# WOOD ANATOMY OF THE PALAEOTROPICAL MELASTOMATACEAE

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#### SUMMARY

The wood anatomy of the palaeotropical Melastomataceae is described in detail on the basis of 134 samples of 107 species from 36 genera. On the wood anatomy, three subfamilies are recognized, Memecyloideae, Melastomatoideae, and Crypteronioideae. The Memecyloideae stand out through their fibre-tracheids, the deviating fibre length/vessel member length ratio, and the scanty paratracheal to aliform parenchyma. The Melastomatoideae are characterised by libriform fibres showing fibre dimorphism and rays composed of erect, square, and weakly procumbent cells (also in Memecyloideae p.p.). The subfamily Astronioideae is abolished; Pternandra is transferred to Memecyloideae, the Astronieae fit perfectly in the Melastomatoideae. Within Melastomatoideae the tribes are not easy to separate. The subtribe Dissochaetineae (all climbers) of the Dissochaeteae stands out because of its multiseriate rays, subtribe Medinillineae has scalariform inter-vessel pits; Astronieae have longest vessel members of the palaeotropical Melastomataceae, uniseriate rays, and bands of deviating fibres in which axial parenchyma is scarcely present: in the Osbeckieae apotracheal parenchyma bands (probably originated through fibre dimorphism) characterise the wood of Dichaetanthera; it is proposed to combine Oxysporeae and Sonerileae to one tribe Sonerileae; on the basis of the inter-vessel pitting two subtribes are recognized, different in delimitation from the two original tribes.

The family Crypteroniaceae s.s. (Axinandra, Crypteronia and Dactylocladus) is incorporated in Melastomataceae as a separate subfamily.

The scalariform inter-vessel pits, present in palaeotropical Melastomataceae only, must be interpreted as a specialization from the alternate pattern.

Raphides are present in one species of *Bredia*, *B. tuberculata*. Clustered crystals are observed in the axial parenchyma and rays of *Dichaetanthera*. Large elongate crystals are present in the parenchyma of the strands of axially included phloem of the *Memecyloideae*.

Variation in quantitative characters (vessel member length, vessel diameter and frequency) can partly be explained from the ecological preference of the species concerned. Wood anatomical differences between lianas and erect relatives are discussed.

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# INTRODUCTION

# Aims of this study.

The wood anatomy of the family Melastomataceae is known from a limited number of genera only. This is due to the fact that only a few genera contain sizable trees, of which the wood is not of economic value. The largest part of the family is made up of shrubs, climbers, and herbs or semi-woody perennials. The taxonomy of this very large family of over 240 genera with at least 3000 species is not very up to date. Since Cogniaux (1891) and Krasser (1893) no further attempt has been made to reconsider the classification of the family as a whole. Revisions of parts of the family are known from later date. For the palaeotropical area the most relevant papers are by Bakhuizen van den Brink (1943), Mansfeld (1926), and Wickens (1975).

This paper deals with the wood anatomy of the palaeotropical Melastomataceae only. The neotropical representatives of this family are the subject of a series of papers by Ter Welle & Mennega (1977), Ter Welle & Koek-Noorman (1978, 1981 this issue) and by Koek-Noorman et al. (1979).

The implications from these papers for the over-all taxonomy of the family and for its relationships with other representatives from the Myrtales will be the subject of a separate paper (Van Vliet, Koek-Noorman & Ter Welle, 1981 this issue).

In this paper an attempt will be made to compare a grouping based on external morphological characters with one based on wood anatomical data obtained from 36 genera, covering 107 species (134 samples). Of several genera only stems of small diameter ( $\emptyset$  1–5 cm) were available, wood anatomical data of some other representatives were obtained from twig material, removed from herbarium sheets. This series of papers on Melastomataceae forms part of an extensive study on the wood anatomy of the Myrtales. Other papers in this project are on Crypteroniaceae (Van Vliet, 1975; Van Vliet & Baas, 1975), Rhizophoraceae (Van Vliet, 1976a), Lythraceae (Baas & Zweypfenning, 1979), Punicaceae (Bridgwater & Baas, 1978), Combretaceae (Van Vliet, 1976b, 1978, 1979); a final paper on the wood anatomy of this order is in preparation (Van Vliet & Baas, in prep).

# Historical.

Cogniaux (1891) and Krasser (1893) divided the family into three subfamilies; the Memecyloideae – Memecylon (Africa, Asia) and Mouriri (S. America); the Astronioideae – Pternandra, Kibessia, Astronia, Beccarianthus, Astrocalyx, Astronidium (all palaeotropical); and the Melastomatoideae – all other genera, divided over 11 tribes, 7 from the neotropics and 4 from the palaeotropics.

This subfamily classification has never been challenged, although the position of some individual genera in the tribes has induced much debate. The subfamily *Memecyloideae* should in the opinion of some (Airy Shaw, 1973) be raised to family rank. The classification of the various genera, treated in this paper is given in table 4.

The subfamily Astronioideae has been subject of the most differing opinions. Naudin (1849) and Miquel (1855) already suggested that Pternandra should be placed in a separate taxon, together with Memecylon. The remaining genera should be united with the Melastomatoideae. Wood anatomical (Moll & Janssonius, 1918) and leaf- and twig anatomical evidence (Van Tieghem, 1891) was forwarded to support this opinion. Janssonius (1950) even suggested a family rank for the two taxa. These suggestions have, however, hardly found any support.

The subfamily *Melastomatoideae* is the largest taxon. Many of the tribes are poorly known or understood. Of the ones of interest here, the *Dissochaeteae* are rather well known, and wood anatomy may contribute to a better understanding of the relationships patterns between the genera involved. Another point of interest is the position of *Creochiton*, placed in various tribes of this subfamily, and by some (Bakhuizen van den Brink, 1943; Mansfeld, 1926) even in the subfamily *Astronioideae*. The taxonomy of the other tribes is less consistently known, and from the wood anatomical point of view only tentative suggestions for reconsidering the positions of these genera can be presented.

Only a limited number of publications dealt with the wood anatomy of the palaeotropical Melastomataceae, mainly referring to the genera Astronia, Medinilla, Melastoma, Memecylon, and Pternandra (here also including Kibessia).

In the following list of publications dealing with the wood anatomy of the Melastomataceae those genera illustrated with plate or figure are indicated with °. Cooper & Record, 1931 (Memecylon); Desch, 1954 (Memecylon°, Pternandra°); Hayashi et al, 1973 (Memecylon° only); Kanehira, 1921 (Astronia, Blastus°, Melastoma); 1924 (Medinilla); Metcalfe & Chalk, 1950; Moll & Janssonius, 1918 (Astronia°, Kibessia (=Pternandra)°, Medinilla°, Melastoma°, Memecylon°); Normand, 1960 (Dichaetanthera°, Memecylon°); Reyes, 1938 (Memecylon), and Solereder (1899).

## MATERIALS AND METHODS

Wood samples were obtained from several institutional wood collections, and these will be referred to using Stern's (1978) abbreviations; when no such references are given, the material was obtained from the Rijksherbarium collections. Wood collection numbers, and/or institutional references are given between brackets; herbarium vouchers are listed when known. Mature wood samples are listed without further indications, 'immature' samples are listed with the branch or stem diameter.

Sections and macerations for light microscopy and surfaces for scanning electron microscopy were prepared according to standard techniques (cf. Baas, 1973).

For each sample 25 measurements were made for vessel member length (including the tails), vessel diameter, and fibre length. Data on vessel frequency are based on at least five counts in areas of  $1 \text{ mm}^2$ ; data on ray frequency are based on at least five counts over tangential distances of 1 mm each.

Species marked with <sup>+</sup> were studied using a scanning electron microscope.

When possible, the names of the species and genera were adjusted to revisions and studies by Airy Shaw (1960), Bakhuizen van den Brink (1943, 1964), Furtado (1963), Krasser (1893), Mansfeld (1926), Markgraf (1934), Maxwell (1978, 1980 a & b, 1981) Nayar (1966, 1975), Perrier de la Bâthie (1951), Veldkamp (1978a & b), Veldkamp et al. (1978), and Wickens (1975). The more recent publications are given preference over the earlier ones. Most of the information on habit and ecological preference are obtained from these papers.

Several of the above authors have united two or more genera to one. The resulting name changes are given in table 1. These taxonomic decisions are discussed in the notes at the end of each individual description.

# DESCRIPTIVE PART

Explanatory notes to the descriptions:

The genera are presented in alphabetical sequence.

The absence of characters is not always recorded, unless this appears relevant for identification purposes.

For quantitative characters no size classes are used, except for the thickness of the fibre walls, as seen in transverse section. These size classes follow Van Vliet (1976a).

Quantitative characters are presented as full range, with the range of means in between the extreme values; in cases where only two specimens of one genus were studied, the means are connected with &. If more than two species or samples in one genus were studied, the quantitative characters are presented in table 2, specified for each sample.

The vesturing is described following the types recognized by me in an earlier paper (Van Vliet, 1978). Only the letters referring to these types are indicated in the descriptions. Their morphology will more elaborately be dealt with in the discussion on the wood anatomical characters.

Fibre dimorphism is of general occurrence in the Melastomataceae.

In transverse section these deviating fibres have a parenchyma-like appearance. The deviating fibres are described under the subheading Fibres. There is, however, a gradient to axial parenchyma. Parenchyma present in these fibre bands is for this reason also described there.

Not uncommonly used generic names which because of recent taxonomic decisions are reduced to synonymy, are given in table 1.

 Table 1 – Commonly used generic names of palaeotropical genera of the Melastomataceae which in recent times have been reduced to synonymy.

Anplectrella Furtado; included in Creochiton Bl. (Veldkamp, 1978a).

Anplectrum A. Gray; included in Diplectria Bl. (Veldkamp et al., 1978).

Backeria Bakh. f.; included in Diplectria Bl. (Veldkamp et al., 1978).

Dalenia Korth.; p.p. included in Diplectria Bl., p.p. included in Dissochaeta Bl. (Maxwell, 1980b). Hederella Stapf = Catanthera F. Muell.

Kibessia DC. = Pternandra Jack. (Maxwell, 1981).

Marumia Bl. = Macrolenes Naud.

Neodissochaeta Bakh. f.; included in Dissochaeta Bl. (Maxwell, 1980b).

Phaulanthus Ridl.; included in Anerincleistus Korth. (Nayar, 1975).

Sakersia Hook. f.; included in Dichaetanthera Endl. (Jacques-Félix, 1955).

Tashiroea Matsum.; included in Bredia Bl. (Li, 1944).

# Allomorphia B1. — Plate 6:42

Shrubs of lowland forests.

M a t e r i a l s t u d i e d: A. malaccensis (Miq.) Guill.: Malaya, Phyt. Surv. Mal.  $2403^+$ , Ø 2.5 cm (ex K-Jw). — A. racemosa (Ridl.) Bakh. f.: Sumatra, Rahmat Si Boeea 10513 (USw 29233).

Growth rings faint. Vessels diffuse, in A. mallacensis (55-) 66 (-74)/mm<sup>2</sup>, in A. racemosa (50-) 54 (-59) /mm<sup>2</sup>, solitary and in radial multiples up to 4, occasionally also in tangential multiples of 2 or 3, 55 & 65% solitary, round to polygonal in transverse sections, tangential diameter (23-) 39 & 41 (-53) μm, radial diameter up to 55 μm, walls 2-3 μm thick. Vessel member length in A. mallacensis (500-) 710 (-910) um, in A, racemosa (210-) 490 (-630) um. Perforations simple in oblique end walls. Inter-vessel pits crowded, alternate, round to polygonal  $(3-5 \mu m)$  to elongate (up to 12  $\mu m$ ), in A. racemosa also frequently tending to opposite and more elongate (up to 19 µm). Vestures of type A. Vessel-ray and vessel-parenchyma pits predominantly large and almost simple and infrequently half-bordered, biseriate to  $\pm$  scalariform, infrequently alternate-opposite and  $\pm$  diffuse. Vestures similar to the inter-vessel pits, but many of the simple pits not or only partly vestured. Granular contants infrequently filling the vessels, but more often lining the vessel walls. Thin-walled tyloses infrequently present in A. mallacensis. Fibres (600-) 830 (-1020) µm long in A. mallacensis, (530-) 600 (-810)  $\mu$ m long in A. racemosa, septate in A. mallacensis (first formed xylem excepted), dimorphous; ground tissue composed of 'normal' fibres with thin to medium thick walls with frequent simple or minutely bordered pits on both radial and tangential walls; more rounded fibres with intercellular spaces present in parenchyma-like continuous or confluent bands, in association with part of the vessels only; bands infrequently including some axial parenchyma. Granular contents infrequent in both fibre types. Parenchyma scanty paratracheal and infrequent in the bands of the deviating fibre type. Strands of (3-) 4 & 5 (-7) infrequently septate cells. Rays (11-) 16 & 18 (-21) /mm, uniseriate, rarely with a biseriate portion, composed of erect and infrequent square cells, (4-) 7 & 9 (-25) cells high.

N o t e: This genus is traditionally assigned to the tribe Oxysporeae. This tribe is rather heterogeneous in some of its wood anatomical characters (cf. table 8) and in need of revision; possibly it must be united with the tribe Sonerileae. See also the chapter on the classification of the family.

# **Amphorocalyx** Baker

Shrub from moist forests.

M a t e r i a l s t u d i e d: Twig only. A. multiflorum Baker: Madagascar, D'Alleizette s.n. ( $\emptyset$  6 mm, pith 3 mm).

Growth rings indistinct. Vessels diffuse, solitary and frequently in radial multiples. Inter-vessel pits alternate, round to polygonal (6–8  $\mu$ m), and infrequently elongate and curved (up to 15  $\mu$ m), apertures infrequently coalescent; vestured, but not seen with SEM. Vessel—ray and vessel—parenchyma pits large and almost simple, opposite (infrequently tending to alternate) to scalariform or uni- and biseriate. Vestured. Thin-walled tyloses infrequent. Fibres dimorphous, septate: normal fibres with walls of medium thickness, septa absent in the fibres of the first formed secondary xylem; more rounded fibres with slightly thinner walls and frequent intercellular spaces present in tangential bands of 2–4 cells wide, mixed with infrequent axial parenchyma, bands in contact with part of the vessels only. Parenchyma scanty paratracheal and infrequent in the bands of deviating fibres. Rays uniseriate, composed of erect cells only.

N o t e. Amphorocalyx is traditionally placed in the tribe Osbeckieae in which it does not seem out of place wood anatomically (cf. table 8).

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# Anerincleistus Korth. (including Phaulanthus Ridl.; cf. Nayar, 1975). Shrubs from moist forests.

M a t e r i a l s t u d i e d: A. pauciflorum Ridl.; Malaya, Carrick 1520<sup>+</sup> (Ø 3 cm). Twig: A. spec.: Malaya, SFN 35110 (Ø 3 mm, pith 1 mm).

Growth rings faint. Vessels diffuse, (45-) 52 (-61) /mm<sup>2</sup>, solitary and in radial multiples of 2-3 (-5), rarely forming some tangential multiples, tangential diameter (30-) 43 (-53) µm, radial diameter up to 63 µm, walls 1-2 µm thick. Mean vessel member length (430-) 630 (-780) µm.

Perforations simple in oblique end walls. Inter-vessel pits crowded, alternate, round to polygonal  $(2-5 \,\mu\text{m})$  but in some vessel elements frequently elongate (up to 23  $\mu\text{m}$ ), resulting in a more or less transitional pattern. Vestured of type A. Vessel—parenchyma and vessel—ray pits large and simple, less frequently half-bordered, round to oval  $(3-5 \,\mu\text{m})$  to elongate (up to 12  $\mu\text{m}$ ), alternate/opposite to transitional and infrequently scalariform or reticulate, rarely unilaterally compound. Vestures similar to those of the inter-vessel pits, but pits with reduced borders often not or only partly vestured. Fibres dimorphous, (610–) 815 (–1070)  $\mu\text{m}$  long, septate: ground tissue composed of 'normal' thinwalled fibres, walls with simple pits (1–2  $\mu\text{m}$ ) most frequent on the radial walls, partly gelatinous; more rounded fibres with thinner walls and frequent intercellular spaces forming narrow tangential bands, frequently intermingled with axial parenchyma and in association with part of the vessels. Parenchyma scanty paratracheal and frequent in the bands of deviating fibres, strands of 2–4 cells, infrequently septate. Rays uniseriate, composed of erect cells only, up to 13 cells high.

Secondary xylem of twig. Similar to that of the branch described above, but the vessels are slightly narrower and the parenchyma-like fibres are less abundant, forming narrow tangential arcs only.

N o t e: Nayar (1975) included Phaulanthus Ridl. in Anerincleistus. A comparison between a branch of Anerincleistus and a twig of Phaulanthus (which can only be superficial because of the immature state of the material studied) did not provide evidence to oppose this conclusion.

Anerincleistus is traditionnaly placed in the tribe Sonerileae (Melastomatoideae) in which it seems out of place because in the material studied it is the only one with alternate inter-vessel pits (cf. table 8), the others have scalariform intervascular pit fields. Transfer to Oxysporeae (or Osbeckieae) seems more in accordance with wood anatomy. However, both the tribes Sonerileae and Oxysporeae are in need of revision and may even be united (cf. Bakhuizen van den Brink, 1943).

#### Astrocalyx Merr. Plate 9/57-59.

Small tree from moist forests.

M a t e r i a l s t u d i e d: Mature wood: A. calycina (Vid.) Merr.: Philippines (FPRI 1114). Twig: same species, Philippines, PNH 9836 (Ø 6 mm, pith 2.3 mm).

M a t u r e w o o d. Growth rings indistinct. Vessels diffuse (4-) 5 (-7) /mm<sup>2</sup>, solitary and in radial multiples of 2-3, 60% solitary, tangential diameter (70-) 90 (-108) µm radial diameter up to 147 µm, walls 2-4 µm thick. Vessel member length (420-) 890 (-1280) µm. Perforations simple in horizontal to oblique end walls. Inter-vessel pits crowded, alternate, round to slightly oval, 8-10 (-12) µm in diameter, with wide, oval apertures, frequently coalescent over 2-3 pits; vestured, but not seen with SEM.

Vessel—ray pits large and simple, alternate/opposite, biseriate to scalariform and reticulate, oval (up to 10  $\mu$ m) to elongate (up to 28  $\mu$ m), long axis usually horizontal, but also oblique or vertical; vessel—parenchyma pits more or less similar, but rarely reticulate and more frequently diffuse, elongate pits up to 42  $\mu$ m; vestured. Fibres dimorphous (620–) 1140 (–1380)  $\mu$ m long, septate: ground tissue composed of 'normal' fibres, walls thin to medium thick, with simple or minutely bordered pits confined to the radial walls, one septum per fibre; more rounded fibres with frequent intercellular spaces, forming bands of 4–9 cells wide, in association with part of the vessels only, infrequently including some parenchyma strands. Granular contents frequent in both fibre types. Parenchyma scanty paratracheal and infrequent in bands of deviating fibres; strands of (4–) 5(–7) cells. Rays (15–) 17 (–19) /mm, uniseriate, occasionally with a small biseriate portion, composed of weakly procumbent, square and erect cells, (2–) 9 (–18) cells high. Granular contents frequent in rays and axial parenchyma.

Secondary xylem of twig. As mature wood, but with the following deviations: Vessels more frequent, in multiples of up to 4, less than 40% solitary, inter-vessel pits sometimes tending to opposite, infrequently elongate up to 29  $\mu$ m, apertures infrequently coalescent; vessel—ray pits predominantly scalariform, vessel—parenchyma pits more frequently uni- to biseriate. Fibres frequently gelatinous, thin-walled fibres with intercellular spaces less frequent forming an aliform-like pattern. Rays uniseriate, composed of erect cells only.

N ot e: The anatomy of the secondary xylem of the twig is, quantitative characters excepted, hardly different from that of the mature wood. The differences are those that may be expected when comparing mature and immature wood.

Astrocalyx is traditionally placed in the tribe Astronieae in which it does not seem out of place, sharing most of its wood anatomical characters with Astronia, Astronidium, and Beccarianthus. (cf. table 5)

## Astronia Bl. - table 2; Plate 9: 54-56

Small to medium-sized trees, from moist forests.

M a t e r i a l s t u d i e d: A. hollrungii Cogn.: New Guinea, BW 6999; (FPRL 26649<sup>+</sup>) — A. papetaria Bl.: New Guinea, BW 4309.

Growth rings indistict. Vessels diffuse,  $(3-)5-9(-11)/mm^2$ , solitary and in radial multiples of 2-3, 40-70% solitary, tangential diameter (68-) 110- 130 (-178) µm, radial diameter up to 220 µm, walls 2-4 (-7) µm thick. Vessel member length (340-) 540-730 (-980) µm. Perforations simple in horizontal to oblique end walls. Inter-vessel pits crowded, alternate, round to oval, 5-7  $\mu$ m, apertures very rarely coalescent in A. hollrungii. Vestures of type A. Vessel-ray and vessel-parenchyma pits large and simple or with narrow borders, alternate to reticulate and  $\pm$  scalariform, oval (7-11 µm) to elongate (up to 41 µm), vessel-parenchyma pits more often alternate/opposite and biseriate or infrequently diffuse. Vestures similar to those of the inter-vessel pits, but many of the simple pits not or only partly vestured. Thin-walled tyloses infrequent. Vessel walls warted, warts continuous into the pit chamber. Fibres dimorphous (620-) 810-1035 (-1350) um long: ground tissue composed of 'normal' fibres, walls thin with frequent simple or minutely bordered pits  $(1-2 \mu m)$  mainly confined to the radial walls septate, (1-) 2-3 septa per fibre in A. hollrungii, 3-4 septa in A. papetaria, partly gelatinous; more rounded fibres with slightly thinner walls and frequent intercellular spaces present in  $\pm$  oblique bands of 8–12 cells wide, forming a parenchyma-like, confluent to banded pattern in association with part of the vessels only, septation as normal fibres; granular contents infrequent. Parenchyma scanty paratracheal and very infrequent in the bands of deviating fibres; strands of 4-5 (-7) cells. Rays (19-) 20 (-22) /mm in A. hollrungii, (13-) 14 (-17) /mm in A. papetaria, uniseriate, in B.W. 6999 of A. hollrungii infrequently with a small biseriate portion, composed of square to erect and weakly procumbent cells, (1-) 8-12 (-28) cells high. Solid amorphous contents and granular contents frequent in the rays.

N o t e: Moll & Janssonius (1918) recorded for A. spectabilis Bl. a higher vessel frequency (9-25  $/mm^2$ ) and shorter vessel members (average length 400-450  $\mu$ m) and fibres (average length 750  $\mu$ m). Data presented by Kanehira (1921) on A. formosana Kanehira agree well with the above description; the wavy lines of septate fibres, mentioned by him, may refer to the parenchyma-like fibre type.

Astronia (Astronicae) is wood anatomically very similar to the other genera placed in this tribe (see table 5). See also note under Astronidium.

Differences in type of perforation between Astronia and Astronidium (Metcalfe & Chalk, 1950) were not observed by me. Observation of scalariform inter-vessel pits (Metcalfe & Chalk, 1950) are probably based on a wrongly identified sample.

#### Astronidium A. Gray.

Small trees (up to 15 m) from moist forests.

M a t e r i a l s t u d i e d: A. palauense (Kan.) Mgf.: Solomon I., Dep. Sant. Isabel 8353. — A. storckii Seem.: Fiji, (FHOw 11648<sup>+</sup>).

