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COMPARATIVE ANATOMY OF THE CRYPTERONIACEAE sensu lato

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SUMMARY

The leaf, twig, and nodal anatomy of *Alzatea*, *Axinandra*, *Crypteronia*, *Dactylocladus*, and *Rhynchocalyx* is described in detail. This family, as newly delimited by Van Beusekom-Osinga and Van Beusekom, appears to be very heterogeneous, a conclusion supported by the wood anatomical diversity reported in another paper. The nodes may be simply unilacunar, unilacunar with a complete girdling trace, of the common gap (or split lateral) plus median trace type, or trilacunar. Cortical bundles may be present in addition. Further diversity is present in e.g. cuticular texture, stomatal type, hypodermal development, arrangement of vascular bundles in petiole and midrib, mechanical support of the veins, the crystal complement, foliar sclereids, and cork origin.

Anatomical evidence only supports the Myrtalean character of all genera, and a close mutual affinity of *Axinandra* and *Crypteronia*. These genera, together with *Dactylocladus* show several features characteristic for some *Melastomataceae*, which family with its wide anatomical range would also cover most of the anatomical diversity of *Lythraceae*, *Sonneratiaceae*, *Oliniaceae*, *Alzatea*, and *Rhynchocalyx*. *Rhynchocalyx* appears to be closer in its anatomy to some *Lythraceae*, *Oliniaceae*, and *Melastomataceae* than to the other members of *Crypteroniaceae*. *Alzatea* shows affinities with all families mentioned, but remains problematic with its trilacunar node not known to occur in the other families. The complex pattern of overlapping anatomical ranges of *Crypteroniaceae s.l.*, *Melastomataceae*, *Lythraceae*, *Oliniaceae*, and *Sonneratiaceae* may be interpreted as evidence of intimate relationships between these families.

INTRODUCTION

In the present issue of Blumea, Van Beusekom proposes a new delimitation of the family *Crypteroniaceae*, uniting *Alzatea*, *Axinandra*, and *Rhynchocalyx* with *Crypteronia* and *Dactylocladus*. These five genera share a number of supposedly primitive relic characters, absent or of rare occurrence in other Myrtalean families, implying that mutual affinities between the individual genera are not necessarily very close. Furthermore, they are also characterized by a combination of more specialized features by which the delimitation of the *Crypteroniaceae* in the new sense appears to have a factual base comparable to that of *Melastomataceae* and *Sonneratiaceae*. The naturalness of the family remains, however, open to some doubt. A detailed anatomical study was therefore undertaken to contribute to our understanding of intra and inter-family relationships of these genera, and to compare the results on macromorphology (Van Beusekom, 1975) and pollen morphology (Muller, 1975) with those of wood anatomy (Van Vliet, 1975, and this paper) and leaf, twig, and nodal anatomy (this paper).

The complicated taxonomic history of all five genera has been reviewed by Van Beusekom. Since the anatomical evidence clearly supports a Myrtalean affinity for all genera (presence of vestured pits in the wood and intraxylary phloem in leaf and twig) only families from this order, mentioned in the literature as putative relatives (e.g. *Melastomataceae*, *Lythraceae*, *Sonneratiaceae*) will be considered in the comparisons.

Data on leaf and twig anatomy of the *Crypteroniaceae s.l.* are very scanty. Hallier (1911) and Stant (in Lourteig, 1965) briefly described the vegetative anatomy of *Alzatea*. Niedenzu (1892) recorded some anatomical characters for *Crypteronia*, and Sprague & Metcalfe (1937) did so for *Rhynchocalyx*. Metcalfe & Chalk (1950) in compiling data from the older literature only included some information on *Axinandra* and *Crypteronia*. Reference to these publications will only be made as far as is relevant for the discussion of the present results.

Apart from a detailed histological study of leaf and twig, special attention is given to the course of vascular bundles in the nodal region.

MATERIALS AND METHODS

Only herbarium specimens were available for this study. Collecting data will be given for each species. Since the specimens used in this study were also used for the revision (Van Beusekom-Osinga & Van Beusekom, 1975) no herbaria of origin will be cited. Sections and macerations were prepared according to standard techniques (Baas, 1970; Bongers, 1973). Serial sections were made of unembedded twigs of nodal and large parts of internodal regions. These serial sections were only bleached and studied in semi-permanent glycerin mounts. All nodal regions were studied at some stage of secondary thickening. Specimens used for the study of nodal anatomy are marked with an asterisk. The anatomical terminology employed, as far as of uncommon use, is the same as explained elsewhere (Jansen & Baas, 1973; Bongers 1973; Van Staveren & Baas, 1973).

RESULTS AND DISCUSSIONS

Nodal anatomy (Fig. 1—4)

In the literature the term node has been applied in different ways. For this study the following definition is employed: the node is that part of the stem in which the course of the vascular bundles from the leaf to the stele (or vice versa) produces a deviation of the vascular pattern in the stem. For practical reasons the course of vascular bundles will be described as descending from the leaf into the stem. This should not be taken as a developmental interpretation, since no data on the ontogeny of the vascular bundles in *Crypteroniaceae* are available. The classification of nodal types based on the number of gaps and traces (Sinnott, 1914) provides a useful descriptive tool (Howard, 1974). However, in some *Crypteroniaceae* the pattern is such a complex one that this classification cannot be employed for all genera or species.

In all *Crypteroniaceae* the leaves are oppositely arranged. Serial sections through one nodal region therefore afford the study of vascular connections of two leaves with the stele. It appeared that even within a single node differences may exist between the vascular patterns at the opposite sides of the stem. More evidence of variability within a species was found in the few instances that several nodes per species or specimen were studied.

In *Crypteronia* three traces descend from the leaf. The large median bundle fuses immediately with the stele in all species. In *C. griffithii* and *C. macrophylla* (fig. 1a) lateral traces girdle around the stele and fuse with those from the opposite leaf to enter a common gap, conforming to the split lateral or common gap condition described by Howard (1970) for several families e.g. *Rhizophoraceae*. In *C. cumingii* an additional centric bundle (lateral anastomosis) splits off from each lateral trace to enter the stele at a level just below or in the same gap as the median bundle (fig. 1b). In *C. paniculata* var. *paniculata* (*Kochummen 97773*, fig. 1c) the situation is comparable to that in *C. cumingii* but the girdling lateral traces fail to enter the stele after fusion on the place where one would expect a common gap. On one side of the node the lateral anastomosis was found to fuse with the median

