WOOD ANATOMY, CLASSIFICATION AND PHYLOGENY
OF THE MELASTOMATACEAE

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SUMMARY

A classification of the Melastomataceae, modified on the basis of wood anatomical evidence, is discussed. Three subfamilies (Crypteronioideae, Memecyloideae and Melastomatoideae) are recognized. Astronioideae, recognized in other classifications, are abolished and their constituent genera are classified in Memecyloideae (Pternandra) and Melastomatoideae (four genera of the tribe Astronieae). Wood anatomically Melastomataceae show affinities with a number of Myrtalean families, notably with Lythraceae, Onagraceae and Myrtaceae. The wood anatomy of ancestral 'Protomelastomataceae' is hypothesized and a tentative phylogeny is suggested for the extant subfamilies and tribes.

INTRODUCTION

A detailed account of the wood anatomy of the Melastomataceae has been given in two separate papers dealing with the palaeotropical (van Vliet 1981, this issue) and the neotropical representatives (ter Welle & Koek-Noorman 1981, this issue). In these papers, comprehensive descriptions are presented, as well as discussions on the wood anatomical variation and its bearing on the generic, tribal and subfamily delimitation in their main distribution areas. The synthesis with respect to classification and phylogeny of the whole family is presented here.

CLASSIFICATION OF THE MELASTOMATACEAE

The classification of the Melastomataceae, modified on the basis of wood anatomical evidence is presented in table 1. In the short wood anatomical diagnoses of subfamilies and tribes, exceptions from the general pattern or irrelevant characters of isolated occurrence have been omitted. For the wood anatomical characteristics of some genera of uncertain alliance we refer to ter Welle & Koek-Noorman (1981, this issue). Arguments in favor of the modifications from the traditional classifications are given in our previous papers, and here a brief summary must suffice.

The main aspects in which the classification presented here deviates from previous ones, based on macromorphological characters alone, is the abolishment of the subfamilie *Astronioideae*. The main components of this subfamily, tribes *Kibessieae (Pternandra*

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Table 1 — Synopsis of the wood anatomical characteristics of the Melastomataceae.
(P) = Palaeotropics; (N) = Neotropics.

Subfamily Crypteronioideae	Fibre tracheids; fibre length to vessel member length ratio (F/V) 1.32–1.67; rays heterogeneous, uni- or uni- and multiseriate, composed of central portions of strongly procumbent cells and tails of erect cells; parenchyma vasicentric and diffuse in aggregates or aliform and confluent; vessel–parenchyma and vessel–ray pits half-bordered, in *Dactylocladus* vessel–ray pits also simple.
Axinandra (P)	Av. vessel member length 390–440 μm, F/V 1.53–1.56, parenchyma aliform to confluent, rays heterogeneous II (–III).
Crypteronia (P)	Av. vessel member length 650–900 μm, F/V 1.64–1.67, parenchyma vasicentric and diffuse in aggregates, rays heterogeneous I–II.
Dactylocladus (P)	Av. vessel member length 950–1100 μm, F/V 1.32–1.37, parenchyma aliform to confluent, rays uniseriate, strongly procumbent cells infrequent.
Subfamily Memecyloideae	Fibre tracheids; axially included phloem; F/V (1.66–)1.85–2.56; rays heterogeneous, uni- or uni- and multiseriate, either composed of central portions of strongly procumbent cells and tails of erect cells, or of erect, square and weakly procumbent cells; parenchyma vasicentric, or aliform and confluent; vessel–ray and vessel–parenchyma pits half-bordered, in *Pternandra* vessel–ray pits also simple.
Tribe Memecyleae (P, N)	Av. vessel member length 260–440 μm, F/V (1.72–)1.85–2.56; parenchyma vasicentric to aliform and confluent; rays heterogeneous II(–III) or uni- and multiseriate and composed of erect, square and weakly procumbent cells (*Mouriri* p.p.).
Tribe Pternandreae (P)	Av. vessel member length 350–500 μm, F/V (1.66–)1.85–2.02; parenchyma vasicentric, rays uniseriate and composed of erect to weakly procumbent cells.
Subfamily Melastomatoideae	Libriform fibres; F/V ratio 1.11–1.63(–1.74); rays heterogeneous, composed of erect to weakly procumbent cells, rarely homogeneous; fibres dimorphous (pseudoparenchyma); apotracheal parenchyma as a result from a development from fibre dimorphism present in part of the tribes; paratracheal parenchyma scanty; inter-vessel pits alternate, infrequently scalariform; vessel–ray and vessel–parenchyma pits frequently large and simple.
Tribe Astronieae (P)	Av. vessel member length 540–890 μm, F/V 1.39–1.61, rays uniseriate, bands of deviating fibres without or with scarce axial parenchyma.
Tribe Blakeeae (N)	Av. vessel member length 425–735 μm, F/V 1.14–1.60, rays 1–4-seriate, parenchyma apotracheally banded; clustered crystals frequent.
Tribe Dissochaeteae	
subtribe Dissochaetinae (P)	Av. vessel member length 410–540 μm, F/V 1.20–1.50, vessels with very wide diameter, inter-vessel pits alternate, rays up to 7-seriate, axial parenchyma often vasicentric.
subtribe Medinillinae (P)	Av. vessel member length 330–600 μm, F/V 1.34–1.49, inter-vessel pits scalariform, rays 1–2-seriate.
Tribe Merianieae (N)	Av. vessel member length 390–760 μm; F/V 1.25–1.64, half-bordered vessel–ray and vessel–parenchyma pits also present, rays mostly uniseriate, homogeneous rays scarce, apotracheal parenchyma bands present in most samples, clustered crystals scarce.