Growth rings faint to absent. Vessels diffuse,  $(23-) 26 (-30)/mm^2$  in A. palauense,  $(18-) 21 (-26)/mm^2$  in A. storckii, solitary and in radial multiples of 2-4, 65% respectively 50% of the vessels

solitary, tangential diameter (55-) 85 & 87 (-105) μm, radial diameter up to 120 & 155 μm, walls 1-3 μm, rarely up to 5 μm thick. Vessel member length (250-) 620 & 650 (-830) μm. Perforations simple in oblique end walls. Inter-vessel pits crowded, alternate, round to oval (7-10 µm), infrequently elongate (up to 21 µm) and slightly curved, apertures occasionally coalescent in A. palauense, more frequently so in A. storckii. Vestures of type A. Vessel--ray and vessel-parenchyma pits large and simple or with narrow borders, alternate/opposite to scalariform and reticulate, oval (6-12 µm) to elongate (up to 41 µm), elongate pits infrequently curved, vessel-parenchyma pits more often opposite to biseriate and infrequently diffuse. Vestures similar to those of the inter-vessel pits, but many of the simple pits not or only partly vestured. Thin-walled tyloses infrequent. Vessel walls with fine warts. Fibres dimorphous, (650–) 815 & 890 (–1060) µm long: ground tissue composed of normal fibres, walls thin with simple or minutely bordered pits (1–2 µm) frequent on the radial walls, partly gelatinous, in A. storckii with thin septa when bordering the vessels; more rounded fibres with thinner walls and large intercellular spaces present in bands of 2-5 cells wide, up to 7 cells wide in A. storckii, forming a parenchyma-like, confluent to banded pattern in association with part of the vessels only, septate in A. storckii. Parenchyma scanty paratracheal, strands of (2-) 3 (-5) cells. Rays (11-) 12 (-14) /mm in A. palauense, (14-) 17 (-19) /mm in A. storckii, uniseriate, very rarely with a small biseriate portion, (2-) 8 & 11 (-24) cells high, composed of square, erect and weakly procumbent cells.

N o t e: Metcalfe and Chalk (1950) mentioned moderately numerous, procumbent ray cells (ray type heterogeneous III), this observation is probably based on a wrongly identified sample.

The genus Astronidium is closely related to Astronia (cf. Markgraf, 1934) and placed in the same tribe (Astronieae). Wood anatomically (as based on this limited number of samples studied, cf. table 5) the two genera differ only in the abundance of septa in the fibres (abundant in Astronia, absent or scarce in Astronidium) and in the vessel frequency (5–9/mm<sup>2</sup> in Astronia). Differences in type of perforation between Astronia and Astronidium (Metcalfe & Chalk, 1950) were not observed by me.

#### Barthea Hook. f.

Shrubs from mountainous regions

M a t e r i a l s t u d i e d: Twig only. B. formosana Hayata: Taiwan, Suzuki s.n. + (Ø 3 mm, pith 1 mm).

Growth rings faint. Vessels solitary and in frequent radial multiples. Perforations simple in oblique end walls. Inter-vessel pits scalariform, infrequently transitional; vestures of type A, continuous on pit canal and pit apertures. Vessel—ray and vessel—parenchyma pits mostly large and simple, alternate/opposite to uniseriate and scalariform, infrequently unilaterally compound. Fibres thinwalled, walls with simple or minutely bordered pits, frequent on the radial walls, septate, partly gelatinous. Parenchyma scanty paratracheal, strands of 1–3 cells, frequently septate. Rays uniseriate, composed of erect cells only.

N o t e: Barthea is traditionally placed in the tribe Sonerileae (Melastomatoideae) in which it does not seem out of place wood anatomically (cf. table 8).

#### Beccarianthus Cogn.

Small trees or shrubs from primary forests.

M a t e r i a 1 s t u d i e d: Mature wood. B. spec.: New Guinea, Kalkman 5191; Solomon I., Schodde & Craven 3827 + (ex K-Jw).

Twigs. B. pulcherrima Merr.: Philippines, PNH 10542 (Ø 4 mm, pith 2 mm); New Guinea, NGF 39789 (Ø 5 mm, pith 3 mm).

M a t u r e w o o d. Growth rings indistinct. Vessels diffuse, (11-) 13 & 16 (-19) /mm<sup>2</sup>, solitary and in radial multiples of 2 (-3), 55% of the vessels solitary, tangential diameter (48-) 99 & 101 (-145)µm, radial diameter up to 178 µm, walls 2-4 µm thick. Vessel member length (370-) 570 & 630 (-890) µm. Perforations simple in horizontal to oblique end walls. Inter-vessel pits crowded, alternate, round to polygonal (6-7  $\mu$ m) to elongate (up to 32  $\mu$ m) and slightly curved, elongate pits more frequent in Schodde & Craven 3827 than in Kalkman 5191, apertures wide and frequently coalescent in Kalkman 5191, less frequently so in Schodde & Craven 3827. Vestures of type A. Vessel-ray and vessel-parenchyma pits large and simple, oval (6-11 µm) to elongate and slightly curved (up to 42  $\mu$ m), vessel—ray pits scalariform to reticulate, vessel—parenchyma pits mostly in an alternate/opposite to  $\pm$  transitional pattern and infrequently diffuse. Vestures similar to those of the inter-vessel pits, but many of the simple pits not or only partly vestured; vestures also present on the apertures of the vessel-parenchyma pits. Thin-walled tyloses infrequent in Schodde & Craven 3827. Vessel walls with fine warts. Fibres dimorphous, (610-) 830 & 870 (-1090) µm long: ground tissue composed of 'normal' fibres, walls thin to very thin with simple or minutely bordered pits  $(1-2 \mu m)$ , mainly on the radial walls, very rarely septate, in Kalkman 5191 infrequently with some branched tips; more rounded fibres with thinner walls and large intercellular spaces in ± oblique bands and arcs of 3 cells wide, in association with infrequent (Kalkman 5191) or frequent axial parenchyma (Schodde & Craven 3827). Parenchyma scanty paratracheal and in the bands of the deviating fibres; in Kalkman 5191 mostly in 'radial multiples', in Schodde & Craven 3827 constituting large patches of these bands. Strands of (2-) 4 (-7) cells. Rays uniseriate (13-) 14 & 16 (-20) /mm, composed of square and erect cells, (2-)6&7(-16) cells high. Amorphous contents frequent in the ray cells of Kalkman 5191.

Secondary xylem of twigs. As mature wood, but vessels more frequent and in multiples up to 4, inter-vessel pits more or less transitional in the vessels of the first formed secondary xylem, vessel—parenchyma pits rarely alternate/opposite. Fibres frequently septate and gelatinous.

N o t e: Apart from the quantitative data and the frequent septate fibres is the secondary xylem of the twigs hardly different from that of the mature wood. Beccarianthus is placed in the tribe Astronieae of the subfamily Astronioideae (table 5) in which it does not seem out of place wood anatomically.

#### Blastus Lour. — Plate 4: 22; 6: 39

Shrubs from moist forests.

Material studied: B. cogniauxii Stapf.: Sumatra, Rahmat Si Boeea 5232 + (= USw 28726, Ø 2 cm).

Growth rings faint. Vessels diffuse  $(50-)58(-67)/mm^2$ , solitary and in radial multiples of 2–4, 20% solitary, tangential diameter  $(28-)37(-51) \mu m$ , radial diameter up to 62  $\mu m$ , walls 2–3  $\mu m$  thick. Vessel member length  $(450-)610(-790) \mu m$ . Perforations simple in oblique end walls. Inter-vessel pits transitional to scalariform. Vestures of type A, small vestures present on pit apertures. Vessel—ray and vessel—parenchyma pits large and simple or with narrow borders, uni- to biseriate to transitional and scalariform, vessel—parenchyma pits also infrequently diffuse. Vestures similar to those of the inter-vessel pits, but many simple pits not or only partly vestured. Thin-walled tyloses and solid amorphous contents infrequent. Fibres dimorphous,  $(610-)790(-1020) \mu m$  long: ground tissue composed of 'normal' fibres,  $(1-2 \mu m)$ , more frequent on the radial than on the tangential walls; more rounded, septate fibres with slightly thinner walls and large intercellular spaces forming a parenchyma strands. Parenchyma scanty partarcheal, infrequently some strands and fusiform cells in the bands of thinner-walled fibres. Strands of 3–5 cells. Rays (1-1)3(-15)/mm, uniseriate, rarely with a biseriate portion, composed of erect cells, (1-)7(-18) cells high.

N o t e: Data presented by Kanehira (1921) on B. cochinchinensis Lour. agree rather well with the above description, although he recorded frequent septate fibres and did not mention the bands of thin-walled fibres.

Blastus is traditionally placed in the tribe Oxysporeae (Melastomatoideae; cf. table 8). This tribe is rather heterogeneous in its intervascular pit pattern. Based on this character a position in the tribe Sonerilae could be justified as well. Both Sonerilae and Oxysporae are in need of revision, and may even be united into one tribe (Bakhuizen van den Brink, 1943).

# Bredia Bl. (Including Tashiroea Matsum.; cf. Li, 1944). — Plate 6: 38 Small shrubs; in forests and along streams.

M a t e r i a 1 s t u d i e d : Twigs only. B. hirsuta Bl.: Kyushu, Tagawa & Konta 255 (Ø 3 mm, pith 1 mm). — B. okinawensis Li: Okinawa, Sonohara, Tawada & Aman 6279 (Ø 3 mm, pith 1 mm); Taniyudake, Hatusima 17895 (Ø 3 mm, pith 1 mm). — B. oldhamii Hook.f.: Taiwan, Mirushima & Liao 10883 (Ø 3.5 mm, pith 0.5 mm). — B. tuberculata Diels: Yunnan, D'Alleizette s.n. (Ø 5 mm, pith 3 mm). — B. yaeyaemensis Li.: Ryukyu, Hatusima 23083 (Ø 3 mm, pith 1.5 1.5 mm).

Growth rings faint or distinct. Vessels more frequently solitary than in multiples, tangential diameter 19-43  $\mu$ m, radial diameter up to 45  $\mu$ m, walls 1 (-2)  $\mu$ m thick. Perforations simple. Inter-vessel pits alternate/opposite to transitional in B. okinamensis and B. yaeyaemensis, predominantly transitional to scalariform in the other species. Vestured, but not seen with the SEM. Vessel-ray and vessel-parenchyma pits mostly large and simple or half-bordered, round to oval to elongate, 3-11 (-16)  $\mu$ m; vessel—ray pits mainly transitional to scalariform, vessel—parenchyma pits alternate/opposite (and often halfbordered) to transitional in B. okinawensis and B. yaeyaemensis, opposite/transitional to scalariform in the remaining species. Solid amorphous contents infrequent in the vessels of B. hirsuta. Fibres dimorphous: ground tissue composed of normal fibres with simple pits, partly gelatinous; more rounded fibres with intercellular spaces present in widely spaced, more or less continuous tangential bands of 1-2 cells wide, but 3-4 cells wide in B. hirsuta and B. tuberculata, infrequently including some axial parenchyma cells. Parenchyma scanty paratracheal, composed of up to 5, infrequently septate cells. Rays uniseriate, composed of erect cells only. Raphide crystals present in the axial parenchyma of B. tuberculata.

N o t e: In Bredia some species have scalariform inter-vessel pits, and some (B. okinawensis and B. yaeyaemensis) have alternate/opposite inter-vessel pits. These two species were assigned to the genus Tashiroea Matsum. Li (1944) however, incorporated Tashiroea in Bredia. One of the very few wood anatomical characters that seem to be of taxonomic value in this family is in fact the inter-vascular pitting. Reinstalment of the genus Tashiroea seems therefore more than justified from the wood anatomical point of view. A close relationship between Tashiroea and Bredia as based on macromorphological characters and implied in Li's combination of the two genera, would than make Tashiroea and Bredia an alliance serving as link between genera with alternate and those with scalariform inter-vessel pits in the tribe Oxysporeae (eventually united with the genera of the tribe Sonerileae, where also a similar difference in inter-vessel pitting can be observed).

The sporadic occurence of raphides in the wood of B. tuberculata is noteworthy. One would expect this character to occur throughout the genus.

# Campimia Ridl.

Shrubs from moist forests

Material studied: Twig only. C. wrayi King: Malaya, Mohnd, Shah & Sidek 1111 (Ø 4 mm, pith 1,5 mm).

Growth rings indistinct. Vessels diffuse, solitary and in radial multiples of 2–4. Perforations simple in oblique end walls. Inter-vessel pits scalariform, infrequently transitional. Vestured, but not studied with SEM. Vessel—ray and vessel—parenchyma pits large and simple or with narrow borders, uniseriate to alternate/opposite and scalariform. Thin-walled tyloses infrequent. Fibres dimorphous, septate; ground tissue composed of thin-walled fibres with simple pits, partly gelatinous (and than thick-walled); more rounded fibres with intercellular spaces very infrequent in tangential arcs of 1–2 cells wide, rarely including some axial parenchyma strands. Parenchyma scanty paratracheal. Rays uniseriate, composed of erect cells only.

N o t e: Campimia is traditionally placed in the tribe Sonerileae in which it does not seem out of place wood anatomically.

Bakhuizen van den Brink (1943) is of the opinion that the differential character of the inflorescence may not be sufficient to maintain Campimia as a separate genus, and that it is probably better to consider it as a section of Driessenia. The wood anatomy of the twig material that was studied of these genera would not be in conflict with such a decision (cf. table 8). Catanthera F. Muell. — Fig. 1; Plate 2: 6–12; 4: 21; 5: 29 Syn: Hederella Bl. Lianas from moist forests.

The stems show anomalous structure when viewed in transverse section (also visible with the naked eye!) The older stems are composed of numerous, irregularly lobed bundles of secondary xylem, embedded in phloem tissue. The young twigs still have a narrow ring of first formed secondary xylem, but show in the undulating outline of the xylem the first signs of the peculiar growth pattern. For a further treatment of the anomalous growth in Catanthera see Discussion of the wood anatomical characters.

M a t e r i a 1 s t u d i e d: C. paniculata (Nayar)Nayar: New Guinea, Jacobs 9080<sup>+</sup>. Twigs. C. brassii (Nayar)Nayar: New Guinea, Ridsdale, Henty & Galore NGF 31786. — C. tetrandra (Stapf.) Nayar: Borneo, Chew, Corner & Stainton 1326. — C. spec.: Borneo, S. 21131; New Guinea, Schodde 2125.

Growth rings absent, although local tangential bands of very thin-walled parenchyma may give the impression of ring boundaries. Vessels diffuse, (19-) 22 (-24) /mm<sup>2</sup>, solitary and in radial and tangential multiples or in clusters of up to 3 (-4), 40% solitary, tangential diameter (55-) 140 (-252) μm, radial diameter up to 315 μm thick. Perforations simple in horizontal to slightly oblique end walls. Vessel member length (330-) 540 (-760) µm. Inter-vessel pits crowded, alternate, round to oval or polygonal, 8-11 µm in diameter, apertures infrequently coalescent over 2-3 pits. Vestures of type A. Vessel-ray and vessel-parenchyma pits large and simple and less frequently also half-bordered, alternate to biseriate to transitional and scalariform, round to oval (9-13 µm) to elongate (up to  $22 \mu m$ ), infrequently unilaterally compound and elongate, up to  $31 \mu m$ . Vestures similar to those of the inter-vessel pits, but many of the simple pits not or only partly vestured. Infrequent or frequent bead-like warts on the vessel walls or walls with a thin cover of a fungus-like matting of interwoven thin vestures (Plate 4: 21 and 5: 29). Thin-walled or very thick-walled sclerotic tyloses present in some of the vessels. Fibres (500-) 650 (-830) µm long, walls medium thick and with frequent simple or minutely bordered pits  $(1-4 \mu m)$ , more abundant on the radial than on the tangential walls, septate, often with solid amorphous contents, Parenchyma vasicentric, largely embedding the vessels. Very thin-walled fusiform parenchyma or parenchyma strands with unlignified walls present in narrow tangential bands and in isolated patches of various sizes. Rays uniseriate, composed of erect to weakly procumbent cells, (1-) 5 (-7) cells high. Thin-walled rays cells with unlignified walls sometimes bordering the normal ray tissue. Solid amorphous contents frequent in rays and thickwalled axial parenchyma.

S e c o n d a r y x y l e m o f t w i g. Similar to mature wood, but with the following deviations: Vessels more abundant, up to 100 /mm<sup>2</sup>, in multiples up to 6, and with smaller diameter; vessel members shorter (440  $\mu$ m on average). Fibres shorter (520  $\mu$ m on average); narrow bands and patches of thin-walled unlignified parenchyma less common.

N ot e: The average values for vessel member length and fibre length are constant within one bundle, or when comparing different xylem bundles.

Mansfeld (1926) and Bakhuizen van den Brink (1943), the latter with hesitation, included Catanthera in Medinilla. This is not in agreement with the wood anatomical evidence (cf. table 7), because Catanthera has alternate inter-vessel pits and Medinilla scalariform ones.

Gilg (1897) referred Catanthera to Dissochaeta. The wood anatomy of Catanthera is very similar to that of Dissochaeta, as well as to that of the closely related genera Diplectria and Macrolenes. This similarity points to a close affinity between the genera mentioned above. The peculiar anomalous growth may, however, serve as a decisive differential character to support a separate generic status for Catanthera.

Creaghiella Stapf.

Shrub from wet forests.

Material studied: Twig only. C. spec: Borneo, S 22688 (Ø 4 mm, pith 2 mm).

Growth rings indistinct. Vessels frequently in tangential multiples. Perforations simple in oblique end walls. Inter-vessel pits scalariform, infrequently transitional and with some curved pits; vestured, but vestures not studied with SEM. Vessel—ray and vessel—parenchyma pits large and simple or with narrow borders, uniseriate to alternate/opposite and scalariform. Fibres dimorphous, septate; ground tissue composed of thin-walled fibres with simple or minutely bordered pits, infrequently gelatinous; more rounded fibres with large intercellular spaces present in tangential arcs of 1–2 cells wide, frequently mixed with axial parenchyma strands. Parenchyma scanty paratracheal. Rays uniseriate and composed of erect cells only.

N o t e: This genus is traditionally placed in the tribe Sonerileae (Melastomatoideae) in which it does not seem out of place wood anatomically (cf. table 8).

# Creochiton Bl. (Including Anplectrella Furtado; cf. Veldkamp, 1978a) Scandent shrubs of moist forests.

M a t e r i a 1 s t u d i e d: Twigs only. C. anomale (King) Veldk.: Malaya, Burkill 1792<sup>+</sup> (Ø 5 mm, pith 1 mm) — C. ledermannii Mansf.: New Guinea, v. Leeuwen 10382 (Ø 1 cm, pith 2 mm) — C. novoguineensis (Baker f.) Veldk. & Nayar: New Guinea, Clemens 1116<sup>+</sup> (Ø 4 mm, pith 3 mm) — C. pudibunda (Bl.) Bl.: Java, Bl. s.n. (Ø 4.5 mm, pith 3 mm).

Growth rings indistinct. Vessels more frequently solitary than in radial multiples. Perforations simple in oblique end walls. Inter-vessel pits alternate, in C. anomale infrequently elongate (up to 16  $\mu$ m) and slightly curved. Vestures of type A. Vessel—ray and vessel—parenchyma pits large and simple or with reduced borders, infrequently half-bordered, alternate/opposite and uniseriate to transitional and scalariform. Vestures similar to those of the inter-vessel pits but many of the simple pits not or only partly vestured; in pits with reduced borders, vestures often tend (through reduction) to type B, form 1. Fibres dimorphous: normal fibres with thin to medium thick walls, and frequent simple or minutely bordered pits on radial and tangential walls, frequently gelatinous; more rounded fibres with large intercellular spaces present in narrow tangential arcs of 1–2 cells wide, in C. ledermannii tending to a more banded pattern, in C. anomale forming bands of up to 3 cells wide, parenchyma-like fibres frequently mixed with axial parenchyma; all fibres septate, but in C. novoguineensis not in the later formed secondary xylem. Parenchyma scanty paratracheal and in the bands of parenchyma-like fibres; fusiform or in strands of (2–) 4 (–7) partly septate cells. Rays uniseriate and composed of erect, square and infrequent weakly procumbent cells.

N o t e: Bakhuizen van den Brink (1943) and Mansfeld (1926) placed Creochiton in the subfamily Astronioideae, as subtribe Creochitoneae or close to Beccarianthus respectively. Recent opinions favour a position in the tribe Dissochaeteae of the subfamily Melastomatoideae. A position near Beccarianthus is not in accordance with wood anatomy since all genera of the tribe Astronieae have uniseriate rays only, whilst some of the young branches of Creochiton already have biseriate rays, so in older material even broader rays may be expected. In this and other wood anatomical characters Creochiton is very similar to many genera of the Dissochaeteae (Diplectria, Dissochaeta, Macrolenes, cf. table 8). Placement in that tribe seems therefore justified.

## Dichaetanthera Endl. — Table 2; Fig. 5; Plate 5: 23; 7: 43-45

Shrubs or small trees from sclerophyllous forests and rocky soils (D. rhodesiensis) and wet forests.

M a t e r i a 1 s t u d i e d: D. africana Hook. f.: Cameroon, Foury 66 (= CTFT 621) - D. cordifolia Bak. var. reticulata (Cogn.) H. Perr.: Madagascar, Thouvenot 39<sup>+</sup> (= CTFT 614) - D. rhodesiensis A. & R. fernandez: Zambia, Milne-Redhead 3232<sup>+</sup> (ex K-Jw). Twig: D. laurentii Cogn.: Congo, Mendinckx 6079 (Ø 4 mm, pith 2 mm).

Growth rings faint or absent (D. cordifolia). Vessels diffuse (3-) 4-13 (-16) /mm<sup>2</sup>, solitary and in radial multiples, 30-80% solitary, tangential diameter (58-) 107-156 (-235)  $\mu$ m, radial diameter up to 30  $\mu$ m, walls 1-3  $\mu$ m thick. Vessel member length (260-) 340-680 (-880)  $\mu$ m. Perforations simple in oblique to almost horizontal end walls. Inter-vessel pits crowded, alternate, polygonal or round to

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oval (8-11 µm), but in D. rhodesiensis infrequently elongate up to 18 µm, in D. cordifolia elongate up to 45 µm and slightly curved, apertures rarely coalescent. Vestures of type B, form 1, tending to form A. Vessel—ray and vessel—parenchyma pits large and simple or with narrow borders, rarely halfbordered, alternate/opposite to scalariform and reticulate,  $oval (7-13 \,\mu\text{m})$  to elongate (up to 41  $\mu\text{m}$ ), rarely unilaterally compound or with coalescent apertures; vessel-parenchyma pits also infrequently diffuse. Vestures similar to those of the inter-vessel pits, but many of the simple pits not or only partly vestured. Thin-walled tyloses infrequent in D. cordifolia. Fibres (250-) 440-1020 (-1220)  $\mu$ m, walls thin, up to medium thick in D. cordifolia, with simple or minutely bordered pits (1-2  $\mu$ m) more frequent on the radial than on the tangential walls. Fibres septate but septa absent from the fibres of D. cordifolia; frequently with shouldered, variously branched or blunt ends in D. rhodesiensis (Fig. 5); frequently gelatinous in D. rhodesiensis, rarely so in D. africana. Parenchyma apo- and paratracheal; apotracheal parenchyma banded, bands 3-6 cells wide, in unilateral contact with part of the vessels; paratracheal parenchyma scanty vasicentric; in D. africana also in a more aliform to confluent pattern. Strands of (2-)3 (-5) cells. Rays uniseriate (D. cordifolia and D. africana); uni- and biseriate in D. rhodesiensis, (7-) 8-13 (-15)/mm, uniseriate rays up to 23 cells high, composed of erect to square and infrequent weakly procumbent cells, biseriate rays composed of central portions of square to weakly procumbent cells and tails of erect cells. Small radial intercellular canals, rarely completely separating the rays cells, present in D. cordifolia. Clustered crystals present in slightly swollen, chambered cells of the axial parenchyma of D. cordifolia; oval to rounded crystals scarce in the axial parenchyma of D. rhodesiensis. Globular bodies (of gummy or resinous substance?) present in the ray cells of D. rhodesiensis.

S e c o n d a r y x y l e m o f t w i g. As mature wood but with the following deviations: Growth rings absent. Vessels more abundant, narrower and mainly solitary, inter-vessel pits frequently elongate up to 31  $\mu$ m. Parenchyma aliform to confluent. Rays uniseriate, composed of erect cells only.

N ot e: Observations by Normand (1960) on D. africana (CTFT 5232) agree well with the above description. Of the species studied here D. cordifolia is outstanding because of the occurrence of clustered crystals in the axial parenchyma. D. rhodesiensis is characterized by its frequent biseriate rays and the various forms of the fibres. The fibres and vessel elements of this species are distinctly shorter that those of the other species studied. This difference might be accounted for by the fact that this species grows on dry laterite soils and rocky hill tops; the other species have a more mesic ecology.

