LEIDEN BOTANICAL SERIES, No. 3, pp. 20–75, 1976

WOOD ANATOMY OF THE RHIZOPHORACEAE

G. J. C. M. VAN VLIET

Rijksherbarium, Leiden, The Netherlands

Summary. The wood anatomy of 127 samples of 65 species of all 18 genera of the Rhizophoraceae is described in detail; features not observed here, but recorded in the literature are added. Wood anatomically several groups can be recognized. Three distinct groups are very homogeneous, coinciding with the Rhizophoreae (*Bruguiera*, *Ceriops*, *Kandelia*, and *Rhizophora*), the Anisophylleae (*Anisophyllea*, *Combretocarpus*, *Poga*, and *Polygonathus*), and the Macarisieae (*Anopyxis*, *Blepharistemma*, *Cassipourea*, *Comiphyton*, *Macarisia*, and *Sterigmapetalum*), as recognized by several taxonomists. One group, the Gynotrocheae (*Carallia*, *Crossostylis*, *Gynotroches*, and *Pellacalyx*), is rather heterogeneous. The family as a whole is wood anatomically very heterogeneous, but this diversity can be interpreted as the result of divergent xylem specialisation in the different groups. Although the woods of the mangrove genera (Rhizophoreae) are very different from all inland representatives of the family, there are no arguments to regard their character complex as a special adaptation to an unusual environment. Other ecological considerations are also discussed. A key to the woods is presented. Most of the genera can easily be identified, using xylem characters only. Some are, however, difficult to separate wood anatomically.

CONTENTS

INTRODUCTION

Aims of this study

The last more or less comprehensive account of the wood anatomy of the Rhizophoraceae was by Marco (1935). Since Marco's time more material has become available and large parts of the family have been critically revised by taxonomists, justifying a new wood anatomical survey on a more complete basis than Marco could afford. With 18 woody genera, of which 4 inhabit the mangrove forest, the Rhizophoraceae constitute an interesting family from the ecological and anatomical point of view. A fully satisfactory classification below the family level has not yet been proposed, and it is hoped that this study of 127 samples of species belonging to all 18 genera will contribute to our understanding of relationship patterns within the Rhizophoraceae. The affinities of Rhizophoraceae with families constituting the order Myrtales have also become controversial, and it is intended to discuss this subject in a future publication, following the wood anatomical study of several undisputed families of the Myrtales. The first paper in this series dealt with Crypteroniaceae (van Vliet, 1975).

Historical

A survey of the several opinions on the affinities within the Rhizophoraceae is given in Table 1. Almost all of the students of this family have used external morphological characters only. Marco (1935), however, used wood anatomical characters; Geh & Keng (1974) studied morphological and palynological as well as anatomical characters.

From Table 1 it is clear that the views on the position of the mangrove genera (*Bruguiera*, *Ceriops*, *Kandelia*, and *Rhizophora*) have almost always been unanimous. Only Schimper (1893) did not classify them in one group. He assumed that the remarkable structure of the fruit and the mode of germination of these mangrove trees (viviparous) were mere adaptations to the tidal habitat and thus provided artificial, systematic characters. For this reason he mixed them with the inland genera. This was not supported by wood anatomical characters, as has been previously pointed out by Solereder (1899), Moll & Janssonius (1918) and Marco (1935). Schimper's classification has never been accepted.

The Macarisieae, either as a subfamily or as a tribe, have never been subject to much discussion. However, most studies on Rhizophoraceae have been confined to Malesian representatives mainly. Most of the Macarisieae inhabit Africa and S. America, and are in Asia restricted to the mainland.