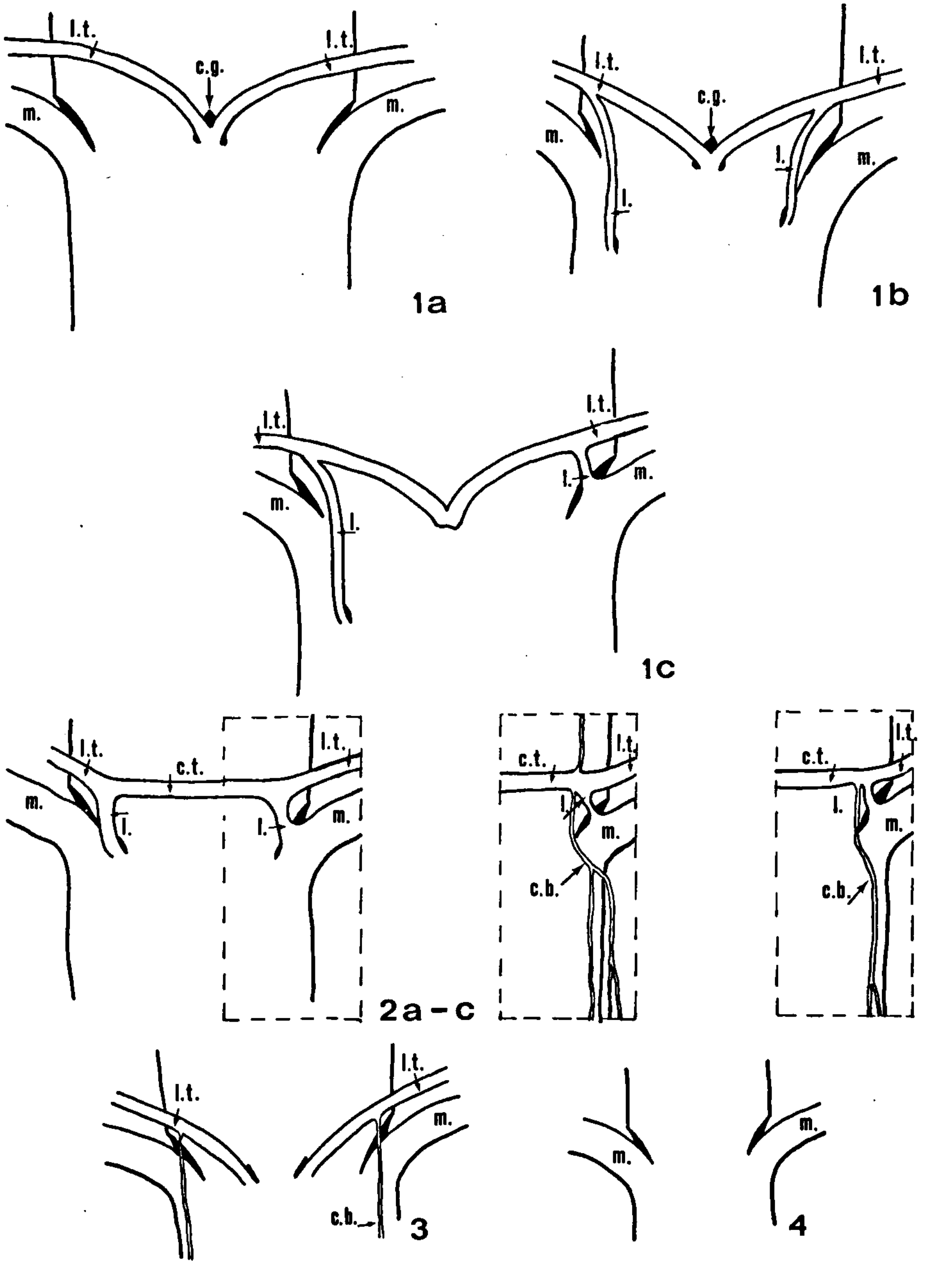

Fig. 1—4. Idealized three-dimensional diagrams of nodal types. 1. *Crypteronia*; 1a. *C. griffithii*, similar to *Dactylocladus*; 1b. *C. cumingii*; 1c. *C. paniculata* var. *paniculata* (*Kochummen KEP. F. 97773*). — 2. *Axinandra*; 2a. *A. beccariana* (similar to *Crypteronia paniculata p.p.*); 2b. *A. alata*; 2c. *A. zeylanica*. — 3. *Alzatea verticillata*. — 4. *Rhynchocalyx lawsonioides*.
c.b. = cortical bundle; c.g. = common gap; c.t. = complete girdling trace; l = lateral anastomosis; l.t. = lateral trace; m = median trace.

bundle above the level of its entrance into the stele. In the other three specimens of *C. paniculata* the laterals form a complete horizontal girdling path showing no special locus of fusion; the lateral anastomoses from both leaves enter the stele in the same gaps as the median traces (similar to the situation pictured in fig. 2a for *Axinandra beccariana*). The fact that in *Crypteronia* these lateral anastomoses vary in their connections with the stele from a three-traced condition at the median gap (*C. paniculata* var. *affinis*, and partly in *C. paniculata* var. *paniculata* and *C. cumingii*) to a situation where these anastomoses have their own gaps at a lower level (partly in *C. paniculata* var. *paniculata* and *C. cumingii*) makes it impossible to fit them into the nodal classification of Sinnott. Their absence in two other *Crypteronia* species and the above reported variability makes it difficult to assess the systematic value of these lateral anastomoses. In the formal descriptions the different conditions will be referred to as follows: Nodes with a common gap will be described as having a common gap with split laterals plus one median trace (to distinguish these from types where several lateral traces and gaps may be present as reported by Howard, 1970). The nodal pattern as in *C. paniculata* will be referred to as a complete girdling trace plus one median bundle. Lateral anastomoses, if present, will be mentioned in addition.

In *Axinandra* the nodal patterns are all similar to that in *Crypteronia paniculata* var. *affinis* (fig. 2a—c). Cortical bundles may, however, be present in addition. These bundles may be collateral or, if sufficiently large, centric (amphicribal). In transverse sections through the internode these bundles are situated at the four corners, sometimes in wing-like extensions, and occasionally arranged in radial rows with the bundles decreasing in size towards the periphery. In the latter instance the bundles are always fused with each other just below the node. In the nodal region the cortical bundles descend from the lateral traces at the points of insertion of the lateral anastomoses and bend into the outer cortical region, passing through the layer of cork tissue. In *Axinandra zeylanica* the cortical bundles end in the outer cortex at various distances from the node. In *A. alata* no complete internodes were sectioned but the fact that both above and below the lateral trace a (the same?) cortical bundle is attached, is suggestive of a cortical bundle system continuous over several nodes (fig. 2b). In *A. coriacea* two successive nodes of one twig (*Meijer SAN 37494*) were sectioned and a cortical system as in fig. 2c was found to be present in only one node and part of an internode, the other node and internode being devoid of cortical bundles. In *A. beccariana* no cortical bundles were found at all. As far as we are aware, complete girdling traces as in *Axinandra* and *Crypteronia paniculata* var. *affinis* have only been reported as part of cortical systems (Howard, 1974; Lignier, 1886, 1887) and by the latter author as additional to situations with a split lateral or common gap girdling trace. The complete girdling traces of *Axinandra* and *Crypteronia paniculata* cannot, however, be interpreted in this way since they are also present in species without cortical bundles. The variability of the cortical system in *Axinandra* limits its use as a systematic character.

In *Dactylocladus* the nodal anatomy conforms to the type described for *Crypteronia macrophylla* and *C. griffithii* (fig. 1a).

In *Alzatea* (fig. 3) three bundles from each leaf enter the stele in separate gaps, thus conforming to the well known trilacunar condition with three traces. Cortical bundles, present in the internodes are attached to the lateral traces but apparently do not form a continuous system. Scarcity of material made it impossible to trace the endings of the cortical bundles.

In *Rhynchocalyx* only one leaf trace is present and enters the stele at the site of leaf insertion: a simple unilacunar node with one trace (fig. 4).

The unusual diversity of nodal anatomy in this small family calls for some comment. Although it would be entirely unjustified to attempt phylogenetic derivations of one nodal type from the other, it is possible to construct morphological series of part of the diversity reported here. We regard the simple unilacunar condition of *Rhynchocalyx* as an isolated condition within this family, but the other genera show some similarities. Differences between the trilacunar nodes of *Alzatea* and the common gap situation in *Dactylocladus* and *Crypteronia p.p.* are not so great, if one considers that Howard (1970, 1974) succeeded in changing the nodal pattern of *Alloplectus (Gesneriaceae)* from split lateral or common gap plus one median trace to a trilacunar condition or vice versa by merely transferring plants from native to greenhouse environment and back again. Within *Crypteronia* there are, moreover, transitions between the normal common gap plus median trace situation and the unilacunar nodes with a complete girdling trace of *C. paniculata* and *Axinandra*: *Kochummen 97773* of *C. paniculata* var. *paniculata* (fig. 1c) represents this more or less intermediate condition.

Howard (1974) recently stressed the importance to use the entire pattern of changes in vascular arrangement in the stem—node—leaf continuum for taxonomic purposes. Applying this to the *Crypteroniaceae* there is a good correlation between petiole vasculature and nodal anatomy, accepting the trilacunar node and common gap plus median traces as fundamentally similar types. In *Alzatea*, *Dactylocladus*, and *Crypteronia* a closed ring or a separate adaxial and abaxial plate plus latero-dorsal bundles is found in the distal end of the petiole and usually also in the midrib. In *Axinandra* and *Rhynchocalyx* the main petiole bundle is arc-shaped throughout, connected as it is with a complex or simple unilacunar node. The combinations of midrib, petiole, and nodal anatomy present in the *Crypteroniaceae* represent only few of the possibilities classified by Howard (1963), though he did not even include the common gap plus median trace condition in his scheme.

Generic descriptions

Leaf, node, and twig anatomy of the individual genera are described below. Secondary xylem of twigs and trunks is the subject of a separate publication (Van Vliet, 1975). Quantitative values are given as the full range only, or as full range and range of means.

ALZATEA Ruiz & Pavon

Material studied. *A. verticillata* Ruiz & Pavon: PERU, *Ule 6750**; *Woytkowski 6196**.