Jacques-Félix (1955) reduced the genus Sakersia to Dichaetanthera. This is supported by wood anatomy, because D. africana, formerly treated in Sakersia fits well in Dichaetanthera on account of its banded parenchyma. Banded parenchyma only occures in one other Old World genus of the Melastomataceae, viz. Dionycha of the tribe Osbeckieae, to which Krasser also assigned Dichaetanthera. An allience with the tribe Dissochaeteae, as implied from Krasser's treatment of Sakersia in this tribe, finds no support in wood anatomy.

#### Dionycha Naud.

M a t e r i a l s t u d i e d: Twig only. D. bojerii Naud.: Madagascar, D'Alleizette s.n. (Ø 4 mm, pith 2 mm).

Growth rings indistinct. Vessels diffuse, solitary and infrequently in tangential multiples. Perforations simple in oblique end walls. Inter-vessel pits alternate, oval (up to 13  $\mu$ m) and infrequently elongate (up to 25  $\mu$ m) and curved, apertures infrequently coalescent; vestured, but not seen with SEM. Vessel—ray and vessel—parenchyma pits large and simple or with narrow borders, alternate/ opposite to scalariform, vessel—ray pits also reticulate, round to oval (5–14  $\mu$ m) to elongate (up to 27  $\mu$ m). Fibres dimorphous: ground tissue formed by normal fibres with thin walls and simple pits, frequently gelatinous; more rounded septate fibres with large intercellular spaces bordering the parenchyma bands on both sides, in rows of 1 (–2) cells. Parenchyma scanty paratracheal and in more or less continuous apotracheal bands of 2–(3) cells wide, in contact with only a part of the vessels. Strands of 2(–4) cells, frequently septate when bordering vessel elements. Rays uniseriate, composed of erect cells only.

N o t e: Dionycha is traditionally placed in the tribe Osbeckieae (Melastomatoideae; cf. table 8), where it does not seem out of place wood anatomically. Dionycha and Dichaetanthera are the only

genera in the subfamily Melastomatoideae with banded true parenchyma. Contrary to what is observed in the wood of Dichaetanthera, the parenchyma bands are bordered by deviating fibres. In this Dionycha may serve to connect Dichaetanthera to the other members of the subfamily Melastomatoideae, which have bands that are largely formed by parenchyma-like fibres, variously mixed with axial parenchyma.

Since no mature sample of Dionycha was available for study, it cannot be established whether the intermediate stage between bands of exclusively axial parenchyma or of deviating fibres only, reflects a juvenile stage. In the twig material of Dichaetanthera the parenchyma distribution was also less distinct than in the more mature wood.

Diplectria Bl. (Including Anplectrum A. Gray, Backeria Bakh.f. (cf. Veldkamp et al., 1978) and Dalenia p.p. (cf. Maxwell, 1980b)). — Plate 5; 8: 53

Straggling shrubs and climbers from moist forests.

M a t e r i a l s t u d i e d: Mature wood. D. conica Bakh.f.: Malaya, J.C. 1569<sup>+</sup> (Ø 2.5 cm) — D. viminalis (Jack.) O. Kuntze: Malaya, P.S.M. 2623<sup>+</sup> (Ø 1 cm) – SEM only: D. divaricata (Willd.) O. Kuntze: Malaya, Carrick 1575<sup>+</sup> (Ø 8 mm). Twigs. D. beccariana (Cogn.) O. Kuntze: Borneo, Havilland & Hose 144 (Ø 4.5 mm, pith 3 mm). — D. viminalis (Jack.) O. Kuntze: Java, Bakhuizen v.d. Brink 6401<sup>+</sup> (Ø 4.5 mm, pith 3 mm); Borneo, SAN 74345 (Ø 3 mm, pith 2 mm).

Secondary xylem of branches. Growth rings indistinct. Vessels diffuse, 8-11/ mm<sup>2</sup> in D. conica, 29-55/mm<sup>2</sup> in D. viminalis, solitary and in radial multiples of 2-3 (-4), 15% and 65% of the vessels solitary, tangential diameter 165-332 µm in D. conica, 42-107 µm in D. viminalis, radial diameter up to 450 and 115 µm respectively, walls 1-2 µm thick. Perforations simple in horizontal or oblique end walls. Vessel member length (210-) 530 (-820) µm in D. conica, (230-) 400 (-580) µm in D. viminalis. Inter-vessel pits crowded, alternate, round to polygonal 5-7 µm, infrequently elongate up to 21 µm and slightly curved, apertures frequently coalescent in D. conica, infrequently so in D. viminalis. Vestures intermediate between type A and type B from 1. Vessel-ray and vessel-parenchyma large and simple or with narrow borders, alternate/opposite to biseriate and scalariform, vessel-ray pits also reticulate, round to oval (5-11 µm) to elongate (up to 21 µm). Vestures similar to those of the inter-vessel pits, but many of the simple pits not or only partly vestured. Thin-walled and infrequently sclerified tyloses present in D. conica. Vessel walls of all samples studied covered with fine warts. Fibres dimorphous, (480-) 670 (-830) µm long in D. conica, (590-) 660 (-830) µm in D. viminalis, septate: ground tissue composed of 'normal' fibres, walls thin to medium thick, with simple or minutely bordered pits, equally frequent on both radial and tangential walls, infrequently gelatinous; more rounded fibres with intercellular spaces present in narrow tangential arcs, forming a faint, aliform to confluent, parenchyma-like pattern in association with part of the vessels. Parenchyma scanty paratracheal, strands of 2-5 cells. Rays in D. viminalis (8-) 10 (-11)/mm, uniseriate, rarely with small biseriate portions, composed of erect cells only; in D. conica uni- and 3-7-seriate (3-) 5 (-9)/mm, composed of weakly procumbent and infrequent square cells, up to 7 mm high, infrequently with some sheath cells. Pith flecks infrequent.

S e c o n d a r y x y l e m o f t w i g s. Similar to the secondary xylem of the branches, but vessels more abundant and with narrower diameter, vessel-parenchyma pits frequently scalariform. The more rounded fibres of the deviating type are present in a more banded pattern in the latest formed xylem of D. viminalis (SAN 74345); fibres in D. beccariana with 2-3 septa, in D. viminalis only one.

N ot t e: Diplectria is placed in the tribe Dissochateae and has the same wood anatomy as the other genera of the subtribe Dissochatinae (cf. table 7). Differences between D. conica and D. viminalis can be accounted for by the difference in diameter of the samples studied (near the pith in the sample of D. conica most rays are also uniseriate or at most biseriate).

Backeria Bakh.f. (Bakhuizen van den Brink, 1943) is an incorrect name for Anplectrum Gray (Merrill, 1952; Airy Shaw, 1960). Veldkamp (1978b) reduced Anplectrum Gray to Diplectria Reichenbach, because he could not find decisively differentiating characters between the two. This conclusion is not in conflict with anatomical evidence, because the samples studied of 'Backeria' (now D. viminalis; Bakh. v.d. Brink 6401) and 'Anplectrum' (now D. viminalis, remaining samples) are very similar to the Diplectria material. It must, however, be mentioned that all genera of the subtribe Dissochaetinae are very similar in their wood anatomy.

Maxwell (1980b) included Dalenia furfuraceae Ridl. in Diplectria as D. beccariana (Cogn.) Kunt-

ze. The one immature sample only differs in the abundance of the septa in the fibres. The decision of Maxwell can, however, not be evaluated wood anatomically, since material of the other species of Dalenia (transferred by him to Dissochaeta) was not available for this study.

Dissochaeta Bl. (Including Neodissochaeta Bakh.f.; cf Maxwell (1980b)) — Table 2; Fig. 6; Plate 8: 49, 50; 8:52

Mainly climbers from humid forests.

M at e r i a 1 st u d i e d: D. annulata Hook.f. ex Triana var. annulata: Malaya, Maxwell 77-359<sup>+</sup> ( $\emptyset$  2.5 cm) — D. beccariana Cogn.: Borneo, Fuchs 12352<sup>+</sup> (ex K-Jw,  $\emptyset$  3.5 cm) — D. celebica Bl.: Malaya, Maxwell 78-24 ( $\emptyset$  1.5 cm, pith 2 mm) — D. gracilis (Jack.) Bl.: Malaya, T & P 1<sup>+</sup> ( $\emptyset$  1 cm, pith 3 mm). — D. hirsuta Hook.f.: Malaya, Maxwell 78-31 ( $\emptyset$  2 cm, pith 2 mm) — D. velutina Bl. var. velutina: Malaya, J.C. 1574<sup>+</sup> ( $\emptyset$  1 cm, pith 3 mm). Twigs. D. beccariana Cogn.: Borneo, Clemens 30342 ( $\emptyset$  6 mm, pith 4 mm) — D. vacillans (Bl.) Bl.: Sumatra, Meijer 6020 ( $\emptyset$  12 mm, pith 8 mm).

Growth rings faint. Vessels diffuse, in the latest formed growth rings (8-) 10-36 (-46)/mm<sup>2</sup>, solitary and in radial or infrequent tangential multiples of 2-3 (-4), infrequently including some very narrow elements, tangential diameter (58-) 96-215 (-283) µm, radial diameter up to 425 µm, walls 2-4  $\mu$ m thick, common walls up to 7  $\mu$ m thick. Perforations simple in horizontal to oblique end walls. Mean vessel member length (310–) 410–500 (–790)  $\mu$ m. Inter-vessel pits crowded, alternate, round to polygonal, 6-9 µm, infrequently elongate (up to 21 µm) and slightly curved, apertures often coalescent in D. annulata, D. beccariana, D. celebica and D. velutina. Vestures of type A, in D. annulata apertures covered with a more or less closed mat of vestures. Vessel-ray and vessel-parenchyma pits large and simple or with narrow borders, round to oval  $(7-13 \ \mu\text{m})$  to elongate (up to 29  $\mu\text{m}$ ), alternate/opposite to transitional and infrequently scalariform and reticulate. Vestures similar to those of the inter-vessel pits, but more often tending to type A; part of the simple pit not or only partly vestured. Thin-walled tyloses present in the vessels of D. annulata, D. beccariana, D. celebica and D. hirsuta. Vessel walls warted in D. velutina and D. beccariana. Fibres dimorphous, (380-) 560-770 (-1020) µm, septate; ground tissue composed of 'normal' fibres, walls thin to medium thick, with frequent simple or minutely bordered pits  $(2-4 \mu m)$ , more abundant on the radial walls than on the tangential walls, partly gelatinous; more rounded fibres with less lignified walls and intercellular spaces forming narrow tangential arcs or continuous bands of 1-2 (-4) cells wide in D. beccariana and D. velutina, bands of 2-5 cells wide in D. annulata, in the remaining samples up to 11 cells wide so that the parenchyma-like fibres are more abundant than the normal fibres; bands frequently mixed with axial parenchyma. Parenchyma paratracheal, vasicentric and in the bands of the parenchymalike fibres; fusiform (particulary abundant in D. annulata) or in strands of (2-) 5-8 (-9) sometimes septate cells. Rays of varying width; uniseriate, rarely with a small biseriate portion, (9-) 11 (-13) /mm, fully composed of erect cells and (1-) 22 (-46) cells high in D. velutina; uni- and biseriate (6-) 8-10(-11)/mm, composed of square to weakly procumbent cells and up to 1.9 mm high in D. annulata and D. gracilis; uni- and 3-7-seriate 3-6 (-9)/mm, composed of weakly procumbent and square cells and infrequent strongly procumbent and erect cells, up to 7.7 mm high and with infrequent sheath cells present in D. beccariana, D. celebica and D. hirsuta. Pith flecks present in the xylem of D. hirsuta.

S e c o n d a r y x y l e m o f t w i g s. Similar to that of the stems described above, but vessels narrower and more abundant, fibres frequently gelatinous, parenchyma-like fibres arranged in widely spaced tangential bands of 1-2 cells wide, rays uniseriate and composed of erect cells only.

N o t e: The variation in ray width between the samples studied is correlated with the diameter of the material (the narrowest rays in the narrowest samples), a tendency commonly observed. The inclusion of Neodissochaeta Bakh.f. in this genus (Maxwell 1980b) is not in contradiction with the wood anatomical evidence. The characters of the one species studied of Neodissochaeta (now D. beccariana) fall within the range of the generic description. It should be stressed, however, that all genera of the subtribe Dissochaetinae have a very similar wood anatomy (cf. table 7).

Dissotis Benth. — Table 2; Plate 7: 46-47

Shrubs and small trees, from grasslands and evergreen forest over 1800 m.

Material studied.: D. glandulicalyx Wickens: Tanzania, Newbold & Jefford 1772<sup>+</sup>, 1947 (ex K-Jw) — D. polyantha Gilg.: E. Africa, (FHOw 11640).

Growth rings very faint. Vessels diffuse (8-) 13-21 (-27)/mm<sup>2</sup>, solitary and in radial multiples of 2-3 (-4), rarely also in oblique or tangential multiples or in clusters, tangential diameter (40-) 65-73 (-93) µm, radial diameter up to 116 µm, walls 1-2 µm. Perforations simple in horizontal or oblique end walls. Vessel member length (160)-230-350 (-520) µm. Inter-vessel pits crowded, alternate, round to polygonal (5-7 µm) to elongate (up to 31 µm) and curved. Vestures of type B form 1. Vessel—ray and vessel-parenchyma pits large and simple or with narrow borders, alternate/opposite to scalariform and reticulate, round to oval (6-11 µm) to elongate (up to 51 µm) and curved, vessel-parenchyma pits sometimes half-bordered, vestures similar to those of the inter-vessel pits, but simple pits not or only partly vestured. Granular contents infrequently lining the vessel walls in Newbold & Jefford 1947 of D. glandulicalyx. Fibres dimorphous, (250-) 350-495 (-610) µm long; ground tissue composed of 'normal' fibres, walls thin to very thin with frequent simple or minutely bordered pits (1-2 µm) mainly confined to the radial walls, infrequently gelatinous; in D. glandulicalyx frequently with minutely branched or shouldered tips, only rarely so in D. polyantha, more rounded fibres with intercellular spaces present in widely spaced bands of varying conspicuousness of 1-3 cells wide, mixed with axial parenchyma. Parenchyma scanty paratracheal and in the bands of deviating fibres, fusiform or in strands of (2-) 3 (4-) cells. Rays (12-) 13-16 (-18)/mm, uniseriate in D. polyantha, uniand biseriate, rarely 3-seriate in D. glandulicalyx, (1-) 3-5 (-13) cells high, composed of erect and square and infrequently weakly procumbent cells; rays cells in D. glandulicalyx comparitively large  $(21-39 \times 51-124 \,\mu\text{m})$  when viewed in tangential section. Granular contents frequent in rays and axial parenchyma.

N o t e: Dissotis is traditionally placed in the tribe Osbeckieae, in which it fits well wood anatomically (table 8).

#### Driessenia Korth.

Shrubs up to 2 m, from moist forests.

M a t e r i a l s t u d i e d: Twig only. D. glandulifera Stapf.: N. Borneo, Chew, Corner & Stainton 1347 ( $\emptyset$  5 mm, pith 3 mm).

Growth rings faint. Vessels diffuse, solitary and in radial or tangential multiples. Perforations simple in oblique end walls. Inter-vessel pits scalariform, infrequently transitional; vestured, but not studied with SEM. Vessel—ray and vessel—parenchyma pits large and simple or with narrow borders, predominantly scalariform, infrequently alternate/opposite to biseriate. Fibres dimorphous: ground-tissue composed of thin-walled, frequently glatinous, septate fibres with simple pits; more rounded fibres with slightly thinner walls and frequent intercellular spaces present in infrequent tangential arcs of 1–2 cells wide, including some axial parenchyma strands. Parenchyma scanty paratracheal and in the bands of parenchyma-like fibres; strands of 2–3, infrequently septate cells. Rays uniseriate and composed of erect cells only.

N o t e: Generally Driessenia is placed in the tribe Oxysporeae (cf. Gilg, 1897) but Bakhuizen van den Brink (1943) transfered the genus to the tribe Sonerileae, on account of its resemblance to Phyllogathis (not studied by me). In this tribe it does not seem out of place (cf. table 8). A position in the tribe Oxysporeae can, however, also be defended from the wood anatomical point of view, for Driessenia shares most of its wood anatomical characters with Blastus, Bredia (p.p.) and Kendrickia. According to Bakhuizen van den Brink (1943) Sonerileae and Oxysporeae should probably be united. See further the discussion on the taxonomic delimitation within the family.

Gravesia Naud. (Including Veprecella Naud.; cf. Perrier de la Bâthie, 1951.) Small shrubs from moist forests.

M a t e r i a l s t u d i e d: Twigs only. G. baroni Perr.: Madagascar, Lam & Meeuwse 5606<sup>+</sup> (Ø 3 mm, pith 1.5 mm). –G. lutea (Naud.) Perr.: Madagascar, D'Alleizette s.n. (Ø 3 mm, pith 1.5 mm).

Growth rings indistinct. Vessels diffuse, solitary and in radial multiples of 2–3, infrequently also forming small clusters. Perforations simple in horizontal to oblique end walls. Inter-vessel pits scalariform, infrequently transitional to opposite. Vestures of type A, sometimes tending to type B form 1. Vessel—ray and vessel—parenchyma pits large and simple or with narrow borders, scalariform to biseriate, infrequently alternate/opposite or reticulate. Vestures similar to those of the inter-vessel pits, but many of the simple pits not or only partly vestured. Fibres dimorphous in G. lutea only: ground tissue composed of 'normal' thin-walled fibres with simple or minutely bordered pits (1–2 µm) on both radial and tangential walls; narrow tangential bands of more rounded fibres with intercellular spaces are present in G. lutea, forming a  $\pm$  confluent parenchyma-like pattern in G. lutea. Parenchyma scanty paratracheal. Strands of 2–4 infrequently septate cells, in G. lutea also fusiform or up to 7 cells long. Rays uniseriate, composed of erect cells only, in G. baroni 1–2 cells high.

N o t e: Perrier de la Bâthie (1951) included the genus Veprecella (now G. lutea) in Gravesia. The twig samples studied differ in the occurrence of the tangential arcs of parenchyma-like fibres, the septation of the fibres and the height of the rays. The two first differences are also present in other genera (cf. Medinilla), whilst the third alone is not sufficient to oppose the correctness of Perrier de la Bâthie's decision.

Gravesia is traditionally placed in the tribe Sonerileae (subfamily Melastomatoideae, cf. table 8) where it shares its wood anatomical characteristics with many of the other genera.

## Hypenanthe Bl.

Shrub from moist forests

M a t e r i a l s t u d i e d: Twig only. H. bracteatum (Bl.) Bakh. f.: Borneo, San 29360 (Ø 4 mm, pith 1 mm).

Growth rings faint. Vessels diffuse, solitary and in radial multiples of 2–3, tangential diameter up to 38  $\mu$ m, radial diameter up to 39  $\mu$ m, walls 1–2  $\mu$ m. Perforations simple in oblique end walls. Inter-vessel pits scalariform, vestured, but not studied with SEM. Vessel—ray and vessel—parenchyma pits large and simple or with narrow borders, alternate/opposite to biseriate and scalariform, round to oval to elongate (up to 21  $\mu$ m). Solid amorphous contents infrequent in the vessels. Fibres dimorphous, septate; 'normal' fibres with thin to medium thick walls and simple or minutely bordered pits (1–2  $\mu$ m) present on both radial and tangential arcs, in the latest formed xylem tending to tangential bands. Parenchyma scanty paratracheal, fusiform or in strands of 2–3 cells, frequently septate. Rays uniseriate and composed of erect cells only.

N o t e: Hypenanthe is traditionnally placed in the Dissochaeteae (Melastomatoideae) being allied to Medinilla (Bakhuizen van den Brink, 1943). Wood anatomy, in particular through the shared scalariform inter-vessel pits, favours such a position (cf. table 7).

#### Kendrickia — Plate 1: 1-5; 3-B; 6: 40 & 41

Climbers, from moist forest.

M a t e r i a l s t u d i e d: K. walkeri Hook.f.: Sri Lanka, Kostermans 24784<sup>+</sup> (Ø 4.5 cm). – Twig: Sri Lanka, D'Alleizette s.n. (Ø 4 mm, pith 2 mm).

A n o m a l o u s g r o w t h. Secondary xylem cylinder lobed with four radial flanges of largely unlignified phloem tissue reaching up to a very narrow, initially continuous ring of first formed secondary xylem. In two of the xylem lobes of the stem studied here new flanges are formed (cf. Plate 1: 1). Cambium continuous over the largest part of the lobes though not very active in the flanges.

S e c o n d a r y x y l e m. Growth rings indistinct. Vessels diffuse, (29-)33 (-36)/mm<sup>2</sup>, solitary and in radial multiples of 2-3 (-4), 45% solitary, tangential diameter (55-) 100 (-145)µm, radial diameter up to 210 µm, walls 4-7 µm thick. Vessel member length (410-) 550 (-720) µm. Perforations simple in horizontal to oblique end walls. Inter-vessel pits transitional to scalariform, pits frequently curved. Vestures of type A. Vessel—ray and vessel—parenchyma pits large and simple or with narrow borders; mostly transitional and scalariform, also alternate/opposite uniseriate, vessel—ray pits also reticulate. Vestures similar to those of the inter-vessel pits, but many of the simple pits not or only partly vestured. Fibres dimorphous, (610-) 720 (-850) µm long, septate: 'normal' fibres with walls of medium thickness and frequent simple pits on tangential, and more abundant, on radial walls; thinner walled fibres with frequent intercellular spaces, forming tangential bands and arcs of varying width, 2 to 12 cells wide, in a slightly oblique pattern, incidentally mixed with axial parenchyma. Parenchyma scanty paratracheal. Fusiform or in strands composed of 2-3 (-5) cells. Rays uniseriate and less frequently biseriate, composed of erect and square cells, up to 19 cells high.

S e c o n d a r y x y l e m o f t w i g. Similar to that of the thick branches, but vessels more narrow, present in higher frequency, deviating fibres present in narrow, tangential arcs of 1-2 cells wide, associated with a limited number of vessels. Rays exclusively uniseriate and composed of erect cells only.

N o t e: The anomalous growth of the stem of Kendrickia, resulting in four or more distinct xylem lobes (cf. Plate 1: 1), makes this genus easily recognisable. Kendrickia is placed in the tribe Oxysporeae, in which there are more genera with the same wood anatomical characteristics. In some wood anatomical characters this tribe is rather heterogeneous, and in need of a thorough taxonomic revision. A merger with the tribe Sonerileae cannot be excluded. If that were the case, Kendrickia would share most of its wood anatomical characters with the greatest part of the genera of the Sonerileae as well, being unique only in its anomalous secondary growth.

#### Macrolenes Naud. - Plate 5: 34; 8: 51

Climbers from humid forests.

M at e r i a l s t u d i e d: M. dimorpha (Craib.) Maxw.: Malaya, T & P 26<sup>+</sup> ( $\emptyset$  1.5 cm) – M. nemorosa (Jack) Bakh.f. var. bancana (Scheff.) Bakh.f.: Malaya, Maxwell 77-397<sup>+</sup> ( $\emptyset$  2 mm).

Growth rings faint to fairly distinct. Vessels diffuse, 18–15/mm<sup>2</sup> in M. dimorpha, 17–19/mm<sup>2</sup> in M. nemorosa, solitary and in radial multiples of 2-3 (-4) infrequently including some very narrow elements, tangential diameter 85-140 µm in M. dimorpha, 110-240 µm in M. nemorosa, radial diameter up to 195 and 280 µm respectively, walls 2-5 µm thick. Vessel member length (320-) 475 & 485 (-710) μm. Perforations simple in horizontal to oblique end walls. Inter-vessel pits crowded, alternate, round to polygonal (7-10  $\mu$ m) infrequently elongate (up to 19  $\mu$ m) and slightly curved, apertures infrequently coalescent over 2-3 pits. Vestures of type A. Vessel-ray and vessel-parenchyma large and simple or with narrow borders, round to oval  $(7-13 \,\mu\text{m})$  to elongate (up to 20  $\mu\text{m})$ ) alternate/opposite to transitional and scalariform, vessel-ray pits also reticulate. In some crossfields the vessel wall is very thin (Plate 5:34). Vestures similar to those of the inter-vessel pits, but part of the simple pits not or only partly vestured. Branched vestures/warts present on the walls of the vessels of M. dimorpha, often situated on delicate wall thickenings or pit apertures; in M. nemorosa vestures are abundant on the vessel walls, covering it with a thick 'carpet' (illustrated in Van Vliet, 1978). Fibres dimorphous, (390-) 600 & 610 (-820) µm: ground tissue composed of 'normal' fibres, walls thin to medium thick with frequent simple pits, more abundant on the radial walls; more rounded fibres with intercellular spaces are present in bands of 2-6 (-11) cells wide, including some fusiform, septate parenchyma cells; both fibres types with 2-3 septa per cel. Parenchyma scanty paratracheal,  $\pm$  vasicentric, fusiform or in strands composed of (2-) 3-4 (-6), frequently septate cells. Rays uniseriate in M. dimorpha and composed of erect cells only, uni- and 3-5-seriate in M. nemorosa, and composed of erect to square and weakly procumbent cells, up to 1.4 mm high. Pith flecks infrequent in M. nemorosa.