(Table 1 continued)

Tribe Miconieae (N)	Av. vessel member length 315–1000 μm, F/V 1.16–1.51, half-bordered vessel–ray and vessel–parenchyma pits also present, apotracheal parenchyma bands scarce, rays mainly uniseriate, megastyloids infrequent.
Tribe Microlicieae (N)	Av. vessel member length 300–510 μm, F/V ratio 1.26–1.34, rays 1–3-seriate.
Tribe Osbeckieae (P)	Av. vessel member length 230–620 μm, F/V 1.32–1.61, apotracheal parenchyma bands infrequent, rays 1(–2)-seriate, clustered crystals infrequent.
Tribe Rhexieae (N)	Av. vessel member length 300–420 μm, F/V 1.07–1.32, rays mainly uniseriate.
Tribe Sonerileae	
subtribe Sonerilinae (P)	Av. vessel member length 550–610 μm, F/V 1.29–1.31, inter-vessel pits scalariform, rays 1–2-seriate.
subtribe Oxysporinae (P)	Av. vessel member length 330–710 μm, F/V 1.17–1.38, inter-vessel pits alternate, rays 1–2-seriate.
Tribe Tibouchineae (N)	Av. vessel member length 300–900 μm, F/V 1.11–1.63(–1.74), apotracheal parenchyma bands scarce, rays uni- or uni- and multiseriate, clustered crystals scarce.

only) and *Astronieae* (four genera) are transferred to *Memecyloideae* and *Melastomatoi-deae* respectively. The main criteria on which this modification is based are difference in fibre type (fibre-tracheids in *Memecyloideae;* libriform fibres in *Melastomatoideae*) and presence (*Memecyloideae*) or absence (*Melastomatoideae*) of included phloem. One might also derive an additional argument, albeit a weak one, from the fibre length to vessel member length ratios. These ratios have been analysed statistically for the whole family: The equality of the mean elements ratios was tested by analysis of variance (F=84.7; df=12 221; p≦0.00005). The outcome of this test allowed for an *a posteriori* simultaneous test procedure using the least significant difference (LSD) criterium in order to detect the actual heterogeneity. The outcome of this test is illustrated in Fig. 1 for LSD values of α=0.01 and α=0.05. The horizontal lines connecting the taxa with a similar mean element length ratio demonstrate that *Melastomatoideae* are at both probability levels seperate from *Pternandra*, *Mouriri* and *Memecylon*. However, *Pternandra* also remains distinct from *Mouriri* and *Memecylon* in this quantitative feature so that it would be misleading to use fibre length to vessel member length ratio as a strong argument in favour of the broader delimitation of the subfamily *Memecyloideae*.

The abolishment of *Astronioideae* was earlier suggested by Janssonius (1950), basing his conclusions on wood anatomical data from some palaeotropical genera, and by van Tieghem (1891) who studied well over 100 palaeo- and neotropical genera.

