

LEAF ANATOMY OF THE MELASTOMATACEAE, MEMECYLACEAE, AND CRYPTERONIACEAE

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SUMMARY

The leaf anatomy of the Melastomataceae, Memecylaceae and Crypteroniaceae is surveyed on the basis of 179 samples representing 151 genera. The Melastomataceae appear to be leaf anatomically very heterogeneous. An unusual diversity of hair types is present, varying from simple unicellular hairs to very complex multicellular, non-glandular or glandular trichomes. Elongate multiseriate unbranched non-glandular hairs and short-stalked glandular hairs are most common. Stomata generally are polo-, dia-, tetra-, and anomocytic; other types and intermediate kinds also occur. A hypodermis is sometimes present. The mesophyll is usually dorsiventral, rarely isobilateral. Sclereids of various types are present in some genera. Crystals are usually druses, sometimes styloids. The vascular bundles in midrib and petiole are almost always bicollateral and only in some genera enclosed by sclerenchyma. The petiole contains an arc composed of widely spaced vascular bundles, sometimes accompanied by accessory bundles. The Memecylaceae are leaf anatomically rather homogeneous in the absence of multicellular hairs, mainly paracytic stomata, a simple vascularisation pattern, and xylem with alternating layers of tracheary elements in the midrib and petiole. The Crypteroniaceae are leaf anatomically characterized by the absence of hairs, mainly paracytic stomata, druses and styloids, and a complex vascular pattern.

Leaf anatomy is used to discuss the (sub)families and tribal delimitation of the Melastomataceae alliance and modifications suggested by Van Vliet (1981) (subfamily Crypteronioideae) and Renner (1989a, c and 1992 in press and pers. communication). Leaf anatomy can support a family status of the Crypteroniaceae and also of the Memecylaceae. Within the Melastomataceae the Astronioideae (without *Pternandra*) are leaf anatomically so distinctive that they deserve a subfamily status. The phylogenetic affinities of *Pternandra*, which phenetically show an intermediate position between Astronioideae and Memecylaceae, remain at this stage unresolved. The Melastomatoideae are leaf anatomically very diverse and this heterogeneity does not lend support to the traditional classification into 12 tribes nor to alternative tribal classifications.

INTRODUCTION

The present study forms part of a project on the comparative vegetative anatomy of the Myrtales to result in a volume of the second edition of 'The Anatomy of the Dicotyledons' (eds. D.F. Cutler, M. Gregory, and W.C. Dickson).

For the Melastomataceae, Memecylaceae and Crypteroniaceae 179 species representing 151 genera were studied and together with data in the literature this material showed so much diversity that separate publication of the leaf anatomical survey of this family seems justified.

The Melastomataceae, a large mainly tropical family, consist of about 170 genera and at least 4550 species of trees, shrubs, herbs, lianas, and epiphytes. The species are represented in Africa, Asia, Australia and two thirds occur in America. The Memecylaceae consist of 6 genera with c. 430 species from Africa, Madagascar, Asia and America; the Crypteroniaceae, all trees, of 3 genera and 10 species from Asia. At various stages of their taxonomic history all three families have been incorporated in the Melastomataceae *sensu lato* (cf. Dahlgren & Thorne, 1984; Raven, 1984; Renner, 1992, in press; Van Vliet, 1981). Especially Memecylaceae have usually been considered to be a subfamily in the Melastomataceae. Below we will refer to this broad alliance as Melastomataceae *s.l.*

The most recent monograph of the family in the broad sense is by Cogniaux (1891) and forms the basis of nearly all subsequent work in the family. Three classical studies by Gottschall (1900), De Palézieux (1899) and Pflaum (1897) gave anatomical descriptions of the leaves of the Melastomataceae. Solereder (1899 and 1908) and Metcalfe & Chalk (1950) summarized the limited leaf anatomical data available. After 1950 Baumgratz (1980, 1989–1990), Baumgratz & Ferreira (1980, 1984), Hansen (1980, 1982, 1985a–d), Hansen & Wickens (1981), Jacques-Félix & Leuenberger (1980), Jacques-Félix et al. (1978), Judd (1986, 1989), Karatela & Gill (1988), Keating (1984), Maxwell (1980, 1982), Morley (1953, 1976, 1989), Nayar (1974), Renner (1989b), Todzia & Almeda (1991), Weber (1982), and Winkler (1964, 1965) studied a number of species of the Melastomataceae leaf anatomically. Wurdack (1986) made an extensive SEM survey of hairs of the neotropical taxa of the family and Feissly (1964) gave anatomical data of hairs of the calicinal tube of some African genera of the tribe Osbeckieae. Baas (1981) recorded data of stomatal types and cell inclusions in leaves. Klucking (1989) explored leaf venation patterns of the family. Almeda (1989), Brouwer & Clifford (1990), Costa (1977), Gregory (1990), Pemberton & Turner (1989), Schnell (1966, 1967) and Solereder (1920) investigated domatia. Rao (1957), Rao & Bhattacharya (1977), Rao & Dakshni (1963), Rao & Jacques-Félix (1978), Rao et al. (1980, 1983) published on foliar sclereids. Van Beusekom-Osinga & Van Beusekom (1975), Van Vliet (1975) and Van Vliet & Baas (1975) studied the morphology and anatomy of the Crypteroniaceae. A wood anatomical survey of the Melastomataceae *s.l.* has been given by Van Vliet (1981), Van Vliet et al. (1981) and Ter Welle & Koek-Noorman (1981).

Despite all these contributions our knowledge of the leaf anatomy of the Melastomataceae and Memecylaceae is very fragmentary. Previous anatomical studies on the Melastomataceae indicated conflicting evidence with respect to the classification into three subfamilies or families (Van Vliet, 1981; Baas, 1981). The traditional subdivision into Astronioideae, Memecyloideae and Melastomatoideae (Triana, 1865, 1871) has been challenged by several authors (Airy Shaw, 1973; Dahlgren in Dahlgren & Thorne, 1984; Johnson & Briggs, 1984; Klucking, 1989; Raven, 1984; Renner, 1989a, c and 1992, in press). Following Cogniaux (1891) the Astronioideae and the Memecyloideae are generally recognized as consisting of only one tribe each with mainly paleotropical distribution, while the Melastomatoideae consist of eleven tribes which mainly occur in tropical America and of which three tribes are exclusively paleotropical.

In this paper generic classification is based on Cogniaux (1891) with complements and modifications by Van Vliet (1981) and Renner (1989a, c, 1992, in press and pers. communication). Van Vliet (1981) proposed on the basis of wood anatomical characters the recognition of the following three subfamilies: Crypteronioideae, Memecyloideae (including *Pternandra*), and Melastomatoideae. For this reason the Crypteroniaceae are included in this study and in agreement with Van Vliet (1975, 1981) the Crypteroniaceae comprise the genera *Axinandra*, *Crypteronia*, and *Dactylocladus* only.

Renner (1989a, 1992, in press and pers. communication) gave an overview of the traditional tribal arrangement based on fruit, seed, and stamen characters. Renner stated that the tribes recognized by or known to Old and New World workers vary considerably. She noted that Gleason's (1929) neotropical Cyphostyleae (3 genera) are usually not known to Old World specialists and that Van Vliet's (1981) recognition of Pternandreae (incl. Kibessieae) as a tribe of the Memecyloideae and of Astromieae as a tribe of Melastomatoideae in turn is usually disregarded in the New World.

It is undesirable to base classifications on leaf anatomical characters only, but when interpreted carefully, leaf anatomy does have considerable systematic value, as Keating (1982) demonstrated for the Onagraceae, a family also belonging to the order Myrtales. Hopefully the present leaf anatomical study will contribute to our understanding of intrafamilial relationships. Although in general only one species per genus is studied, which is not enough for detailed generic descriptions, it must be realized that this survey of the Melastomataceae is the most extensive leaf anatomical one ever conducted with respect to the number of genera and species covered.

MATERIAL AND METHODS

Mature leaves from herbarium specimens were rehydrated by boiling in water. Transverse sections of the mid-portion from each lamina, including midrib and leaf margin, and of the petiole were prepared on a sledge microtome. Paradermal free hand sections were taken of the upper and lower leaf surface. Free hand sections and half of the transverse sections were bleached in household bleach and all sections were stained with a safranin-haematoxylin mixture (94:6).

Cuticular macerations were obtained after incubation of leaflet fragments overnight in a mixture of equal volumes of 30% hydrogen peroxide and glacial acetic acid and stained with Sudan IV. Leaf clearings of thin leaves were prepared in chloral-lactophenol enriched with hydrogen peroxide. The cuticular macerations were mounted in glycerin jelly and all others in euparal.

Many of the leaves [see genera marked with (s) in the list of specimens studied] were also studied with a Jeol JSM-35 scanning electron microscope (the lower leaf surface) after critical point drying of rehydrated herbarium material with dimethoxymethane and using a Polaron E 5100 series II sputter-coater.

Material for anatomical research was obtained from the Rijksherbarium in Leiden (L) and from several other herbaria (Utrecht, Wageningen and Århus). The specimens studied are listed below.