Leaf (Fig. 5, Plate I, 2; II, 7)

In surface view. Indumentum absent. Cuticle granular, anticlinal flanges well developed, straight to slightly curved. *Stomata* confined to abaxial epidermis, mainly anomocytic or intermediate between anomocytic and cyclocytic, with 3—7 neighbouring (subsidiary) cells, which are hardly submersed below the guard cells. Guard cell pairs 27—30 & 32—33 μm long, 26—28—31 μm wide. Outer stomatal ledges well developed. Polar T-pieces absent. Cork warts infrequently present in *Ule 6750* and of irregular outline, probably of traumatic origin. Veins not prominent. In transverse section. Lamina dorsiventral, 380—440 μm thick. Abaxial cuticle 7—11 μm thick, adaxial cuticle 11—15 μm thick. Unspecialized cells of adaxial epidermis mainly square, slightly larger than the square to erect abaxial epidermal cells. *Stomata* in the same level as unspecialized cells. Adaxial *hypodermis* of 1 cell-layer locally present on either side of midrib. Mesophyll composed of 2 layers of palissade tissue and rather compact mostly lignified spongy tissue. *Midrib* adaxially flattened or slightly raised, abaxially prominently raised, supplied with an abaxial shallow arc-shaped bicollateral vascular bundle and one to several smaller adaxial bicollateral bundles. Whole system embedded in sclerenchyma, abaxially interspersed with lignified parenchyma. Ground tissue lignified in 'pith', unlignified in periphery but interspersed with sclereids. Major *veins* with bicollateral, smaller veins with collateral vascular bundles, embedded in mesophyll and with a lignified parenchymatous bundle sheath, enclosing adaxial and abaxial sclerenchyma caps. Caps absent from smallest veins. Vascular system of *petiole* composed of a strongly incurved, almost closed, bicollate-

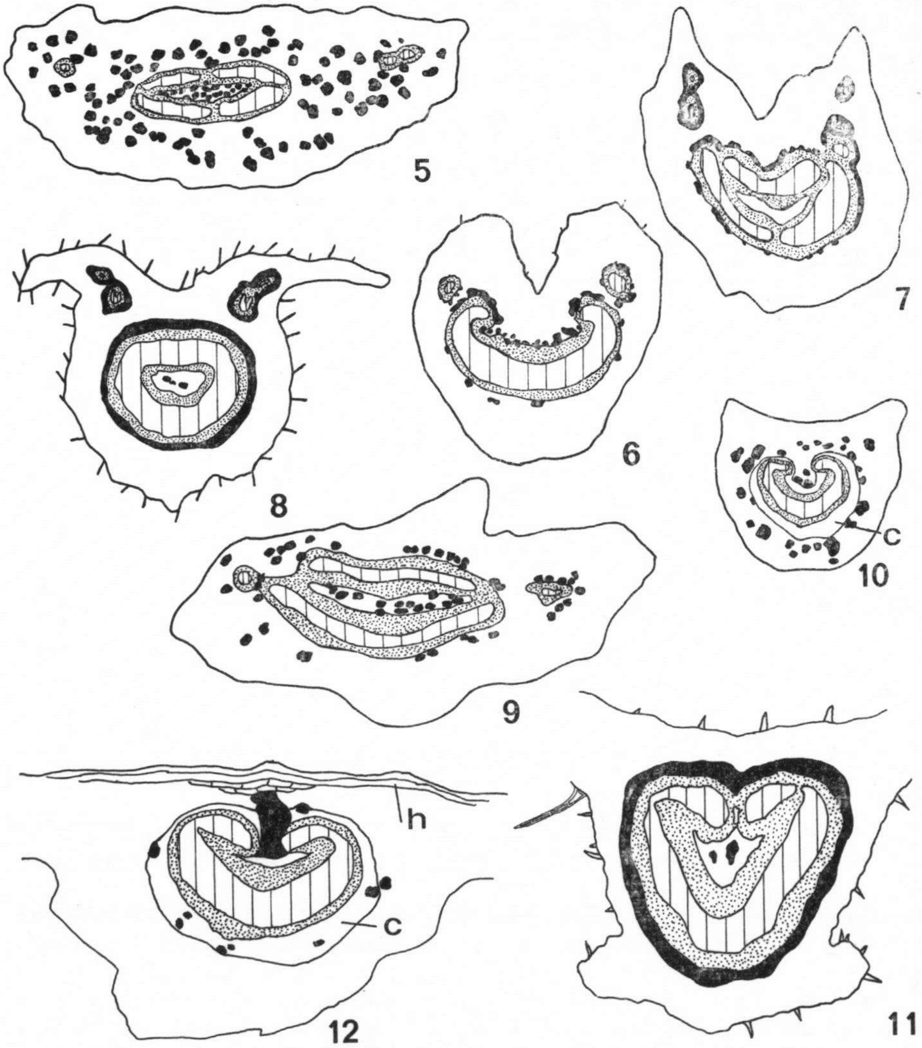

Fig. 5—12. Camera lucida drawings of vascular systems in petiole (5—10) and midrib (11 & 12). 5—10, ×25; 11 & 12, ×68.

5. *Alzatea verticillata* (*Ule 6750*), basal part. — 6. *Axinandra zeylanica* (*Thwaites 2668*), distal part. — 7. *Crypteronia cumingii* (*Edaño PNH 37179*), distal part. — 8. *Crypteronia paniculata* var. *affinis* (*Kostermans 255*), distal part. — 9. *Dactylocladus stenostachys* (*Teysmann s.n.*), central part. — 10. *Rhynchocalyx lawsonioides* (*de Joncheere s.n.*), distal part. — 11. *Crypteronia paniculata* var. *affinis* (*Kostermans 255*) midrib. — 12. *Rhynchocalyx lawsonioides* (*Strey 7750*), midrib.

xylem hatched; phloem dotted; sclerenchyma black; c = collenchyma; h = hypodermis.

ral vascular bundle, in the distal part forming a closed ring, sheathed by a strongly interrupted sclerenchyma ring, and with 2—3 latero-dorsal centric wing bundles on either side. Ground tissue collenchymatous with numerous large sclereids (probably fusiform parallel to axis of petiole). *Crystals* present as druses in ground tissue of lamina and petiole. *Sclereids* in lamina of two types: large, little branched, ± isodiametric asterosclereids in palissade tissue (Plate II, 7), and idioblastic sclerified cells of spongy tissue.

Node (Fig. 3)

Trilacunar with three traces. Cortical bundles departing from lateral traces and probably ending somewhere in the internode below.

Axis (material studied 1—6 mm in diameter; Plate II, 6)

Young twigs square, older twigs rounded in transverse section. Epidermal cells square; cuticle 12—14 μm thick, with conspicuous anticlinal flanges. Cortex of 6—11 parenchymatous cell-layers interspersed with stone cells, with in each corner of the twig 1—3 more or less centric cortical bundles (Plate II, 6). Perivascular sclerenchyma scanty, in an interrupted ring. *Cork* arising in pericycle adjacent to perivascular sclerenchyma, first formed phellem cells square and thin-walled, in later stages layers of square cells with unilateral wall thickenings alternating with flattened thin-walled cells. Greater part of primary phloem sclerified in older material. Secondary phloem composed of sieve tubes, companion cells, chambered parenchyma, and (in older material) infrequently scattered phloem fibres. Primary xylem and internal phloem in a continuous ring; phloem with infrequent sclerenchymatous elements. Pith quadrangular to oval in transverse section, composed of lignified parenchyma, in older material with some strongly sclerified cells. *Crystals* present as druses in cortex and pith, abundant in chambered phloem parenchyma. Sclereids, see cortex and pith.

AXINANDRA Thw.

Material studied. *A. alata* Baill.: BORNEO, *Beccari P.B. 3651**. — *A. beccariana* Baill.: BORNEO, *Beccari P.B. 3423**, *3458**; *Jaheri s.n. (1893)*; *Teysmann s.n. (=HB 8299)*. — *A. coriacea* Baill.: BORNEO, *Chew Wee Lek 1393*; *Jacobs 5116**; *Meijer SAN 37494**, *49845*; *Smythies S 15661*. — *A. zeylanica* Thw.: CEYLON, *d'Alleizette 2485*; *Meijer 492*, *555**; *Thwaites C.P. 2668*.

Leaf (Fig. 6, 13, 14; Plate I, 3, 4; II, 8)

In surface view. Usually glabrous, but indumentum of short unicellular *hairs* sparsely present on petiole and abaxial side of midrib in *A. beccariana*, on petiole and lamina in *A. zeylanica p.p.* (*Meijer* 492) and on abaxial side of lamina in *A. alata*. Cuticle coarsely granular, anticlinal flanges indistinct to absent. Anticlinal walls of unspecialized cells straight to slightly undulated in abaxial epidermis; curved to undulated in adaxial epidermis, with thin areas of periclinal wall in loops of undulations or cell corners. Unspecialized cells with thin, straight anticlinal division walls in part of the material, more frequently in adaxial than in abaxial epidermis. *Stomata* confined to abaxial epidermis, paracytic, subsidiary cells for a minor or major part submersed below the guard cells and one of them occasionally subdivided perpendicular to the pore. Guard cell pairs 11—13—17—20 μm long, 12—14—17—20 μm wide. Outer stomatal ledges fairly well developed. Polar T-pieces absent; cuticular 'cross-pieces' rarely present, only distinct in *A. coriacea p.p.* (*Chew Wee Lek 1393*). Giant stomata infrequently present. Cork warts infrequently present and of irregular outline, probably of traumatic origin. Primary veins and some secondary veins prominent in *A. beccariana* and *A. zeylanica*, not prominent in