N ot e: The difference in ray width, vessel frequency and vessel-diameter can largely be explained through the difference in age of the samples studied.

# Medinilla Gaud. - Table 2; Plate 3: 14-19; 4: 24; 5: 33

Epiphytic or terrestrial shrubs from moist forests; species of the section Heteroblemma are root creepers.

M a t e r i a l s t u d i e d: M. crassinervia Bl.: Malaya, T. & P. 420<sup>+</sup> (Ø 1.5 cm) – M. heterophylla A. Gray: Fiji, (FHOw 11647) – M. magnifica Lindl.: Philippines (ex K-Jw) – M. spec.: Philippines, Jacobs 7053.

Secondary xylem of twigs. M. alternifolia Bl.: Borneo, Chew Wee Lek 346 ( $\emptyset$  15 mm, pith 1 mm), Endert 3867 ( $\emptyset$  6 mm pith 2 mm), Achmad 1315<sup>+</sup> (SEM only) – M. anisophyllea Merr.: Philippines, Ramos & Edano 29203 ( $\emptyset$  4 mm, pith 2 mm) – M. barbata Bakh.f.: New Guinea, Vink BW 8404 ( $\emptyset$  7 mm, pith 2 mm) – M. ericoidea Steen.: New Guinea, Lam 7-11<sup>+</sup> ( $\emptyset$  3 mm, pith 1 mm) – M. homoeandra Stapf.: Borneo, Clemens 28121 ( $\emptyset$  4 mm, pith 0.5 mm), Clemens 30341 ( $\emptyset$  2 mm, pith 0.5 mm) – M. dentata Veldk.: New Guinea, Darbyshire 341 ( $\emptyset$  3 mm, pith 1 mm), NGF 42845 ( $\emptyset$  2 mm, pith 0.5 mm) – M. lorata Stapf: Borneo, Haviland & Hose 3388 ( $\emptyset$  5 mm, pith 1 mm) – M. myrtiformis (Naud.) Triana; Java, Boerlage 263 (M 2 mm, pith 0.5 mm), Cuning 753 ( $\emptyset$  4 mm, pith 0.5 mm) – M. ramiflora Merr.: Philippines, Elmer 7482 ( $\emptyset$  3 mm, pith 1 mm) – M. serpens Stapf.: Borneo, SAN 12912 ( $\emptyset$  12 mm, pith 1 mm).

A n o m a l o u s g r o w t h; observed in the species studied from the section Heteroblemma: M. anisophyllea, M. barbata, M. lorata, M. serpens.

Secondary xylem cylinder lobed with radial to irregularly shaped flanges of unlignified parenchymatous tissue, presumably with potential for originating new centres of meristimatic activity. Cambia with a radial orientation producing tangential files of xylem cells noted in such flanges of M. alternifolia (Chew Wee Lek 346). Unlignified flanges sometimes with tangential extensions. Islands or tangential stretches of unlignified tissue also present within lignified xylem and possibly partly derived from these lateral extensions. Large idioblasts with druses present in the radial flanges. In M. serpens flanges partially broken up by differentiation into more or less normal axial elements (see further the chapter on anomalous growth).

X y l e m o f s t e m s. Growth rings faint. Vessels diffuse, (32-) 41-52 (-62)/mm<sup>2</sup>, solitary and in radial and infrequent tangential multiples or clusters of up to 4, incidentally including some very narrow elements or vascular tracheids, 25-70% solitary, tangential diameter (35-) 46-85 (-115) µm, radial diameter up to 130 µm, walls 2-4 µm thick. Vessel member length (160-) 330-600 (-740) µm. Perforations simple in oblique to almost horizontal end walls. Inter-vessel pits scalariform, infrequently transitional. Vestures of type A. Vessel-ray and vessel-parenchyma large and simple or with narrow borders, mostly scalariform, also opposite/alternate and transitional, vessel-ray pits also reticulate, round to oval (up to  $13 \,\mu$ m) to elongate (up to  $53 \,\mu$ m). Vestures similar to those of the inter-vessel pits, but many of the simple pits not or only partly vestured. Solid amorphous contents present in the vessels of the first formed secondary xylem of M. heterophylla. Fibres dimorphous, (340-) 460-820 (-950) um long, septate; ground tissue composed of 'normal' fibres, walls thin to very thin, but thin to medium thick in M. magnifica, with simple or minutely bordered pits on both radial and tangential walls, granular contents frequent, in M. spec. frequently with branched tips; more rounded fibres with intercellular spaces, scarce in M. crassinervia, M. magnifica and M. spec.; in short tangential arcs and, in the latest formed xylem of M. crassinervia, also widely spaced bands of 2-4 cells wide; in M. heterophylla forming tangential bands of 3-7 cells wide, frequently mixed with axial parenchyma. Parenchyma scanty paratracheal fusiform or in strands of 2-5, infrequently septate cells. Rays (8-) 9-13 (-14)/mm, uniseriate or with a small biseriate portion, composed of square to erect and infrequent weakly procumbent cells, up to 36 cells high. Patches of included phloem of traumatic origin present near one growth ring of M. magnifica. Pith flecks infrequent in M. crassinervia.

S e c o n d a r y x y l e m o f t w i g. Similar to that of the branches and mature wood, but vessels more frequent and with narrower diameter; F/V ratio of M. anisophyllea 1.25 (average values for vessel member length and fibre length 370  $\mu$ m and 475  $\mu$ m respectively); vessel walls warted in M. anisophyllea; fibres frequently gelatinous, more rounded fibres scarce in most samples, in more distinct tangential arcs in M. dentata (Boerlage 357) and M. ramiflora; in M. ericoidea and M. dentata (NGF 42845) infrequent broad rays with radial strands of included phloem, probably of traumatic origin. Pith fleckes of unlignified parenchyma infrequent in M. anisophyllea and M. ramiflora.

N o t e: Data presented by Kanehira (1924) on M. spec. fall within the range of the above description. Moll & Janssonius (1918) studied M. javanensis Bl. The quantitative data are within the range found for the mature wood studied here; they recorded thin-walled fibres in a distinctly banded pattern for this species. Medinilla is, within the tribe Dissochaeteae rather oustanding because of the scalariform inter-vessel pits and the narrow rays. Together with some small, closely related genera (cf. table 7) with a similar wood anatomy it constitutes the subtribe Medinillinae. The wood anatomical differences between the two subtribes are – in view of the diversity in the subfamily Melastomatoideae – of such consistency that each can be raised to tribal rank. The deviating

secondary growth of the species of the section Heteroblemma supports the taxonomic status. Inclusion of Catanthera (syn: Hederella) is not justified wood anatomically (see Note on Catanthera).

#### Melastoma L. — Table 2; Plate 4: 26; 7: 48.

Shrubs or small trees, from moist forests.

M a t e r i a l s t u d i e d: M. denticulatum Kab.: Melanesia, (SJRw 22667,  $\emptyset$  3 cm). – M. malabathricum L.; Ponape, H.A. Miller 6681 (=Uw 16691,  $\emptyset$  2 cm). – M. sanguineum Soms.: Malaya, Carrick 1475<sup>+</sup> (ex K-Jw,  $\emptyset$  4 cm); Carrick 1594<sup>+</sup> (ex K-Jw,  $\emptyset$  3.5 cm).

Growth rings faint to absent, discontinuous growth rings present in M. sanguineum Vessels diffuse. (24-) 27-42 (-58)/mm, solitary and in radial multiples of 2-3 (-4), in M. sanguineum p.p. (Carrick 1475, Ridley s.n.) in multiples and clusters of up to 8, including some very narrow elements, 35-70% solitary, tangential diameter (28-) 54-82 (-120) µm, radial diameter up to 126 µm, walls 2-3 (-4) µm thick. Vessel member length (190-) 350-410 (-640) µm. Perforations simple in oblique to almost horizontal end walls. Inter-vessel pits alternate, round to polygonal (6-9 µm), infrequently elongate (up to  $12 \mu m$ ). Vestures of type A. Vessel—ray and vessel—parenchyma pits large and simple or with narrow borders, the latter pit-contacts infrequently half-bordered, round to oval to elongate (up to 32 µm), alternate/opposite to transitional and scalariform, vestures similar to those of the inter-vessel pits, but many of the simple pits not or only partly vestured. Thin-walled tyloses infrequent in M. sanguineum p.p. Fibres dimorphous, (380-) 530-640 (-770) µm long, septate in M. malabathricum and M. sanguineum p.p. (Ridley s.n.): ground tissue composed of 'normal' upres, walls thin, with frequent simple pits, more abundant on the radial than on the tangential walls; more rounded fibres with slightly thinner walls and intercellular spaces present in tangential bands of 2-4 cells wide, forming a confluent to banded pattern in association with part of the vessels only, bands 1-2 cells wide and widely spaced in M. malabathricum, in M. denticulatum bands well developed in the latest formed xylem only, scarce in the earlier formed xylem, bands sometimes mixed with axial parenchyma cells. Parenchyma scanty paratracheal, and infrequent in the bands of deviating fibres; strands of 2-3 (-4) cells, infrequently septate. Rays (9-) 11-14 (-17)/mm, uniseriate, rarely with a small biseriate portion in M. malabathricum and M. sanguineum p.p. (Carrick 1475), uni- and biseriate in the other samples studied, composed of erect, square and weakly procumbent cells, and with some strongly procumbent cells in M. sanguineum (Carrick 1594), uniseriate rays up to 17 cells high, biseriate rays up to 350 µm high. Pith flecks present in M. sanguineum.

N o t e: Quatitative data given by Kanehira (1921) for M. candidum Don. agree well with the above description, although he did not mention the bands of fibres of the deviating type. Moll & Janssonius studied M. aperum Bl. (= M. zollingeri Naud.), M. lanuginosum Bl., M. molkenboerii Miq. (= M. setigerum Bl. var. molkenboerii (Miq.) Back, and M. setigerum Bl. Their quantitative data are within the range observed by me; they found the bands of deviating fibres to be very distinct not containing parenchyma with shorter elements, septa were observed in the deviating fibres only, M. lanuginosum excepted where all the fibres are septate.

#### Memecylon L. — Table 2; Plate 5: 28; 10: 62-65

Shrubs and trees up to 20 m; from coastal sites, dry and humid forests.

M a t e r i a 1 s t u d i e d: M. amabile Bedd.: India (FPRL 4152<sup>+</sup>). – M. amaniense (Gilg.) A. & R. Fernandez: Tanzania, For. Dept. 470 (= FHOw 18205). – M. blakeoides G. Don: Guinea, Jacq-Félix s.n. (= CTFT 3687). – M. brachybotrys Merr.: Philippines, Stearn 31 (= FPRL 22085) M. cantley Ridl.: Malaya, Carrick 1639. – M. cinnamomoides G. Don.: Ghana, C. Vigne 2833 (= FHOw 8477); Africa (FHOw 10029); (SEM only: GABON, Normand 314). – M. coerulum Jack.: Malaya, P.S.M. 2949 (Ø 1.5 cm). – M. cumingianum Tr.: Philippines, Stearn 44<sup>+</sup> (= FPRL 22099). – M. danguyanum Perr.: Madagascar, Thouvenot 123 (= CTFT 618). – M. edule Roxb.: Burma (FHOw 3053, Ø 6 cm); Sri Lanka, Gamble s.n. (= FHOw 760). – M. fasciculare (Planch. ex. Benth.) Naud.: Guinea, Jacq.-Félix 428 (= CTFT 9274). – M. garcinioides BI.: Malaya, KEP 7553 (= W.T. 4379, KEPw). – M. golaense Bakh.f.: Ivory Coast, Leeuwenberg 3785 (= Uw 10872). – M. laterifolium (G. Don.) Brem.: Ghana, C. Vigne 1969 (= FHOw 5910). – M. membranifolium Hook.f.: Gabon, Normand 249 (= CTFT 5213). – M. myrsinoides BI.: Malaya, S. 11318 (= W.T. 4401, KEPw). – M. nudum BI.: Sumatra, Krukoff 4250 (= FPRL 8086). – M. oligoneurum BI.: Borneo, Jacobs 5350. – M. pseudoangulatum Perr.: Madagascar, Thouvenot 104 (= CTFT 615). – M. pubescens King: Malaya, KEP 30100 (= W.T. 2871, KEPw), W.T. 3991 (= KEPw). – M. rostratum Thw.: Sri Lanka, Gamble s.n. (= FHOw 761). – M. subfurfuraceum Merr.: Philippines (FHOw 1834). – M. varians Thw.: Sri Lanka, Gamble s.n. (= FHOw 762).

Growth rings absent in most species, but faint in M. amabile, M. brachybotrys, M. nudum, and M. edule (Gamble s.n.) and distinct in FHOw 3053 of M. edule. Vessels diffuse (8-) 9-126 (-144)/mm<sup>2</sup>, solitary and in radial and infrequent (frequent in M. oligoneurum) oblique or tangential multiples of 2-3 (-4), infrequently with some very narrow vessels or vascular tracheids, 50-95% solitary, round to oval in transverse section, tangential diameter (25-) 38-113 (-153) µm, radial diameter up to 165 µm, walls 2-4 µm thick, up to 7 µm thick in M. blakeoides, M. cinnamomoides, M. edule (Gamble s.n.), M. fasciculare, M. membranifolium and M. subfurfuraceum. Perforations simple in horizontal to oblique end walls. Mean vessel member length (160-) 260-440 (-730) µm. Inter-vessel pits crowded, alternate, round to polygonal, 3-5 (-6) µm in diameter in most species but 6-9 µm in diameter in M. blakeoides, M. brachybotrys, M. fasciculata and M. rostratum, infrequently elongate up to 9 µm in M. cinnamomoides (Vigne 2833), up to 23 µm long and slightly curved in M. oligoneuron; apertures coalescent in M. amaniense, M. blakeoides, M. cinnamomoides, FHOw 3053 of M. edule, M. fasciculare, M. nudum, M. membranifolium, and M. subfurfuraceum, very infrequently so in the other species. Vestures of type A. Vessel—ray and vessel—parenchyma pits half-bordered, but part of the pits with reduced borders in M. brachybotrys, M. cinnamomoides (Normand 314), M. danguyanum, M. fasciculare, M. nudum, and M. oligoneurum, mostly in an alternate pattern, but vessel-parenchyma pits also uni- to biseriate and diffuse in M. cumingianum, M. dangyuanum, M. myrsinoides, M. nudum, M. pubescens, M. rostratum and M. subfurfuraceum; pits slightly larger than inter-vessel pits, and infrequently elongate up to 25 µm, some vessel—ray pits unilaterally compound in M. rostratum; apertures infrequently coalescent in species that have inter-vessel pits with frequent coalescent apertures. Vestures similar to those of the inter-vessel pits, in pits with slightly reduced borders (thinner walls) continuous on the aperture. Tyloses frequent in the vessels of M. cumingianum, W.T. 2187 of pubescens, and M. pseudoangulatum, scarce in FHOw 3053 of M. edule; amorphous or granular contents frequent in the vessels of M. pseudoangulatum and W.T. 2187 of M. pubescens, infrequent in those of M. cantleyi, M. cumingianum, FHOw 3053 of M. edule, M. membranifolium and M. subfurfuraceum. Warts infrequent on the walls of M. cinnamomoides (Normand 314). Axial strands of included phloem (foraminate type) present in all samples studied. Fibres (fibre-tracheids) (440-) 650-1040 (-1430) µm long, walls thick to very thick in most species, but mostly of medium thickness in M. amabile and M. brachybotrys; walls with bordered pits of  $3-5 \,\mu\text{m}$ , up to  $8 \,\mu\text{m}$  in M. fasciculare, equally numerous on both radial and tangential walls or mainly confined to the radial walls in M. amaniense, M. cinnamomoides, M. fasciculare, M. garcinioides, and M. oligoneurum. Small branched and unbranched vestures present in the pits. Parenchyma paratracheal and apotracheal, abundant to rather scarce; paratracheal parenchyma vasicentric, aliform and infrequently confluent in most species, but predominantly aliform to confluent in M. oligoneurum, embedding only part of the vessels, wings and confluent bands 1-2(-4)cells wide; apotracheal parenchyma diffuse and in narrow tangential aggregates, also bordering the abaxial sides of the included phloem strands, but scarcely so in M. amabile, M. garcinioides and M. laterifolium. Strands composed of (3-) 4-5 (-7) cells. Rays heterogeneous II, sometimes tending to heterogeneous III, (8-) 9-18 (-23)/mm, 1-3-seriate in most species, but up to 4-seriate in M. garcinioides, and up to 5-seriate in M. membranifolius, M. myrsinoides, and M. nudum; multiseriate rays (150-) 340-550 (-750) µm high, composed of multiseriate parts of procumbent cells and uniseriate tails of erect cells of 1-3 (-8) cells high, uniseriate rays (3-) 6-14 (-17)/mm, composed of erect cells only, (1-) 3-4 (-6) cells high. Radial bundles of included phloem, probably of traumatic origin present in the rays of M. cantleyi. Large styloids, 140-240 µm long and 25-55 µm in diameter, frequent in the parenchyma of the included phloem strands, and also in the xylem parenchyma surrounding the phloem bundles of M. cantleyi and M. rostratum.

Pith flecks often present.

N o t e: Data presented by Desch (1954), Hayashi et al. (1973), Moll & Janssonius (1918), Normand (1960) and Reyes (1938) agree well with the above description. Quantitative data given by Moll & Janssonius for M. paniculatum Jack are: 25-30 vessels/mm<sup>2</sup>, tangential diameter 30-130 µm, radial diameter up to 140 µm, vessel member length (not including tails) 120-300 µm, fibre length 600-1000 µm. Jacques-Félix (1978) reinstated the satellite genera Spathandra Guill. et Perr. and Warneckea Gilg. The wood anatomy of the Memecylon species transferred to Spathandra (M. blakeoides, M. danguyanum) or Warneckea (M. amaniense, M. cinnamomoides, M. fascicularis) is not different from that of the remaining species. The wood anatomy does therefore not give arguments to support this taxonomic division. Through its fibre-tracheids, fibre length/vessel member length ratio and the occurrence of axial strands of included phloem, Memecylon has a wood anatomy that is distinctly different from almost all other members of the Melastomataceae (cf. table 5). In the Old World tropics only Pternandra (including Kibessia) shows the same set of characters, being different in the ray type only. In the New World tropics the closely related genus Mouriri has a similar wood anatomy (cf. Ter Welle & Koek-Noorman, 1981 this issue). A separate taxonomic status for Memecylon, Pternandra and Mouriri (at least as subfamily Memecyloideae, but the family status, Memecylaceae, can also be supported) is therefore justified.

## **Omphalopus** Naud.

Climber of wet forests.

M a t e r i a l s t u d i e d: Young twig only. O. fallax (Jack) Naud.: Sumatra, Bünnemeijer 4515 (Ø 4 mm, pith 3 mm).

Growth rings faint. Vessels diffuse, solitary and in infrequent radial multiples of 2-3. Perforations simple in oblique end walls. Inter-vessel pits alternate, vestured but not seen with SEM. Vessel—ray and vessel—parenchyma pits large and simple, alternate/opposite to biseriate and transitional, vestured. Fibres septate, dimorphous: 'normal' fibres with thin to medium thick walls and simple pits; more rounded fibres with intercellular spaces in widely spaced infrequent narrow tangential arcs. Parenchyma scanty paratracheal, fusiform or in strands of 2-4, frequently septate cells. Rays uniseriate and composed of erect cells only.

N o t e: Naudin (1849) separated Omphalopus from Dissochaeta as a subartificial genus; according to Bakhuizen van den Brink (1943) a justified decision, based on stamen characters. The wood anatomy of this twig does not deviate from that of the twig material studied of species from Dissochaeta, but all genera of the subtribe Dissochaetinae are very similar in their wood anatomy (cf. table 7).

Oxyspora DC. - Plate 4: 25; 6: 36-37

Shrubs up to 4 m, from moist forests.

Material studied: O. paniculata DC: India, Darjeeling 3144 E<sup>+</sup> (ex K-Jw0

Growth rings faint. Vessels diffuse, (30-) 32 (-37)/mm<sup>2</sup>, solitary and in radial or oblique multiples of 2 & 3 and infrequent clusters of up to 5, sometimes including some very narrow elements, 30% solitary, tangential diameter (45-) 72 (-88)µm, radial diameter up to 107 µm, walls 2-3 µm. Perforations simple in oblique end walls. Vessel member length (240-) 330 (-430) µm. Inter-vessel pits crowded, alternate, round to polygonal (4-6  $\mu$ m), and infrequently elongate and curved (up to 19  $\mu$ m), apertures frequently coalescent over 2-3 pits. Vestures of type A, continuous on pit canal wall; small bead-like and frequent branched vestures present on apertures, fading away on the vessel wall. Vessel-ray and vessel-parenchyma pits half-bordered to almost simple, round to oval (5-9 µm) to elongate (up to 17 µm), alternate/opposite to transitional, vessel-ray pits also scalariform and reticulate, infrequently unilaterally compound or with coalescent apertures. Vestures similar to those of the inter-vessel pits. Vessel infrequently with granular contents. Fibres dimorphous, septate; ground tissue composed of 'normal' fibres, (310-) 490 (-630) µm long, walls thin to medium thick with simple or minutely bordered pits (1-2 µm) mainly confined to the radial walls; more rounded fibres with intercellular spaces in narrow tangential arcs of 1-2 (-4) cells wide, including axial parenchyma, hardly in contact with any of the vessels. Parenchyma scanty paratracheal and apotracheal in the arcs of deviating fibres, fusiform or in strands of 2-3 cells. Rays (11-) 13 (-14)/mm, uniseriate, rarely with a small biseriate portion, composed of square to erect and infrequent, weakly procumbent cells. Pith flecks infrequent.

N ot e: Oxyspora is the type genus of the tribe Oxysporeae, sharing most of its wood anatomical characters with Allomorphia, Bredia (p.p.) and Poikylogyne and with Anerincleistus from the Sonerileae (table 8). See further the chapter on the classification of the family.

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# Pachycentria Bl.

Epiphytic shrub, of moist forest.

Material studied: Twig only. P. constricta (Bl.) Bl.: Sumatra, v. Borssum Waalkes 2878 (Ø 6 mm, pith 1 mm).

Growth rings indistinct. Vessels diffuse, in multiples of 2-5, infrequently solitary. Perforations simple in oblique end walls. Inter-vessel pits scalariform, infrequently transitional, vestured, but not studied with SEM. Vessel-ray and vessel-parenchyma pits large and simple or with narrow borders, mostly scalariform, also alternate/opposite to transitional, oval (up to  $9 \mu m$ ) to elongate (up to 19 µm). Thin-walled tyloses and solid amorphous contents infrequent. Fibres septate, dimorphous: 'normal' fibres with thin to medium thick walls and simple pits on both radial and tangential walls forming the ground tissue, frequently gelatinous; more rounded fibres with intercellular spaces in faint tangential arcs of 1-2 cells wide, present in the latest formed xylem. Parenchyma scanty paratracheal. Strands composed of 2-4, infrequently septate cells. Rays uniseriate, rarely with a small biseriate portion, composed of erect to square cells.

N ot e: The wood anatomy of Pachycentria is not in conflict with its position in the tribe Dissochaeteae, subtribe Medinillinae (cf. table 7). The genus is closely allied to Pogonanthera, with which it shares most of its anatomical characters; Pogonanthera, however, has 2-3 septa per fibre, Pachycentria only one.