Acanthella sprucei Hook. f., Venezuela, Breteler 4890 — *Aciotis rostellata* (Naud.) Triana, Panama, Colon prov., Liesner 1095 — *Acisanthera alsinaefolia* (DC.) Triana var. *alsinaefolia*, Brazil, Santa Catarina, Klein 3678 — *Adelobotrys ciliata* Triana, French Guiana, Santini 2409 (s) — *Allomaieta grandiflora* Gleason, Colombia, Lawrance 487 — *Alloneuron ulei* Pilger, Peru, Loreto, Ule 6417 (s) — *Amphiblemma riparium* Gilg, Cameroon, Bipinde, Zenker 4860 — *Amphorocalyx multiflorus* Baker, Madagascar, Herb. de Ch. d'Alleizette s.n. (L) — *Anaetocalyx latifolia* Cogn., Venezuela, Steyermark 91552 — *Anerincleistus pauciflorus* Ridley, Malaya, Carrick 1520 — *Antherotoma naudinii* Hook. f., Transvaal, Codd 7896 — *Appendicularia thymifolia* DC., French Guiana, Cogniaux 242 — *Arthrostemma lanceolatum* Griseb., Central America, St. Kilts., Eggers 812 — *Astrocalyx calycina* (Vid.) Merr., Philippines, Ramos 23537 (s) — *Astronia spectabilis* Blume, Bali, Kostermans et al. 122 (s) — *Astronidium pallidum* Maxw. (type), Australia, Cowmeadow BSIP 3138 (s) — *Axinaea nitida* Cogn., California, Hutchinson & Wright 5590 — *Axinandra coriacea* Baillon, Borneo, Chew Wee Lek 1393 — *Barthea formosana* Hayata, Formosa, Mt. Taiheizan, Suzuki s.n. (L) (s) — *Beccarianthus spec.*, New Guinea, Pullen 583 (s) — *Behuria parvifolia* Cogn., Brazil, São Paulo, Markgraf & Brade 2/274 — *Bellucia acutata* Pilger, Brazil, Rio Madeira, Ule 6097 (s) — *Benevidesia organensis* Sald. & Cogn., Brazil, Rio de Goyas, Vincent 2406 (s) — *Bertolonia acuminata* Gardn. subsp. *paranensis* Wurdack, Brazil, Parana, Hatschbach 13190 — *Bisglaziovia behurioides* Cogn., Brazil, Rio de Janeiro, Glaziou 16821 — *Blakea trinervia* L., Jamaica, Mandeville, Lam 7968 (s) — *Blastus sumatranus* Merr., Sumatra, Padang Si Dimpoean, Rahmat 4803 — *Brachyotum rostratum* (Naud.) Triana (type), Peru, Dombey, Cogniaux 273 — *Bredia okinawensis* (Matsum.) Li, Okinawa, Japan, Walker et al. 77031 (s) — *Bredia oldhamii* Hook. f. (type), Taiwan, Mizushima & Liao 891 — *Brittenia subacaulis* Cogn., Borneo, Kapit dist., Anderson S 28851 (s) — *Bucquetia glutinosa* Triana, Colombia, San Cristobal, Pinael s.n. (L) (s) — *Calvoa monticola* A. Chev., Africa, Ivory Coast, De Bryant 2432 (s) — *Calycogonium apleura* (Urban & Ekman) Judd, Haiti, Ekman 2366 — *Calycogonium krugii* Cogn., Puerto Rico, Adjuntas, Sintenis 4435 (s) — *Cambessedesia pityrophylla* (Cham.) A.B. Martins, Brazil, Minas Gerais, Claussen s.n. (L) (s) — *Cambessedesia rugosa* Cogn., Brazil, Minas Gerais, Claussen 590 — *Campimia auriculata* (Ridley) Nayar, Sarawak, Long Kapa, Richards 1447 (s) — *Carionia elegans* Naud., Philippines, Luzon, Celestino 7952 (s) — *Castratella piloselloides* Naud., Colombia, Andes de Bogota, Apollinaire 6376 — *Catanthera spec.*, New Guinea, Van Royen & Sleumer 7633 — *Catocoryne linnaeoides* Hook. f., Colombia, Luteyn et al. 10585 — *Centradenia floribunda* Planch. (type), Cult. Hortus Leiden — *Centronia crassiramis* Triana, Brazil, Amazonas, Ule 8678 (s) — *Chaetolepis saturioides* (Griseb.) Triana, West India, Isla de Piños, Curtiss 459 (s) — *Chaetostoma fastigiatum* Naud., Brazil, Minas Gerais, Glaziou 1604s — *Charianthus corymbosus* Cogn., Martinique, Hahn 457 — *Cinnobotrys oreophila* Gilg, Zaire, Stauffer 10455 — *Clidemia hirta* (L.) D. Don, Malaya, Carrick 1417 — *Clidemia spec.* (*Calophysa retropila* Triana), Mexico, Hnitamalco 34 (s) — *Comolia neglecta* Cogn., French Guiana, Santini 2385 — *Conostegia subcrustulata* (Beurl.) Triana, Panama, Chiriqui, Liesner 217 (s) — *Creochiton diptera* Elmer, Philippines, Elmer 14119 (s) — *Crypteronia cuminghii* Blume, Philippines, Edaña PNH 37179 — *Cyanandrium spec.*, Sarawak, Paie S.41637 — *Cyphostyla strigosa* Gleason, Colombia, Lawrance 419 — *Dactylocladus stenostachys* Oliver, N Borneo, Anderson 8541 — *Desmoscelis villosa* (Aubl.) Naud. var. *fuscescens* Cogn., Surinam, Paramaribo, Samuels 437 — *Dicellandra barteri* J.D. Hook., Cameroon, Leeuwenberg 5589 (s) — *Dichaetanthera corymbosa* (Cogn.) Jacq.-Fél., Burundu, Ndora, Henri 254 — *Dichaetanthera lancifolia* H. Perrier (type), Madagascar, Lam & Meeuse 5866 (s) — *Dinophora spenneroides* Benth., Liberia, Van Harten 163 — *Dionycha bojerii* Naud., Madagascar, Ankazobe 7466 (s) — *Dionycha triangularis* Jum. & Perr., Madagascar, Herb. de Ch. d'Alleizette s.n. (L) — *Diplectria barbata* (C.B. Clarke) Fr. & Roos, Thailand, Geesink & Santisuk 5098 (s) — *Dissochaeta pallida* (Jack) Blume, Malaya, Maingay 793 (s) — *Dissotis pellegriniana* Boissieu, Thailand, Smitinand & Floto 6091 — *Dissotis senegambiensis* (G. & P.) Triana, Madagascar, Herb. de Ch. d'Alleizette s.n. (L) — *Driessenia axantha* Korth. (type), Borneo, Korthals s.n. (L) — *Dries-*

senia winkleri (Cogn.) Backer ex Bakh. f., Java, Bakhuizen van den Brink Jr 681 — *Ernestia glandulosa* Gleason, Guyana, Granville 7251 — *Fordiophyton fordii* (Oliv.) Krass., China, Kwangtung, K'ung 6216 — *Frittschia erecta* Cham. & Schl., Brazil, Minas Gerais, Cogniaux 285 (s) — *Graffenrieda latifolia* (Naud.) Triana, B. W. I., Dominica, W. & B. Hodge, Knowlton 3852 (s) — *Graffenrieda scandens* (Gleason) Wurdack (type), Colombia, Cuatrecasas 15807 (s) — *Graffenrieda spec.* (*Calyptrilla granatensis* Cogn.), Colombia, Santa Marta, Smith 3 (s) — *Gravesia laxiflora* (Naud.) Drake, Madagascar, Lam & Meeuse 6016 — *Gravesia lutea* (Naud.) H. Perrier, Madagascar, Em. & Beforma s.n. (L) (s) — *Guyonia intermedia* Cogn., Africa, Ivory Coast, De Bryant 2391 — *Henriettea spruceana* Cogn., Brazil, Ule 6049 (s) — *Henriettea fascicularis* (Sw.) Triana, Panama, Née 8488 — *Heterocentron elegans* Kuntze, Wisley, Gardens RHS, Cult, Boom 22305 — *Heterocentron subtripplinervium* A. Br. & Bouché, Hawaii, Fosberg 47738 — *Huberia glabrata* Cogn., Brazil, Glaziou 16815 — *Huilaia macrocarpa* L. Uribe, Colombia (type), Boyaca, Uribe 5439 (s) — *Itatiaia cleistopetala* Ule, Rio de Janeiro, Markgraf & Brade 21275 — *Kendrickia walkeri* (Wight & Gardn.) Triana, Ceylon, Nootboom & Huber 3124 (s) — *Killipia quadrangularis* Gleason, Colombia, Uribe U 6547 — *Lavoisiera pulcherrima* DC., Brazil, HLB 908.129-1727 (L) — *Leandra clidemioides* (Naud.) Wurdack, French Guiana, Santini 24080 — *Leandra cuneata* (Mart.) Cogn., Brazil, Martius 496 (s) — *Leandra fragilis* Cogn., Brazil, Hatschbach 20191 — *Lijndenia capitellata* (Arn.) Bremer, Ceylon, Kostermans 27139 — *Lithobium cordatum* Bong., Brazil, Minas Gerais, Irwin et al. 22887 — *Llewelynina williamsii* Pittier, Venezuela, Williams & Alston 151 (s) — *Loreya nigricans* Triana, Brazil, Amazonas, Ule 5344 (s) — *Loricalepis duckei* Brade, Rio de Janeiro, Ducke 35068 (s) — *Macairea theresiae* Cogn., Brazil, Amazonas, Ule 6153 — *Macrocentrum cristatum* Triana, French Guiana, Cogniaux 280 (s) — *Macrolenes nemorosa* (Jack) Bakh. f., Sumatra, Rahmat si Toroes 3287 — *Maieta guianensis* Aublet, Peru, Loreto, Croat 18391 (s) — *Mallophyton chimantense* Wurdack (type), Venezuela, Steyermark & Wurdack 766 (s) — *Marcetia taxifolia* DC., Brazil, Amazonas, Ule 8675 — *Mecranium amygdalinum* (Descr.) C. Wright, Jamaica, Proctor 26755 — *Medinilla cauliflora* Hemsley, Solomon Islands, BSIP 8871 — *Medinilla mirabile* (Gilg) Jacq.-Fél., Cameroon, Bos 6744 — *Medinilla spec.*, Central Sumatra, Meijer 195 (s) — *Melastoma polyanthum* Blume, Borneo, Kadir & Kambatan A 3560 — *Memecylon beccariana* Cogn., N Borneo, SAN 22217 — *Meriania paniculata* Triana, Brazil, Rio de Janeiro, Vincent 2410 (s) — *Miconia bailloniana* Macbr., Peru, Loreto, Ule 6741 (s) — *Miconia mirabilis* (Aublet) L. Williams., Suriname, Den Outer 974 (s) — *Miconia theaezans* Cogn., Paraguay, Pedersen 9288 (s) — *Miconia tuberculata* (Naud.) Triana, Venezuela, Breteler 4107 — *Microlepis oleaefolia* (DC.) Triana, Brazil, Parana, Hatschbach 18803 — *Microlicia euphorbioides* Mart., Brazil, Minas Gerais, Glaziou 16776 (s) — *Monochaetum lineatum* (D. Don) Naud., Colombia, Sibundoy, Bristol 310 — *Monolena spec.*, Panama, Kennedy et al. 2407 — *Mouriri grandiflora* DC., Brazil, HLB 908.132-631 (L) — *Myriaspora egensis* DC., Brazil, Burchell 347 — *Myrmidone macrosperma* Mart., Brazil, Amazonas, Ule 8942 (s) — *Myrmidone macrosperma* (Mart.) Mart. (*Hormocalyx hirsutus* Gleason), Brazil, Amazonas, Krukoff 7098 — *Neblinantha cumbrensis* Wurdack, Venezuela, Née 31126 — *Neodriessenia tectiflora* C. Hansen (type), Borneo, Sarawak, Ilias Paie S 19955 (s) — *Nepsera aquatica* (Aublet) Naud., Trinidad, Van Steenis 20312 — *Nerophila gentianoides* Naud., Africa, Gabon, Courtet 2390 — *Ochthocharis bornensis* Blume (type), Borneo, Korthals s.n. (L) (s) — *Ochthocharis dicellandroides* (Gilg) Hansen & Wick., Cameroon, Yaninde, Zenker 1418 (s) — *Omphalopus fallax* (Jack) Naud., Sumatra, Van Borssum Waalkes 1532 — *Opisthocentra clidemioides* Hook. f., Venezuela, Amazonas, Wessels Boer 2287 — *Osbeckia chrysophylla* (DC.) H. Perrier, Madagascar, Herb. de Ch. d'Alleizette (s) — *Osbeckia gracilis* Bedd., Kerala, Kramer & Nair 6297 — *Ossaea micrantha* (Sw.) Macf., Panama, Croat 22988 (s) — *Ossaea quinquenervia* (Mill.) Cogn., Panama, Chiriqui, Liesner 392 (s) — *Otanthera bracteata* Korth., Australia, N Johnstone, Irvine 1299 (s) — *Oxyspora microflora* Maxw., Sarawak, Chai S 39480 — *Oxyspora spec.*, Borneo, Nootboom & Chai 2237 — *Oxyspora sublepidota* (King) Maxw., Malaysia, Pahang, Maxwell 78-138 — *Pachyanthus urbanianus* Cogn., Santo Do-