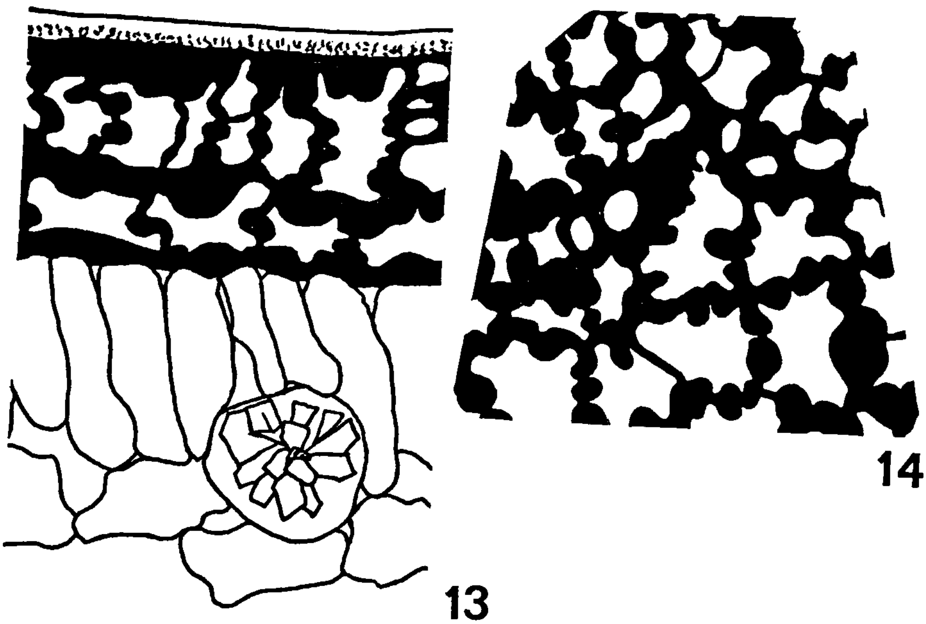

Fig. 13 & 14. *Axinandra zeylanica* (*Meyer 555*). Camera lucida drawings, ×970. — 13. Transverse section of lamina showing irregular wall thickenings of epidermis and hypodermis. Granular cuticular layer indicated with dots. — 14. Paradermal section of hypodermis.

other material. In transverse section. Lamina dorsiventral, 130—340 μm thick. Abaxial cuticle 1—4 μm thick, adaxial cuticle 3—6 μm thick. Unspecialized epidermal cells square to flattened or of irregular outline, adaxially larger than abaxially and the former with irregularly thickened outer periclinal walls (cf. thin wall areas in surface view) and fairly thin and slightly wavy (*A. alata*) to irregularly thickened anticlinal walls (fig. 13). *Stomata* in the same level as the unspecialized cells. Adaxial *hypodermis* clearly differentiated in *A. coriacea*, *A. beccariana*, and *A. zeylanica p.p.* (*Meyer 555*), only present over midrib and major veins of other *A. zeylanica* specimens, and absent from *A. alata*. Hypodermis composed of thick-walled collenchyma cells with very irregular wall thickenings (fig. 13, 14), cells occasionally subdivided by thin anticlinal and periclinal walls. *Mesophyll* composed of 1—3 layers of palissade cells and unlignified spongy tissue. *Midrib* adaxially grooved, abaxially slightly to prominently raised, supplied with a flat to arc-shaped, rarely interrupted, bicollateral vascular bundle, with or without incurved edges; whole system sheathed with sclerenchyma, ground tissue unlignified, parenchymatous to collenchymatous. Major *veins* usually bicollateral, sheathed by sclerenchyma with or without extra polar caps. Minor veins collateral, also usually sheathed by sclerenchyma which is more abundant at the poles except in smallest veins. Outer bundle sheath of unlignified parenchyma variously distinct. All veins embedded in mesophyll. *Petiole* with ± similar vascular pattern as midrib, but with extra latero-dorsal wing bundles except in basal part of petiole of *A. alata*, sheathed by various amounts of sclerenchyma, without sclerenchyma in *A. alata*. Ground tissue parenchymatous to collenchymatous. *Crystals* abundant to rather infrequent; as druses in ground tissue of lamina and petiole as styloids in phloem of major vascular bundles. Idioblastic *sclereids* absent.

Note on individual species. Most of the restricted species-to-species variation in *Axinandra* is recorded in the generic description. The thinnest leaves are found in *A. alata*, in which irregular wall thickenings of the epidermis are least developed. *A. zeylanica* shows the strongest development of irregular wall thickenings in the adaxial epidermis; *A. coriacea* and *A. beccariana* being somewhat intermediate. *A. coriacea* has the thickest leaves.

Node (Fig. 2)

Complete girdling trace plus one median bundle. Lateral anastomoses present, fusing with the basal part of the median trace. Cortical bundles mostly present (absent in *A. beccariana p.p. Beccari 3423* and one of the successive nodes of *A. coriacea SAN 37494*), ending in cortex of internode or continuous over at least two nodes (*A. alata*, fig. 2b).

Axis (material studied 1—4 mm in diameter)

Twigs rectangular to rounded in transverse section. Indumentum of short unicellular hairs present except in *A. alata*. Epidermal cells mainly square to erect. Cuticle 1—2 μm thick in *A. alata*, 2—4 μm thick in *A. beccariana* and *A. zeylanica*, and 5—7 μm thick in *A. coriacea*. Cortex of 5—9 parenchymatous cell layers, in all species with centric cortical bundles in the twig corners. Perivascular sclerenchyma fibres in an interrupted ring, sometimes very infrequent. *Cork* arising in pericycle adjacent to perivascular sclerenchyma, cells square to rectangular in T.S. with unilaterally thickened adaxial walls, alternating with thin-walled layers. Pericycle *c.* 4 cell layers wide and composed of an outer parenchymatous portion, and variously differentiated inner layers of sclereids with U-shaped adaxial wall thickenings. These layers are, if present, continuous with a massive ring of thick-walled sclereids differentiated from outer phloem of older twigs. Phloem fibres restricted to the region of primary phloem, and interspersed with sclereids. Secondary phloem composed of sieve tubes, companion cells, and axial- en ray parenchyma. Primary xylem and internal phloem in a continuous ring. Pith quadrangular to oval, parenchymatous, partly lignified, with rare to frequent thick-walled stone cells; in *A. zeylanic* mainly bordering on internal phloem. Pith caducous in older twigs. *Crystals* present as sparse to frequent druses in cortex and pith, and as long thin styloids in outer and internal phloem. Sclereids, see pith.

CRYPTERONIA Bl.

Material studied. *C. cumingii* (Planch.) Endl.: CELEBES, *b.b. 9704*; MOLUCCAS, *Pleyte 382*; PHILIPPINES, *Edaño PNH 37179*★. — *C. griffithii* Clarke: BORNEO, *Ampuria SAN 41449*★; MALAYA, *Wyatt-Smith KEP. F. 76336*. — *C. macrophylla* Beus.—Osinga: BORNEO, *Banying ak Nyudong S 19193*★, *Anderson & Paie S 28537*★; *Hallier 3180; Kostermans 13012*. — *C. paniculata* Bl. var. *paniculata*: LAOS, *Poilane 11924*; INDIA, *Hooker & Thomson s.n.*★; PHILIPPINES, *Edaño PNH 17897*; MALAYA, *Kochummen KEP. F. 97773*★. — *C. paniculata* var. *affinis* Beus.-Osinga; MALAYA *KEP. F. 98861*★; THAILAND, *Kostermans 255*★.

Leaf (Fig. 7, 8, 11; Plate I, 5)

In surface view. Usually glabrous, but indumentum of short unicellular *hairs* (up to 20 μm long) and long uniseriate, multicellular hairs (up to 160 μm long) present on adaxial and abaxial epidermis of *C. paniculata* var. *affinis*. Cuticle mostly coarsely granular, rarely finely granular, adaxially striated or not, abaxially infrequently striated over veins, with or without thin areas in loops of undulations in adaxial epidermis. Anticlinal flanges rather indistinct to conspicuous, adaxially curved to undulated, abaxially straight to undulated. *Stomata* confined to abaxial epidermis, paracytic, subsidiary cells only for a minor part submersed below the guard cells. Guard cell pairs 12—14—19—22 µm long, 11—14—19—20 µm wide. Giant stomata infrequently present over veins, more rarely in areolae, anomocytic to complex cyclocytic. Polar T-pieces faint to absent, but fairly distinct in *C. griffithii*, outer stomatal ledges well developed. Cork warts infrequently present and of irregular outline, probably of traumatic origin. Primary and secondary veins prominent on both surfaces; elaborate network of minor veins sometimes prominent. In transverse section. Lamina dorsiventral, 110—300 µm thick. Adaxial cuticle 2—6 µm thick, abaxial cuticle 1—3 µm thick. Unspecialized cells mainly flattened, adaxially larger than abaxially. *Stomata* in the same level as unspecialized cells. Adaxial *hypodermis* of 1—2 layers of usually thick-walled lignified cells present, not differentiated in some parts of lamina of *C. paniculata* var. *paniculata p.p.* (*Hooker & Thomson s.n.*), absent from *C. paniculata* var. *affinis*. Hypodermal cells square to flattened, larger than adaxial epidermal cells. *Mesophyll* composed of 1—3 layers of palissade cells, and rather compact, wholly or partly lignified, spongy tissue, not lignified in *C. paniculata*. *Midrib* adaxially flattened to slightly raised, abaxially prominently raised, supplied with a usually closed, more or less triangular bicollateral vascular system, frequently composed of distinct vascular bundles separated by lignified 'pith'—'cortex' connections, with small additional medullary bundles in *C. macrophylla*; whole system sheathed by sclerenchyma. Ground tissue wholly or partly lignified, sometimes sclerified in 'pith' region adjacent to internal phloem. Major *veins* bicollateral, minor veins collateral. Most veins with an inner one- to many-layered sclerenchymatous bundle sheath and/or polar sclerenchyma caps or girders, and a lignified or unlignified parenchymatous outer bundle sheath. Smallest veins with little or no sclerenchyma. Major veins vertically transcurrent by lignified or unlignified sclerenchymatous to parenchymatous bundle sheath extensions, except in *C. paniculata* which has embedded veins. *Petiole* with ± similar vascular pattern as midrib, often not entirely closed in basal part, and kidney shaped to circular in distal part, less frequently fragmented by 'pith'—'cortex' connections; with two to several latero-dorsal bicollateral to centric wing bundles on either side. Vascular system sheathed by various amounts of sclerenchyma. Ground tissue parenchymatous to collenchymatous. *Crystals* present as druses in ground tissue of lamina and petiole, and as styloids in phloem of petiole and midrib. Large unbranched *sclereids* infrequently present in ground tissue of petiole of *C. cumingii*, rarely clustered.