## **Phaeoneuron** Gilg.

Small shrubs, from moist forests.

M a t e r i a 1 s t u d i e d, Twig material only: P. dicellandroides Gilg .: Cameroon, Zenker 904 (Ø 4 mm, pith 2 mm).

Growth rings absent. Vessels diffuse, solitary and in radial multiples of 2-3. Perforations simple in oblique end walls. Inter-vessel pits alternate, round to oval and frequently elongate (up to  $16 \mu m$ ) and slightly curved. Vessel-ray and vessel-parenchyma with narrow borders, mostly scalariform, also alternate/opposite to biseriate. Vessel pits vestured, but not seen with SEM. Fibres mostly septate, weakly dimorphous: ground tissue composed of normal fibres with simple pits (1-2 µm), mainly confined to the radial walls, frequently gelatinous; more rounded fibres with intercellular spaces present in short tangential arcs of 1-2 (-3 cells wide), in association with part of the vessels. Parenchyma scanty paratracheal. Rays uniseriate and composed of erect cells only.

N o t e: Gilg (1897) placed Phaeoneuron in his key to the tribe Dissochaeteae in one group with Medinilla. The alternate inter-vessel pits, however, point to an affinity with the Dissochaeta-alliance. Medinilla has scalariform inter-vessel pits (cf. table 7).

## Plethiandra Hook.f.

Epiphytic shrubs from moist forsts.

M a t e r i a l s t u d i e d: Twig only. P. tenuinervis Ohwi: Borneo, Hallier 1950<sup>+</sup> (Ø 5 mm, pith 3 mm).

Growth rings indistinct. Vessels solitary and in radial multiples of 2-3. Perforations simple in oblique end walls. Inter-vessel pits scalariform, infrequently transitional often with very wide gash-like apertures. Vessel-ray and vessel-parenchyma pits large or with reduced borders, mostly scalariform, also alternate/opposite and biseriate to transitional. Vestures similar to those of the inter-vessel pits, but many of the simple pits not or only partly vestured. Fibres infrequently septate, dimorphous: 'normal' fibres with thin to medium thick walls, and simple or minutely bordered pits on both radial and tangential walls, frequently gelatinous; more rounded fibres with intercellular spaces present in narrow tangential arcs of 1-2 cells wide, often in association with the vessels, including some axial parenchyma. Parenchyma scanty paratracheal and in the arcs of deviating fibres, fusiform or in strands of 2-4, often septate cells. Rays uniseriate and composed of erect cells only.

N o t e: Krasser (1893) placed Plethiandra in the tribe Kibessieae of the subfamily Astronioideae. The scalariform inter-vessel pits, the dimorphous libriform fibres and the absence of included phloem form wood anatomical evidence for another position. The more recent placement in subtribe Medinillinae (Bakhuizen v.d. Brink, 1943) of tribe Dissochaeteae is fully in agreement with the wood anatomy. (Compare table 5 and 7).

#### Pogonanthera Bl. - Plate 4: 20

Epiphytis shrubs of moist forest.

M a t e r i a l s t u d i e d: P. pulverulenta (Jack.) Bl.: Malaya, Enah 1405 ( $\emptyset$  5 mm, pith 1.5 mm); Sumatra, Van Steenis 3467<sup>+</sup> ( $\emptyset$  7 mm, pith 2.5 mm).

Growth rings indistinct. Vessels diffuse, solitary and less frequently in radial multiples of 2–3. Perforations simple in oblique end walls. Inter-vessel pits scalariform. Vestures of type A. Vessel—ray and vessel—parenchyma pits large and simple, mostly similar to those of the inter-vessel pits, but many of the pits not or only partly vestured. Granular contents and thin-walled tyloses infrequent in the vessels; warts infrequent on the vessel walls. Fibres septate (2–3 septa per fibre), dimorphous: ground tissue composed of thin-walled fibres with simple or minutely bordered pits, frequently gelatinous; more rounded fibres with large intercellular spaces present in narrow tangential arcs of 1–2 cells, more abundant in the later formed secondary xylem of Van Steenis 3467. Parenchyma scanty paratracheal; strands of 2–4, infrequently septate cells. Rays uniseriate infrequently with a biseriate portion, composed of erect and infrequent square and weakly procumbent cells.

Note: Pogonanthera is closely allied to Pachycentria (tribe Dissochaeteae, subtribe Medinillinae) but in Pachycentria there is mostly only one septum per fibre (cf. table 7).

## Poikilogyne Baker f.

Shrubs or small trees up to 5 m, from moist forests.

Material studied: P. cordifolia (Cogn.) Mansf.: New Guinea, NGF 3211+ (Ø 3 cm).

Growth rings indistinct. Vessels diffuse,  $(30-) 37 (-42)/mm^2$ , solitary and in radial multiples of 2-3, 50% solitary, round to oval in transverse section, tangential diameter  $(38-) 74 (-93) \mu m$ , radial diameter up to 103  $\mu m$ , walls 1-2  $\mu m$  thick. Vessel member length  $(370-) 580 (-710) \mu m$ . Perforations simple in horizontal to oblique end walls. Inter-vessel pits crowded, round to polygonal  $(7-10 \ \mu m)$  and elongate (up to 17  $\mu m$ ) forming an alternate to opposite pattern, infrequently pits more elongate (up to 32  $\mu m$ ) and slightly curved. Vestures of type A. Vessel—ray and vessel—parenchyma pits large and simple, frequently half-bordered, opposite to transitional and scalariform. Vestures similar to those of the vessel pits, but many of the simple pits are not or only partly vestured. Fibres frequently septate, dimorphous,  $(650-) 800 (-920) \mu m$  long: ground-tissue composed of 'normal' fibres, walls thin to medium thick with simple or minutely bordered pits  $(1-2 \ \mu m)$ , mainly confined to the radial walls; more rounded fibres with intercellular spaces present in widely spaced, tangential bands of 2 (-3) cells wide, frequently including some axial parenchyma. Parenchyma scanty paratracheal and in the bands of deviating fibres; fusiform or in strands of 2-3 cells. Rays (7-) 10 (-11)/mm, uniseriate, rarely with a small biseriate portion, (1-) 5 (-16) cells high, composed of erect and frequent square cells.

N o t e: Poikilogyne is traditionally placed in the tribe Sonerileae (Table 8), sharing its wood anatomical characters with part of the genera only. See further the discussion on the taxonomic delimitations of the family.

#### Pseudodissochaeta Nayar.

Scandent shrubs of moist forests.

M a t e r i a l s t u d i e d: Young twigs only: P. assamica (C.B. Clark) Nayar: India, coll. unknown ( $\emptyset$  7 mm, pith 4 mm). – P. septentrionalis (W.W. Smith) Nayar: Thailand, Put 3461 ( $\emptyset$  4 mm, pith 2 mm).

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Growth rings indistinct. Vessels diffuse, solitary and in radial multiples of 2–3, tangential diameter up to 84  $\mu$ m, radial diameter up to 102  $\mu$ m. Perforations simple in oblique end walls. Inter-vessel pits alternate, round to polygonal (5–8  $\mu$ m). Vessel—ray and vessel—parenchyma pits large and simple or with narrow borders, mostly scalariform and transitional, also alternate/opposite. Vestured, but not seen with SEM. Thin-walled tyloses infrequent. Fibres dimorphous: normal fibres with thin to medium thick walls and simple or minutely bordered pits; more rounded fibres with intercellular spaces in narrow bands of 2–3 cells wide, present in the later formed xylem; fibres septate, but in P. assamica only in the first formed xylem and the deviating fibre bands. Parenchyma scanty paratracheal, and infrequent in the deviating fibre bands, rarely fusiform, mostly in strands of 3–5, frequently septate cells. Rays uniseriate and composed of erect cells only.

N ot e: Pseudodissochaeta belongs to the tribe Dissochaetae (subtribe Dissochaetinae) in which taxon it is not out of place wood anatomically (cf. table 7).

Pternandra Jack (Including Kibessia DC; cf. Maxwell, (1981); Nayar (1975). — Table 2; Fig. 2; Plate 5: 31-32; 10: 60-61

Shrubs and small trees from moist forests.

M a t e r i a l s t u d i e d: P. coerulescens Jack: Malaya, T & P 211 (K-Jw,  $\emptyset$  2 cm), T & P 76<sup>+</sup> (K-Jw,  $\emptyset$  4 cm), (KEPw 1745); Sumatra, Krukoff 4021 (= FPRL 7945). – P. coriacea (Cogn.) Max.: Sarawak, S 2606 (= FHOw 19187). – P. echinata Jack: Malaya, Carrick 1482<sup>+</sup> (K-Jw). – P. galatea (Korth.) Ridl.: New Guinea, Van Rooyen 4006. – P. hirtella (Cogn.) Max.: Sarawak, R 2427 – P. spec.: Sumatra, Krukoff 270 (= FHOw 8367). SEM only: P. cordata, (Korth.) Baill.: E. Indies, (FHOw 5229).

Growth rings absent to distinct. Vessels diffuse, (4-) 9-29 (-32)/mm<sup>2</sup>, solitary and in radial or infrequent oblique or tangential multiples of 2-3, infrequently or frequently including some very narrow vessels or tracheids, 70-100% solitary, tangential diameter (30-) 64-112 (-145) µm, (very narrow elements rarely exceding 37 µm), radial diameter up to 181 µm, walls 2-4 µm thick; Vessel member length (210-) 340-430 (-610) µm; very narrow elements (210-) 370-570 (-810) µm long. Perforations simple in horizontal to oblique end walls. Inter-vessel pits crowded, alternate, 6-8 µm in diameter, infrequently oval and up to 10 µm long, in T & P 76 of P. coerulescens also frequently elongate and up to 14 µm. Vestures of type A. Vessel-ray pits half-bordered and frequently with reduced borders, alternate/opposite to  $\pm$  diffuse, round to oval (7-10 µm) to elongate (up to 18 µm), infrequently unilaterally compound; vessel-parenchyma pits mainly alternate and infrequently with reduced borders, in P. coriacea and P. hirsuta also tending to uniseriate and diffuse, infrequently with some coalescent apertures. Vestures similar to those of the inter-vessel pits, but also present over the pit apertures, more abundant over vessel-parenchyma than over vessel-ray pits. Vessel-fibre pits with vestures that completely cover the apertures and that spread on the vessel wall. Thin-walled tyloses infrequent in P. coerulescens (T & P 211). Warts infrequent on vessel walls. Axial strands of included phloem (foraminate type) present in all samples studied. Fibres (400-) 610-760 (-960) µm long, walls medium thick to thick with frequent, distinctly bordered pits (5-6 µm) on both radial and tangential walls, in P. cordata more frequent on the radial than on the tangential walls, pits less frequent in P. galatea; fibre tips infrequently minutely branched. Pits with minute vestures, mainly situated on the pit aperture. Intermediates with vascular tracheids infrequent. Parenchyma apo- and paratracheal; apotracheal parenchyma scantily diffuse and forming a vasicentric to aliform-like pattern around the included strands of axial phloem; paratracheal parenchyma scanty, in T & P 76 en KEPw 1745 of P. coerulescens also continuous with the parenchyma around the included phloem bundles. Strands of 2-3 (-4) cells. Rays (9-) 12-18 (-24)/mm, uniseriate, infrequently with a small biseriate portion, but rays with included radial strands of phloem up to 4-seriate, composed of erect to weakly procumbent cells, (1-)3-5(-12) cells high. Radial strands of phloem present in the rays of all samples studied. Solitary crystals present in the parenchyma around the included axial strands of phloem of T & P 211 of P. coerulescens and of P. echinata.

N o t e: Data given by Moll & Janssonius (1918) on Kibessia azurea (= Pternandra azurea (Korth.). Maxw. agree well with the above description. The decission to merge Kibessia with Pternandra (Nayar, 1975; Maxwell, 1981) is fully supported by wood anatomy. The wood of species studied from Kibessia (P. coriaceae, P. hirtella) is similar to that of species studied from Pternandra.

Pternandra is placed in a separate tribe Kibessieae (= Pternandreae) in the subfamily Astroniodeae. If differs wood anatomically from the other members of this subfamily in the fibre type and the included axial phloem strands (sharing these characters with Memecylon of the Memecyloideae) and is intermediate between Memecylon and the remaining Melastomataceae in the fibre length to vessel member length ratio. Pternandra differs from Memecylon in ray type, radially included phloem and the parenchyma distribution around the axially included phloem bundles.

An inclusion of Pternandra in the same group as Memecylon seems therefore better than retaining it in the subfamily Astronioideae. When doing so the remainder of the Astronioideae should be transferred to the Melastomatoideae, resulting in abolishing the subfamily Astronioideae.

# Tristemma Juss.

Shrubs from moist forests.

M a t e r i a l s t u d i e d: Twig only. T. virusanum Comm.: Madagascar, D'Alleizetta s.n. ( $\emptyset$  3 mm  $\times$  4 mm, pith 2 mm  $\times$  3 mm).

Growth rings absent. Vessels diffuse, more often solitary than in multiples. Perforations simple in horizontal to oblique end walls. Inter-vessel pits alternate, crowded, round to polygonal,  $4-6 \,\mu m$  in diameter, infrequently elongated up to 15  $\mu m$ . Vestured, but not seen with SEM. Vessel—ray and vessel—parenchyma pits large and simple or with narrow borders, alternate to opposite, round to oval (4-9  $\mu m$ ) to elongate (up to 15  $\mu m$ ), vessel—ray pits more often biseriate to scalariform. Vestured. Fibres thin-walled with simple or minutely bordered pits ( $1-2 \,\mu m$ ), mainly confined to the radial walls, infrequently septate when bordering vessels or axial parenchyma; part of the fibres gelatinous. Parenchyma scanty paratracheal, strands of 2-4 cells, frequently septate. Rays uniseriate and composed of erect cells only.

N o t e: Tristemma is traditionally assigned to the tribe Osbeckieae (table 8) of the subfamily Melastomaoideae, in which it fits well wood anatomically.

Species and/or Specimen	average vessel frequency/mm2	% solitary vessels	average tangential diameter (μm)	maximum radial diameter (μm)	vessel member length (μm)	average fibre length (µm)	fibre length/vessel member length ratio
Astronia							
hollrungii							
<b>B.W. 6999</b>	6	40	130	220	540	810	1.50
Wageningen 11050	6	70	126	180	730	1015	1.39
papetaria	9	55	110	142	720	1035	1.43
Dichaetanthera							
africana	6	30	155	280	630	1020	1.61
cordifolia var. reticulata	4	80	145	330	680	900	1.32
rhodesiensis	13	60	110	210	340	440	1.29
Dissochaeta							
annulata var. annulata	22	50	160	245	530	660	1.25
beccariana	10	15	215	425	500	750	1.50
celebica	10	35	220	330	40.0		
gracilis	21	30	120	220	490	665	1.36
hirsuta	16	30	165	280	410	490	1.20
velutina var. velutina Dissotis	36	50	95	185	460	560	1.22
glandulicalyx							
Newbould & Jefford 1772	13	50	73	103	220	250	1.50
Newbould & Jefford 1947	15	35	65	103	230 230	350 360	1.52 1.56
polyantha	21	55 60	63 68	103	350	360 495	1.30
Polyanona	21	00	00	103	350	473	1.41

Table 2 – Quantitative characters of the genera of which more than two samples were studied.

							.o
(Table 2 continued)	12	els	Itial	[a]			fibre length/vessel member length ratio
	/mu	vess	ngen µm)	hm (m	nber (	e C	h/ve ingtl
	e ve: ncy	ary	e tai ter (	ter (	Len Len	fi fi	er le
	average vessel frequency/mm <sup>2</sup>	% solitary vessels	average tangential diameter (μm)	maximum radial diameter (µm)	vessel member length (µm)	average fibre length (µm)	fibre length/vessel member length ra
Species and/or Specimen	ave	8	dia	dia	ve: len	ave ler	£ ŭ
Medinilla							
crassinervia	41	70	62	99	600	820	1.34
heterophylla magnifica	. 44 51	45 25	85 46	128 95	370 410	500 610	1.35 1.49
spec.	45	30	40 60	108	330	460	1.49
Melastoma	,	20	00		200		
denticulatum	42	50	55	105	390	630	1.61
malabathricum	27	65	65	110	380	540	1.42
sanguineum	41	70	70	125	240	5.40	1.60
J.C. Carrick 1475 J.C. Carrick 1594	41 40	70 45	70 80	125 110	340 410	540 640	1.59 1.56
Ridley s.n.	33	35	65 /		350	530	1.50
Memecylon		00	00	00	000	220	
amabile	27	85	83	124	340	840	2.47
amaniense	50	85	45	90	380	860	2.26
blakeoides	16	70	92	155	320	820	2.56
brachybotrys cantleyi	31 35	90 85	70 60	105 90	340 460	800 1040	2.35 2.26
cinnamomoides	55	05	00	90	400	1040	2.20
C. Vigne 2833	22	75	78	113	370	910	2.46
FHOw 10029	53	85	65	90	430	950	2.21
coeruleum	61	80	38	58	330	730	2.21
cumingianum	25	80	71	108	440	910	2.07
danguyanum edule	32	90	74	106	270	660	2.44
FHOw 3053	39	85	51	83	350	750	2.14
Gamble s.n.	126	25	38	70	260	660	2.54
fasciculata	22	50	96	158			
garcinioides	21	80	81	180	370	890	2.41
(Memecylon)	44	85	52	78	420	850	2.03
golaense lateri folium	34	75	72	120	400	970	2.43
membranifolium	34	75	81	125	395	850	2.15
myrsinoides	26	80	49	66	440	870	1.98
nudum	14	90	105	138	320	680	2.13
oligoneurum	53	75	53	103	440	760	1.72
pseudoangulatum	17	90	80	120			
pubescens W.T. 3991	14	90	98	143	440	865	1.97
W.T. 2187	9	95	113	165	430	950	2.21
rostratum	30	80	81	133	370	800	2.16
subfurfuraceum	25	75	77	140	300	650	2.17
varians	21	90	66	123	400	900	2.25
Pternandra coerulescens							
Krukoff 4021					370	750	2.02
T. & P. 211	29	90	64	108	360	610	1.66
T. & P. 76	27	85	80	115	420	720	1.71
KEPw 1745	17	70	75	133	360	700	1.94
coriacea	12	97	102 88	141 140	500 350	925 610	1.85 1.74
echinata	23 17	85 85	122	140	430	760	1.74
galatea hirtella		÷ 97	81	155		,	
spec.	17	100	75	118	340	620	1.82
-							

# DISCUSSION OF THE WOOD ANATOMICAL CHARACTERS

G r o w t h r i n g s. Growth rings occur in several genara, but are mostly faintly delimited. Only in one sample of *Memecylon* and several of *Pternandra* the growth rings are distinct. Irregular,  $\pm$  undulating growth rings occur in some liana species only. The undulation is mainly caused by the large vessel diameter, a feature commonly observed in lianas. In *Melastoma sanguineum* the growth rings may be limited by relatively broad bands of deviating fibres (Plate 7:48). The presence or absence of growth rings is of no diagnostic value; when more than one species per genus or specimen per species were studied there appeared to be variation in presence or absence.

A n o m a l o u s g r o w t h. Most Melastomataceae show normal secondary growth. In a small number of genera anomalous growth of different types occurs.

In *Memecylon* and *Pternandra* included (interxylary) phloem is produced in regularly distributed axial bundles (foraminate type; Plate 10:60, 63). Its constant occurrence in these two genera, as well as in the neotropical genus *Mouriri*, makes it an important diagnostic and taxonomic character.

In *Pternandra* all samples have moreover radial bundles of included phloem in multiseriate rays (Plate 10:61), occasionally connected with the axial bundles. Radial included phloem strands as an isolated feature also occur in some *Medinilla* species, but are variable below the species level and perhaps of traumatic origin.

Kendrickia, Catanthera and section Heteroblemma of Medinilla show a markedly anomalous stem structure, each of a different type. Detailed ontogenetic studies on living material would be necessary for a complete understanding of the different growth patterns. The material available to me only allowed the following, generalized observations to be made.

In Kendrickia walkeri, the only species of this genus from Sri Lanka, older stems are deeply lobed in transverse section (Plate 1:1). In young branches this lobing is initiated through differential cambium activity, after a closed cylinder of secondary xylem has been formed first. At four equidistant positions the cambium produces, towards the xylem side, thin-walled unlignified parenchymatous tissue, including crystalliferous cells with druses and lignified cells, reminiscent of phloem fibres or sclereids rather than xylem fibres! The presence of darkstaining cells also recalls phloem parenchyma (Plate 1:3-5).

The production of 'normal' xylem is at a maximum in between the sites producing the abnormal tissue. This ultimately results in the distinctly lobed xylem body. The narrow cylinder of secondary xylem formed before the lobe initiation is often broken in older stems. The cambium (active or not) is continuous over the largest part of the xylem lobes and the initially formed patches of abnormal tissue (Plate 3:13). In his detailed account of the anomalous thickening of *Kendrickia*, Clarke (1907) also noted that in the flanges of thin-walled tissue, dilatation through cell enlargement and cell division occurs, resulting in the penetration of parenchyma between the contiguous xylem elements. This leads to a breaking up of the ring of first-formed secondary xylem, so that the flanges of thin-walled tissue become connected with the pith. Clarke also recorded tyloses in tracheids (he probably meant fibres) and hypothesized that they might cause, by mechanical force and absorption, the disappaerance of the elements in which they were formed. Thus space for

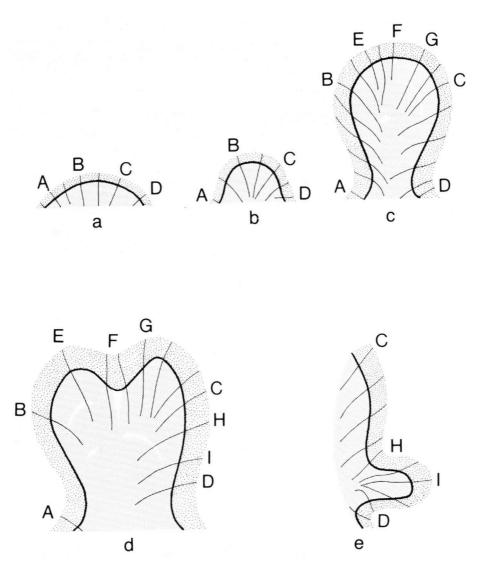


Fig. 1. Diagramatic representation of the possible secondary growth pattern in the stems of *Catanthera* (tribe *Dissochaetae*); cambium: solid line; phloem: dots widely spaced; xylem: densely dotted; unlignified parenchymatous tissue: open areas. —  $a. \pm 1/5$  of a portion of a young twig, where cambium activity is equally high. At the positions A and D the cambium is forming thin-walled, unlignified tissue on the side of the xylem. b. Division activity of the cambium at the position A and D is extremely low or nil, at the positions B and C much higher, resulting in the formation of xylem lobes. The phloem tissue has all around the xylem lobe more or less the same width and the cells have a regular arrangement. c. At position F, thin-walled unlignified tissue is formed, finally followed by decreasing activity of the cambium at that point, leading to a splitting of the xylem lobe. (d). e. At a point (I) lower on the lobe the cambium is 'reactivated', forming a new lobe with a growth direction perpendicular to that of the original lobe.

outgrowth of the thin-walled tissue would be created. Tyloses in fibres were not observed by me and one can only view Clarke's interpretation with great scepticism. The data at my disposal do not allow a choice between the alternative explanations, presented by Clarke.

At the end of his paper Clarke made a very interesting remark: 'No formation of secondary cambium in the large-celled parenchyma of the ingrowth (in the pith) was ever observed, but it seemed as if the quiescent cambium, lying between the original (internal) phloem groups and axial woody ring, had, stimulated apparently by the arrival of cells of the growth, become active once again, and cut of xylem to the one side and phloem to the other! Only four of such groups were noted. These four centres of activity were not observed by me in the pith of *Kendrickia*. They were, however, present in the pith of *Catanthera*, and crucial in the further development of the anomalous pattern in that genus.