mingo, Turckheim 3146 (s) — *Pachycentria constricta* (Blume) Blume, Malaya, Mandi, Whitmore 12064 (s) — *Phainantha laxiflora* (Triana) Gleason, Venezuela, Steyermark 89424 — *Phyllagathis tuberculata* King, Malaya, Pahang, Stone 13779 — *Pleiochiton glaziovianum* Cogn., Brazil, Parana, Hatschbach 8943 — *Plethiandra hookeri* Stapf, Borneo, RSNB 1059 & 4950 — *Pogonanthera pulverulenta* (Jack) Blume, Malaya, Perak, Whitmore 3010 (s) — *Poikilogyne diastematica* Maxw. (type), Papua, Carr 15101 — *Preussiella kamerunensis* Gilg, Cameroon, Hall 46989 — *Pseudodissochaeta septentrionalis* (W.W. Smith) Nayar, Thailand, Van Beusekom et al. 1761 — *Pternandra echinata* Jack, Malaya, H.M. Burkill 1033 (s) — *Pterogastra divaricata* Naud., Colombia, Guyana, Schomburgk 721 — *Pterolepis glomerata* (Rottb.) Miq., Brazil, Paranagua, Pedersen 7777 — *Purplella grossa* L. f., Colombia, Schultes 18745 — *Rhexia nashii* Small, Florida, Ray Jr 11059 (s) — *Rhynchanthera brachyrhyncha* Cham., Brazil, Monte Christa, Reitz & Klein 10452 — *Sagraea sessiliflora* Triana, Venezuela, Korthals s.n. (L) — *Salpinga secunda* Schr. & Mart. ex DC., Brazil, Amazonas, Prance & Pennington s.n. (U) (s) — *Sandemania hoehnei* (Cogn.) Wurdack, Brazil, Amazonas, Renner 954 (s) — *Sarcopyramis napalensis* Wall., Sumatra, De Wilde et al. 14239 — *Schwackaea cupheoides* Cogn., Colombia, Smith 772 — *Scorpiothyrus spec.*, Borneo, Brooke 8995 (s) — *Siphanthera fasciculata* (Gleason) Almeda, Colombia, Maguire et al. 36278 (s) — *Siphanthera paludosa* Cogn. var. *glabrata* Br., Brazil, Langstriff s.n. (L) (s) — *Sonerila crassicaulis* Lundin (type), Ceylon, Robyns 7168 — *Stenodon suberosus* Naud., Brazil, Rio Corumba, Hatschbach 38804 — *Svitramia pulchra* Cham., Brazil, Minas Gerais, Glaziou 16820 — *Tateanthus duidae* Gleason, Venezuela, Steyermark et al. 109259 — *Tessmannianthus heterostemon* Markgraf, Ecuador, Pastaza, Lőjtnant & Molau 13514 (s) — *Tetrazygia bicolor* (Mill.) Cogn., Miami, Boom 38594 (s) — *Tibouchina pauciflora* Cogn., Brazil, Parana, Hatschbach 18058 — *Tibouchinopsis mirabilis* Brade & Markgraf, Morro do Chapau, Bahia, Hatschbach 44242 — *Tococa guianensis* Aublet, Peru, Loreto, Croat 19841 — *Topobea urophylla* Standley, Panama, Liesner 1257 (s) — *Trembleya neopyrenaica* Naud., Brazil, Est. de Goias, Anderson 10439 — *Triolena amazonica* (Pilger) Wurdack, Brazil, Amazonas, Ule 5826 (s) — *Triolena hirsuta* (Benth.) Triana, Panama, Liesner 1354 (s) — *Tristemma coronatum* Benth., Liberia, Van Harten 157 — *Votomita guianensis* Aubl., French Guiana, Billiet & Jadin 1072 — *Warneckea bebaiensis* (Gilg ex Engl.), Gabon, Breteler & De Wilde 171 — *Warneckea cinnamomoides* (D. Don) Jacq.-Fél., Liberia, Jansen 1658.

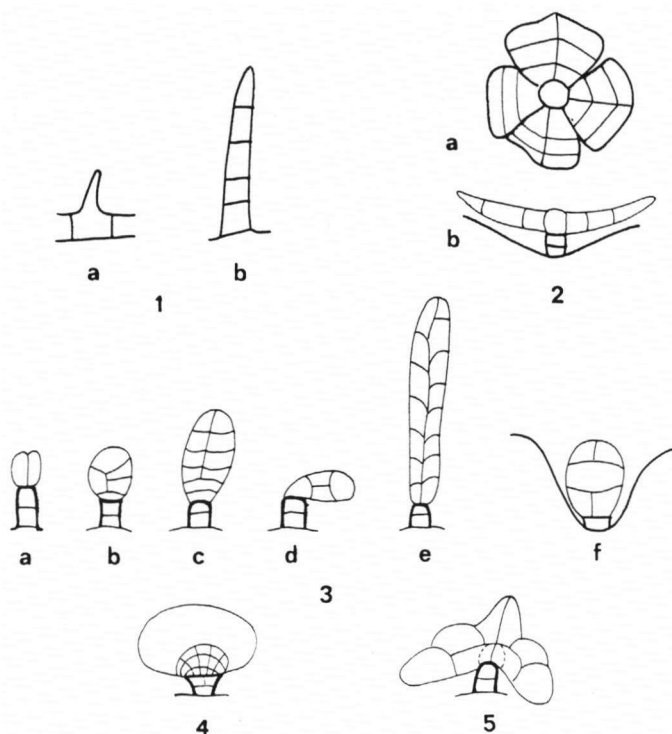
Survey of the leaf anatomical characters (with comments on their diagnostic and systematic significance)

Most descriptive data are given in Table 1 A & B. The range of leaf anatomical diversity is described and discussed below.

Indumentum (Table 1A)

In the Melastomataceae an unusual diversity of hair types is present, varying from simple unicellular hairs to very complex multicellular, non-glandular or glandular trichomes. In the material studied glabrous leaves only occur in *Acanthella*, the Memeceylaceae (except *Votomita*) and the Crypteroniaceae; however, species of a number of unrelated genera, e.g. some species of *Charianthus*, *Conostegia*, *Graffenrieda*, *Miconia* and *Tococa* may also be glabrous.

Hairs mostly occur as multiseriate non-glandular hairs and short-stalked glandular trichomes. Simple hair types are comparatively rare, while complex types occur frequently. Complex trichomes are often branched or have a special kind of hair base. A great diversity of intermediate hair types is recorded and these exceptional types of trichomes cannot be satisfactorily placed in any of the recognized categories of hair



Figs. 1–5. Hair types of the Melastomataceae (semi-diagrammatic); 1a: unicellular non-glandular hair; b: uniseriate non-glandular hair; 2a: non-glandular peltate scale in surface view; b: ditto in transverse section; 3a–f: short-stalked glandular hairs; 4: bladder-like glandular hair; 5: glandular scale.

types. It is not always feasible to make a clear distinction between non-glandular and glandular trichomes. Some types of hairs occur both with and without glandular heads.

Thus no entirely satisfactory classification of trichomes can be constructed for the Melastomataceae, and the one given below is therefore partly artificial.

1 — *Unicellular or uniseriate non-glandular hairs* (Fig. 1; Photo 1)

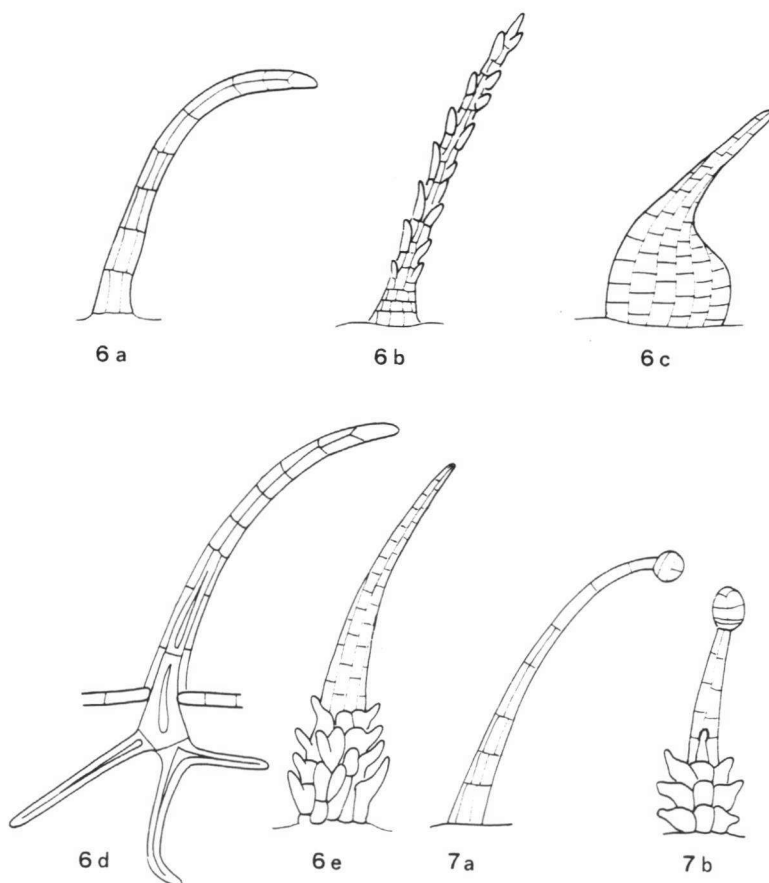
Unicellular hairs resembling papillae occur in *Macairea*, *Sandemania* and *Votomita*. Uniseriate hairs, with a length varying between 25–400 μm , are present in *Acisanthera*, *Bellucia*, *Neblinantha*, *Pternandra* and *Sandemania*.

2 — *Non-glandular peltate scales* (Fig. 2)

Peltate scales may vary from sessile to short-stalked. They occur frequently in sunken areas in the genus *Axinaea* and the tribe *Astronieae*. Sometimes the scales show appendices and have an irregular outline.

3 — *Sessile or short-stalked glandular hairs* (Fig. 3; Photo 2)

Short-stalked glands occur with various shapes of heads, for example globular, elliptic, elongate and intermediate forms. The head is always multicellular. Stalks



Figs. 6 & 7. Hair types of the Melastomataceae (semi-diagrammatic); 6: multiseriate unbranched non-glandular hair; a: smooth; b: with cellular protrusions; c: with swollen base; d: with root-like base embedded in the mesophyll; e: with cellular protrusions on its base; 7: multiseriate unbranched glandular hair; a: with smooth stalk; b: with cellular protrusions on its base.