Note on individual species. Most of the variation from species to species in *Crypteronia* is recorded in the generic description. The leaves of *C. paniculata* are typically thin, and the lesser amount of lignification in the supporting tissues around the veins and in the ground tissue of petiole and midrib characterizes this species as the most mesomorphic in *Crypteronia*. *C. paniculata* var. *affinis* has a slightly aberrant arrangement of vascular tissue in the petiole with a not entirely closed, deeply arc-shaped bicollateral bundle with strongly incurved edges (fig. 11). Most of the other characters reported to vary within the genus (e.g. cuticular striations, conspicuousness of thin areas of cuticle in loops of anticlinal wall undulations etc.) appear to be variable within some individual species as well.

Node (Fig. 1)

Typically common gaps with split laterals and one median bundle. In *C. paniculata* without common gaps but with complete girdling traces, showing distinct places of fusion or not. Lateral anastomoses present between lateral traces and median bundle in *C. paniculata p.p.*, but entering the stele in individual gaps below the level of leaf insertion in *C. cumingii* and *C. paniculata p.p.*, after having traversed the cortex.

Axis (material studied 1.5—4 mm in diameter; Plate II, 9)

Twigs rounded in transverse section. Mostly glabrous, but with indumentum of infrequent unicellular hairs in *C. paniculata* var. *affinis*. Epidermal cells square to flattened, cuticle 2—4 µm thick. Cortex of 5—8 parenchymatous cell-layers, interspersed with sclereids in *C. griffithii*, without cortical bundles except just below leaf insertion in some species (see under node). Perivascular fibres in a continuous ring, but in *C. paniculata* poorly developed (var. *paniculata*) or absent (var. *affinis*). Cork arising in outer pericycle adjacent to perivascular sclerenchyma (if the latter is present). *Cork* cells square to flattened, with adaxial unilateral wall thickenings; in *C. paniculata* and *C. griffithii* layers of unilaterally thick-walled cells alternating with thin-walled cells; in other species thin-walled cells irregularly distributed between unilaterally thick-walled cork cells. Secondary phloem composed of sieve tubes, companion cells, parenchyma, and frequent phloem fibres. Primary xylem and internal phloem in a more or less continuous ring, sometimes traversed by lignified pith—xylem connections. Pith oval to rectangular in T.S., composed of mostly lignified parenchyma interspersed with sclereids; the latter most frequent near internal phloem. In *C. griffithii* whole outer part of pith strongly sclerified (Hallier's 'Hartbastbündel', 1911: 31). Pith caducous in older material. *Crystals* present as druses in cortex and pith, as styloids in phloem. Sclereids, see cortex and pith.

DACTYLOCLADUS Oliv.

Material studied. *D. stenostachys* Oliv.: BORNEO, *Anderson 8541; b.b. 32378*; Teysmann s.n. (= HB 7930).*

Leaf (Fig. 9; Plate I, 1)

In surface view. Glabrous. Cuticle smooth to very faintly granular; abaxially conspicuously striated, adaxially faintly striated to smooth. Anticlinal flanges distinct, straight to curved. *Stomata* confined to abaxial epidermis, typically anomocytic, rarely anomocytic to cyclocytic, with 4—7 neighbouring (subsidiary) cells, which are for a minor part only submersed below the guard cells. Guard cell pairs 21—24—29 µm long, 16—19—21 µm wide. Polar T-pieces indistinct. Outer stomatal ledges well-developed. Cork warts of irregular outline and probably of traumatic origin frequent on abaxial epidermis of *Anderson 8541*, infrequent in *Teysmann s.n.* Veins not prominent, except for some primary veins in *Teysmann s.n.*

In transverse section. Lamina dorsiventral, 330—450 µm thick. Adaxial cuticle 7—10 µm thick, abaxial cuticle 2—5 µm thick. Unspecialized cells of adaxial epidermis erect, taller than the square to erect abaxial cells. *Stomata* in the same level as unspecialized cells. *Hypodermis* absent. *Mesophyll* composed of 2—3 layers of palissade cells, and spongy tissue which is faintly lignified in central part. *Midrib* adaxially flattened or slightly raised, abaxially faintly or prominently raised, supplied with a shallowly arc-shaped abaxial bicollateral bundle and a flatter adaxial bicollateral bundle; whole system sheathed by interrupted fibre ring. Ground tissue parenchymatous to collenchymatous, partly lignified. Major *veins* bicollateral, with unlignified parenchymatous bundle sheath enclosing polar fibre caps. Minor veins with little or no sclerenchyma. All veins embedded in mesophyll. Vascular system of *petiole* in distal end similar to that of midrib, but with 1 or 2 latero-dorsal wing bundles on either side; in basal part with a strongly incurved, almost closed bicollateral bundle. *Crystals* present as druses in ground tissue of lamina and petiole, as coarse crystal sand (fragmented druses?) in phloem. Thick-walled fusiform *sclereids* present in ground tissue of lamina and petiole.

Note. The fusiform sclereids in the mesophyll are connected with the polar sclerenchyma caps of the vascular bundles of the veins. They are therefore of an entirely different type than the sclereids of *Alzatea.*

Node (cf. Fig. 1a).

Common gaps with split laterals and one median trace.

Axis (material studied 1.5—3 mm in diameter)

Young twigs more or less rectangular, older twigs rounded in transverse section. Epidermal cells mainly square, cuticle 8—10 μm thick. *Cork* arising in subepidermal layer. Cork cells flattened with lignified anticlinal and inner periclinal wall thickenings; in older twigs 2—3 layers of thickened cells alternating with 1 layer of thin-walled cells. Cortex of 7—9 parenchymatous cell-layers, interspersed with branched and unbranched sclereids. Perivascular sclerenchyma cylinder not or poorly developed in young twigs, almost closed and composed of thick-walled fibres in older material. Secondary phloem composed of sieve tubes, companion cells, and parenchyma, and with infrequent scattered fibres in older material. Primary xylem in a more or less closed cylinder. Internal phloem in more or less discrete units opposite major primary xylem poles. Pith oval to rectangular in transverse section, composed of unlignified parenchyma interspersed with thick-walled fusiform sclereids, and medullary phloem bundles at periphery. Pith caducous in older material. *Crystals* present in phloem as druses and crystal sand, in cortex and pith as infrequent druses. Sclereids, see cortex and pith.

Note. The medullary phloem strands are difficult to distinguish from the internal phloem because of their predominantly peripheral position in the pith. Apparently they fuse occasionally with the internal phloem. Without ontogenetic studies it is not possible to know whether they are merely part of the internal phloem system, separated from each other by phloem parenchyma, or whether the interpretation of them as medullary strands separated by pith parenchyma is the correct one. Their course in the nodal region has not been traced because of difficulties in identifying them in herbarium material.

RHYNCHOCALYX Oliv.

Material studied. *R. lawsonioides* Oliv.: S. AFRICA. *De Joncheere s.n.* (1973); *Strey 7550*, 7565, 7750.*

Leaf (Fig. 10, 12)

In surface view. Glabrous. Cuticle adaxially striated, abaxially smooth to finely granular, and striated over veins. Anticlinal flanges well-developed, straight to slightly curved. *Stomata* confined to abaxial epidermis, intermediate between anomocytic and cyclocytic, occasionally seemingly paracytic (see note), with 4—7 neighbouring/subsidiary cells, submersed below the guard cells for a minor part only. Guard cell pairs 16—17—20—22 μm long, 13—15—16—18 μm wide. Outer stomatal ledges well-developed. T-pieces absent. Cork warts infrequently present and of irregular outline, probably of traumatic origin. Network of primary and secondary veins prominent.

