investigation is lacking, Dusén's illustration shows a leaf with typical melastome venation, and the identification appears reliable according to E. Zastawniak who has studied the specimen (Pingen, in litt. 1992).

Combining all available evidence, the most likely place of origin of the Melastomataceae appears to be East Gondwana (Antarctica + Australia + New Guinea; Fig. 5); because the family exhibits much greater fundamental diversity in the east-Gondwanan region; because the most

plesiomorphic groups (Kibessieae and Astronieae) occur in the Malesian region; because there is a fossil record from Antarctica; and because there are three tribes that span from Southeast Asia to South America. Africa has a number of Melastomeae (13 genera) and Sonerileae (7 genera), but lacks all other tribes, most notably the Miconieae, except for two introduced species of *Medinilla*. This may indicate that the Miconieae originated at a time when the distance between South Africa and East Gondwana was already too large for Africa to be entered from the south, while it was still possible to reach South America. The suggestion of Madagascar as a possible cradle (Fernandez & Fernandez 1954) is unlikely because Madagascar harbours none of the basal groups. It does have some Sonerileae (*Gravesia*) and Melastomeae (a few species of *Osbeckia*, an introduced species of *Melastoma*, a few representatives of African genera (*Dissotis*, *Dichaetanthera*, *Antherotoma*, *Tristemma*) and two endemics, *Amphorocalyx* and *Dionycha*), but lacks all Miconieae except *Medinilla* (Perrier de la Bâthie 1951). *Osbeckia* and *Medinilla* probably arrived in Madagascar from Asia where they comprise numerous species, whereas they have no native representatives in Africa. India, suggested by Nayar (1972) as a place of origin for the Melastomataceae, can be excluded because of the unbalanced representation of the family there, which consists of weeds and relatively derived species, e.g., of *Sonerila* (Lundin, pers. comm. 1991).

A west-Gondwanan origin, favoured by Raven & Axelrod (1974), is contradicted by the present distribution of the tribes and the restriction of the Kibessieae and Astronieae to Malesia, while an east-Gondwanan origin not only agrees with the fossil record but also with a possible ancestry from crypteronioid-lythroid stock.

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