Other elements in our classification differ less from traditional ones (but for the inclusion of *crypteronioideae* in the Melastomataceae, see van Vliet 1981, this issue). Especially the tribal classification in the *Melastomatoideae* hardly deviates from systems based on macromorphological characters because of the lack of a sufficiently great and patterned wood anatomical diversity in this subfamily. Only in the *Sonerileae-Oxyspo-reae* complex adjustments have been made. The two original tribes have been combined to one tribe composed of two subtribes, each containing genera from both the original tribes. This subtribal separation is based on the difference in inter-vessel pit patterns.
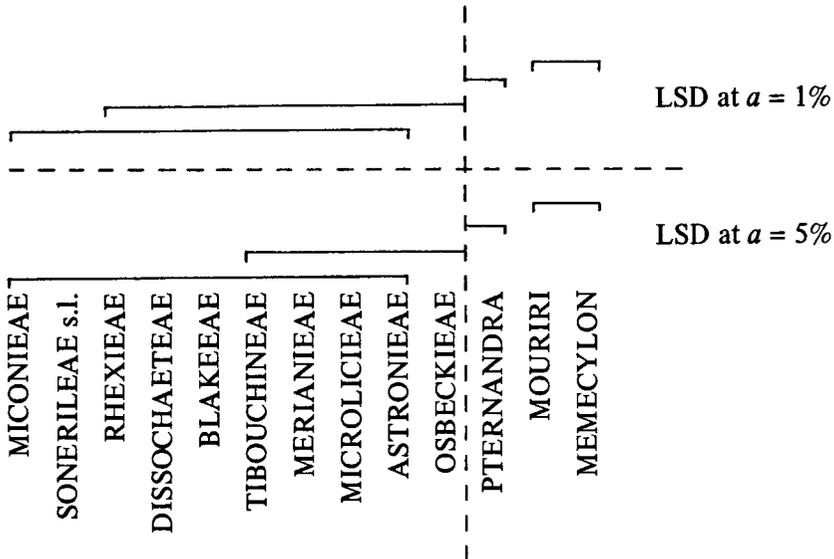
Fig. 1. Graphic representation of a simultaneous test procedure on the average fibre length to vessel member length ratios, using the least significant difference (LSD) criterium to analyse the actual heterogeneity when comparing the tribes of the Melastomatoideae and the genera of the Memecyloideae.

AFFINITIES WITH OTHER MYRTALES

Especially through the two basically different fibre types present in the Melastomataceae (fibre-tracheids in *Crypteronioideae* and *Memecyloideae;* libriform fibres in *Melastomatoideae*) it is possible to suggest affinities, as based on wood anatomical similarities, with all large families of the order. This may point to either a more or less central position of the Melastomataceae in Myrtales or to abundance of parallel and convergent wood anatomical development within the order.

Lythraceae share many wood anatomical characters with the subfamily *Melastomatoideae* (cf. Baas & Zweypfenning, 1979). Their 'Protolythraceae' may very well serve as the ancestral base for the *Melastomatoideae,* and apart from the fibre type, also for the whole Melastomataceae. Fibre dimorphism, present throughout the *Melastomatoideae* is of more restricted occurrence in Lythraceae, and has probably arisen independently in both families. The coarse vessel—ray and vessel—parenchyma pits, present in many *Melastomatoideae,* are only rarely found in Lythraceae.

The wood of *Alzatea* (cf. Baas, 1979; van Vliet, 1975) recalls Melastomataceae in many aspects, such as the alternate inter-vessel pits, low F/V ratio, simple vessel—ray and

vessel—parenchyma pits, vestures of type A, and the heterogeneous II rays. Baas & Zweypfenning's suggestion (1979) that *Alzatea* is an isolated remnant of an ancestral stock that gave rise to Lythraceae and Melastomataceae seems therefore plausible.

Onagraceae (cf. Carlquist, 1975b, 1977) have in the alternate intervessel pits that sometimes tend to elongate, the ray type, the scanty paratracheal parenchyma and the infrequently reduced borders of vessel—ray and vessel—parenchyma pits, characters that recall the *Melastomatoideae*. Fibre dimorphism was not observed, although Carlquist recorded many living fibres. Raphides in axial parenchyma are very unusual in dicotyledonous woods. The presence of this crystal type in one species of *Bredia* (*Sonerileae*, subtribe *Sonerilinae; Melastomatoideae*) may indicate affinities with Onagraceae, where this crystal type is present in many representatives.

Subfamily *Combretoideae* of the Combretaceae (cf. van Vliet, 1979) has some resemblance with the *Melastomatoideae* but differs in many respects. Subfamily *Strephonematoideae* (one, rather aberrant genus) has several characters in common with *Memecyloideae* and to lesser extent with *Crypteronioideae*. Combretaceae are probably the least related of the three families mentioned this far.