In transverse section. Lamina dorsiventral, 200—270 μm thick. Adaxial cuticle 3—7 μm thick, abaxial cuticle 2—4 μm thick. *Stomata* above level of unspecialized cells. Unspecialized cells square to flattened, adaxially lower, but slightly broader than abaxially. Adaxial *hypodermis* of 1 collenchymatous to parenchymatous layer present; cells larger than those of adaxial epidermis. *Mesophyll* composed of 2 layers of palissade cells, and unlignified spongy tissue. *Midrib* adaxially flattened, abaxially prominently raised, supplied with a single, crescentiform, bicollateral vascular bundle (with incurved edges in *Strey 7550*), linked to adaxial hypodermis by a sclerenchyma girder, abaxially with little or no sclerenchyma (fig. 12). Ground tissue parenchymatous to collenchymatous. Vascular bundles of major and most minor *veins* bicollateral, with a collenchymatous to parenchymatous unlignified bundle sheath extending to upper and lower epidermis, and enclosing an adaxial sclerenchyma girder; smallest veins embedded in mesophyll. *Petiole* with a slightly incurved single bicollateral vascular bundle, sheathed by collenchyma, without latero-dorsal wing bundles. *Crystals* present as druses in ground tissue of lamina and petiole, and as solitary prismatic crystals in phloem. Thick-walled (probably fusiform) *sclereids* frequent in ground tissue of petiole, infrequent in ground tissue of midrib and lamina.

Note. In the seemingly paracytic stomata 2 cells of the ring of anomocytic to cyclocytic subsidiary/neighbouring cells are arranged parallel to the pore.

Node (Fig. 4)

Unilacunar with one trace.

Axis (material studied 1—4 mm in diameter; Plate II, 10)

Twigs rounded in transverse section. Epidermal cells flattened, early caducous, cuticle 1—2 μm thick. Cortex of 8—12 parenchymatous cell layers. *Cork* arising in 3rd to 5th cortex layer from the periphery, composed of layers of thin-walled cells, alternating with 1 to several layers of flattened cells with unilateral adaxial wall-thickenings. Perivascular sclerenchyma virtually absent in young twigs, interrupted and composed of very thick-walled sclereids in older material. Secondary phloem composed of sieve tubes, companion cells, chambered parenchyma cells, and infrequent thick-walled sclereids. Primary xylem and internal phloem in a continuous cylinder. Pith oval in transverse section, composed of unlignified parenchyma interspersed with infrequent thick-walled sclereids, caducous in older material. *Crystals* present as clusters and (sometimes irregular) solitary prismatic crystals in pith and cortex, as solitary prismatic crystals in chambered phloem parenchyma (Plate II, 10). Sclereids, see pith.

Systematic and diagnostic value of some of the anatomical characters

The anatomical characters recorded in the descriptive part are usually of good diagnostic value at the species and often also at the genus level within the *Crypteroniaceae*. Their systematic value is often much more difficult to evaluate and depends on the problems one wants to solve. For instance, the stomatal type, in combination with several other characters, provides good evidence of a close affinity between *Axinandra* and *Crypteronia*, but its taxonomic value becomes of little help in comparisons of *Crypteroniaceae* with *Melastomataceae* which both are heterogeneous in this respect. Styloid crystals also serve to indicate relationships between *Axinandra* and *Crypteronia*, but provide very strong evidence of Melastomataceous affinities too, because some representatives of this family also show this feature, which is of very rare occurrence in the Dicotyledons as a whole (*cf.* Metcalfe & Chalk, 1950). In view of this variability in systematic value, the only possibility for the systematic anatomist is to list as many characters as possible and to judge mutual affinities and relationships with other families on the basis of a good overall

Table I. Some anatomical characters of Crypteroniaceae and putative relatives

	Crypteroniaceae													
	Alzatea	Axinandra	Crypteronia	Dactylocladus	Rhynchocalyx	Oliniaceae	Sonneratiaceae[1])	Lythraceae	Lagerstroemia	Lafoensia	Melastomataceae	Memecyloideae	Astronioideae	Melastomatoideae
Leaf														
Cuticle granular	×	×	×	—	—	—	—	o	—	—	o			
smooth	—	—	—	×	×	+	+	o	×	×	o			
Stomata paracytic	—	×	×	—	—	—	?	—	—	—	o			
anomocytic (to cyclocytic)	×	—	—	×	×	+	+	+	×	×	o			
Hypodermis present	×[2])	×	×	—	×	o	—	o	×	—	o			
absent	—	×	—	×	—	o	+	o	—	×	o			
Vascular system petiole-midrib A[3])	—	×	—	—	×	o	S	o	×	×	o			
petiole-midrib B[4])	×	—	×	×	—	—	D	—	—	—	o			
Veins vertically transcurrent	—	—	×[5])	—	×[6])	—	—	o	×[7])	—	o			
Crystals outside phloem clustered	×	×	×	×	×	o	+	o	×	×	o			
in phloem clustered	×	—	—	—	—	—	D	o	—	×	o			
in phloem crystal sand	—	—	—	×	—	—	—	—	—	—	—			
in phloem solitary prismatic	—	—	—	—	×	+	—	o	×	—	o			
in phloem styloids	—	×	×	—	—	—	—	—	—	—	o			
Unbranched sclereids in petiole	×	—	×[8])	(×)	×	o	o	o	—	—	o			
Branched foliar sclereids	×	—	—	—	—	o	S	—	—	—	o			
Axis														
Site of cork origin. subepidermal	—	—	—	×	—	+	+	—	—	—	o			
in pericycle	×	×	×	—	—	—	—	o	×	—	o			
in cortex	—	—	—	—	×	—	—	o	—	×	o			

Wood (Van Vliet, 1975)[9]														
Vesturing intervessel pits. type 1	×	—	—	—	×									
type 2	—	×	—	×	—									
type 3	—	—	×	—	—									
Vessel—ray and vessel—parenchyma pits alternate	—	×	×	—	×[10]	o	S	o	×[11]	×	o	+	o	o
reticulate to scalariform, larger	×	—	—	×	—	—	D	o	—	—	o	—	o	o
Fibre pits distinctly bordered	—	×	×	×	—	—	—	—	—	—	o	+	+	—
simple to minutely bordered	×	—	—	—	×	+	+	+	×	×	o	(o)	(o)	+
Fibres partly septate	×	—	—	—	×	+	+	o	×	×	o	—	o	o
Parenchyma														
aliform-confluent	—	×[12]	—	×[12]	—	—	(D)	o	×	—	o	o	—	—
paratracheal vasicentric	(×)	—	(×)	—	(×)	+	D	o	—	(×)	o	(o)	o	o[13]
diffuse in aggregates or short lines	—	—	×	—	—	—	—	o	—	—	o	o	o	—
Septate fibres with crystals present	—	—	—	—	×	+[14]	—	o	×	—	—	—	—	—
Rays: Heterogeneous III[15]	—	—	—	×	—	—	—[16]	o	—[16]	×	o	(o)	o	+
Heterogeneous I	×	×	×	—	×	+	—	—	—	—	o	o	o	—
Intercellular canals in rays	—	—	×	×	—	—	—	—	—	—	o	—	o	—

× = species or genus character. o = character present in part of the family only.
\+ = characteristic for (sub)family. — = character absent or not recorded. ( ) = rarely present.

[1] S = character recorded for *Sonneratia* only; D = character recorded for *Duabanga* only.

[2] hypodermis only over midrib and largest veins

[3] arc-shaped, with or without incurved edges in petiole and midrib

[4] composed of an abaxial and adaxial part or completely closed in distal part of petiole and midrib

[5] veins not transcurrent in *Crypteronia paniculata*

[6] midrib also adaxially transcurrent by sclerenchyma

[7] midrib also adaxially transcurrent by collenchyma

[8] only present in *Crypteronia cumingii*

[9] of *Alzatea* only twig material was studied

[10] smaller than in *Axinandra* and *Crypteronia*

[11] alternate to reticulate, larger than in *Rhynchocalyx*

[12] with very narrow wings

[13] parenchyma scanty-paratracheal to vasicentric

[14] it is not evident from Mujica and Cutler's descriptions whether the chambered crystals occur in parenchyma cells or in fibres

[15] according to Kribs (1950)

[16] in these taxa the rays are homogeneous III.

similarity or of consistent differences in a number of characters. This has been done in table I for the 5 Crypteroniaceous genera and several putative relatives. Data on wood anatomy have been included as well and are taken from Van Vliet, 1975.

Of the characters listed, those referring to hypodermis, unbranched sclereids, and probably also the cuticle are of very little value for comparison with other families, yet they are included because within the *Crypteroniaceae* they have a good diagnostic value. The systematic value of the wood anatomical characters is discussed elsewhere (Van Vliet, 1975).The implications of the diversity in nodal anatomy are discussed separately on p. 192.

We have found no reasons to believe that the anatomical diversity employed in the systematic discussions is due to different ecologies of the taxa studied.