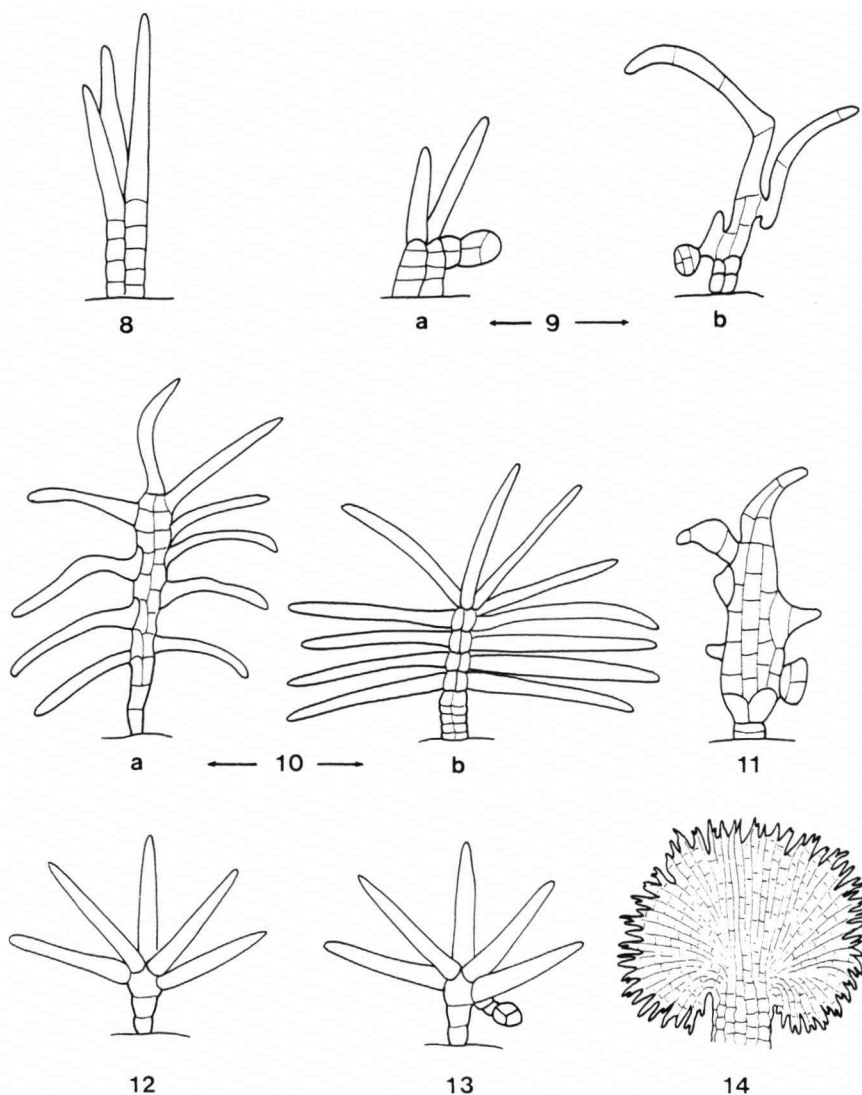
may be uni- or biseriate, rarely multiseriate. Generally the stalks are two cells long. Sometimes there are appendices present on the heads, rarely on the stalks. Most glands are erect, but bent stalks also occur.

Short-stalked glands are present in nearly all tribes except in Astronieae and Pternandreae (= Kibessieae). They are also absent from the Crypteroniaceae and Memecylaceae.

Sessile glandular hairs look like short-stalked glands, but the stalk is absent. They occur mostly in sunken areas.

4 — Bladder-like glandular hairs (Fig. 4; Photo 3)

Glands with bladder-like heads, sessile or stalked, occur mainly in the tribes Microlicieae and Oxysporeae. They resemble the glandular hairs of the Labiatae.



Figs. 8–14. Hair types of the Melastomataceae (semi-diagrammatic); 8: few-armed non-glandular hair; 9a, b: few-armed glandular hairs; 10a, b: complex multiserial branched non-glandular hairs; 11: complex multiserial branched glandular hair; 12: stellate non-glandular hair; 13: stellate glandular hair; 14: single-tiered multiserial non-glandular scale.

5 — Glandular scales (Fig. 5; Photo 4)

These are short-stalked trichomes with a multicellular, glandular shield. Sometimes they show gradations to globular short-stalked glands. Appendices may occur on the shield and cause irregularities of form of the scale. Glandular scales are present in the tribe Merianieae.

6 & 7 — *Multiseriate unbranched non-glandular or glandular hairs* (Figs. 6, 7; Photos 5–9)

- 6) Multiseriate unbranched non-glandular hairs generally vary in length between 750–1000 μm . Short multiseriate hairs (250 μm) are sometimes present and very long ones (4000 μm) occur in *Clidemia spec.*

Some hairs are smooth, others have cellular protrusions approaching papillae (Fig. 6b).

The hair base may be swollen, have a smooth to papillate surface, or have an elongate root-like base. Hairs with a raised, swollen, conical base have been reported by Wurdack (1986) as bulla-based hairs. Sometimes the hair base has cellular protrusions and shows gradations to branched hair types. The elongate root-like base of some hairs is embedded in the mesophyll, mostly vertically or horizontally extended as a prolongation of the hair, and often branched.

Many trichomes are sclerenchymatous and a few have a vascular strand, generally present in the root-like base.

Druses (see crystals) are sometimes present in the elongate root-like bases, mostly in the tribe Osbeckieae.

Combinations of many of the above-mentioned features are possible.

Some genera show intermediate hair types, especially when protrusions along the surface of multiseriate hairs intergrade for example with branched hairs consisting of a long axis and short arms.

The shape of the multiseriate hairs is mostly elongate with a fairly blunt tip. Vermiform multiseriate hairs are sometimes present. Conical shapes also occur, varying from short- to long-conical.

Multiseriate hairs may be surrounded by clusters of short-stalked glandular trichomes. *Sandermania* possesses multiseriate non-glandular hairs with short-stalked glands and short unicellular non-glandular hairs on the surface of the hair base.

- 7) Sometimes multiseriate hairs occur with glandular heads and long stalks (Fig. 7). The glandular heads are mostly small, globular, and multicellular. Intermediate types between short- and long-stalked glands occur frequently and elongate stalks are sometimes present (2500 μm long in *Myrmidone*).

Two glandular heads seldom occur on one stalk. Protrusions are rarely found on the stalk.

Multiseriate unbranched hairs, non-glandular or glandular, are present in nearly all tribes except in Astronieae, Blakeae and Pternandreae. They are also absent from the Crypteroniaceae and Memecylaceae.

8–11 — *Multiseriate branched non-glandular or glandular hairs* (Figs. 8–11; Photos 10–15)

- 8) Few-armed hairs possess a uniseriate or multiseriate axis with mostly 2–5 arms (Fig. 8). The arms may also be branched. The hair shape sometimes approaches that of stellate and more complex branched types.

- 9) Few-armed hairs may be present with a glandular head (Fig. 9).
A special form is the lateral gland (Wurdack, 1986): the stalk is knee-shaped with a glandular head and one or more finger-shaped protrusions are often found on the outer bend of the stalk (Fig. 9a). This type is restricted to Miconieae and according to Wurdack (1986) also occurs in Blakeeae.
- 10) Complex multiseriate branched hairs display a great variety of features (Fig. 10). The axis may vary from short to long, from narrow to broad (uni- to multiseriate). The arms may vary from short to long, from few to many, and may be branched or not. Arms are generally inserted all along the trichome axis, but sometimes they are lacking on the base. Combinations of these different features occur frequently.
Many genera show gradations from branched hairs to other trichome types such as unbranched multiseriate hairs and stellate hairs. These intermediate types of trichomes cannot be satisfactorily classified.
- 11) Complex branched hairs sometimes have a multicellular glandular head (Fig. 11). In that case generally one (exceptionally two or more) of the arms possesses a glandular, mostly multicellular head. The arm with the gland may vary from short to long and this arm can be placed anywhere on the trichome axis. Sessile multicellular glandular heads also occur.
Complex branched hairs (non-glandular or glandular) are mostly present in the tribes Blakeeae and Miconieae and are totally absent from Astronieae, Bertoniaceae, Pternandreae, Rhexieae, the Crypteroniaceae and Memecylaceae.
- 12 & 13 — *Stellate non-glandular or glandular hairs* (Figs. 12, 13; Photo 16)
 - 12) Stellate hairs are star-shaped and may be sessile or stalked, with short to long arms.
 - 13) Sometimes one of the arms of the stellate hairs bears a multicellular glandular head. Intermediate types with other hair groups may be present. The stellate hair type occurs mostly in the tribe Miconieae.
- 14 — *Multiseriate non-glandular scales* (Fig. 14; Photos 17, 18)
Single-tiered, multiseriate, non-glandular scales with a lateral base and with the radii fused for 2/3 to their complete length are present in *Loricalepis* (Photo 17).
Several-tiered, multiseriate, non-glandular, stalked scales with the radii fused for about half their length occur in the genera *Calycogonium* (*apleura*) and *Tetrazygia*.
Scale-like, multiseriate, non-glandular, flattened, and laterally attached trichomes occur in the genera *Chaetolepis* and *Dichaetanthera* (*lancifolia*) (Photo 18).

Species often possess more than one type of trichomes; especially in the tribe Miconieae several types are commonly found together.

The great diversity of types of hairs within the Melastomataceae offers a powerful diagnostic tool at the species level (cf. Jacques-Félix & Leuenberger, 1980; Renner,

1989b; Wurdack, 1986). At the generic level and above their value seems very restricted (Renner, 1989b and pers. communication). Yet the presence or absence of some kinds of hairs in certain tribes is of taxonomic interest. In the Melastomataceae complex branched hairs (without or with glandular heads) are present mostly in the tribes Blakeeae and Miconieae and stellate trichomes (glandular or not) in the Miconieae. Non-glandular peltate scales occur in the Astronieae and glandular scales in the Merianieae. The most common hair types (multiseriate unbranched non-glandular hairs and short-stalked glandular trichomes) are absent from the tribes Astronieae and Pternandreae. They are also absent from the Crypteroniaceae and Memecylaceae.

Distribution of hairs

Hairs are present on the upper and lower surface of the leaf and the petiole, but generally more abundant on the lower surface.

Leaves with hairs restricted to the abaxial surface occur in a number of genera. The exceptional kinds of intermediate trichomes with irregular shapes and, for example, branched hairs with broad well-developed axis and short arms, are mostly present in the axils of lateral veins.

Multiseriate unbranched non-glandular hairs are often inserted on the leaf margin.

Cuticle

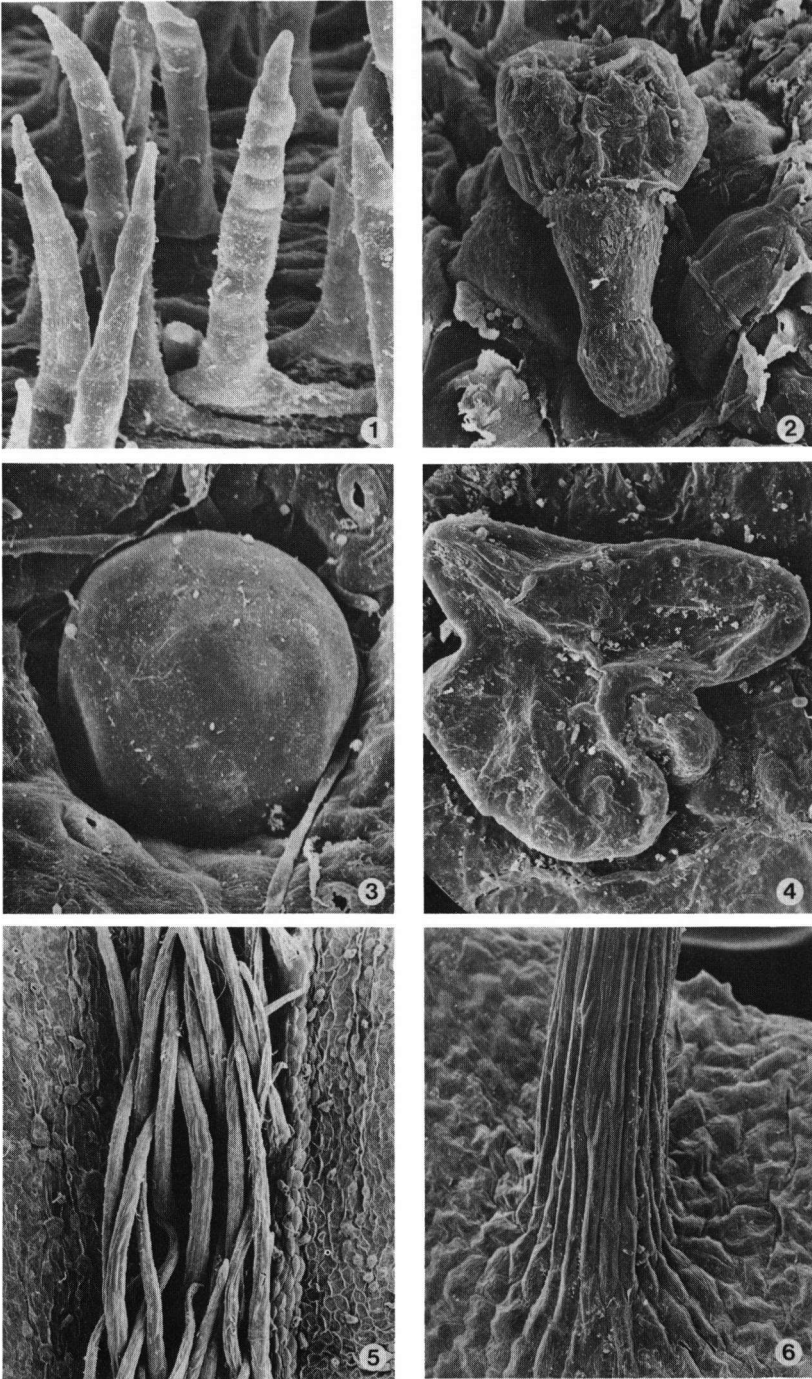
The cuticle may be smooth, but cuticular striations occur frequently, especially near stomata and hair bases.