Catanthera (syn. Hederella, also a climber) shows a very complex anomalous pattern in mature stems (Plate 2:11 & 12). Young stems (Plate 2:6 & 7) are, however, similar to *Kendrickia*. There are four centres of reduced xylem growth. The starting points for new lobes are, however, more numerous and there are also more numerous patches and tangential stretches of unlignified tissue in the xylem lobes. The variable direction and activity of the cambial growth results in the formation of butterfly- to star-shaped secondary xylem bundles (cf. Fig. 1) embedded in phloem tissue. The most interesting phenomenon is the reactivation of the connective tissue (procambium?) between the internal phloem and the primary xylem, leading to the formation of lobed bundles in the pith (Plate 2: 8–12), so that the earlier formed secondary xylem ring, are pushed towards the periphery of the growing stem.

In the species studied from section *Heteroblemma* of *Medinilla* the anomalous growth is only slightly different from that encountered in *Kendrickia* (Plate 3:14-19). There are usually more lobes (up to 10). No distinct cambium zones could be localized on the sides of the xylem lobes, bordering the flanges of unlignified tissue. Cell division presumably occurs throughout the tissue of the flanges in a predominantly radial direction. Sometimes radially oriented cambia were noted, producing tangential files of cells against a xylem lobe (Plate 3:14). The xylem lobes have fairly frequent islands or tangential stretches of unlignified tissue within them.

The anomalous growth in *Catanthera*, *Kendrickia* and *Medinilla p.p.* is highly diagnostic, and can easily be detected with the unaided eye in stems thicker than 0.5 cm. The restriction of the phenomenon to the section *Heteroblemma* of *Medinilla* also indicates a taxonomic value, below the genus level.

V e s s e l s. The vessels in the wood of the palaeotropical Melastomataceae have a diffuse distribution, either solitary or in tangential multiples. In the xylem of twigs, and infrequently also in mature wood, some clusters or tangential multiples can be observed as well. The vessels in older stems and mature wood are round to oval in transverse section. In twigs and stems of narrow diameter vessels can be more angular to polygonal in outline. Very narrow elements, associated with the normal multiples, are scarcely present in the wood of genera with a climbing habit (*Catanthera, Diplectria, Dissochaeta*)

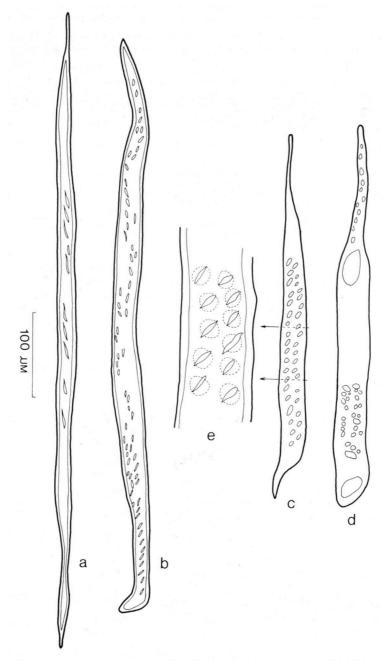


Fig. 2. Camera lucida drawings of the fibre-tracheids and intermediates towards very narrow vessels elements, as observed in the macerations of the wood of *Pternandra caerulescens* (J.C. 1482). — a. & b. fibre-tracheids; c. tracheid; d. very narrow vessel element; e. detail of the pit fields of the tracheid drawn under c.

and *Macrolenes*), and are slightly more common in the wood of *Memecylon* and *Pternandra*. These two genera have a ground tissue composed of fibre-tracheids, and intermediates between these axial elements and narrow vessels occur as well (cf. Fig. 2).

Vessel member length ranges from 260  $\mu$ m to 730  $\mu$ m. The shortest elements are commonly found in *Memecylon* and *Pternandra* (in general between 300 and 450  $\mu$ m, with highest averages up to 500  $\mu$ m). Short elements are also frequent in the tribe *Osbeckieae*. This can partly be explained from ecological influences (see further the chapter on ecological considerations.)

When comparing the range of the average vessel frequencies of the species, the overlap within the genera is such that no diagnostic value can be attached to this character. When comparing genera within tribes, the same arguments can be used. When comparing the range of the vessel member length of the tribes a similar strong overlap is present (cf. Fig. 3A). The average vessel member length can also be presented differently. In Fig. 3B the average is indicated of the average vessel member lengths of the samples studies from a given tribe. To the left and the right twice the standard error is indicated. This total forms the 95% reliability range (95% of any new average calculated for a similar number of samples will fall within the range depicted here for the taxa concerned). In this case a more general representation of the vessel member length is given, and the extreme values causing the overlap, are toned down. The resulting picture facilitates discussions on vessel member length and trends amongst tribes. Perforations are simple in all Melastomataceae studied. Reports in the literature on scalariform perforation plates in *Astronia* (Metcalfe & Chalk, 1950) are probably based on a wrongly identified sample.

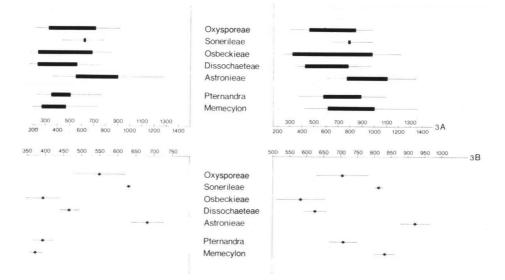


Fig. 3.-A. Diagrammatic representation of the range of the average vessel member length and fibre length for tribes and some genera of the Melastomataceae. (— range of the extreme values; range of the average values). — B. Diagrammatic representation of the 95% reliability limits for the tribes and some genera of the Melastomataceae. \* average of the average range indicated in 3 A; — to the left and to the right twice the standard error.

Perforations are generally present in oblique end-walls; horizontal end walls are also present in the vessels of the species with a climbing habit.

Inter-vessel pits in most genera are arranged in an alternate pattern. Generally the pits are round to polygonal, incidentally some elongate pits can be present (Fig. 4a). In some genera the elongate inter-vessel pits can be rather abundant (Fig. 4b Plate 8:52), sometimes completely covering the common wall.

The longitudinal axis of the pit aperture is not horizontal as is the case in the common opposite and transitional pit patterns, but oblique and frequently curved. The curve of the elongate pits generally follows the arrangement of the alternate pattern, as if the alternate pits are fused. The abundance of the elongate inter-vessel pits seems not correlated with the age of the sample, they are present in both mature and immature wood samples.

Inter-vessel pits with a rather distinct scalariform arrangement are present in part of the palaeotropical Melastomataceae only (Fig. 4c; Plate 6:41). In the neotropical ones a tendency towards such a pattern only incidentally occurs (cf. Ter Welle & Koek-Noorman 1981, this tissue). The term scalariform is applied because almost all inter-vessel pits of a given vessel element completely extend over the common wall. Transitional is used to describe the presence of shorter pits. However, contrary to what is generally observed in transitional patterns one long pit is not replaced by several small pits. Only one shorter pit is present and the neighbouring long pits curve along both sides, to fill the gap. This phenomenon, and the fact that even the scalariform patterns have an oblique arrangement, have induced me to regard these scalariform pits as derived from an alternate pattern with frequent elongate pit (a morphological series illustrated in Fig. 4), rather than to treat them as the traditional primitive type of vessel wall pitting.

The presence of alternate or scalariform intervessel pits is constant in a genus. Only in the genus *Bredia* species are found with either alternate or scalariform/transitional inter-vessel pits. However, the reinstalment of a genus, recently incorporated in *Bredia*,

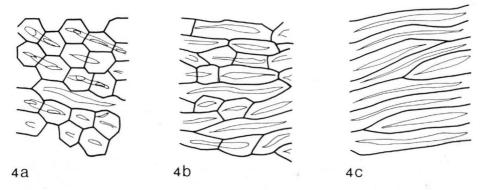


Fig. 4. Camera lucida drawings of some inter-vessel pit fields. — 4a. Alternate inter-vessel pits, most of the pits are polygonal, occasionally some elongate pits are present. 4b. The elongate inter-vessels pits are more abundant than the polygonal pits and frequently curved. The basic alternate pattern can still be recognized. 4c. All pits are elongate, and extend more or less completely over the common wall; some shorter pits are present; the neighbouring pits are curved. This strongly resembles the traditional scalariform pit patterns, but differs in the oblique arrangement of the pits and the curved pits around the shorter ones.

would lead to the removal of all species with alternate inter-vessel pits. The presence of either scalariform/transitional or alternate inter-vessel pits in a given genus can be of diagnostic and taxonomic value on the supra-generic level. It can serve to separate the two groups of genera in the tribe *Dissochaeteae*, a segregation that is also supported by differences in other wood anatomical features. It may turn out to be a valuable character for solving the taxonomic problems in the *Oxysporeae–Sonerileae* complex.

Vessel—ray and vessel—parenchyma pits are generally large and simple, but predominantly half-bordered in *Memecylon. Pternandra* is intermediate in the sense that half-bordered and simple pits are  $\pm$  equally abundant. The arrangement of the pits is more or less correlated with the shape of the cells. Vessel—parenchyma pits and erect ray cells generally show an alternate/opposite to biseriate and scalariform arrangement (scalariform more common in the vessel—ray pits). Reticulate patterns are found in the contacts between vessels and square ray cells; a tendency towards this type can also be found in the infrequent, broad axial parenchyma cells bordering the vessels in the wood of lianas. The half-bordered pit contacts are found in an alternate pattern, with the vessel—parenchyma pits sometimes tending to diffuse and biseriate.

Unilaterally compound pits are infrequent. In some genera the fields sometimes seem to be completely sunken in the vessel wall (Plate 5: 34) because of the reduced thickness of the vessel wall between all pits towards a given ray cell.

Tyloses (rarely sclerotic) and granular or amorphous contents in vessels are sometimes observed, but never abundant. No diagnostic value can be indicated. Vessel elements in some genera have very delicate wall thickenings, on which warty structures are often deposited (illustrated in Van Vliet, 1979).

V e s t u r e d p i t s. Melastomataceae, like all true members of the Myrtales, have vestures in their bordered vessel pits. The type of vesturing is described following Van Vliet (1978). In this family two closely allied forms are present, which in some cases may integrade.

The vesturing in the inter-vessel pits is mostly of type A: the vestures are attached to all parts of the roof of the pit chamber and branch into a compact mass of vestures of  $\pm$  equal thickness completely filling the pit chamber (Plate 4: 20-22). Viewed from the pit floor into the pit chamber this results in a compact mass of bead-like endings of the terminal branches (Plate 4:26). In *Dichaetanthera* the vesturing in the inter-vessel pits is of type B, form 1 (Plate 4:23); to the roof of the pit chamber, near the pit canal, a ring of comparitively thin vestures is attached, pointing into the pit chamber, dichotomizing into slightly thinner branches. Vesturing in some of these inter-vessel pits tends towards type A. Vesturing in the chamber of half-bordered vessel—ray and vessel—parenchyma pits is similar to that in the inter-vessel pits. In the Melastomataceae many of the pits have strongly reduced or no borders. Then vesturing is often absent or present in only a part of the pit chamber (Plate 5: 27, 33, 34). The abundance of the vestures on reduced pit borders shows in several genera a more or less balanced decrease: the vestures form only one ring, attached to the thin remainder of the pit border. Because of the basically dichotomous branching of each individual vesture these pits shows a vesturing that must be described as type B, form 1. Fully bordered vessel pits of these genera still have a type A vesturing.

The bordered pits in the fibre-tracheids of *Memecylon* and *Pternandra* are frequently vestured. In some pits only a few, bead-like vestures are present on the pit chamber roof (Plate 5:32). In others the vesturing is more abundant and the vestures are evenly branched (Plate 5:28). This variation in vesturing as well as some non-vestured fibre pits can be observed in one sample.

Vesturing on pit apertures may also be present. In *Pternandra* these vestures are more abundant over the pit aperture of the vessel—parenchyma pits than over those of the vessel—ray pits, where they are generally only present on the edges of the pit apertures. This difference in abundance of vestures on apertures follows the same pattern as I have described for genera of the Crypteroniaceae, Combretaceae, and some other families (Van Vliet, 1975, 1978, 1979).

The apertures of the vessel to fibre-tracheid pits in *Pternandra* are fully covered with a thick layer of vestures which spread out over part of the vessel wall (Plate 5:30, 31).

In the other genera of the Melastomataceae it is very difficult to differentiate between warts and vestures (see also Van Vliet, 1978). This is the more a problem, since the occurrence of warts on vessel walls with vessel—ray and vessel—parenchyma pit fields is restricted to those parts of the wall, where bordered pits are present (Plate 5:27).

F i b r e s, f i b r e d i m o r p h i s m a n d a x i a l p a r e n c h y m a. With the exception of *Memecylon* and *Pternandra*, all Melastomataceae have fibres of the libriform type. The pits are simple or have minute borders, in diameter rarely exceeding  $2 \mu m$ . In the genera *Pternandra* and *Memecylon* the fibres have distinctly bordered pits (diameter 9  $\mu m$ ) and are thus fibre-tracheids. Generally the walls of the fibres are thin (lumen one to three times the thickness of the wall), but may infrequently also be very thin or of medium thickness. The fibre-tracheids have mostly thick to very thick walls, which are only infrequently of medium thickness.

Septa are found in almost all the genera with libriform fibres, but not in all species or samples. Even in one sample some variation in the occurrence of septa can be observed. Generally only one septum per fibre is found, but in some genera (Astronia, Pogonanthera) 2–3 (sometimes even 3–4) septa are common.

In all genera the fibres have pointed, very rarely minutely branched, tips. Only *Dichaetanthera rhodesiensis* forms an exception, having variously branched and forked or in other ways deformed fibres (cf. Fig. 5).

Fibre dimorphism of a type that was earlier reported for Lythraceae (Baas & Zweypfenning, 1979) and the neotropical Melastomataceae (Ter Welle & Koek-Noorman, 1978) is also present in the greater part of the palaeotropical Melastomataceae (Tables 5, 7 & 8). The ground tissue is formed by 'normal' libriform fibres. Fibres with slightly thinner walls and well developed intercellular spaces (resulting in a more rounded outline of the fibres in transverse section) are present in vague to well-defined bands or tangential arcs of varying width. Fusiform or pleuricellular strands of axial parenchyma are frequently present in these bands, but in frequencies varying from scarce to abundant. The deviating type of fibres is not observed in the first formed secondary xylem, but it soon appears as short tangential arcs of 1–2 cells wide, often forming an aliform to confluent, parenchymalike pattern, in association with part of the vessels only (Plate 8:51). In mature samples the deviating fibres are present in varying patterns: in bands of 2–3 up to 8 cells wide (Plate 9: 54, 57) (widely spaced or not), in tangential patches or in  $\pm$  confluent, parenchyma-like bands (Plate 8:51). Mostly these walls of deviating fibres were hardly thinner than those of the normal fibres, and the bands can only be recognized by the intercellular spaces. Only in woods with fibre walls of medium thickness the differences in wall thickness were such, that with the unaided eye, these bands can be mistaken for parenchyma bands (Plate 9:54).

Axial parenchyma elements are frequently present in the bands of deviating fibres. They can be found as isolated elements, or in radial multiples. In *Dionychia* (twig material only) the parenchyma forms a more or less continuous band of one, rarely two cells, wide, on both sides bounded by one or two rows of deviating fibres.

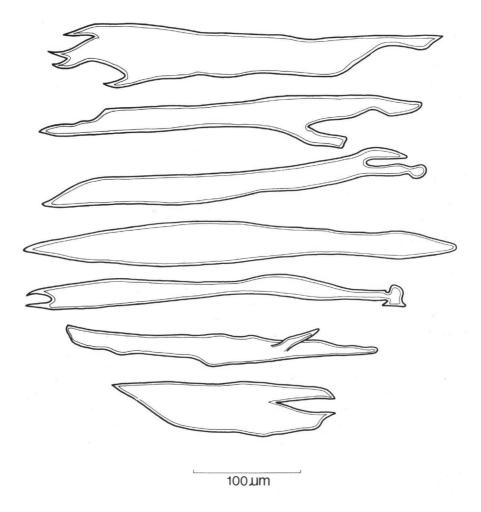


Fig. 5. Camera lucida drawings of several of the peculiar forms of fibres, frequently found in macerated preparations of the wood of *Dichaetanthera rhodesiensis*.

Very distinct gradients from axial parenchyma to deviating fibres were observed. In the bands one often finds a mixture of deviating fibres, axial strands of 2–5 cells (part of the latter often septate), septate fusiform parenchyma, and thin-walled (septate p.p.) fibre elements with pits with a more oval outline and a diameter that decreases when going in the direction of true libriform fibres (Plate 8:53).

Septation in the deviating fibre type is generally similar to that of the normal fibres. Sometimes only the deviating fibres are septate (*Blastus, Dionychia*). A distinct difference in length between normal fibres and the deviating ones was not observed. Baas & Zweypfenning (1979) observed such a difference in the Lythraceae. Intrusive growth is in that family larger (Fibre length/Vessel member length ratio 2 or more) than in the Melastomatoideae (F/V = 1.2-1.5). It seems therefore very likely that the range of the length of the shorter, deviating fibres is covered by that of the normal fibres.

Ter Welle & Koek-Noorman (1981, this issue) treat all expressions of fibre dimorphism (i.e. bands purely composed of deviating fibres, or bands mixed with various amounts of fusiform and strand parenchyma) under the heading pseudo-parenchyma. For reasons of precision I have chosen to describe the occurrence of deviating fibres and of parenchyma under the appropriate headings of fibres and parenchyma.

The relative amount of true parenchyma in the bands of deviating fibres is of little taxonomic significance. For instance in the very closely knit group of Astronidium, Astronia, Astrocalyx and Beccarianthus, the first genus has bands purely composed of deviating fibres, Astronia and Astrocalyx have very little axial parenchyma mixed with the deviating fibres, and in Beccarianthus the associated parenchyma varies from infrequent to frequent. Moreover, the distribution of the deviating fibres throughout the secondary xylem is not constant for a particular genus or species (cf. Melastoma, Medinilla) and is therefore of limited diagnostic and taxonomic value.

I agree with Baas & Zweypfenning (1979) that the morphological series from normal fibre, via thinner-walled (shorter) fibres and fusiform (septate) parenchyma, to normal parenchyma probably reflects a phylogenetic specialization trend. The final stage of this morphological series – apotracheal bands of axial parenchyma – is found in one genus only, *Dichaetanthera*. In the other genera parenchyma is in various quantities present in the bands of deviating fibres, and additionally as scanty paratracheal parenchyma. Only in the lianas a more or less closed ring of parenchyma cells can be found around the vessels. Like in Lythraceae, the condition of scanty paratracheal can be interpreted as the primitive condition for the Melastomataceae. In *Pternandra* and *Memecylon* the paratracheal parenchyma is slightly more abundant than in the *Melastomatoideae*. The resulting vasicentric to aliform and confluent patterns may be interpreted as a specialization.

R a y s. The composition of the rays of the palaeotropical Melastomataceae shows an interesting diversity which is only partly of diagnostic value.

The rays in *Memecylon* are typically heterogeneous II (according to Kribs' definitions of 1950). The multiseriate parts (up to 5 cells wide) are composed of procumbent cells, bearing tails of erect cells of more than 2 (up to 8) cells high. Part of the rays have tails of only one cell high, and must be referred to as heterogeneous III. The uniseriate rays are composed of erect cells only.

The other genera also show a considerable variation in the ray tissue, but are never heterogeneous in the sence of Kribs' definitions nor are the they truly homogeneous. The twig material studied invariably showed uniseriate rays, composed of erect cells only. Branch material studied from genera of the *Sonerileae* and *Oxysporeae* (table 8) has uniseriate rays of erect cells, but also biseriate rays and in the latter the ray cells tend to be of a more squarish shape.

The mature wood of the genera of the Osbeckieae (Table 8; Plate 7:44), the Astronieae (table 5; Plate 9:56, 59), the Medinilla-alliance of the Dissochaeteae (table 7; Plate 3: 19), and of Pternandra (table 5, Plate 10:61) almost all have uniseriate rays, largely composed of erect, square and weakly procumbent cells; small biseriate portions are infrequently present, and more common in some samples studied of the Osbeckieae.

The genera of the *Dissochaeta*-alliance of the *Dissochaeteae* show a distinct tendency towards multiseriate rays, when going from immature wood to mature wood. Rays can become up to seven cells wide and are made up of square and weakly procumbent and infrequent erect cells.

In the uniseriate rays of the mature wood (small biseriate portions are infrequently present) the erect cells are more abundant, but infrequent square or weakly procumbent cells also occur. The variation in ray type lends itself very well for taxonomic and sometimes also diagnostic purposes. The differences do, however, not necessarily deny mutual affinities between the taxa concerned. An evaluation of the phylogenetic value of this range of variation in rays is made for the family as a whole (Van Vliet et al., 1981, this issue). Referring to this paper it suffices to mention here that the heterogeneous II type of ray can be interpreted as the primitive condition for the family. One phylogenetic development from this ancestral type, involving reduction and paedomorphosis, presumably resulted in the presence of uniseriate rays of square and erect cells in mature wood. The further widening of rays (e.g. in *Dissochaeteae*) can also be interpreted as a more derived condition, being the result of an opposite phylogenetic trend, which still is partly recapitulated in the ontogeny of individual stems.

Crystals and other inclusions. Until recently crystals were not observed for this family, but the wood of only a limited number of genera and species was ever studied. Recent studies on neotropical Melastomataceae revealed that crystals are not completely wanting (Ter Welle & Mennega, 1979; Koek-Noorman et al., 1979; Ter Welle & Koek-Noorman, 1981, this issue) and also in the palaeotropical Melastomataceae crystals are not completely absent.

In one species of *Bredia*, *B. tuberculata*, raphides are present in the axial parenchyma (Plate 6:38). The unique occurrence of this very unusual crystal type in dicotyledonous wood is very noteworthy, and might be of significance as the expression of a relict character yet indicating affinities with families such as Onagraceae, possessing the crystals in many of their representatives.

Files of up to 4 idioblasts, containing large druses are infrequently present in the axial parenchyma of *Dichaetanthera cordifolia* var. *reticulata;* oval to rounded crystals are scarce in the axial parenchyma of *D. rhodesiensis;* crystals are absent from the wood of a third species studied from this genus, nor was their presence reported by Normand (1960) for the same species.

Idioblasts containing druses were observed in the patches of thin-walled tissue, formed in the anomalous secondary xylem of *Kendrickia* and *Catanthera*.

Large elongated crystals are common in the parenchyma of the axially included strands of phloem in the wood of *Pternandra* and *Memecylon* (Plate 10:62), and may also occur in the xylem parenchyma surrounding the phloem strands.

Silica was not observed in this family, nor has it been reported in the literature.

The ray cells of *Dichaetanthera rhodesiensis* contain large, dark staining globular bodies which could not be removed after treatment with domestic bleach. A study with the scanning electron microscope showed that these bodies had granular surfaces (Plate 5:35). Their nature could not be established.

### LIANAS VERSUS TREES AND SHRUBS

Various types of anomalous growth have been recorded for lianas (cf. Obaton, 1960, Schenck, 1893). Some of these anomalies are already discussed in an earlier chapter. Axially included phloem, common in many lianas, is in this family restricted to two genera (*Memecylon, Pternandra*) composed of erect shrubs and trees only.

Earlier studies (cf. Van Vliet, 1979) have demonstrated quantitative wood anatomical differences between lianas and relatives with an erect habit. From table 3 it appears that the climbing representatives of the tribe *Dissochaeteae* have wider vessel elements in lower frequencies than relatives from the same tribe with an erect habit. Similar to observations in Combretaceae (van Vliet, 1979) the lianas have longer vessel elements (fibre length is hardly different). This is contrary to findings by Carlquist (1975) who suggested that lianas have shorter vessel elements, in order to offer a better resistence to collapse through even only moderate negative pressures. In Combretaceae this deviation may find its basis in the drier habitats of the erect representatives. In the comparison in table 3, only *Medinilla* species are included. Several of the erect species have an epiphytic habit. Because of the precarious water availability, this may result in change in the wood anatomy, also found in trees from dry sites. Ecological data on the samples studied here were, unfortunately, too limited for a sufficient support of this suggestion.