Relationships within the Crypteroniaceae

Within the genus *Crypteronia* there is some anatomical diversity supporting Niedenzu's (1892) subdivision into two sections, *Crypteronia* (*C. paniculata*) and *Basisperma* (the other species), a subdivision also adopted by Van Beusekom-Osinga & Van Beusekom (1975). *Crypteronia paniculata* is the only species with a complete girdling trace in the node, with veins embedded in the mesophyll and not vertically transcurrent, and abundant coalescent apertures in the secondary xylem vessels of the twigs (Van Vliet, 1975).

The subgeneric division of *Axinandra* into the monotypic section *Axinandra* (*A. zeylanica*) and section *Naxiandra* (the other species) is not correlated with anatomical differences. *Axinandra alata* of the latter section is anatomically slightly different from the remainder of the genus by its lack of wing bundles in the basal part of the petiole, total absence of a hypodermis, and rather regular outline of the epidermal cell walls.

From table I and from the descriptions it appears that *Axinandra* and *Crypteronia* share many anatomical characters. Particularly the common occurrence of paracytic stomata and styloid crystals, not found elsewhere in the *Crypteroniaceae*, suggest close affinities. Supporting evidence is provided by the overlap in nodal conditions, and similarities in cuticular texture, cork origin, and overall wood anatomy. Differences in petiole anatomy and parenchyma distribution of the wood are minor ones. The peculiar collenchymatous thickening of the cell walls of epidermis and/or hypodermis in species of *Axinandra* is not constant throughout the genus, and does therefore not provide a good distinctive character.

Dactylocladus shares its nodal type with *Crypteronia*, but differs from both *Axinandra* and *Crypteronia* in stomatal type, crystal complement, cork origin, vessel—ray pitting, and ray type. These differences are not sufficiently outweighed by anatomical similarities with either *Crypteronia* or *Axinandra* to be able to advocate a strong affinity as suggested by Van Beusekom-Osinga & Van Beusekom (1975) who placed *Crypteronia* and *Dactylocladus* into one tribe, or by Muller (1975) who reported a similar pollen type for *Axinandra* and *Dactylocladus*.

Alzatea differs strongly from the above mentioned genera in its wood anatomy (Van Vliet, 1975) and also bears little resemblance to these in its other anatomical characters. With its sclereids, clustered crystals in chambered phloem cells, and trilacunar node the genus stands out from all other *Crypteroniaceae*, though it is possible to derive the nodal condition in *Crypteronia* and *Dactylocladus* from that in *Alzatea* or vice versa. The presence of cortical bundles might indicate similar tendencies as in *Axinandra*. From *Crypteronia* and *Axinandra* the genus differs, however, in stomatal type and septate fibres as well as in the characters restricted to *Alzatea*. *Dactylocladus*, sharing the same stomatal type with *Alzatea*, differs from it moreover in cork origin and ray type. The few similarities remaining (see table I) do not compensate for the above mentioned differences, indicating that relationships of *Alzatea* with the other three genera is at most remote.

Rhynchocalyx is also very aberrant in this group of genera; its wood anatomy shows similarities with that of *Alzatea* (Van Vliet, 1975) but is very different from the other three genera. Within *Crypteroniaceae* it is the only genus to have a simple unilacunar node, crystalliferous fibres in the wood, cork arising in the cortex, and solitary prismatic crystals in the phloem. If compared with each of the other four genera, most similarities are with *Alzatea* (stomatal type, and overall wood histology) but considerable differences remain in cuticular texture, mechanical support of veins, petiole anatomy, and vessel—ray pitting, besides the important characters restricted to either *Alzatea* or *Rhynchocalyx*. Differences with *Crypteronia*, *Axinandra*, and *Dactylocladus* are most outspoken, the number of characters in common with each of these genera being extremely limited (see table I).

Accepting Van Beusekom's family delimitation the anatomist is faced with a very heterogeneous group of genera, in which the anatomical evidence only supports a close affinity between *Axinandra* and *Crypteronia*. Remarkably enough this is not supported by macromorphology or palynology. It is possible to advocate some remote anatomical relationships of these genera with *Dactylocladus* if the anatomical characters shared by the three genera are weighted more heavily than the differentiating characters. *Alzatea* would even be much further removed from this assemblage, and anatomical characters provide no evidence at all of affinities of *Rhynchocalyx* with *Axinandra*, *Crypteronia*, and *Dactylocladus*, except that all belong to the *Myrtales*. The anatomical affinities between *Rhynchocalyx* and *Alzatea* appear to be of the same remoteness as those between *Dactylocladus* and both *Crypteronia* and *Axinandra*, and may be taken to support the tribe level to which *Alzatea* and *Rhynchocalyx* have been raised by Van Beusekom-Osinga & Van Beusekom (1975).

As an alternative one might reject Van Beusekom's concept of the *Crypteroniaceae* and search for the closest relatives of each individual genus in other families. This alternative will be explored below.

Position in the Myrtales and affinities with other families

As stated before, the anatomical evidence fully supports inclusion of all genera of the *Crypteroniaceae* in the *Myrtales*. Besides the presence of vestured pits in the wood (Van Vliet, 1975) and intraxylary phloem in twig and leaf, characteristic for most *Myrtales*, there are many more characters in each of the genera witnessing affinities with one or several Myrtalean families (see table I). Affinities with *Cunoniaceae* or other families suggested in the past are not supported by anatomical evidence.

The comparisons have been limited to those families of the *Myrtales* which have been suggested as close relatives of the individual Crypteroniaceous genera in the systematic literature (see comprehensive survey by Van Beusekom in this issue). These families are *Lythraceae* and *Melastomataceae*. *Oliniaceae* have been added because a striking similarity between the wood of *Rhynchocalyx* with that of *Olinia* was noted in a superficial survey of the anatomy of all *Myrtalean* families (Van Vliet, 1975). Both *Oliniaceae* and *Sonneratiaceae* have been included in the *Lythraceae* at some stage of botanical history. The comparisons as summarized in table I are mainly based on data from the literature (Metcalfe & Chalk, 1950; Mujica & Cutler, 1974) but additional observations have been made of most relevant genera using the Rijksherbarium slide collection. It should be borne in mind that the body of anatomical information, although very substantial for the families compared, is by no means complete, rendering conclusions about the lack of affinities with certain groups tentative. For *Lythraceae* separate additional columns for *Lagerstroemia* (*Lagerstroemieae*) and *Lafoensia* (*Diplusodontineae*) are given because of suggestions of close affinities with *Rhynchocalyx* and *Alzatea* respectively (see survey by Van Beusekom, 1975). The two genera of *Sonneratiaceae*, *Duabanga* and *Sonneratia*, are presented individually for those characters in which they differ or which have only been studied in one of the genera. For *Melastomataceae* separate columns have been added as far as wood anatomy is concerned; for the other anatomical characters data in the literature were insufficient to do this.

Before discussing the affinities as based on the overall vegetative anatomy, summarized in table I, the implications of nodal anatomy will be dealt with.

Comparative nodal anatomy

The nodal anatomy of the families compared is only incompletely known. In the literature Sinnott (1914) and Lignier (1886, 1887) provide useful information for *Lythraceae* and *Melastomataceae*, and for these families Dr. R. A. Howard (Arnold Arboretum) provided us with his as yet unpublished data on a substantial number of genera. All *Lythraceae* so far studied are unilacunar with one trace. *Melastomataceae* are unilacunar with one trace or show a common gap with a median trace. Howard furthermore found complete girdling traces in *Rhexia* and *Arthrostemma* 'derived from cortical bundles', a situation perhaps comparable to some of our *Axinandra* species (fig. 2). Cortical and medullary bundles are present in a number of genera (*cf.* Metcalfe & Chalk, 1950). Oe each of the species *Duabanga moluccana* and *Sonneratia caseolaris* (*Sonneratiaceae*) and *Olinia cymosa* (*Oliniaceae*) one node was sectioned for comparison. All nodes appeared to bf unilacunar. It may be interesting to cite Dr. Howard's letter in response to our report o the nodal diversity in *Crypteroniaceae*: "(the diversity of) the 'new' components of the *Crypteroniaceae* is broader than I have found in any family of the *Myrtales*".

In comparing the nodes of *Axinandra*, *Crypteronia*, and *Dactylocladus* with those of the above mentioned families the affinities are obviously with *Melastomataceae*, which family covers the range of these — elsewhere in the Dicots — very unusual nodes; the unilacunar node of *Rhynchocalyx* occurs in all families compared, and the situation reported for *Alzatea* is unique in *Myrtales* as far as known at present. Therefore, general nodal anatomy cannot indicate which taxa have the closest affinities with these two genera. However, the presence of cortical bundles in *Alzatea* and the suggested similarity of its trilacunar node with the common gap plus median trace condition would favour a Melastomataceous affinity rather than relationships with the other families mentioned.

In *Rhizophoraceae*, a family of disputed Myrtalean affinity, the nodes are also characterized by common gaps (Howard, 1970). Evidence from other anatomical features (notably the unvestured pits and the absence of intraxylary phloem in *Rhizophoraceae*) pleads, however, against close affinities of *Rhizophoraceae* with those *Crypteroniaceae* showing similar nodes.