Penaeaceae (Carlquist & Debuhr, 1977) show similarities with *Memecyloideae* (different in the absence of axially included phloem and the F/V ratio) and *Crypteronioideae*. The mostly uniseriate rays of erect cells in the wood of many Penaeaceae tends to heterogeneous II in older stems, thus affirming affinities.

The very large family Myrtaceae shares wood anatomical characters with *Memecyloideae* and *Crypteronioideae*, but also to a lesser extent with *Melastomatoideae*. The wood of the 'Protomelastomataceae', hypothesized in the following chapter of this paper contains many characters still extant in Myrtaceae.

A more detailed account of the affinities of the families of the Myrtales will be presented by van Vliet & Baas (in prep.).

PHYLOGENETIC CONSIDERATIONS

A hypothetical reconstruction of the phylogeny of the Melastomataceae, a family occurring both in the Neotropics and the Palaeotropics, can be approached in two different ways. Firstly one may assume separate, monophyletic lines for each of these major distribution areas. The wood anatomy of the common ancestor would have been rather similar to that of the present *Memecyloideae* (see below), and after the separation of Africa from South America wood anatomical specialization would have gone along almost strictly parallel lines. Although this possibility cannot be completely discarded it seems more fruitful to consider the relationship patterns of the family as a whole on the more reasonable assumption that there are several phylogenetic affinities bridging the present oceans.

The problems one can be faced with when analysing the wood anatomical data following a rigid cladistic approach have already been expounded by ter Welle & Koek-Noorman (1981, this issue). The likelihood of parallel developments in several taxa complicates the issue and leaves the more traditional approach as the only possibility. We will base our discussion on the phylogenetic trends as established on the basis of studies

in large plantgroups. These trends have initially been exemplified by Bailey and his contemporaries (cf. Tippo, 1946) and were later extended by several other students in this field.

The characters discussed below are useful in the discussion on the hypothetical phylogeny of this family. Although the presentation of the information may suggest an one-way development, reversions can never be excluded.

Wood with long *vessel* members is thought to be more primitive than wood with shorter vessel members. This tendency can be intensified or interfered with through ecological adaptations (cf. Carlquist, 1975a, van der Graaff & Baas, 1974; van den Oever et al., 1981). The scalariform inter-vessel pits, present in some of the palaeotropical Melastomataceae may, contrary to the general accepted theories, be interpreted as a specialization, rather than as a primitive character state (cf. van Vliet 1981, this issue). The vessel—ray and vessel—parenchyma pits with strongly reduced or without borders are thought to be derived from half-bordered pit contacts of ± the same size as the inter-vessel pits. Solitary vessels are interpreted as more primitive than vessels in multiples.

Wood with libriform *fibres* is more specialized than wood with fibre-tracheids. High values for the fibre length to vessel member length ratios indicate an increased intrusive growth and are interpreted as more specialized than low values. In some families, the morphological series from normal fibres via thin-walled (shorter) fibres and fusiform septate parenchyma to axial parenchyma reflects a specialization tendency (Carlquist, 1958; Baas & Zweypfenning, 1979; ter Welle & Koek-Noorman, 1978). In Melastomataceae this is reflected in bands almost wholly composed of deviating fibres, bands with various quantities of fibres and parenchyma and bands wholly composed of parenchyma.

The phylogenetic development of apotracheal *parenchyma* bands goes through fibre dimorphism. A second tendency for axial parenchyma specialization in this family goes from a scanty paratracheal condition – through increase of the amount of parenchyma tissue – via aliform to confluent patterns (cf. Carlquist, 1961). Apotracheal parenchyma in diffuse aggregates is another primitive condition.

The development of the *ray* types in the Melastomataceae probably followed a pattern similar to that which Baas & Zweypfenning (1979) hypothesized for the Lythraceae. From the ancestral heterogeneous I–II rays, the 1+2–3-seriate rays composed of erect, square and weakly procumbent cells have originated under the influence of juvenilistic tendencies (paedomorphosis; Carlquist, 1962). Uniseriate rays, composed of erect and square cells may be the result of a reduction from the multiseriate condition. The 1–7-seriate rays are considered to be the result of a reverse process, leading to an increase of the ray width.

The uniseriate rays may also be derived directly from the ancestral type through loss of multiseriate rays in association with juvenilistic tendencies.

The homogeneous rays that are very infrequently found in neotropical Melastomataceae are most likely the result of a specialization from these multiseriate or uniseriate rays.