Legends to Photos 1–18:

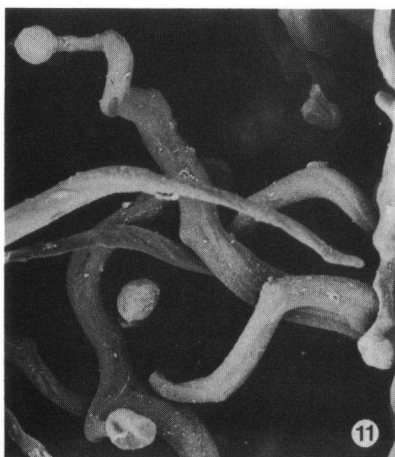
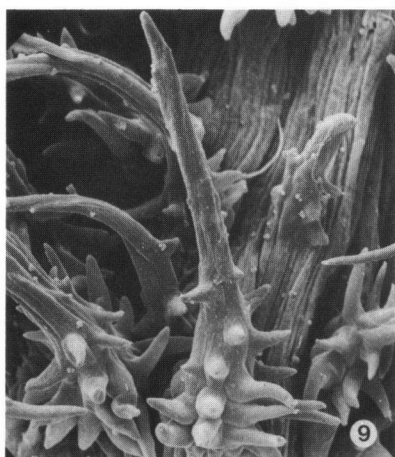
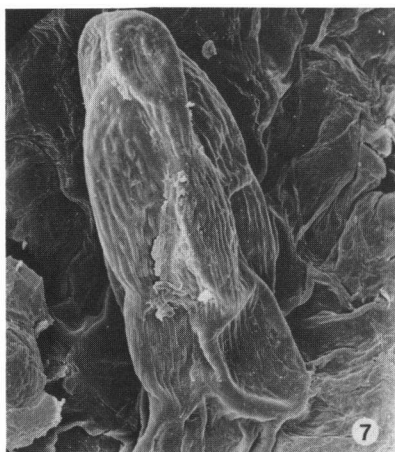
Photos 1–6. Scanning electron micrographs of foliar hairs of the Melastomataceae. – 1. *Pternandra echinata*. Uniseriate non-glandular hairs; $\times 305$. – 2. *Kendrickia walkeri*. Short-stalked glandular hair; $\times 750$. – 3. *Microlicia euphorbioides*. Bladder-like glandular hair; $\times 800$. – 4. *Graffenrieda latifolia*. Glandular scale; $\times 800$. – 5. *Pachycentria constricta*. Multiseriate unbranched non-glandular hairs; $\times 55$. – 6. *Myrmidone macrosperma*. Base of multiseriate unbranched non-glandular hair; $\times 235$.

Photos 7–12. Scanning electron micrographs of foliar hairs of the Melastomataceae. – 7. *Macrocentrum cristatum*. Conical multiseriate unbranched non-glandular hair; $\times 550$. – 8. *Calycogonium krugii*. Multiseriate unbranched non-glandular hair with swollen base; $\times 120$. – 9. *Dionycha bojerii*. Multiseriate unbranched non-glandular hair with protrusions; $\times 265$. – 10. *Myrmidone macrosperma*. Multiseriate branched glandular hair; $\times 450$. – 11. *Mallophyton chimantense*. Multiseriate branched glandular hairs; $\times 200$. – 12. *Dissochaeta pallida*. Complex multiseriate branched non-glandular hair; $\times 365$.

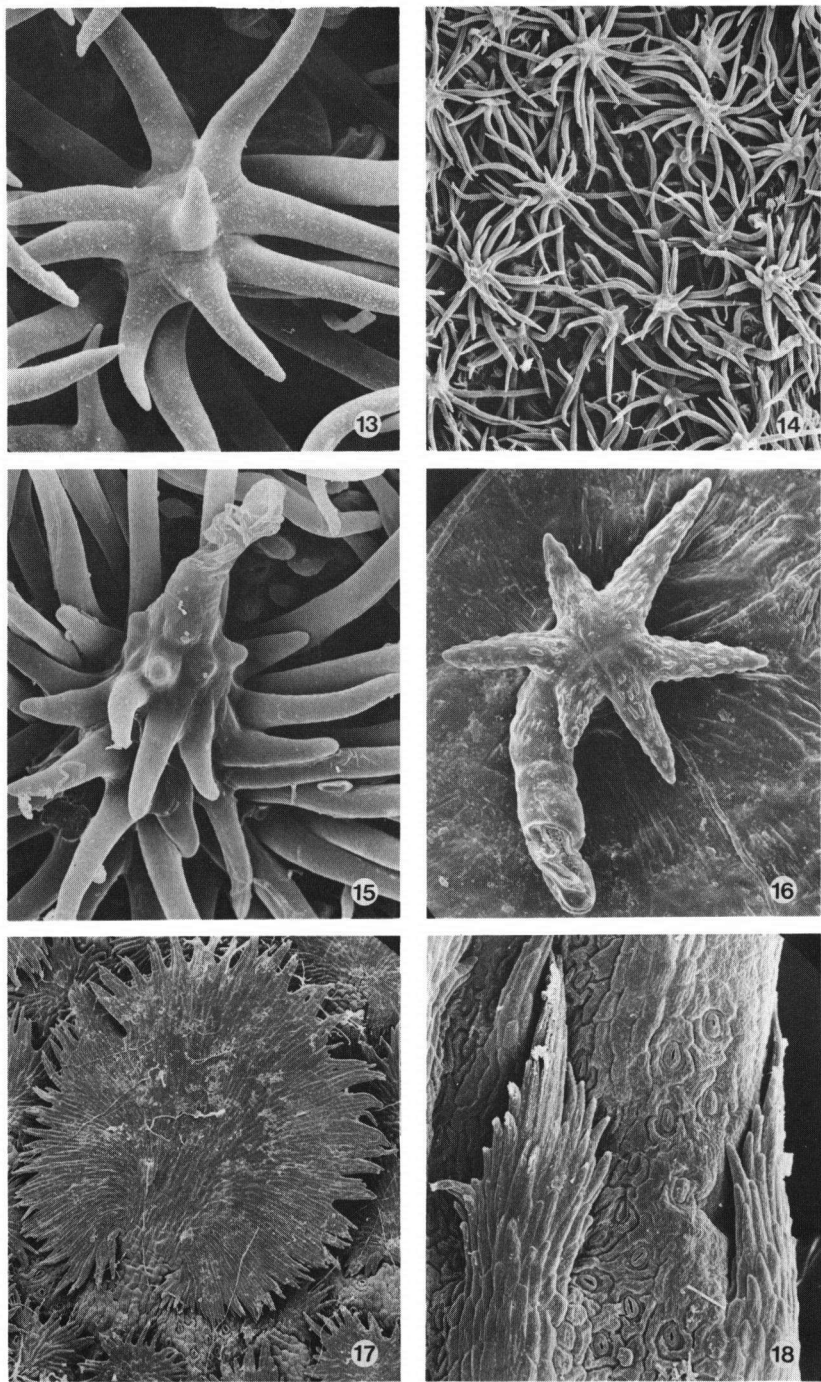
Photos 13–18. Scanning electron micrographs of foliar hairs of the Melastomataceae. – 13. *Miconia mirabilis*. Detail of complex multiseriate branched non-glandular hair; $\times 950$. – 14. *Miconia mirabilis*. Complex multiseriate branched non-glandular hairs; $\times 165$. – 15. *Henriettea spruceana*. Complex multiseriate branched glandular hair; $\times 700$. – 16. *Leandra cuneata*. Stellate glandular hair; $\times 800$. – 17. *Loricalepis duckei*. Multiseriate non-glandular scale; $\times 105$. – 18. *Chaetolepis saturioides*. Scale-like multiseriate non-glandular trichome; $\times 225$.



Photos 1–6. For legend, see page 200.



Photos 7–12. For legend, see page 200.



Photos 13–18. For legend, see page 200.

Table 1.

A: Indumentum of genera of the Melastomataceae s.l. — B: Some leaf anatomical characters of genera of the Melastomataceae s.l.
A & B both arranged alphabetically by tribe or subfamily.

Legends: + = present, - = absent, ± = few, ++ = many, • = character state unknown, 0 = sessile leaf.

A		B	
Column		Column	
1 =	unicellular or uniseriate non-glandular hairs (Fig. 1)	15 =	diacytic stomata
2 =	non-glandular pellate scales (Fig. 2)	16 =	polocytic stomata
3 =	sessile or short-stalked glandular hairs (Fig. 3)	17 =	tetracytic stomata
4 =	bladder-like glandular hairs (Fig. 4)	18 =	anomocytic stomata: ± = few or intermediate type
5 =	glandular scales (Fig. 5)	19 =	anisocytic stomata
6 =	multiseriate unbranched non-glandular hairs (Fig. 6)	20 =	paracytic stomata
7 =	multiseriate unbranched glandular hairs (Fig. 7)	21 =	cyclocytic stomata: ± = few or intermediate type
8 =	few-armed non-glandular hairs (Fig. 8)	22 =	number of cell layers of adaxial hypodermis
9 =	few-armed glandular hairs (Fig. 9)	23 =	adaxial local hypodermis
10 =	complex multiseriate branched non-glandular hairs (Fig. 10)	24 =	domatia: b = bladder-domatium, p = pocket-domatium, ± = tending to pocket-domatium
11 =	complex multiseriate branched glandular hairs (Fig. 11)	25 =	druses
12 =	stellate non-glandular hairs (Fig. 12)	26 =	styloids
13 =	stellate glandular hairs (Fig. 13)	27 =	sclereids in midrib
14 =	multiseriate non-glandular scales (Fig. 14)	28 =	sclereids in petiole
		29 =	sclereids in mesophyll
		30 =	midvein: so = simple open, sc = simple closed, co = complex open, cc = complex closed
		31 =	petiole: so = simple open, sc = simple closed, co = complex open, cc = complex closed
		32 =	sclerenchyma around midrib vascular system: - = absent, + = ring of sclerenchyma fibres, ± = few sclerenchyma fibres
		33 =	sclerenchyma around petiole vascular system: - = absent, + = ring of sclerenchyma fibres, ± = few sclerenchyma fibres

(Table 1 continued)