In table 3 also the quantitave values are listed for the species from the Oxysporeae with a climbing (Kendrickia only) or erect habit. The conclusions are more or less similar to those found in the Dissochaeteae as far as vessel frequency and vessel diameter are concerned, differences in element length are not present.

 Table 3 – Quantitative features of lianas compared with their erect relatives, presented for

 Dissochaeteae and Oxysporeae separately.

 Data are presented as the range of the average values of the individual samples.

	Disso	chaeteae	Oxy	sporeae
	Dissochaetinae (climbers)	Medinillinae (erect)	Kendrickia (climber)	other genera (erect)
vessel frequency/mm <sup>2</sup>	8-22	41-45	33	32-66
vessel diameter in µm	120-250	46-85	100	39-88
vessel member length in $\mu m$	410-620	330-410(-600)	550	330-710
fibre length in $\mu m$	490-690	460-610(-820)	720	490-830

### ECOLOGICAL ASPECTS

The role of the ecology in relation to the wood anatomy has, in recent years been a subject of increasing importance in wood anatomical research (Baas, 1973, 1976; Van der Graaff & Baas, 1974; Van der Oever et al., 1981; and Carlquist, 1975, 1977).

One of the ecological trends to be discussed here is the alleged theory that a decrease in moisture availability corresponds with a decrease in vessel member length.

Since collecting data accompanying the wood samples were insufficient, 14 samples of 12 species from *Memecylon* (incl. *Spathandra* and *Warneckea*) were arranged in three groups of decreasing moisture availability on the basis of ecological data from the literature (Bremer, 1979; Hutchinson & Dalziel, 1954; Perrier de la Bathie, 1951; Ridley, 1922; Wickens, 1975). The ranges of vessel frequencies in each of these groups were rather similar. Rain- and swamp forests: 320–380  $\mu$ m; shaded forests, lowland forests, secondary woods and thickets: 270–440  $\mu$ m; sandy open spots and dry spots: 260–350  $\mu$ m. In this case it can only be concluded that the above mentioned trend is not clearly manifested in the average vessel member lengths of *Memecylon*.

The differences in altitudinal distribution of the species studied (from sea level up to 1200 m) were too small to be expressed in substantial differences in vessel element length (see also Van den Oever et al., 1981).

Environmental conditions may very well form the cause for the variation in vessel member length, observed in some genera of the Osbeckieae.

The ecological data of the species concerned were obtained from Perrier de la Bathie (1951) and Wickens (1975). Quantitative data are presented in table 2. In the genus *Dichaetanthera*, *D. rhodesiensis* from rocky, laterite hills, has much shorter vessel members than the two other species from moist forests. In *Dissotis* both species studied are from fairly high altitudes, but *D. glandulicalyx* with the shorter vessel members is from open vegetations (less mesic), *D. polyantha* occurs in forests.

In *Melastoma* there is little variation and values closely correspond with those for the more xeric species of *Dichaetanthera* and *Dissotis*. Perhaps in *Melastoma* altitudinal influences play an additional role, because M. sanguineum occurs at relatively high altitudes (Ridley, 1922). Other ecological data were unfortunately not available. For reasons explained by Van den Oever et al. (1981) the Melastomataceae would not lend themselves well for an analysis of altitudinal and latitudinal trends.

# CLASSIFICATION OF THE PALAEOTROPICAL MELASTOMATACEAE

The overall taxonomy of the family has hardly received any detailed attention since Cogniaux (1891) and Krasser (1893). Bakhuizen van den Brink (1943) published a monograph on the Malesian representatives, but the material he studied was limited because of the war conditions. The classification, as presented by the above authors, with a few minor additions by others (cf. table 4), will serve as a framework, with which a classification of this family based on wood anatomy alone will be compared.

T a x o n o m i c a l l y r e l e v a n t c h a r a c t e r s. Wood anatomical characters with a very restricted distribution such as the raphides in *Bredia tuberculata*, clustered crystals in *Dichaetanthera cordifolia* var. *reticulata*, or globular bodies in *D*. Table 4 – Classification of the genera of the palaeotropical Melastomataceae studied wood anatomically, following Krasser (1893) and Gilg (1897) with additions and some modifications by other authors,

Subfamily Memecyloideae Tribe Memecyleae	Memecylon.
Subfamily Astronioideae	
Tribe Kibessieae1)	Pternandra,
Tribe Astronieae	Astrocalyx <sup>2</sup> ), Astronia, Astronidium, Beccarianthus <sup>2</sup> ).
Subfamily Melastomatoideae	
Tribe Dissochaeteae	Catanthera <sup>2</sup> ), Creochiton <sup>3</sup> ), Diplectria, Dissochaeta, Hypenan- the <sup>2</sup> ), Macrolenes, Medinilla, Omphalopus, Pachycentria, Phaeo- neuron, Plethiandra <sup>4</sup> ), Pogonanthera.
Tribe Sonerileae	Anerincleistus, Barthea, Campimia (Nayar, 1972), Creaghiella, Driessenia, Gravesia.
Tribe Oxysporeae	Allomorphia, Blastus, Bredia, Kendrickia, Oxyspora, Poikilo- gyne <sup>2</sup> ).
Tribe Osbeckieae	Amphorocalyx, Dichaetanthera, Dionychia, Dissotis, Melastoma, Tristemma.

1) Kibessia is reduced to Pternandra (Maxwell, 1981).

- 2) Bakhuizen van den Brink, 1943.
- Creochiton has also been placed in tribe Astronieae of subfamily Astronioideae (Mansfeld, 1926; Bakhuizen van den Brink, 1943). Recent opinions are, however, in favour of Krasser's decision.

4) Krasser placed *Plethiandra* in the same tribe as *Pternandra*. This decision has never been followed and is also in conflict with wood anatomical evidence.

*rhodesiensis* can obviously not be used for suprageneric classification. Nor can an identical deviation of a certain character state be used to curtail its taxonomic value. Characters which are of importance in search for overall similarities or dissimilarities are the following: fibre type (fibre-tracheids versus libriform fibres); fibre dimorphism associated with parenchyma distribution (scanty paratracheal versus abundant); ray type (heterogeneous II-III versus composed mainly of erect and square cells: uniseriate versus multiseriate); inter-vessel pits (alternate versus scalariform); the ratio of the fibre to vessel member length, absolute average vessel member and fibre length, and axially included phloem.

S u b f a m i l y d e l i m i t a t i o n. The discussion of the subfamily delimitation of the Melastomataceae can be based on the palaeotropical representatives alone. One of the three subfamilies recognized on macromorphological characters, the *Astronioideae*, is fully restricted to the palaeotropics. The other two have a pantropical distribution. The neotropical counterparts, as far as is relevant for this discussion, are not different from the palaeotropical representatives (cf. Ter Welle & Koek-Noorman, 1981, this issue).

Two distinct groups can easily be recognized when using wood anatomical characters alone (cf. table 5). One group consists of two genera only, viz. *Memecylon* and *Pternandra*. These are characterized by a ground tissue of fibre-tracheids, predominantly halfbordered vessel—parenchyma pit contacts, axially included phloem and a significantly deviating vessel member to fibre length ratio. This ratio is graphically illustrated in Fig. 6. *Memecylon* is, on the basis of the fibre to vessel member length ratio, clearly separated from the remainder of Melastomataceae, whereas *Pternandra* occupies a more interme-

Table 5 – Wood anatomical characters of the subfamilies of the Melastomataceae: Melastomatoideae presented by tribal characters, Astronioideae and Memecyloideae by generic characters. Genera arranged as in table 4.	
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	Me	Melastomatoideae	toidea	63		Υ	Astronioideae	ideae		Memecyloideae
						Astronieae	lieae		t	
	Oxysporeae	Sonerilese	Osbeckieze	Dissochaeteae	x{inocal}x	ainortsA.	muibinovteA	suntraineoooal	prbnpmsig	иоүлээшэүү
material1) habit2)	t/b/m s/l	t/b s/tl	t/m s/tl	t/m s/1/e	t/m tl	EΞ	t/ tl	t B	₽ ↔	E +
inter-vessel pits alternate	0	0 <sup>3</sup> )	×	o	×	×	×	x3)	×	×
opposite	<u>)</u>	I	1	I	I	I	I	I	1	I
transitional	<u>)</u>	<u>)</u>	1	(o)	I	I	ł	I	1	I
scalariform	•	x4)	I	0	1	ī	I	I	ļ	I
vessel-ray and vessel-parenchyma pits	.4)	;	;	,	;	;	;	,	9	
predomination sumpre half-bordered	(f)	<b>K</b>	<b>&lt;</b> 1	<b>×</b>	<b>×</b> 1	<b>x</b> I	<b>K</b>	× I	ő ×	×
scalariform to transitional and	;	:								
also alternate/opposite	x4)	<b>x</b> 4)	×	×	×	×	×	×	1	ı
alternate/opposite	03)	(FO	1	I	I	I	i	1	0	0
fibres				:						
dimorphous	×	( <del>4</del> )	•	x4)	×	×	×	×	1	I
libriform only	I	( <u></u>	0	0 <u>3</u> )	ł	I	I	I	I	ı
fibre-tracheids only	I	I	I	I	I	1	ł	I	x	×
septate	0	0	•	×	×	×	0	×	I	ı
thin-walled	×	×	×	×	×	×	×	×	1	I
thick-walled	1	1	I	I	I	I	I	I	x	×
more rounded fibres		÷								
in narrow tangential arcs	( <del>)</del> (	£,	0	0	I	1	I	I		I
in widely spaced bands of $I-2$ cells wide	(00	60)	•	•	1	ı	1	1	ł	I
in bands 4–12 cells wide	I	I	ı	0	×	×	×	×	1	1
only bordering axial parenchyma bands	1	I	0	1	I	I	I	1	ŀ	I

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parenchyma										
scanty paratracheal	×	×	×	×	×	×	×	×	×	0
aliform-confluent	I	I	I	05)	1	I	I	I	I	0
apotracheally banded	I	I	0	r	I	l	T	I	1	I
rays ·										
uniseriate, composed of erect cells only	•	×	0	0	×	×	×	×	x	1
1- & 2-seriate, composed of square and weakly										
procumbent cells	0	1	0	o3)	1	I	I	I	I	I
1-7-seriate, composed of square and weakly										
procumbent cells	I	I	I	0	I	ı	ı	1	1	1
heterogeneous II	1	I	I	1	I	I	ı	1	I	×
radial intercellular spaces	I	I	<b>0</b> 3)	I	I	I	I	I	I	ł
axially included phloem	I	I	1	1	1	ı	I	1	×	×
radially included phloem	1	I	I	0	I	I	I	I	×	0
raphides in axial parenchyma	o5)	I	l i	ł	I	I	1	I	I	I
clusters in axial parenchyma	I	I	05)	1	I	I	ı	I	ţ	I
Υριστικά την			: : :							

x = character present in all samples studied; o = character present in only part of the samples studied; - = character absent; () = character scarcely present.

m = mature sample, diam. > 5 cm; b = branch, diam. 1-5 cm; t = twig, diam. < 1 cm.</li>
 t = tree; tl = small tree; l = liana; s = shrub; e = epiphytic shrub.
 present in one genus only.
 absent from one genus.
 present in one species only.
 simple pits also present.

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diate position. This ratio difference, as well as wood anatomical differences mentioned above, remains equally consistent when all Melastomataceae are compared for this character (cf. Van Vliet et al, 1981, this issue). *Memecylon* itself can be recognized by its aliform to confluent parenchyma and the typically Heterogeneous II-III rays. *Pternandra* has scanty paratracheal parenchyma, frequent simple vessel to ray pits, and uni- to biseriate rays composed of square to erect cells. These three characters are of common occurence in the remaining Melastomataceae, and may emphasize the intermediate position of *Pternandra*. Both genera show a strong tendency towards a solitary arrange-

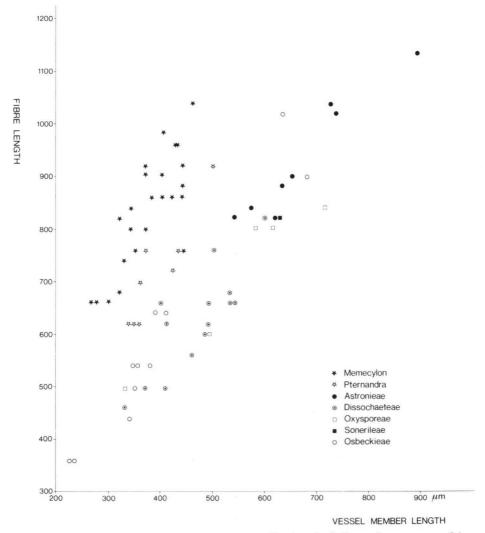


Fig. 6. Average vessel member length plotted against fibre length of tribes and some genera of the Melastomataceae.

ment of the vessels, having percentages of solitary vessels that are generally over 80%.

The other genera of the Melastomataceae have libriform fibres (frequently dimorphous), predominantly large and simple vessel—ray and vessel—parenchyma pits, and no axially included phloem. Rays vary in width from uniseriate to 7-seriate, but are always composed of erect to square and, less frequent, procumbent cells; erect cells tend to be more dominant in the narrow rays, the weakly procumbent cells in the wider rays. Parenchyma is scanty paratracheal. In two genera parenchyma is also apotracheally banded, but this must most likely be interpreted as a further phylogenetic specialization through fibre dimorphism.

The two groups of genera show an evident difference in the structure of their wood. Its seems therefore logical to divide the family Melastomataceae into two subfamilies. One, the *Memecyloideae* is composed of *Memecylon* and *Pternandra* from the palaeotropics, and also includes the neotropical genus *Mouriri*. All the other genera belong to the Melastomatoideae.

In the traditional subdivision of the family, based on macromorphological characters (cf. table 4) the subfamily *Memecyloideae* consists of *Memecylon* and *Mouriri* only. *Pternandra* was always included in the subfamily *Astronioidea*, together with the genera of the tribe *Astronieae*. The differences in the wood anatomy of these two taxa are, however, of such magnitude that I can see no reason to retain *Pternandra* and the *Astronieae* in the same subfamily. I think the differences are consistent enough to place *Pternandra* and *Memecylon* together with *Mouriri* in one taxon. This taxon must have the same status as the remaining Melastomataceae. The same proposition was already made by Van Tieghem (1891) almost a century ago, on the basis of anatomical evidence of leaves and twigs from more than 120 genera.

Janssonius (1950) was of the opinion that the wood anatomical differences between the Melastomataceae he studied were consistent enough to raise the two groups to family rank. However, wood anatomy alone cannot be decisive in this matter; a comparison with other differential characters seems appropriate. The most relevant macromorphological characteristics of the Melastomataceae are listed in table 6. Those most frequently used

	Memecyloideae	Astroni	oideae	Melastomatoideae
		Pternandra	tribe Astronieae	
embryo number of seeds in	large	small	small	small
the fruit	15	many	many	many1)
type of fruit	berry	berry	capsule	capsule/berry
dehiscence of anthers	longitudinal slit	longitudinal slit	longitudinal slit	terminal pore
number of carpels	1-5	4	2-8	2– ∾
placentation	subbasal and axial <sup>2</sup> )	parietal	subbasal	axial
venation	penninerved3)	curvinerved	curvinerved	curvinerved

 Table 6 – Some of the macromorphological characters, used for the subdivision of the family Melastomataceae

1) 5 large seeds present in the Miconieae p.p. (neotropical).

2) subbasal in Memecylon, axial in Mouriri (neotropical).

3) few species are curvinerved, mostly assigned to the satellite genera Spathandra and Warneckea.

to separate the *Memecyloideae* from the remaining Melastomataceae are: size of the embryo, number of seeds in the fruit, and the venation. Because of various transitions found in both groups the two taxa are only rarely raised to family rank. *Memecyloideae* and *Pternandra* have berries for fruits, *Astronieae* capsules, *Melastomatoideae* capsules or berries. Characters that may serve to affiliate *Pternandra* to the *Astronieae* are dehiscense of the anthers and number of ovaries. The type of placentation may point to affinities between *Memecyloideae* and *Melastomatoideae*.

When considering the macromorphological and wood anatomical evidence, my choice for two subfamilies would seem a good combination of the available character sets. The *Melastomatoideae* are macromorphologically hardly more heterogeneous and the new subfamilies are wood anatomically far more coherent. The transfer of *Pternandra* to the subfamily *Memecyloideae* and of the tribe *Astronieae* to the subfamily *Melastomatoideae* implies the abolishment of the subfamily *Astronioideae*. On the grounds of their macromorphology, and in the case of *Pternandra* also of the radial phloem strands, both *Pternandra* and *Astronieae* would merit a tribal status in their new subfamily positions.

A family status for *Memecyloideae* (Memecylaceae – consisting of *Memecylon* and *Mouriri* only) as advocated by Airy Shaw (1973) and Lowry (1976) cannot be supported because of the obvious wood anatomical link of *Pternandra* with those two genera on the one hand, and the convincing macromorphological resemblance of this genus to the *Astronieae* of the *Melastomatoideae* on the other.

### TRIBAL CLASSIFICATION OF THE MELASTOMATOIDEAE

The palaeotropical genera of the Melastomataceae (*Memecylon* and *Pternandra* excepted) are classified in five tribes, all belonging, as I have advanced above, to the subfamily *Melastomatoideae*. The tribal delimitations will be discussed below.

### Tribe ASTRONIEAE

The four genera of this tribe (Astrocalyx, Astronia, Astronidium and Beccarianthus) cannot easily be separated from each other wood anatomically (cf. table 5 and the descriptions). All have alternate inter-vessel pits, clearly distinguishable bands of deviating fibres (in which axial parenchyma is mostly scarce or wanting), scanty paratracheal parenchyma and uniseriate rays (also in thick branches and stem samples). Vessel members and fibres are comparitively long, their values have an overlap with only very few species from other tribes (cf. Fig. 3). An unidentified sample can rather easily be designated to this tribe on the basis of the above mentioned wood anatomical characteristics.

For a discussion on the position of Creochiton: see under tribe Dissochaeteae.

### Tribe DISSOCHAETEAE

On wood anatomical characters the tribe *Dissochaeteae* can be divided into two groups (cf. table 7). One group contains all the genera with a scandent to lianous habit. Their wood is characterized by alternate inter-vessel pit, vessel elements with a wide diameter

Dissochaeteae.
tribe
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s of
character
anatomical
- Some wood
Table 7

Dissochaetinae

Medinillinae

Pogonanthera	x   s t	* ***	×     ×+    + !
Plethiandra	x   « +	× ××0	X I I X + I I + I
pittn92VA2nA	×   ∞ +	× ×××	🗙     ×+    +
əųtuvuədAH	+ ∞   ×	* ***	×     × +     +
pllinib9M	m/t ep ×	× ×××	(o) x + x + x + x + x + x + x + x + x + x +
Pseudodiszochaeta	+ % × I	× ×××	×   ×+     +
นงเทจนงจชนุป	+ × ×	* ***	×     × +     +
sndojvydwO	₩ ×	× ×××	×     ×+    +
ร <b>อก</b> รโองวอM	- × 1,t	× × × ×	× ×+   ×+ ×
Dissochaeta	n∕t − × 1	× ×××	+ × × +   × × ×
Diplectria	m/t sc/l - x	× ×××	×
notihoosiD	I X S +	* ***	0 0   × +   i +
atanthera		× ×   ×	× ×     ×
	material) habit2) inter-vessel pits alternate scalariform vessel-rav and vessel-narenchyma pits	predominantly simple <sup>3</sup> ) alternate/opposite to transitional and scalariform fibres dimorphous septate	rounded fibres in tangential arcs in bands of 1-2 cells wide in bands up to 11 cells wide parenchyma scanty paratracheal rays uniscriate 1-& 2-scriate 1-7-scriate erect cells only erect, square and weakly procumbent cells

# x = character present in all samples studied; o = character present in part of the samples only; - = character absent; () = character only scarcely present; + = character only present in twig material.

m = mature sample, diam. > 5 cm; b = branch, diam. 1-5 cm; t = twig, diam. < 1 cm.</li>
 s = shrub; sc = scandent shrub; ep = epiphyt; 1 = liana.
 vessel-ray pits more frequently scalariform and transitional, vessel-parenchyma pits more frequently alternate/opposite.
 weakly procumbent cells scarce.

(probably due to the climbing habit) and - in the mature samples - rays of up to 7 cells wide. The other group contains, apart from several taxa with a shrub-like habit, the epiphytic representatives of this family. Their inter-vessel pits have a scalariform arrangement, the vessels are more narrow and more abundant, rays are in the mature samples of *Medinilla* not wider than biseriate.

Plethiandra was formerly (Krasser, 1893) placed in Kibessieae of the subfamily Astroniodeae. The scalariform intervascular pits are not in agreement with a position there. The position in the Dissochaeteae is more in accordance with wood anatomy.

Krasser (1893) and more recently Nayar (1973) and Veldkamp (1978b) placed *Creochiton* in this tribe. A position that seems well in accordance with the wood anatomy. Bakhuizen van den Brink (1943) and Mansfeld (1926) optioned for a position in the subfamily *Astronioideae*. A definite conclusion based on wood anatomy is very difficult, because only twig material was available for this study. The occurrence of biseriate rays in the immature wood of two of the four species studied (and which are likely to broaden in the mature samples) points to a position in the *Dissochaeteae*, since *Astronieae* have exclusively uniseriate rays. A position near *Pternandra* is not possible because of the many wood anatomical differences (tables 5 & 7).

Catanthera (syn: Hederella) was placed in the Dissochaeteae by Gilg (1897); Mansfeld (1926) included this genus in Medinilla. Bakhuizen van den Brink (1943) refered it 'with hesitation' also to Medinilla. Wood anatomically Catanthera differs from Medinilla and its allies in the alternate intervascular pitting and the absence of dimorphous fibres. Rays in Catanthera are uniseriate, even in the thicker samples. In this, Catanthera is more like Medinilla than like the other genera of the Dissochaeta-alliance, which have distinct multiseriate rays (up to 7 cells wide). Anomalous growth is also found in both genera, though of a somewhat different type. In Catanthera the stems are made up of many lobed xylem bundles, embedded in phloem. In the species of the section *Heteroblemma* of Medinilla, the stems have a lobed structure as well. Here, however, the one xylem cylinder is traversed by radial flanges of unlignified tissue. The cambium is not continuous along the sides of these flanges, and in this the anomalous structure differs from that found in Catanthera (see also the chapter on anomalous growth). However, the difference in secondary growth between the section Heteroblemma and the remaining Medinilla species is in my opinion so important that a subgenus status for the section seems fully justified.

The subfamily Melastomatoideae is, as I have mentioned before, rather homogeneous in the greatest part of its wood anatomy, as is also the case in the neotropical counterparts. The differences mentioned above may therefore very well serve to characterize two different tribes. The discussion on the taxonomic position of Catanthera and Medinilla p.p. is on the other hand indicative for very close affinities between the two taxa. A division of the tribe Dissochaeteae in subtribes Dissochaetinae (Catanthera, Creochiton, Diplectria, Dissochaeta, Omphalopus, Phaeoneuron, Pseudodissochaeta) and Medinillinae (Medinilla, Hypenanthe, Pachycentria, Plethiandra, Pogonanthera) seems inevitable, although from the wood anatomical point of view, a tribal status for each subtribe can also be defended.

Nayar's suggestion (1973) to separate Dissochaetinae into Creochitoninae (Creochiton and Eisocreochiton) and Dissochaetinae (remaining genera) does not find support in the

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wood anatomy nor in macromorphology (Veldkamp, 1978b). The recognition of subtribes Diplectrinae (Diplectria only) and Dissochaetinae (Maxwell, 1980b) is neither supported by wood anatomy.

The intimate relationship between *Catanthera* and section *Heteroblemma* of *Medinilla* suggest a common ancestral history. Such a derivation is difficult to visualize in terms of wood anatomical specialization, because it would imply the phylogenetic development of normal secondary growth from highly complex anomalous growth. It is much more likely that these anomalous growth patterns represent end points of separate phylogenetic specialization. The deviating (less specialized) ray type of *Catanthera*, compared to the broad rays of the other *Dissochaetinae*, is probably also a consequence of the anomalous growth.