An alternative specialization from the ancestral type is represented in the 'normal' development from heterogeneous II to heterogeneous II–III.

Crystals are of limited value in the discussion on phylogenetic trends in Melastomata-

ceae, and can only be used to support similarities already indicated by other characters. In Melastomataceae, clustered crystals (druses) are invariably associated with apotracheally banded axial parenchyma, although they are not present in all species with this type of parenchyma. Raphides are found in one species only. Megastyloids are recorded in some genera of the *Miconieae* and may point to a somewhat separate (specialized) status of the genera concerned within the tribe.

Taking the most primitive character states of the above mentioned trends as manifested in the Melastomataceae, one can reconstruct a hypothetical 'Protomelastomataceae' with the following wood anatomy:

Vessels predominantly solitary, vessel member length at least 1100 μm, small alternate vessel wall pits, vessel—ray and vessel—parenchyma pits half-bordered, fibre-tracheids forming the ground tissue, fibre length to vessel member length ratio 1.1–1.2, rays heterogeneous I–II, parenchyma scanty paratracheal.

The greatest amount of ancestral characters is found in the *Crypteronioideae*, though not all in one genus. The ground tissue is composed of fibre-tracheids. The vessels are mainly solitary in *Axinandra* and *Dactylocladus,* frequently in multiples in *Crypteronia.* All genera have alternate vessel wall pits, although large vessel—ray and vessel—parenchyma pits are present in *Dactylocladus*. The longest vessels members of the family are found in *Dactylocladus* (900–1100 μm on average), and intrusive growth is lowest for this subfamily (F/V ratio 1.32–1.37). Both *Axinandra* and *Dactylocladus* have aliform to confluent parenchyma; the vasicentric and diffuse in aggregates parenchyma of *Crypteronia* is only a small step from the aliform type (van Vliet, 1975) and may be interpreted as less specialized. The ray type is heterogeneous I–II in *Crypteronia,* slightly more specialized in *Axinandra* (heterogeneous II–III); a different line of specialization is expressed in the uniseriate, heterogeneous rays of *Dactylocladus.*

Axinandra and *Crypteronia* share more specialized character states with each other than with *Dactylocladus*. The phylogeny of this subfamily can be pictured as an early (first?) off shoot from the ancestral stock in which the three extant genera each developed their own wood anatomical identity (cf. Fig. 2).

The *Memecyloideae* also retained the ancestral fibre type and the vessels are only infrequently grouped in radial multiples. The presence of axially included phloem in the wood of all genera studied points to an early introduction of this character in the development of the subfamily. The aliform and confluent parenchyma of the *Memecyleae* may be derived from the scanty paratracheal ancestral condition that is still retained in *Pternandra*. The cambium initials of all members of this subfamily have distinctly shortened, whereas the intrusive growth is the largest of the whole family. *Memecylon* and *Mouriri p.p.* have probably followed an independent line for the development of the ray type (heterogeneous II–III); *Mouriri p.p.* and *Pternandra* exhibit juvenilistic tendencies and reduction in width. Radially included phloem has developed in *Pternandra* only; coarse vessel—ray pits are also restricted to this genus.

The phylogeny of this subfamily may be pictured as an early separation of *Pternandra* from the other two genera, which retained a high degree of similarity in spite of the wide

(and old!) geopgraphical separation (differences between *Memecylon* and *Mouriri* are slight considering their probably long, isolated phylogenetic histories).

Memecylon shares several wood anatomical characters with *Axinandra* of the *Crypteronioideae* (vessel wall pitting, parenchyma distribution, ray type). In the two-dimensional presentation of the putative phylogeny of the Melastomataceae (Fig. 2) these purely phenetic resemblances are expressed by placing *Memecylon* nearest to *Axinandra*. *Pternandra* is placed nearest to the *Melastomatoideae*, being similar in the ray type and the coarse vessel—ray and vessel—parenchyma pits and the scanty paratracheal parenchyma; it is intermediate in the F/V ratio.

In the woods of the *Melastomatoideae* few remnants of the ancestral wood anatomy are evident; scanty paratracheal parenchyma and a low intrusive growth only. The ground tissue of the wood is formed by libriform fibres; the vessels are generally in multiples; the shortage of storage tissue is probably compensated for by the development of apotracheal parenchyma bands via dimorphous fibres and septate, probably living fibres: rays of varying width are composed of erect, square, and weakly procumbent cells (homogeneous rays of procumbent cells are scarce). Vessel—ray and vessel—parenchyma pits are mostly large and simple, although small and alternate half-bordered pits are still extant in some neotropical tribes; inter-vessel pits are alternate, frequently with some elongate and curved pits, or scalariform in some palaeotropical tribes.