Column	A: 1	2	3	4	5	6	7	8	9	10	11	12	13	14	B: 15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33		
(Merianaeae contd)																																			
<i>Bucquetia</i>	-	-	-	±	-	-	-	-	-	-	-	-	-	-	-	+	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•		
<i>Centronia</i>	-	-	-	-	-	+	-	-	-	+	-	-	-	-	-	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
<i>Graffenrieda l.</i>	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	+	±	+	-	-	±	-	+	-	-	-	-	-	-	-	-	-	-	-	
<i>Graffenrieda sc.</i>	-	-	-	-	+	-	-	-	-	-	+	-	-	-	-	+	±	±	-	-	±	-	+	-	-	-	-	-	-	-	-	-	-	-	
<i>Graffenrieda sp.</i>	-	-	+	-	-	-	-	-	-	-	-	+	-	-	-	-	±	±	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Huberia</i>	-	-	+	+	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Meriania</i>	-	-	+	-	-	-	+	+	-	+	-	-	-	-	-	±	+	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Nebelinanthera</i>	+	-	+	-	-	+	+	-	-	-	-	-	-	-	-	±	±	±	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Opisthocentra</i>	-	+	-	-	-	+	-	-	-	-	-	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Phaianantha</i>	-	+	-	-	-	+	±	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Tessmannianthus</i>	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	±	±	+	-	+	-	-	4	-	-	-	-	-	-	-	-	-	-	-	
Miconieae																																			
<i>Anaectocalyx</i>	-	-	+	-	-	+	+	-	±	-	-	-	-	-	-	+	+	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	
<i>Bellucia</i>	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
<i>Calycegonium a.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	+	-	+	-	1	-	+	-	+	-	+	+	-	-	-	-	-	-	
<i>Calycegonium k.</i>	-	-	+	-	-	+	-	+	-	-	-	-	-	-	-	±	±	+	-	-	-	1-3	+	-	+	-	+	+	-	-	-	-	-	-	
<i>Catocoryne</i>	-	+	-	-	-	-	+	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Charianthus</i>	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	+	+	+	-	-	-	2	-	+	-	+	-	+	-	-	-	-	-	-	-
<i>Clidemia h.</i>	-	-	+	-	+	+	+	-	+	-	-	-	-	-	-	±	±	±	±	-	-	-	-	+	-	+	-	+	-	-	-	-	-	-	-
<i>Clidemia sp.</i>	-	-	+	-	-	+	±	-	-	±	-	-	-	-	-	+	+	±	-	-	-	-	-	±	-	+	-	+	-	-	-	-	-	-	-
<i>Conostegia</i>	-	-	+	-	+	+	+	-	++	+	-	-	-	-	-	+	+	±	-	-	-	-	-	-	+	+	+	+	-	-	-	-	-	-	-
<i>Henriettea</i>	-	-	+	-	-	-	+	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	2-3	-	-	-	+	-	-	-	-	-	-	-	-
<i>Henrietteella</i>	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	+	+	+	-	-	1	-	-	-	+	-	-	-	-	-	-	-	-	-
<i>Huilaea</i>	-	-	+	-	-	-	-	-	+	+	-	-	-	-	-	-	+	±	-	+	-	3	-	-	-	+	-	+	-	-	-	-	-	-	-
<i>Killipia</i>	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	±	±	+	-	-	2	-	-	+	-	+	+	-	-	-	-	-	-	-
<i>Leandra cl.</i>	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	+	+	±	-	-	-	-	+	-	+	-	+	+	-	-	-	-	-	-	-
<i>Leandra cu.</i>	-	-	+	-	-	-	-	-	±	-	-	-	+	-	-	+	+	±	-	-	-	-	+	-	+	-	+	-	-	-	-	-	-	-	-
<i>Leandra f.</i>	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	-	+	±	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-
<i>Llewelynina</i>	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-	±	±	+	+	-	-	2	+	-	-	+	-	+	-	-	-	-	-	-	-

Epidermal cells

The unspecialized epidermal cells show generally the whole range from straight to undulating anticlinal walls, varying with the species. Straight walls are common on the adaxial surface and undulating walls dominate in the abaxial epidermis.

Dome-shaped and papillate cells are sometimes present on both surfaces.

The stomatal complex (Table 1B)

Dia-, polo-, tetra- (Metcalf, 1961, 1963), anomo-, aniso-, para- (Wilkinson, 1979) and cyclocytic stomata (Stace, 1963, 1965) are all represented in the Melastomataceae alliance. Intermediate types seldom occur (anomo-cyclocytic in *Axinaea*, *Pternandra* and *Trembleya*). One specimen usually possesses several kinds of stomata.

Nearly all types of stomata occur in each tribe, only the Crypteroniaceae and Pternandreae lack stomata of the polo-, dia-, and tetracytic types. In the subfamily Melastomatoideae, although heterogeneous for stomatal types, there is a tendency for polo-, dia-, and tetracytic types of stomata to predominate, and for paracytic and cyclocytic stomata to be absent.

Stomata usually occur on the lower epidermis, but also on the upper surface in a few genera, mainly in the tribe Osbeckieae. In view of the limited occurrence of adaxial stomata in different tribes the systematic value is restricted.

The stomata are generally superficial. *Mouriri* is a notable exception with stomata both in special crypts and flush with the lamina surface.

Stomatal size mostly varies between 15–20 μm in length and 10–14 μm in width. Small stomata (up to 15 μm long) and giant stomata ($\geq 30 \mu\text{m}$) are sometimes present.

Outer cuticular ledges are present in nearly all genera. Inner cuticular ledges are inconspicuous or absent.

Hypodermis (Table 1B)

A continuous adaxial hypodermis of 1–3 layers, sometimes sclerenchymatous, or a local hypodermis over midrib and veins are present in the Crypteroniaceae (*Axinandra* and *Crypteronia*), the Memecylaceae (*Mouriri*), and in several genera in different tribes of the Melastomataceae. A local abaxial hypodermis in addition to an adaxial hypodermis occurs in *Calycogonium krugii*.

A hypodermis with mucilaginous cells is present in *Mouriri*.

Domatia (Table 1B)

Large bladder-like domatia with two compartments occur in *Allomaieta*, *Maieta*, *Myrmidone* and *Tococa*. The bladders are found on the leaf base of the adaxial surface with the opening abaxially situated. Metcalf & Chalk (1950) recorded such bladders as ant-domatia in *Myrmidone* and *Tococa*. Pocket-domatia (cf. Jacobs, 1966) are present in *Arthrostemma*, *Comolia*, *Mallophyton*, *Osbeckia chrysophylla*, *Pogonanthera*, *Sandemanina* and *Trembleya*. Pockets occur at the leaf base of the lower surface, connecting subparallel longitudinal veins and midrib. The front is open. When the roof which connects the veins in the axil is very small, this has been recorded as 'a tendency' for pocket-domatia. This has been noted in *Cambessedesia rugosa*, *Clidemia spec.*, *Neodriessenia* and *Purpurella*.

Additional records of occurrence of domatia mentioned in the literature are in *Blakea*, *Dissochaeta*, *Dissotis*, *Miconia*, *Ossaea* and *Sakersia* (= *Dichaetanthera*).

According to Gregory (1990) care should be exercised in using domatia as diagnostic characters because, although in many species they may be constantly present, in others they may be rare or restricted to a part of their range.

Mesophyll

The Melastomataceae alliance generally has dorsiventral mesophyll. The palisade tissue consists of 1 to 3 adaxial layers and the spongy zone varies from 2 to 20 cell layers. An intermediate type of adaxial palisade-like parenchyma as a transition to the spongy layers is present in a number of genera, mainly in the tribes Astronieae, Blakeae and Miconieae. A few genera possess an abaxial palisade or palisade-like layer and have isobilateral mesophyll (*Axinaea*, *Bellucia*, *Creochiton*, *Huilaea*, *Laouisiera*, *Loricalepis* and *Miconia bailloniana*).

Lamina thickness

Lamina thickness varies in the Melastomataceae from 25–1400 µm (mainly from 100–200 µm); in the Crypteroniaceae from 200–525 µm and in the Memecylaceae from 70–420 µm.

Crystals (Table 1B)

Crystals are generally present as druses in midrib, petiole and mesophyll, never in the epidermis. Some druses occur in specialized cells, idioblasts, in the mesophyll. Druses deposited in a subepidermal ring in the ground tissue of midrib or petiole occur in *Acanthella*, *Dichaetanthera corymbosa* (incomplete ring), *Phyllagathis*, *Scorpiothyrsus* and *Tristemma*. Most genera have druses with a size between 20–40 µm. Small druses are generally present in the phloem of the vascular bundles. *Calycogonium apleura* has large druses (125 µm). Partly elongate, styloid-like druses occur in *Centradenia*.

Styloids and megastyloids (≥ 200 µm) are present in a number of genera in the tribes Astronieae, Merianieae, Miconieae, and in the families Crypteroniaceae and Memecylaceae.

Rhomboidal crystals are present in *Memecylon* and raphides in *Fordiophyton*. Raphides have also been recorded in the wood of one species of *Bredia*, *B. tuberculata* (Van Vliet, 1981). The occurrence of raphides may be of significance, indicating affinities with families such as Onagraceae, in which all genera possess raphides (Keating, 1982).

Seemingly disintegrating crystals (almost always druses) occur in *Beccarianthus*, *Dicellandra*, *Rhexia*, *Rhynchanthera* and *Warneckea*. Crystal sand (fragmented druses?) is present in *Dactylocladus* and *Phainantha*, and, according to Solereder (1899), also in *Aciotis*.

Crystals are absent from *Loricalepis*, *Myrmidone*, *Neodriessenia* and *Pseudodissochaeta*.

The restriction of druses and/or styloids to special tribes indicates a potential taxonomic value of these features.

Sclereids (Table 1B)

Isolated sclereids of various kinds occur in midrib and petiole, mostly as brachysclereids. Branched fibrous sclereids occur in *Dactylocladus* (Crypteroniaceae), *Lijndenia*, *Mouriri*, *Votomita* (Memecylaceae), *Cincinnobotrys* (in hair bases only), *Plethiandra*, *Stenodon* and *Tateanthus*; filiform sclereids in *Memecylon*. Tracheoidal idioblasts containing spiral thickenings in low angles with the cell wall (length ≥ 600 μm ; diameter c. 18 μm) occur in *Pachycentria*. This special type of sclereid is also found in *Ochthocosmus* of the Ixonanthaceae (Van Welzen & Baas, 1984), *Xanthophyllum* of the Polygalaceae (Dickson, 1973), *Pogonophora* of the Euphorbiaceae (Foster, 1956), *Nepenthes* of the Nepenthaceae (Solleder, 1899) and several Orchidaceae (Olatunji & Nengim, 1980).

The different types of sclereids in species of *Mouriri*, *Memecylon* and other genera of the Memecylaceae have been investigated many times (Bremer, 1979, 1982; Foster, 1946; Jacques-Félix, 1984; Jacques-Félix et al., 1978; Keating, 1984; Morley, 1953, 1989; Rao, 1957; Rao & Dakshni, 1963; Rao & Jacques-Félix, 1978; Rao et al., 1980, 1983; Van Tieghem, 1891). They noticed in species of *Memecylon* filiform, fibre-like, fusiform and ramiform sclereids and in species of *Mouriri* branched or armed sclereids, irregularly stellate with a strong columnar tendency. According to Morley (1953) the distribution of the different types of idioblastic sclereids in the genus *Mouriri* follows to some extent a taxonomic pattern. The character of filiform sclereids was used in distinguishing *Memecylon* from *Lijndenia* (Bremer, 1983) as well as from *Warneckea* and *Spathandra* (Jacques-Félix, 1978). However, varying features of filiform sclereids do not provide satisfactory criteria for identification at the species level (Rao et al., 1983). Solleder (1899 & 1908) mentioned the presence of 'spicular cells', now called idioblastic sclereids (Metcalf, 1979), in species of *Memecylon* and *Mouriri* and he noted that the sclereids are of considerable specific diagnostic value.