Comparative overall vegetative anatomy

Alzatea differs from the *Lythraceae* in which it was included previously, in nodal anatomy, arrangement of the vascular tissue in petiole and midrib, presence of foliar sclereids, and ray type. The common occurrence of mucilage cells in the leaf epidermis provides another distinctive character for most though not all representatives of the *Lythraceae*. Stant (in Lourteig, 1965) reported mucilage cells in the palissade tissue of *Alzatea*, but we have been unable to find them in material of the same collection. The same applies to secretory sacs she mentioned for the petiole. In several anatomical characters there are suggestions of affinity (wood anatomy, stomatal type, etc., see table I).

Diplusodontineae (*Lafoensia* and *Diplusodon*) in particular appear to share features with *Alzatea*. Anatomically the differences of *Axinandra*, *Crypteronia*, and *Dactylocladus* with *Alzatea* are, however, more substantial than those of *Lythraceae* with *Alzatea*. The same applies to *Oliniaceae* and *Sonneratiaceae*. The affinities and differences between *Alzatea* and *Rhynchocalyx* are of about the same order as those with these three families. As a consequence of the wide anatomical range in *Melastomataceae*, *Alzatea* would fit into this family on the basis of most of its anatomical features, except for its trilacunar node. It would be unjustified to use this as absolute evidence of a very close affinity of *Alzatea* with *Melastomataceae*, because we have been unable to find one representative in the *Melastomataceae* with the combination of most *Alzatea* characters, the latter being haphazardly distributed over different genera of *Melastomataceae*. More detailed and comprehensive anatomical studies in *Melastomataceae* would be necessary to judge the anatomical affinities with *Alzatea*.

With the evidence available it is impossible for the anatomist to contribute much to the systematic affinity of *Alzatea*. The presence of links with several families may be used to support the isolated relic character of this genus, also deduced from its unspecialized pollen type (Muller, 1975).

Rhynchocalyx shares a considerable number of anatomical features with *Lythraceae*. The more heterogeneous rays of *Rhynchocalyx* constitute the only (gradual) difference. Within the *Lythraceae* it is, however, impossible to find the complete combination of *Rhynchocalyx* characters in one representative. Both *Lagerstroemia* and *Lawsonia* from the *Lagerstroemieae*, and *Lafoensia* and *Physocalymma* from the *Diplusodontineae* share a fair number of characters with *Rhynchocalyx*. Thus the anatomical affinities of *Rhynchocalyx* appear to be closer to *Lythraceae* than to the other genera of the *Crypteroniaceae*. The wood anatomy of *Olinia* is more or less identical to that of *Rhynchocalyx*. The only major difference in overall vegetative anatomy is in cork origin, the differences in mechanical support of the leaf veins being of minor importance. Affinities of *Rhynchocalyx* with *Oliniaceae* as based on anatomy are therefore also closer than those with other *Crypteroniaceae*. With *Sonneratiaceae* there are similarities too, but here substantial differences are present (see table I; *Sonneratiaceae* differ moreover in having large mucilage cells in the mesophyll). A comparison with *Melastomataceae* results in only one differentiating anatomical character: crystalliferous fibres in the wood. Similarly as with *Alzatea* it is, however, impossible to indicate an individual member of the *Melastomataceae* showing a large portion of the combination of *Rhynchocalyx* characters. *Punicaceae* may also be mentioned in relation to *Rhynchocalyx*; they also have crystalliferous fibres, and have some other characters in common (see Metcalfe & Chalk, 1950). Summarizing, *Rhynchocalyx* shows more affinities to *Lythraceae p.p.*, *Melastomataceae p.p.*, *Oliniaceae*, *Sonneratiaceae p.p.*, and *Punicaceae* than to *Axinandra*, *Crypteronia*, and *Dactylocladus*. Affinities with *Alzatea* are of about the same order as those with the above mentioned families or even more remote. In view of the traditional placement of *Rhynchocalyx* in the *Lythraceae*, it seems appropriate to support this solution by the anatomical evidence presented here. Sprague & Metcalfe (1937) arrived at a similar conclusion.

Dactylocladus shows several anatomical features not present in *Lythraceae*, *Sonneratiaceae*, and *Oliniaceae*, the nodal anatomy and wood anatomy providing the most significant distinctive characters. Affinities with these families, suggested by certain anatomical similarities (table I) are of the same order as those with *Alzatea* and *Rhynchocalyx*. Affinities with *Axinandra* and *Crypteronia* are somewhat closer. *Melastomataceae* show all characters present in *Dactylocladus*, except the crystal sand in the phloem. An intimate relationship with this family is, moreover, supported by the unusual nodal anatomy occurring in both taxa. The medullary phloem strands of *Dactylocladus* would also be suggestive of *Melastomataceous* affinities. Thus, the results from anatomy support the traditional placement of *Dactylocladus* in the *Melastomataceae*, though its inclusion in subfamily *Memecyloideae* could be challanged on wood and nodal anatomical grounds (*cf.* Van Vliet, 1975).

Axinandra is more different from *Lythraceae*, *Sonneratiaceae*, and *Oliniaceae* than *Dactylocladus*, and has an additional Melastomataceous character of rare occurrence in the Dicots as a whole: styloid crystals. Its anatomical affinities with *Melastomataceae* are about equally close as with *Crypteronia*, and much closer than its affinities with *Alzatea* and *Rhynchocalyx*, *Lythraceae*, *Sonneratiaceae*, and *Oliniaceae*. Its anatomical affinities with *Dactylocladus* are somewhat more remote than with *Crypteronia*. Vegetative anatomy on the whole favours the retention of *Axinandra* in the *Melastomataceae*.

Crypteronia shares most of its anatomical characters with *Axinandra*, and would therefore be equally out of place in *Lythraceae*, *Sonneratiaceae*, and *Oliniaceae*. Anatomical affinities with *Melastomataceae* are so striking that the transfer of this genus to the *Melastomataceae* could be supported positively. Similarities with several *Melastomataceae* are anyway stronger than with *Alzatea* and *Rhynchocalyx* and to a lesser extent also than with *Dactylocladus*.

CONCLUSIONS

In the previous sections of this paper two alternative interpretations have been given of the anatomical heterogeneity of the *Crypteroniaceae* in the sense of Van Beusekom. The considerable anatomical heterogeneity of related taxa like the *Melastomataceae*, *Lythraceae*, and *Sonneratiaceae* (see e.g. table I), which are generally considered as very natural groups, strongly weakens the anatomical arguments which have been put forward to retain *Dactylocladus* and *Axinandra* in the *Melastomataceae*, *Rhynchocalyx* in the *Lythraceae*, and to transfer *Crypteronia* to the *Melastomataceae*. Yet these proposals have been made to offer an anatomical alternative and to demonstrate the apparently independent evolution of macro- and micromorphological characters in this plant group. If *Crypteroniaceae* would represent a natural group derived from a common primitive Myrtalean stock, the anatomical diversity and resemblances with other families would exemplify a very peculiar pattern of divergent evolution within the family together with developments parallel or convergent with those in other families (*Melastomataceae*, *Lythraceae*, *Oliniaceae*, *Sonneratiaceae*). A polyphyletic origin would explain the anatomical diversity much better.

There is no general agreement of the anatomical data with those from floral, fruit, and pollen morphology, although the palynological evidence may be interpreted as either supporting the family concept for *Crypteroniaceae* or as supporting the inclusion of several genera in *Lythraceae* and/or *Melastomataceae* (Muller, 1975).

The only possible synthesis of all the conflicting evidence is to accept that floral and fruit specializations have led to the recognition of distinct families like *Melastomataceae*, *Lythraceae*, etc., but that the overlapping of anatomical and palynological ranges witnesses a more intimate relationship between all the taxa discussed than aparent from external morphology alone. This conclusion agrees more or less with Hallier's view from 1918, who used both macro- and micromorphological characters in this intelligent account of the systematic position of amongst others, *Alzatea*, *Rhynchocalyx*, *Axinandra*, *Crypteronia*, and *Dactylocladus*.

The wide anatomical ranges in the putative relatives of *Crypteroniaceae* and consequently the complicated patterns overlapping each other, make it impossible for the anatomist to support or reject Van Beusekom's (1975) proposals for the new delimitation of this family. The only straightforward suggestion based on anatomy would be to keep *Axinandra* and *Crypteronia* together in the same family, be it either *Crypteroniaceae* or *Melastomataceae*. More detailed knowledge of the anatomical characters in all members of *Melastomataceae*, *Lythraceae*, and *Sonneratiaceae* would be useful for more specific suggestions about which representatives are most similar to the individual genera of the *Crypteroniaceae*. Comparative anatomy cannot decide the family delimitation in this part of the *Myrtales*, but the anatomical character complexes are specific and unusual enough to indicate probable relationships and aid in future revisions of those taxa.

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