Although the tribes are rather homogeneous in many aspects, a number of phylogenetic trends are sometimes fully reflected in their wood anatomical variation (fibre dimorphism, inter-vessel pits, vessel—ray and vessel—parenchyma pits). This leaves one with only little wood anatomical variation for a reconstruction of a hypothetical tribal phylogeny for this subfamily. The system we will present is the most plausible to us, although we fully realize that alternatives are very well possible.

Because of the variation in ray type in the *Melastomatoideae* we have accepted an early ray differention, resulting in at least two phylogenetic pathways. One of these could have an ancestral ray type of predominantly uniseriate rays (composed of erect, square, and weakly procumbent cells) derived directly from the Protomelastomataceae-type through loss of multiseriates. This ray type, in association with comparitively long vessel members and *p.p.* small vessel wall pits is found in *Miconieae* and *Merianieae*. The bands of deviating fibres in *Miconieae* frequently contain axial parenchyma; those of the *Merianieae* are more specialized, in most of the species composed fully of axial parenchyma. The more specialized status of the latter tribe is also expressed in the infrequent occurrence of homogeneous rays. The incidental multiseriate rays may be interpreted as a secondary specialization through widening.

Alloneuron and *Llewelynia* can be placed very near or in the *Miconieae*. *Tococa* and *Conostegia* have a wood anatomy that is more or less intermediate between *Miconieae* and *Merianieae* because of their well developed apotracheal parenchyma bands. *Tessmanianthus* is, because of its homogeneous rays, very near to the similarly specialized part of the *Merianieae*. The palaeotropical *Astronieae* seem very well placed near the *Miconieae*, being more primitive in the scarce axial parenchyma in the bands of deviating fibres, yet more specialized in the coarse vessel—ray and vessel—parenchyma pits.

A further specialization from the *Miconieae*-type (involving shortening of the cambium initials and the enlargement and reduction of borders in the vessel—ray and vessel—pa-

renchyma pits) could have resulted in *Rhexieae* and *Tibouchineae*, with *Pachyanthus* possibly intermediate between the two tribes. In *Tibouchina* of the *Tibouchineae*, multiseriate rays are very abundant; the tribe may therefore merit an alternative position in another line of specialization, discussed below (Fig. 2).
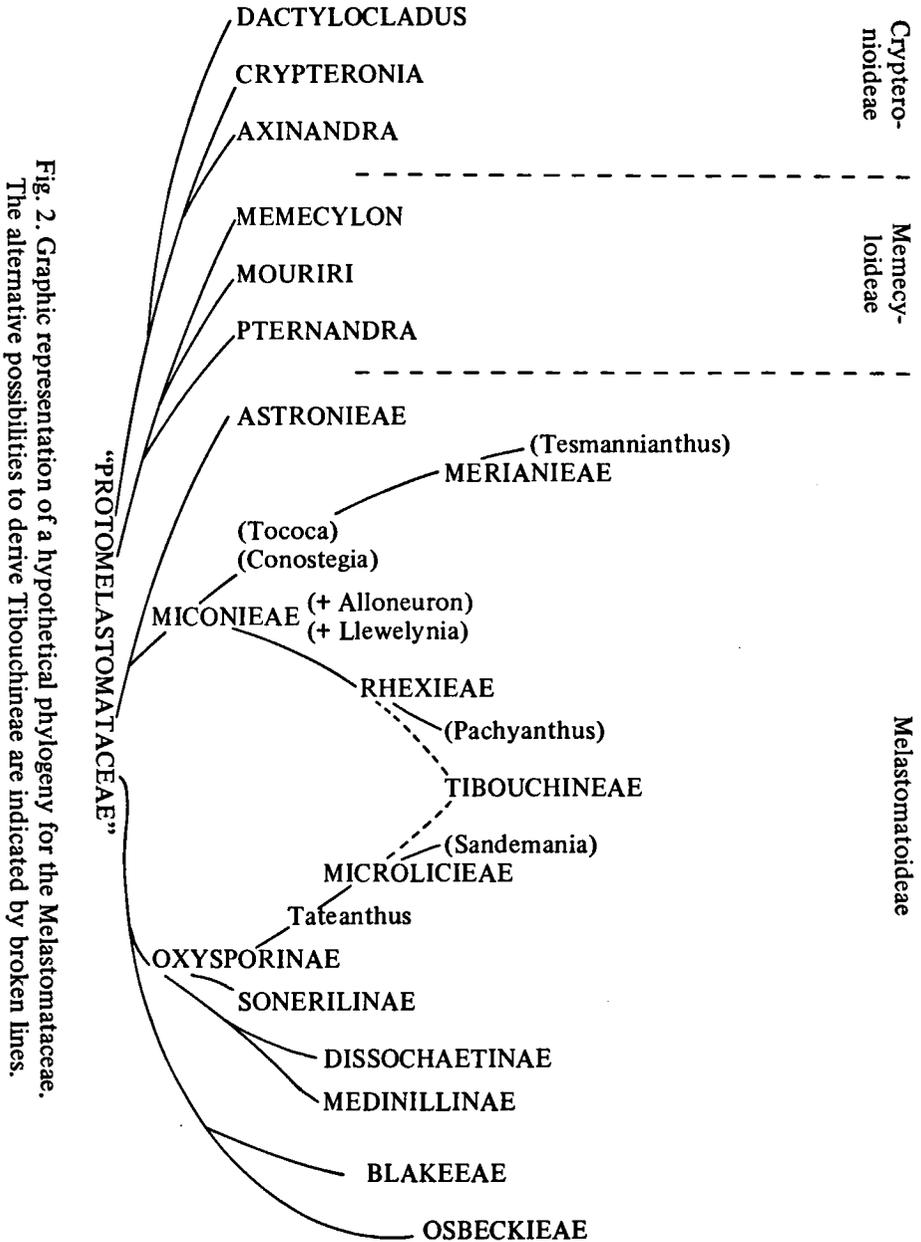
DACTYLOCLADUS