In the family Melastomataceae sclereids are scattered among the genera of all tribes, but they are lacking in Pternandreae and Rhexieae.

Midrib and petiole (Table 1B; Fig. 15)

In the Melastomataceae alliance the midrib is commonly prominently raised on the abaxial surface, and grooved adaxially as seen in transverse section. However, an adaxial ridge occurs in a number of genera. The shape of the petiole in transverse section is variable.

In the midrib, vascular bundles are almost always bicollateral. Collateral bundles are present in *Chaetostoma* and *Siphanthera fasciculata*. In the distal end of the petiole the vascular bundles are bicollateral. The petiole exhibits an arc composed of widely spaced vascular bundles which are frequently accompanied by variously arranged accessory bundles. Xylem with alternating layers of wide and narrow tracheary elements occurs in the Memecylaceae.

The vascular system in midrib and petiole is not usually enclosed by sclerenchyma, but a ring or arc of sclerenchyma fibres is sometimes present. Thick-walled phloem fibres surround the vascular system in *Blakea*, *Huilea*, *Pogonantha* and *Topobea*.

The midvein is embedded in parenchymatous peripheral ground tissue. Palisade parenchyma occurs in the adaxial ground tissue of the midrib in several genera of all

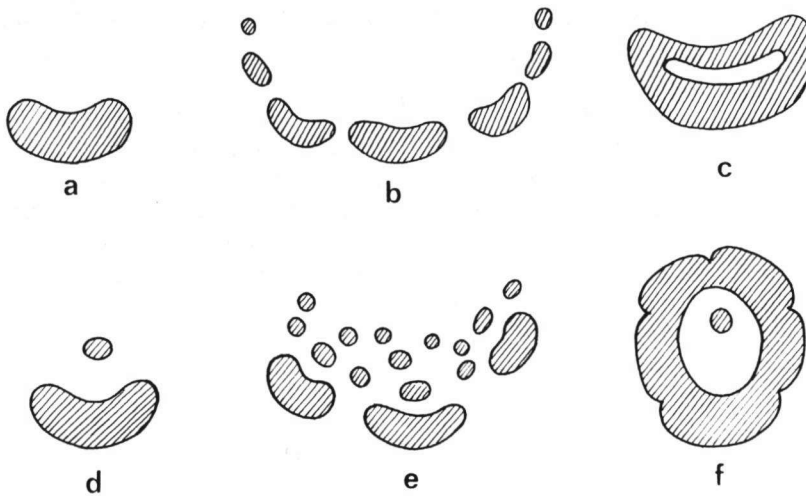


Fig. 15. Types of vascular systems in midrib and distal end of petiole of the Melastomataceae s.l. Bicolateral vascular bundles and cylinders are shaded.; a: arc-shaped, simple open system; b: simple open system of petiole consisting of an arc composed of widely spaced vascular bundles; c: simple closed system; d, e: complex open; f: complex closed with included bundle.

tribes except in Cyphostyleae, Rhexieae and the Memecylaceae. *Chaetostoma* and *Siphanthera fasciculata* have abaxial bundle sheath extensions with sclerenchyma situated not in direct contact with the vascular bundle; in these genera the vascular bundle is enclosed by collenchyma (*Chaetostoma*) or by parenchyma (*Siphanthera fasciculata*).

The range of vascular patterns in the midrib and petiole is illustrated diagrammatically in Figure 15. The vascular pattern in the midrib is simple open (arc-shaped in transverse section) in the Memecylaceae (*Lijndenia* and *Memecylon*) and in half of the genera of most tribes of the Melastomataceae. A simple closed system occurs in the genera *Castratella* (Melastomataceae), *Mouriri*, *Votomita* and *Warneckea* (Memecylaceae). A complex open system in the midrib, consisting of an abaxial arc and a varying number of smaller adaxial bundles, is present in the other half of the genera of most tribes of the Melastomataceae. A complex closed pattern with small medullary bundles occurs in *Crypteronia* (Crypteroniaceae) and *Myriasporea* (Melastomataceae).

The vascular pattern in the petiole both of the Memecylaceae (simple open or closed) and of the Crypteroniaceae (complex open or closed) is similar to the midrib. The vascular pattern in the petiole of the Melastomataceae is simple open in several genera in all tribes except in Astronieae, Blakeae and Cyphostyleae, which have a complex open system. In the petiole a complex open pattern, consisting of an arc of widely spaced bundles accompanied by accessory bundles, occurs frequently in nearly all tribes of the Melastomataceae.

Major and minor veins

Major veins are mostly similar in their anatomy to the midrib. Collateral bundles seldom replace the bicollateral bundles. Minor vein bundles are generally collateral, sometimes bicollateral.

In a number of genera the vascular bundle of the veins is enclosed by a ring or arc of sclerenchyma fibres. Major and minor veins may be vertically transcurrent by both adaxial and abaxial collenchyma bundle sheath extensions, but more frequently the bundle sheath extensions are restricted to the abaxial side only. Sclerenchymatous bundle sheath extensions situated below the epidermis and not always in direct contact with the vascular bundle occur in *Centronia*, *Chaetostoma* (only abaxial), *Crypteronia*, *Dichaetanthera lancifolia* and *Tibouchinopsis*. In several genera the veins are not vertically transcurrent but embedded in the mesophyll.

DISCUSSION

Relationships within the Melastomataceae s.l.

Family Crypteroniaceae

The genera of the Crypteroniaceae (*Axinandra*, *Crypteronia* and *Dactylocladus*) share the absence of trichomes and presence of veins surrounded by sclerenchyma. *Axinandra* and *Crypteronia* are similar in the following characters: paracytic stomata, a hypodermis, druses and styloids. *Dactylocladus* possesses crystal sand (fragmented druses?), which also occurs in *Phainantha* of the Melastomatoideae. *Dactylocladus* is the only genus in this alliance with mainly anomocytic stomata (which is the dominating stomatal type in the Astronioideae), the absence of a hypodermis (as in the Memecylaceae) and weakly developed branched fibrous sclereids, which also occur in the Memecylaceae (*Lijndenia*, *Mouriri* and *Votomita*) and in a few genera of the Melastomatoideae. *Crypteronia* stands out by a complex closed vascular pattern instead of a complex open system which characterizes *Axinandra* and *Dactylocladus*. A complex open vascular pattern is present in all genera of the subfamily Astronioideae and in many genera of many tribes of the Melastomatoideae.

Crypteroniaceae differ from the subfamily Melastomatoideae both leaf anatomically (Table 2) and macromorphologically and according to Van Vliet (1981) also wood anatomically. Between the Memecylaceae and Crypteroniaceae there is some leaf anatomical similarity, particularly the absence of multicellular hairs, the presence of paracytic stomata, druses and styloids. However, the vascular pattern differs: complex in the Crypteroniaceae and simple in the Memecylaceae.

Van Vliet (1981) proposed the inclusion of the Crypteroniaceae as a subfamily in the Melastomataceae. This suggestion of subfamily status was also put forward by Thorne (1981). However, leaf anatomy does not lend support to an inclusion of the Crypteroniaceae in the Melastomataceae.

Family Memecylaceae

In this survey five out of the six genera of the Memecylaceae (*Lijndenia*, *Memecylon*, *Mouriri*, *Votomita* and *Warneckea*) were investigated. No material of *Spathandra* was available for anatomical study.

Table 2. Summary table of important leaf anatomical characters of the Melastomataceae, Memecylaceae and Crypteroniaceae based on Table 1 A & B.

	Melastomatoides	Astronioidae	Pternandreae	Memecylaceae	Crypteroniaceae
Trichomes					
unicellular or uniseriate non-glandular hairs	-/+	-	+	-/+	-
non-glandular peltate scales	-/+	+	-	-	-
short-stalked glandular hairs	+/-	-	-	-	-
multiseriate unbranched non-glandular or glandular hairs	+/-	-	-	-	-
branched non-glandular or glandular hairs	-/+	-	-	-	-
Stomata					
	po, d, t, am (other types)	am (other types)	amc (pa)	pa (other types)	pa (am)
Crystals					
druses	+/-	-	+	+	+
styloids	-/+	+	-	-/+	+/-
Midrib vascular system					
	s, c	c	s	s	c

Legends: + = present in all genera; - = absent in all genera; +/- = mostly present, sometimes absent; -/+ = mostly absent, sometimes present.

Stomata (types mostly present; types that sometimes occur between brackets): am = anomocytic; amc = anomo-cyclocytic; d = diacytic; pa = paracytic; po = polocytic; t = tetracytic.

Vascular system: c = complex; s = simple.

Leaf anatomically the Memecylaceae are rather homogeneous (Tables 1 & 2). The species studied are characterized by the absence of trichomes, except *Votomita* which has unicellular non-glandular hairs. The stomatal type is mainly paracytic except in *Lijndenia* (polo-, dia-, tetra-, and anisocytic) and *Votomita* (anisocytic and intermediate types). *Mouriri* stands out with its stomata both in crypts and superficial. A hypodermis is present only in *Mouriri*. Crystals occur as druses in *Lijndenia* and *Votomita*, druses and styloids in *Memecylon* and *Mouriri*, druses and seemingly disintegrating druses in *Warneckea*. Special types of sclereids are found in *Memecylon* and *Mouriri*. The two species of *Warneckea* lack sclereids. Vascularization pattern in midrib and petiole is simple open (*Lijndenia* and *Memecylon*) or simple closed. Xylem in the vascular bundle of midrib and petiole consists of alternating layers of wide and narrow tracheary elements in all genera. A ring or arc of sclerenchyma fibres surrounding the vascular bundles in midrib and petiole is absent from *Votomita* and *Warneckea*.

bebaiensis. A midrib with and a petiole without sclerenchyma fibres occur in *Warneckea cinnamomoides*.

The Memecylaceae are variously placed within or outside the Melastomataceae. Airy Shaw (1973), Dahlgren (in Dahlgren & Thorne, 1984), Johnson & Briggs (1984), Klucking (1989), Raven (1984), and Renner (1989a, c and 1992, in press) recognized this group as the family Memecylaceae. Van Vliet (1981), however, who only considered *Memecylon* and *Mouriri*, did not support a family status as based on wood anatomical and macromorphological evidence. Leaf anatomy can be invoked in support of a family status of the Memecylaceae, particularly on account of the absence of complex multicellular hairs, the presence of paracytic stomata, druses in combination with styloids, and xylem with alternating layers of tracheary elements in the midrib and petiole. However, some of these characters are present in the subfamily Astronioideae and some tribes of the Melastomatoideae although not as predominating features. At this stage it is impossible to conclude whether these shared features represent synapomorphies or reflect synplesiomorphies or parallel development. Thus it remains questionable whether the leaf anatomical data indicate phylogenetic relationships of the Memecylaceae with the Melastomataceae, especially with *Pternandra* and the Astronioideae.

Family Melastomataceae

Subfamily Astronioideae

This subfamily is leaf anatomically very homogeneous (Tables 1 & 2). The four genera (*Astrocalyx*, *Astronia*, *Astronidium* and *Beccarianthus*) share non-glandular peltate scales, mainly anomocytic stomata, a 1–3-layered hypodermis, (mega)styloids, sclereids and a complex vascular pattern. The veins are not surrounded by sclerenchyma. *Astronidium* possesses mainly anisocytic stomata instead of anomocytic ones, and *Beccarianthus* can be distinguished by the presence of styloids and disintegrating crystals.