### Tribe OSBECKIEAE.

This tribe is rather homogeneous in its wood anatomical characters (cf. table 8) but also the only taxon in which banded axial parenchyma is found (*Dichaetanthera* and *Dionychia*). Fibre dimorphism, present in the remaining genera of the Osbeckiae, is also observed in *Dionychia*, where the deviating fibres border the bands of parenchyma. Although axial parenchyma is frequently observed in the bands of the deviating fibres, sometimes even forming the majority of elements in the bands, this is the only example of a transition from bands of rounded fibres with large intercellular spaces between them to bands wholly composed of axial parenchyma. Fibre dimorphism was not observed in *Dichaetanthera* and *Tristemma*, but of the latter genus only one twig sample was studied. Comparison between twig material and mature sample (*cf. Medinilla*) indicates that fibre dimorphism can be absent from twigs but present in mature samples.

The presence in some genera of bands fully composed of axial parenchyma may seem an exception when considering the palaeotropical Melastomataceae only, but it is present in many of the neotropical tribes (cf. Ter Welle & Koek-Noorman, 1981, this issue). In the tribe *Merianieae* fibre dimorphism is even comparatively rare.

Retaining the tribe Osbeckieae in its present circumscription seems not in conflict with wood anatomy. The differences in the presence of the axial parenchyma bands can be interpreted as a specialization within the tribe.

### Tribes OXYSPOREAE and SONERILEAE.

Both Oxysporeae and Sonerileae are somewhat heterogeneous in their wood anatomy (table 8). Part of the genera have scalariform inter-vessel pits, the remainder has alternate inter-vessel pits. The rays are uniseriate in twigs, branches and stems, and are composed of erect and square cells only. Only Oxyspora has uni- and biseriate rays with frequent square and weakly procumbent cells. In Bredia both types of inter-vessel pits are present, due to the injust incorporation of the genus Tashiroea (see also description and note of Bredia).

Using wood anatomical characters alone, Blastus and Bredia p.p. should be transferred

			Oxysporeae	oreae		1		S I	Sonerileae	leae		I			Osbeckieae	kieae		
	<b>n</b> ihq <b>r</b> omollA	sutenia	Bredia	Kendrickia	proq2vx0	9nv8olihioA	sutsi9ləni19nA.	Barthea	<b>n</b> imiqma)	Creaghiella	Dinseror D	aisəvarə	xAlbooolohqmA	Dichaetanthera	Dissotis	<b>b</b> ihəynoiQ	pm012pl>M	ammsteinT
material 1) habit 2) interessed vite	с s	ф s	s t	- م	E s	ه ل	ъ	s t	s t	s <del>t</del>	+ v	s <del>1</del>	s t	m s/tl	e s	s t	53	s <del>4</del>
alternate	×	I	07) (70	I	×	×	×	I	I	I	1	I	×	×	×	×	×	×
opposite	×	I	<u>)</u>	ł	ĩ	×	ł	I	I	ł		1	I	I	I	I	I	I
transitional	I	×	<u>)</u>	ž	I	1	I	3	ž	ž	e S	(x)	1	I	ł	ł	1	I
scalariform	I	×	( <sup>7</sup> 0	×	I	I	I	×	×	×		¥	١	I	ł	ı	I	ł
vessel-ray and vessel-parenchyma pits																		
transitional to scalariform and also alternate/opposite	×	×	×	×	I	×	I	×	×	×	×	×	×	×	×	×	×	×
alternate/opposite	I	I	I	I	×	I	×	1	I	1	1	I	I	I	I	I	ι	I
fibres																		
dimorphous	×	×	×	×	×	×	×	ł	×	×	×	0	×	I	×	×	×	I
libriform only	I	I	I	I	I	1	I	×	I	I	1	0	I	×	I	t	1	×
septate	<u></u>	1	I	×	×	S	×	×	×	×	×	0	×	•	1	1	•	(x) <del>4</del> )
more rounded fibres in tangential arcs	×	×	×	05)	I	×	×	I	×	×	×	I	I	I	1	1	1	1
in widely spaced bands of 12 cells wide	I	ł	ł	<b>X</b> 6)	×	I	I	ł	ŀ	I	1	1	×	1	×	I	×	I
only bordering axial parenchyma bands	ls –	I	I	I	I	I	I	1	I	I	1	1	I	I	I	×	ł	ł
parenciryma scanty paratracheal aliform-confluent apotrachealiy banded	×	×II	×II	×	×	×	×II	×II	×II	×	×11	×	×II	×°×	×II	×I×	×II	×

Table 8 - Some wood anatomical characters of the genera traditionally placed in the tribes Oxysporeae, Sonerileae, and Osbeckieae

		W	Memecyloideae	ideae					<b>Crypteroniaceae</b>	roniac	sae		
	Memecylon	noi	Mouriri	iri	Pternandra	tra	Dacty	Dactylociadus	A	Axinandra	p	Crypteronia	ronia
fibre-tracheids	×		×		×			×		×		î	
vessel member length/fibre length ratio	1.72-2.54	.54	1.97-2.48	2.48	1.66-2.02	02	1.33	1.32-1.37	1.5	1.53-1.56	9	1.64-	1.64–1.67
axially included phloem	×		×		×			ı		I		•	
radially included phloem	1		1		×			0		I		'	
parenchyma aliform-confluent	×		•		<u>۞</u>			×		×		'	
vasicentric	<u></u>		0		×			1		i		Ξ	0
apotracheal associated with included phloem	×		×		×			I		1		·	
diffuse and in aggregates	I		్ర	_	1			1		I		î	
rays heterogeneous II	×		•		I			I		×		ĥ	
rays uniscriate, composed of erect to								:					
procumbent cells	I		•		×			X <sup>1)</sup>		1		'	1
x = character present in all or almost all of the samples studied: $o =$ character present in only a part of the samples studied; $- =$ character absent;	the sam	ples stud	ied: o =	characte	r present i	n only	a part c	of the sam	oles stud	died; -	- = cha	racter a	ibsent;
() = character only scarcely present.					•	•	•	•					
1) with frequent strongly procumbent cells.													
rays													
uniseriate, composed of erect cells only x	×	××	I	×	×	×	×	×	×	0	×	•	×
uni- and biseriate, composed of square													
and weakly procumbent cells –	ı	1	×	1	1	I	1	1	i	0	۱ ٥	•	1
intercellular spaces in rays	I	1 1	ł	ι	1	1	1	1	i	0	1	I	I
raphides in axial parenchyma	I	ו 0	I	1	1	I	1 1	1	I	1	1	ł	1

# E

×	1	I	١	I
0	0	I	I	I.
×	ı	1	ı	I
•	0	ı	ı	1
0	0	0	1	•
×	I	i	I	I
×	I	I	I	I
×	I	ł	I	I
×	I	I	I	1
×	I	ł	I	1
×	I	I	I	I
×	ł	I	١	I
×	ł	ι	1	I.
I	×	ł	I	I
×	I	I	I	I
×	1	I	0	I
×	I	I	I	I
×	I	I	1	I
rays uniseriate, composed of erect cells only uni- and biseriate, composed of square	and weakly procumbent cells	intercellular spaces in rays	raphides in axial parenchyma	clusters in axial parenchyma

x = character present in all samples studied; o = character present in part of the samples only; - = character absent; () = character scarcely present.

m = mature sample, diam. > 5 cm; b = branch, diam. 1-5 cm; t = twig, diam. < 1 cm.</li>
 s = shrub; t = small tree; l = liana.
 s = shrub; t = small tree; l = liana.
 vessel-ray pits mostly scalariform and transitional; vessel-parenchyma pits frequently alternate/opposite.
 only when bordering vessels or axial parenchyma.
 in twig material only.
 up to 12 cells wide.
 all species formerly assigned to *Tashiroea*; transitional/scalariform in the remaining species of *Bredia*.

to Sonerileae; Anerincleistus would be better placed in Oxysporeae (although a position in the Osbeckieae would also be in accordance with wood anatomy).

Bakhuizen van den Brink (1943) and C. Hansen (private communication) stated that *Oxysporeae* and *Sonerileae* can only be doubtfully separated since there are many resemblances between individual genera. These do, however, not parallel similarities in wood anatomy. The example of *Bredia* has already been mentioned; *Blastus* (scalariform inter-vessel pits) is in seed characters very similar to *Allomorphia* (alternate inter-vessel pit).

On the basis of the data available from this study I can only conclude that there is a striking parallel with the situation encountered in the *Dissochaeteae*: there is a difference in the wood anatomy of two groups of genera of one tribe (in this case inter-vessel pits only) where the macromorphological affiliation of the two groups (illustrated by the debate on combination of two genera) indicates a common phylogenetic background.

The conclusion can therefore only be: one tribe (named either Sonerileae or Osbeckieae) divided in two subtribes, each of which can have a tribal status when judged from the wood anatomical point of view. The subtribe Sonerilinae is then composed of Barthea, Blastus, Bredia, Campimia, Creaghiella, Driessenia, Gravesia and Kendrickia (taken the fact that Sonerila has scalariform inter-vessel pits). The subtribe Oxysporinae is composed of Allomorphia, Anerincleistus, Oxyspora, Poikilogyne and Tashiroea.

### TAXONOMIC POSITION OF CRYPTERONIACEAE.

The palaeotropical genera Axinandra and Dactylocladus, formerly included in subfamily Memecyloideae as tribe Axinandreae, were recently transferred to the family Crypteroniaceae (Van Beusekom-Osinga & Van Beusekom, 1975; Airy Shaw, 1973). In earlier papers, dealing with the anatomy of the Crypteroniaceae (Van Vliet, 1975; Van Vliet & Baas, 1975) it has been stated that the available evidence was as yet insufficient to reject or support the wide family delimitation (also including Alzatea from S. America and Rhynchocalyx from S. Africa). Since then more wood anatomical information on Myrtalean families has become available and a reappraissal of the taxonomic position of the Crypteroniaceae and their affinities with Melastomataceae seems appropiate. The taxonomic positions of Rhynchocalyx (in Lythraceae) and of Alzatea (in or near Lythraceae, but also related to Melastomataceae) have been clarified by Baas & Zweypfenning (1979). The discussion will therefore center on Axinandra, Crypteronia and Dactylocladus.

These three genera are wood anatomically characterised by distinct fibre tracheids, and are diverse in a number of other wood anatomical characters (cf. table 9). The wood histology is very different from that of the *Melastomatoideae* which leaves the three genera of the *Memecyloideae* as the only candidates for comparison.

Table 9 clearly shows numerous wood anatomical similarities between individual genera of *Memecyloideae* and Crypteroniaceae. The main difference between the two taxa is the presence of the axially included phloem. This difference considered on its own would seem insufficient to keep *Memecyloideae* and Crypteroniaceae in separate families. *Crypteronia* is the least similar, *Axinandra* and *Dactylocladus* have more links with *Memecyloideae* (also expressed in a tribal status for the two, cf. Krasser, 1893; Gilg,

1897; Bakhuizen van den Brink, 1943). In view of the differences in external morphological characters (cf. Van Beusekom-Osinga & Van Beusekom, 1975) and in the wood anatomy it seems appropriate to maintain Crypteroniaceae in this restricted sense as a subfamily *Crypteroniodeae* in the Melastomataceae. The suggestion for a subfamily status was recently also brought forward by Thorne (1981), who, however, also still recognized the subfamily *Astronioideae*.

### TAXONOMIC CONCLUSIONS.

The wood anatomical diversity in the palaeotropical Melastomataceae is only partly in harmony with classifications as proposed by Cogniaux (1891), Krasser (1893), Bakhuizen van den Brink (1943), and several others. Based on wood anatomy alone, one would prefer a division into two subfamilies, the *Memecyloideae* and the *Melastomatoideae*. The third subfamily, recognized by many students of the family using other than wood anatomical characters, the *Astronioideae*, must be abolished. The two main components of this subfamily, the genus *Pternandra* (including *Kibessia*) and the tribe *Astronieae* are transferred to the subfamilies *Memecyloideae* and *Melastomatoideae* respectively. Of the four other palaeotropical tribes of the *Melastomatoideae*, the Dissochaeteae could be separated into two closely allied tribes, this on the basis of the inter-vascular pit patterns, ray width and average vessel member diameters. Sonerileae and Oxysporeae are heterogeneous in a more or less similar way.

Alternate and scalariform inter-vessel pits are present in the genera of both tribes. A re-arrangement of the genera traditionaly assigned to these two tribes into one tribe, divided in two subtribes, would seem the best solution. The more since the present tribal delimitation is also open to discussion. The Osbeckieae, although heterogeneous in some aspects, can be retained in the present circumscription. Conclusions from a parallel study on the neotropical Melastomataceae (Ter Welle & Koek-Noorman, this issue) fully support the subfamily delimitation proposed by me. The result from their study and mine will, with respect to the consequences for the whole family, be discussed in a separate paper (Van Vliet et al, 1981, this issue). Using wood anatomical characters alone, the following delimitation can be proposed. Only the genera studied in this paper are cited, but the tribes of the Melastomatoideae are composed of a greater number of genera.

Subfamily Crypteronioideae (Axinandra, Crypteronia, Dactylocladus)

# Subfamily Memecyloideae

Tribe Memecyleae (Memecylon)

Tribe Pternandreae (Pternandra)

# Subfamily Melastomatoideae

Tribe Astronieae (Astrocalyx, Astronia, Astronidium, Beccarianthus) Tribe Dissochaeteae

Subtribe Dissochaetinae s.s. (Catanthera, Creochiton, Diplectria, Dissochaeta, Omphalopus, Phaeoneuron, Pseudodissochaeta)

Subtribe Medinillinae (Medinilla, Hypenanthe, Pachycentria, Plethiandra, Pogonanthera). **Tribe Sonerileae** 

Subtribe Oxysporinae (Allomorphia, Anerincleistus, Oxyspora, Poikilogyne, Tashiroea).

Subtribe Sonerilinae (Barthea, Blastus, Bredia, Campimia, Creaghiella, Driessenia, Gravesia, Kendrickia)

Tribe Osbeckieae (Amphorocalyx, Dichaetanthera, Dissotis, Dionychia, Melastoma, Tristemma).

More detailed studies on other character sets are needed to determine whether the classification here proposed can be refined.

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### LEGENDS TO THE PLATES (PHOTOS)

Plate 1 (Photos 1–5). Some micrographs, illustrating the anomalous secondary growth of Kendrickia walkeri. —1. Transverse surface of a stem ( $\emptyset$  4.5 cm) with 4 lobes, two of the lobes (bottom right and left) are splitting to various extent. —2. Transverse section of mature wood, showing normal fibres and irregular bands of fibres with slightly thinner walls, a more rounded outline and frequent intercellular spaces (arrows) (× 85). —3—5. Young stem. —3. Detail of the xylem showing cambial zone. The cambium has formed thin-walled, parenchymatous tissue, including crystalliferous cells instead of normal xylem (× 85). —4. In this slightly older stem a lobe has been formed. The cambium over the zone of parenchymatous tissue (for detail see 5) has been ceased, or strongly decreased its activity. Formation of a new wedge has already started in the lobe. The change in xylem activity has resulted in isolated patches of thin-walled tissue (arrow) (× 33). —5. Detail of the area where the formation of the first wedge starts. The cells are very similar to those formed on the phloem side of the cambium (× 85).

Plate 2 (Photos 6–12). Some transverse surfaces of twigs of the same specimen of *Catanthera* spec., illustrating its peculiar secondary growth. —6. Young twig with undulating outline of xylem cylinder. —7. The difference in division activity has resulted in four distinct lobes. —8. In the four lobes the changing cambium activity is evident. Wedges of different size are visible. Inside the ring of

primary xylem the activity of new cambia is evident. The, in this picture anti-clockwise, initiation of its activity may be correlated with the natural torsion of the winding stem. -9 & -10. The growth activity in inner and peripheral cambia has resulted in the break up of the ring of first formed secondary xylem. -11. In this older stem the activity of the cambium has resulted in many irregularly lobed bundles of secondary xylem. -12. A more detailed picture where the remainders of the ring of the first formed xylem can still be localized (arrows).

Plate 3 (Photos 13–19). Light micrographs, illustrating anomalous growth and the wood anatomy of *Kendrickia* and *Medinilla*. —13. *Kendrickia walkeri*. Transverse section, showing cambial zone on the sides of the xylem lobes ( $\times$  200). —14. *Medinilla lorata*. Transverse section, showing two xylem lobes with a radial flange in between. Note the absence of cambial activity on the sides of the flanges. Compare also with 13 ( $\times$  33). —15. *M. alternifolia* (*Chew Wee Lek 346*). Transverse section, showing cambia with a radial orientation, present in one of the flanges ( $\times$  20). —16—17. *Medinilla lorata*. —16. Transverse section, showing 10 radial flanges ( $\times$  7). —17. Radial section through a flange, showing parenchymatous tissue and idioblasts with clustered crystals ( $\times$  200). —18. *Medinilla magnifica*. Transverse section, showing vessel distribution, very thin-walled fibres in which fibre dimorphism is not evident, and some scanty paratracheal parenchyma ( $\times$  33). —19. Idem. Tangential section, showing uniseriate rays with infrequent small biseriate portions. The rays are composed of erect square and weakly procumbent cells ( $\times$  33).

Plate 4 (Photos 20-26). Scanning electron micrographs of Melastomataceae wood. Illustrating the structure and distribution of the vestures. -27. Pogonanthera pulverulenta. Section through scalariform inter-vessel pit pairs with vesturing of type A, restricted to the pit chamber (× 4200). -21. Catanthera spec. (Jacobs 9080). Section through vessel-parenchyma pits. The vesturing in the pit chamber is of type A, but vestures are also present on the pit canal and vessel wall (see also 24)  $(\times 4200)$ , -22. Blastus cogniauxii. Vessel-parenchyma pits. The elongate vessel pits have only slightly reduced borders. The pit chambers are completely filled with vesturing of type A. Some minute vestures are present on the aperture (× 1750). -23. Dichaetanthera rhodesiensis. Inter-vessel pits with vestures of type B form 1. Small warts are present on the vessel wall ( $\times$  1300). -24. Medinilla alternifolia. Section through scalariform inter-vessel pit pair. Vesturing in the pit chamber is type A. The small, bead-like structures present on vessel wall, pit canal and pit chamber roof can be interpreted as warts (× 8000). -25. Oxyspora paniculata. Inter-vessel pits with type A vesturing in the pit chamber and small bead-like vestures on the aperture, the latter sometimes merging with those of neighbouring pits (arrow) (× 3350). -26. Melastoma sanguineum (Carrick 1475). Inter-vessel pits with vesturing of type A, seen from the pit floor into the pit chamber, pit floor (p) largely removed ( $\times$  4400).

Plate 5 (Photos 27-35). Scanning electron micrographs of Melastomataceae wood. -27. Diplectria conica. Vessel—ray pit field, illustrating that vesturing in the pit and warts on the vessel wall are associated with bordered pits. Both types of structures are absent from the simple pits (× 4600). -28. Memecylon cinnamomoides. Small, minutely branched vestures in the bordered pit of a fibre-tracheid (× 8500). -29. Catanthera spec. (Jacobs 9080). Thin mat of vestures, completely covering the vessel wall (× 830). -30-31. Pternandra capitellata. -30. Part of a vessel wall (see also 31) (× 1600). -31. Detail of 30 (× 4000). -32. Pternandra cordifolia. Fibre-tracheid pits with minute vestures (× 4700). -33. Medinilla crassinervia. Vessel—ray pits, illustrating the variation in vesturing that can be observed in pits with simple or strongly reduced borders; vesturing type A (× 1700). -34. Macrolenes nemorosa var. bancana. Radial section showing pits to procumbent rays; walls of the pits are strongly reduced, creating large, unilaterally compound pit fields (× 420). -35. Dichaetanthera rhodesiensis. Tangential section showing ray cell with globular body with granular surface of unknown composition (× 1030).

Plate 6 (Photos 36-42). Tribes Oxysporeae and Sonerileae -36-37 Oxyspora paniculata. -36. Transverse section (× 33). -37. Tangential section showing the uniseriate rays with or without a small biseriate portion (× 85). -38. Bredia tuberculata. Tangential section showing raphides in axial parenchyma (× 200). -39. Blastus cogniauxii. Transverse section; the narrow tangential arcs of more rounded fibres with intercellular spaces are hardly visible (arrows) (× 85). -40-41. Kendric-kia walkeri. Tangential section, showing scalariform inter-vessel pits, simple vessel-parenchyma pit fields and uniseriate rays or rays with a small biseriate portion, composed of erect to square cells (× 85). -41. Detail of inter-vessel pit field (× 310). -42. Allomorphia racemosa. Tangential section, showing the uniseriate rays, almost exclusively composed of erect cells (mature sample) (× 85).

Plate 7 (Photos 43-48). Tribe Osbeckieae. -43-45. Dichaetanthera cordifolia var. reticulata. -43. Transverse section showing distinct, apotracheal bands of true parenchyma, including some clustered crystals (arrow) (× 50). -44. Tangential section, showing non-septate fibres and uniseriate rays, infrequently with a small biseriate portion, and composed of erect to square cells (× 50). -45. Radial section, showing clustered crystals in idioblast of axial parenchyma and some square and weakly procumbent rays cells (top) (× 200). -46--47 Dissotis glandulicalyx (Newbold & Jefford 1772). -46. Transverse section, showing distinct narrow bands of deviating fibres (× 33). -47. Tangential section, showing uni- and biseriate rays composed of mainly square to weakly procumbent cells and of limited height (× 85). -48. Melastoma sanguineum (Carrick 1475). Transverse section showing vague, tangential arcs of deviating fibres which are more abundant on the growth ring boundery (× 33).

Plate 8 (Photos 49–53). Tribe Dissochaeteae. -49. -50 Dissochaeta beccariana. Transverse section, showing comparatively wide vessel elements and broad and narrow, wavy bands of deviating fibres (arrows) ( $\times$  33). -50. Tangential section, showing the broad rays, composed of square and weakly procumbent ray cells ( $\times$  20). -51. Macrolenes dimorpha. Transverse section of a branch showing the abrupt change from the narrow vessel elements of the first two or three growth-rings to the wide vessel elements, characteristic for the climbing species of the tribe Dissochaeteae. The deviating fibres are scarce in the first formed xylem, forming a more or less aliform-confluent like pattern in older xylem (arrows) ( $\times$  33). -52. Dissochaetea velutina var. velutina. Tangential section showing parts of uniseriate rays and an inter-vessel pit field. The basic alternate pattern can be recognized, but many elongated and curved pits are present, illustrating a transition towards a more scalariform arrangement ( $\times$  85). -53. Diplecteria viminalis. Tangential section, showing uni- and biseriate rays, composed of square cells mainly; a fusiform parenchyma cell with three septa (p) and above this one a parenchyma cell composed of two, septate cells. The very narrow elements to the right of the lower fusiform parenchyma cell can be interpreted as a transition towards a fibre ( $\times$  85).

Plate 9 (Photos 54–59). Tribe Astronieae. -54-56. Ástronia hollrungii. -54. Transverse section, the light coloured patches in the xylem are broad, tangential arcs or bands of deviating fibres (× 20). -55. Detail of 54. The difference in wall thickness between the normal fibres and the deviating fibres is evident. Intercellular spaces are clearly visible (× 200). -56. Tangential section, showing uniseriate rays and alternate inter-vessel pits (× 85). -57-59. Astrocalyx calycina. -57. Transverses escition, showing bands of deviating fibres (× 20). -58. Detail of 57 (× 85). -59. Tangential section, showing uniseriate rays and alternate inter-vessel pits (× 85).

Plate 10 (Photos 60-65). Subfamily Memecyloideae. --60-61. Pternandra echinata. --60. Transverse section showing  $\pm$  solitary vessel arrangement, paucity of the axial parenchyma and holes of the included phloem (× 33). --61. Tangential section, showing the uniseriate rays, composed of erect, square and weakly procumbent cells, and a broader ray, where the hole points to the previous presence of radially included phloem (× 85). --62. Memecylon membranifolium. Tangential section showing the elongated crystals, present in the parenchyma of the bundles of axially included phloem (× 85). --63. Memecylon polyanthemum. Transverse section, showing islands of axially included phloem, vasicentric to aliform parenchyma, and apotracheal parenchyma around the included phloem bundles (× 33). --64. Memecylon polyanthemum. Tangential section showing heterogeneous II-III rays (× 50). --65. Memecylon polyanthemum. Radial section (× 50).