CRYPTERONIA

AXINANDRA

Cryptero-nioideae

— —

MEMECYLON

MOURIRI

PTERNANDRA

Memecy-loideae

— — — — — — — — — — — — — — — — — — — —

ASTRONIEAE

(Tesmannianthus)
MERIANIEAE

(Tococa)
(Conostegia)

MICONIEAE (+ Alloneuron)
(+ Llewelynia)

RHEXIEAE

(Pachyanthus)

TIBOUCHINEAE

(Sandemania)
MICROLICIEAE

Tateanthus

OXYSPORINAE

SONERILINAE

DISSOCHAETINAE

MEDINILLINAE

BLAKEEAE

OSBECKIEAE

Melastomatoideae

"PROTOMELASTOMATACEAE"

Fig. 2. Graphic representation of a hypothetical phylogeny for the Melastomataceae. The alternative possibilities to derive Tibouchineae are indicated by broken lines.

This line could have as ancestral ray type multiseriate rays composed of erect and weakly procumbent cells. The *Sonerileae s.l.* may have a position near the basis of this line with a closely related neotropical counterpart in the *Bertolonieae* (mainly herbs, not studied wood anatomically; merging of these tribes has been suggested by Bakhuizen van den Brink, 1943 and Wurdack, private communication). The woody neotropical genus *Tateanthus* (closely allied to *Bertolonieae*) is in its wood anatomy very similar to subtribe *Oxysporinae* of *Sonerileae s.l.* thus supporting the suggested link between palaeotropical and neotropical taxa. In this alliance the subtribe *Sonerilinae* of *Sonerileae s.l.* shows a deviating, slightly more specialized wood anatomy with its 'pseudo'-scalariform inter-vessel pits.

The neotropical *Microlicieae* hardly differ from the *Sonerileae s.l.-Tateanthus-Berto-lonieae* alliance (*Sonerilinae* excepted). Derivation of *Tibouchineae* (involving reduction of ray width) might also have been possible from this group, with *Sandemania* in a more or less intermediate position. Further wood anatomical specialization in the palaeotro-pics could have resulted in the *Dissochaeteae* (with increase of paratracheal parenchyma to vasicentric and ray dilatation in the *Dissochaetinae* as an adaptation to a lianous habit, and the development of 'pseudo'-scalariform inter-vessel pits as a separate specialization for the *Medinillinae*).

The position of two tribes remains to be discussed: *Osbeckieae* and *Blakeeae*. Both tribes exhibit wood anatomical specialization in the presence of apotracheal parenchyma bands (more abundant in *Blakeeae*), whereas they are rather primitive in the long vessel members (shortening through ecological influences evident in *Osbeckieae*). Further primitive characteristics in *Blakeeae* are the small vessel—ray and vessel—parenchyma pits. Derivation from these tribes from nearby the *Sonerileae s.l.* stock seems most likely (cf. Fig. 2).