Wood anatomically the four genera of this subfamily are also very similar (Van Vliet, 1981). Van Vliet presented a classification deviating from previous ones in the abolition of the subfamily Astronioideae. He dismembered the subfamily and placed the Astronieae in the Melastomatoideae and *Pternandreae* (= Kibessieae) in the Memecyloideae. Van Vliet et al. (1981) suggested an affinity of Astronieae and Miconieae. The abolition of the Astronioideae of Triana (1865, 1871) was earlier suggested by Janssonius (1950) and a century ago by Van Tieghem (1891).

According to leaf anatomical data the differences of the Astronioideae with the Melastomatoideae are obvious, although some of the leaf features occur scattered over several genera of the Melastomatoideae, in particular the tribe Miconieae. Based on these data it seems justified to maintain a separate subfamily Astronioideae (excluding *Pternandra*) within the Melastomataceae.

The genus *Pternandra*

Pternandra has usually been included in the Astronioideae since Triana (1865, 1871). The differences in leaf anatomy between this genus and the other four genera

are very great and concern the following features (Tables 1 & 2): uniseriate non-glandular hairs, stomatal type (anomo-cyclocytic), druses, absence of a hypodermis and sclereids, vascular pattern and a sclerenchymatous ring surrounding the vascular bundles. *Pternandra* shares more leaf anatomical characters with the Memecylaceae than with the Astronioideae: paracytic stomata (although not as main type), druses, the absence of a hypodermis and sclereids (like *Warneckea*), the occurrence of a simple vascular pattern in midrib and petiole, and sclerenchyma surrounding the veins. Baas (1981) considered *Pternandra* intermediate in leaf anatomy between the subfamilies Astronioideae and Memecyloideae. Van Vliet (1981) suggested the inclusion of the tribe Pternandreae (= Kibessieae) in the Memecyloideae, which is supported by Rao & Nayak (1987) on the basis of veinlet elements morphology. Renner (pers. communication) considers *Pternandra* as a tribe of its own, but without close affinities with the Memecylaceae. In view of the absence of non-glandular peltate scales and the presence of druses and a simple vascular pattern the position of *Pternandra* is probably not in the Astronioideae. Leaf anatomically an intermediate position between Astronioideae and Memecylaceae is indeed indicated, but a conclusion on the phylogenetic affinities of *Pternandra* requires a better understanding of evolutionary specialization in leaf anatomy than we have at present.

Subfamily Melastomatoideae

Most leaf anatomical character states are scattered over the different genera of all the tribes of the Melastomatoideae (Tables 1 & 2).

Nearly all tribes show all the different hair types, but the distribution within tribes is heterogeneous. Multiseriate unbranched non-glandular hairs and short-stalked glandular trichomes are the most common types. Multiseriate unbranched non-glandular hairs are lacking only in the tribe Blakeae and short-stalked glands are present in all tribes. The Bertoloniaeae and Rhexieae are the only tribes without branched or stellate hair types (with or without glandular heads). Glabrous leaves occur in the genus *Acanthella* (tribe Merianieae).

Polo-, dia-, tetra-, and anomocytic stomata are represented as the main types in all tribes of the Melastomatoideae. In Oxysporeae and Sonerileae the polocytic type is generally present and in the Blakeae the anomocytic type. Anisocytic stomata are absent from the Bertoloniaeae, Cyphostyleae, Rhexieae and Sonerileae. Paracytic types occur occasionally in the tribes Dissochaeteae, Merianieae, Miconieae, Osbeckieae, and Rhexieae. This type is also present in the subfamily Astronioideae and as the main type in the Crypteroniaceae and Memecylaceae. Cyclocytic stomata are very infrequently present in the Merianieae, Microlicieae and Tibouchineae.

A continuous or local hypodermis is present mainly in the tribes Dissochaeteae and Miconieae, and is absent from the tribes Cyphostyleae, Microlicieae and Rhexieae.

Large bladder-like domatia occur mostly in the Miconieae and pocket-domatia mostly in the Tibouchineae. Domatia are also found in the tribes Cyphostyleae, Dissochaeteae, Microlicieae, Osbeckieae and Oxysporeae.

In all tribes crystals are present as druses. Styloids occur in the Merianieae, Miconieae and styloid-like druses in Microlicieae (*Centradenia*). Styloids are a feature of the Astronioideae, Crypteroniaceae and Memecylaceae too. Raphides are recorded in the Sonerileae (*Fordiophyton*), crystal sand in the Merianieae. Seemingly disintegrat-

ing druses occur in the Microlicieae, Rhexieae and Sonerileae. They were also noted in the Astronioideae and Memecylaceae.

Sclereids occur in all tribes, mostly as brachysclereids. They are lacking in the tribe Rhexieae. Branched fibrous sclereids are present in the genera *Cinnobotrys* (Sonerileae), *Plethiandra* (Dissochaeteae), *Stenodon* (Microlicieae) and *Tateanthus* (Bertolonieae). They are also present in the Crypteroniaceae (*Dactylocladus*) and in the Memecylaceae (*Lijndenia*, *Mouriri* *Votomita*).

Collateral instead of bicollateral vascular bundles in midrib and petiole are found in *Chaetostoma* and *Siphanthera fasciculata* of the tribe Microlicieae. All other genera have bicollateral bundles. All genera of the tribes Blakeae and Cyphostyleae possess a complex vascular system in midrib and petiole. A simple pattern is present in all genera of the Microlicieae and Rhexieae. All other tribes are heterogeneous for this feature.

This heterogeneity of the leaf anatomical features within the tribes of the subfamily Melastomatoideae does not lend support to current classifications. It may indicate that parallelisms and reversals have been particularly common in the evolution of the leaf anatomical features analysed or that the existing delimitation of tribes is very artificial. Due to a lack of close mutual association of the different anatomical features it is impossible at this stage to suggest alternative groupings. Wood anatomically, however, the Melastomatoideae constitute a rather homogeneous group (Van Vliet, 1981; Van Vliet et al., 1981; Ter Welle & Koek-Noorman, 1981).

The Miconieae are by far the largest tribe of the family. Leaf anatomically this tribe is very heterogeneous. Ter Welle & Koek-Noorman (1981), however, reported that the tribe is rather homogeneous in wood anatomical features. Most genera of the Miconieae show many different hair types and also many stomatal types. Druses and megastyleoids occur. The midvein and petiole are mainly complex, but a simple pattern is present in a number of genera. The affinities with the subtribe Astronioideae have already been mentioned.

Traditionally the Melastomatoideae consisted of eleven tribes (Cogniaux, 1891). Gleason (1929) grouped three neotropical genera, *Allomaieta*, *Alloneuron* and *Cyphostyla*, as a separate tribe Cyphostyleae in the Melastomatoideae. According to Ter Welle & Koek-Noorman (1981) *Alloneuron* shows wood anatomical similarities with the Miconieae. Leaf anatomical features of the three genera are the presence of druses, absence of a hypodermis, a complex open vascular pattern in midrib and petiole and the absence of sclerenchyma surrounding the veins. *Alloneuron* stands out by the occurrence of many hair types and mainly polocytic stomata. *Allomaieta* occasionally possesses bladder-like domatia and lacks sclereids.

Renner (1992, in press and pers. communication) reduced the number of tribes of the Melastomatoideae from 12 to 8, based on distribution of selected characters. She included the Bertolonieae and Oxysporeae in the Sonerileae and the Dissochaeteae in the Miconieae. The Melastomeae are a new tribe, composed out of the traditional tribes Osbeckieae and Tibouchineae. The Rhexieae become monogeneric; the genera *Monochaetum* and *Pachyloma* are placed in the Tibouchineae, now listed as Melastomeae. In the newly created tribes the heterogeneity of the leaf anatomical features is maintained. Leaf anatomical data can, nevertheless, be used to discuss the proposals

by Van Vliet (1981) concerning the Sonerileae-Oxysporeae complex and the division of the tribe Dissochaeteae.

In the Sonerileae-Oxysporeae complex Van Vliet combined the two original tribes to one tribe Sonerileae composed of the subtribes Sonerilinae and Oxysporinae (see also Renner, 1992, in press). Both subtribes contain genera from each of the original tribes Sonerileae and Oxysporeae [the Sonerilinae: *Barthea*, *Blastus*, *Bredia*, *Campimnia*, *Creaghiella* (= *Anerinicleistus*), *Driessenia*, *Gravesia*, *Kendrickia*; the Oxysporinae: *Allomorphia* (= *Oxyspora*), *Anerinicleistus*, *Oxyspora*, *Poikilogyne*, *Tashiroea* (= *Bredia*)]. From a leaf anatomical point of view, however, there is no support for this proposal. Although the two traditional tribes share the presence of polocytic stomata and druses, they differ in the occurrence of sessile glandular hairs (in several genera of the Sonerileae) and bladder-like glandular hairs (in several genera of the Oxysporeae). The two subtribes suggested by Van Vliet are heterogeneous with respect to these hair types.

Based on wood anatomical characters Van Vliet divided the tribe Dissochaeteae into two subtribes: the Dissochaetinae (with the genera *Catanthera*, *Creochiton*, *Diplectria*, *Dissochaeta*, *Omphalopus*, *Phaeoneuron* [= *Ochthocharis*, now Oxysporeae], *Pseudodissochaeta*) and the Medinillinae (with the genera *Hypenanthus*, *Medinilla*, *Pachycentria*, *Plethiandra*, *Pogonanthus*). The present survey includes three more genera of the Dissochaeteae than Van Vliet's study. Leaf anatomically these groups are heterogeneous (Table 1A, B) and there is no support for a subdivision of the Dissochaeteae.

CONCLUSIONS

This study demonstrates that leaf anatomically the subfamily Melastomatoideae and most of its individual tribes are very heterogeneous, while each of the (sub)families Astronioideae, Crypteroniaceae and Memecylaceae are relatively homogeneous.

The leaf anatomy of the Crypteroniaceae is suggestive of a separate position in the Myrtales, but there are some phenetic links with the Memecylaceae and to a lesser extent also with the Astronioideae of the Melastomataceae.

Leaf anatomy can support a family status of the Memecylaceae, but questions remain because of the close phenetic links with *Pternandra* and to a lesser extent with the Astronioideae.

A subfamily status is advocated for the Astronioideae on the base of its unique combination of leaf anatomical characters. The genus *Pternandra* should be removed from the subfamily Astronioideae, but a transfer to the Memecylaceae is also problematic on leaf anatomical grounds, and would not be supported by morphological characters (Renner, pers. communication). The implications of the phenetically intermediate position of *Pternandra* between Astronioideae and Memecylaceae in vegetative anatomical features for a phylogenetic classification of the Melastomataceae are at this stage unresolved.

The leaf anatomical diversity within the tribes of the Melastomatoideae does not lend itself well for support of the traditional classification into 12 tribes or for Renner's classification (1992, in press) into 8 tribes.

ACKNOWLEDGEMENTS

This study has been supported by a grant from the Missouri Botanical Gardens. The authors wish to thank its director, Dr. Peter Raven for encouragement. Dr. Susanne S. Renner's (Århus) advice, critical reading of the manuscript and assistance in obtaining material is gratefully acknowledged. Ms. Mary Gregory (Kew) also kindly scrutinized the manuscript. The curators of the herbaria in Utrecht and Wageningen kindly gave permission to sample their rich holdings of neotropical and African Melastomataceae. Marieke Hardenberg, Bertie Joan van Heuven, Monique Smits and Wim Star are thanked for technical assistance. Jan van Os and Joop Wessendorp made the text figures.

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