As we have admitted earlier in this paper, our interpretation of the wood anatomical diversity of the Melastomataceae, especially of the subfamily *Melastomatoideae* can be challenged. It is for instance quite possible that ray development has proceeded along other lines than those suggested here, or that parallel or convergent ray specialization has occurred even more frequently than we assumed, so that tribal phylogenies cannot be based on this character at all. Affinities between special tribes from the Palaeotropics and Neotropics respectively are also admittedly speculative, with the exception for the doubtless mutual affinities of the pantropical *Memecyleae*. Whatever the shortcomings of the proposed phylogeny, our data point to a considerable degree of wood anatomical differentiation at the subfamily and partly also at the tribal level before the breaking up of Pangea.

Our hypothetical phylogeny for the Melastomataceae can therefore only be used as a framework, to be refined or modified as data from other disciplines – such as palynology, nodal anatomy, floral morphology, phytochemistry, cytology and macromorphology – are analysed. The support for our classification, which can be derived from several independent leaf anatomical characters (Baas 1981, this issue) is gratifying.

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REFERENCES

BAAS, P. 1979. The anatomy of Alzatea Ruiz. et Pavon (Myrtales) Acta Bot. Neerl. 28: 156–158.
BAAS, P. 1981. A note on stomatal types and crystals in the leaves of Melastomataceae. Blumea, this issue.
——. & R. ZWEYPFENNING. 1979. Wood anatomy of the Lythraceae. Acta Bot. Neerl. 28 (2/3): 117–155.
BAKHUIZEN VAN DEN BRINK, R. C. 1943. A contribution to the knowledge of the Melastomataceae occurring in the Malay Archipelago, especially in the Netherlands East Indies. Thesis Utrecht. (Repr. in Rec. Trav. Bot. Neerl. 40, 1946: 1–391).
CARLQUIST, S. 1958. Wood anatomy of the Heliantheae (Compositae). Trop. Woods 108: 1–30.
——. 1961. Comparitive plant anatomy. Holt, Rinehart & Winston, New York.
——. 1962. A theory on paedomorphosis in dicotyledonous woods. Phytomorphology 12: 30–45.
——. 1975a. Ecological strategies of xylem evolution. Univ. of Calif. Press, Berkeley.
——. 1975b. Wood anatomy of Onagraceae with notes on alternative modes of photosynthetic movement in Dicotyledon woods. Ann. Miss. Bot. Gard. 62: 386–424.
——. 1977. Wood anatomy of Onagraceae. Additional species and concepts. Ann. Miss. Bot. Gard. 64: 627–637.
—— & L. DEBUHR, 1977. Wood anatomy of Penaeaceae (Myrtales). Comparitive, phylogenetic and ecological implications. Bot. J. Linn. Soc. 75 (3): 211–227.
GRAAF, N. A. VAN DER, & P. BAAS. 1974. Wood anatomical variation in relation to altitude and latitude. Blumea 22: 101–121.
JANSSONIUS, H. H. 1950. Wood anatomy and relationships. note 3. A subdivision of the Melastomataceae. Blumea 6: 417–418.
OEVER, L. VAN DEN, P. BAAS & M. ZANDEE. 1981. Comparitive anatomy of Symplocos and altitude and latitude of provenance. IAWA Bull. n.s. 2(1): 3–24.
TIEGHEM, PH. VAN. 1891. La structure et les affinitées des Memecylées. Ann. Sc. Nat., sér 7, 13: 23–92.
TIPPO, O. 1946. The role of wood anatomy in phylogeny. Am. Midl. Nat. 36: 362–372.
VLIET, G. J. C. M. VAN. 1975. Wood anatomy of the Crypteroniaceae s.l. J. Micr. 104: 65–82.
——. 1979 Wood anatomy of the Combretaceae. Blumea 25: 141-223.
——. 1981. Wood anatomy of the palaeotropical Melastomataceae. Blumea, this issue.
—— & P. BAAS. in prep. Wood anatomy and Classification of the Myrtales. Ann. Miss. Bot. Gard.
WELLE, B. J. H. TER, & J. KOEK-NOORMAN. 1979. On fibres, parenchyma and intermediate forms in the genus Miconia (Melastomataceae). Acta Bot. Neerl. 27: 1–9.
—— & —— 1981. Wood anatomy of the neotropical Melastomataceae. Blumea, this issue.