Of the remaining genera, *Anisophyllea* and *Combretocarpus* were soon found to be different from the others. Differentiating characters are amongst others: leaves alternate instead of decussate, exstipulate instead of stipulate (cf. Geh & Keng, 1974). *Poga* and *Polygonanthus* were later assigned to this group (see Table 1). The remaining genera of the Legnotideae (the inland genera) viz. *Carallia*, *Crossostylis*, *Gynotroches*, and

TABLE 1. Historical survey of the opinions on the classification of the Rhizophoraceae

	Rhizophora	Bruguiera	Ceriops	Kandelia	Carallia	Gynotroches	Crossostylis	Pellacalyx	Anisophyllea	Combretocarpus	Poga	Polygonanthus 1)	Cassipourea	Macarisia	Blepharistemma	Anopyxis	Sterigmapetalum	Comiphyton
Endlicher, 1840	R	R	R	R	R	L	X						L					
Blume, 1849 2)	R	R	R	R	L	L							L					
Miquel, 1855 2)	R	R	R	R	L	L	L		L				L					
Bentham, 1859; Bentham & Hooker, 1865	R	R	R	R	L	L	L	L	A	A			L	L	L			
Baillon, 1876 3)	R	R	R	R	G	G	G	G	A				M	M	M			
Schimper, 1893	4)—	—	—	—	—	—	—	—	A	A			M	M	M			
Engler, 1900, Sprague & Boodle, 1909																M		
Ridley, 1922 2)	R	R	R	R	L	L		L	A									
Kuhlman, 1925																	M	
Marco, 1935 5)	R	R	R	R	G	G	G	X	G	G	X		M	M	M	M	M	
Croizat, 1943												P						
Kuhlman, 1944												A						
Corner, 1951 6)	R	R	R	R	L	L		L	A									
Desch, 1954 7)	R	R	R	R	L	L		L	A									
Melchior, 1964	R	R	R	R	G	G	G	G	A	A	A		M	M				
Pires & Rodrigues, 1971									A	A	A	A						
Floret, 1974																	M	
Geh & Keng, 1974 7)	R	R	R	R	G	G		G	A	A								

Abbreviations and notes concerning Table 1

R = Rhizophoreae
L = Legnotideae
A = Anisophylleae
M = Macarisieae
G = Gynotrocheae
X = unclassified
P = Polygonanthaceae

[1] Position in other families is not mentioned here, but will be discussed in a later chapter.

[2] The author regarded the several groups as separate families.

[3] Baillon used for the taxon of the Gynotrocheae the name Barraldeieae (*Barraldeia* is a synonym for *Carallia*).

[4] In his classification, Schimper mixed the mangrove genera with some of the inland genera. He recognized two groups: the Gynotrochinae containing *Rhizophora*, *Ceriops*, *Kandelia*, *Gynotrochus*, and *Pellacalyx*, and the Carallinae containing *Bruguiera*, *Carallia*, and *Crossostylis*.

[5] This classification is based on wood anatomical characters only.

[6] Corner regarded the Anisophylleae as a separate family.

[7] Partly based on wood anatomical characters.

Pellacalyx were kept together in one group, the Gynotrocheae. Marco (1935) recognized this group in a different circumscription than was given by other students of this family. Using wood anatomical characters, Marco classified *Anisophyllea*, *Combretocarpus*, *Carallia*, *Gynotroches*, and *Crossostylis* in one group, his Gynotrocheae, and he left *Poga* and *Pellacalyx* unclassified. Desch (1954) was not in agreement with this classification, when he stated: 'the two unclassified genera seem to be no more distinct from *Carallia* and *Anisophyllea*, than is *Gynotroches* from these genera'. Geh & Keng (1974) also treated *Pellacalyx* as a member of the Gynotrocheae. Metcalfe & Chalk (1950) largely accepted Marco's system, and mentioned that the material they examined provided less evidence for a clear distinction between the Gynotrocheae sensu Marco and the Macarisieae.

A considerable amount of wood anatomical data has been published in the past, mainly concerning the mangrove genera *Bruguiera*, *Ceriops*, and *Rhizophora* and the inland genera *Anisophyllea*, *Carallia*, *Combretocarpus*, and *Gynotroches*. Data on the other genera are very scanty or even absent. In the following list of publications on the wood structure of the Rhizophoraceae ° indicates the presence of a figure or plate of the genus concerned. These publication, containing microscopical and/or macroscopical data are by Araujo & Mattos Filho, 1973 (*Cassipourea*°, *Rhizophora*°, *Sterigmapetalum*°); Becking *et al.*, 1922 (*Bruguiera*°, *Ceriops*, *Rhizophora*); Benoist, 1931 (*Cassipourea*); den Berger, 1926 (*Bruguiera*°, *Carallia*°, *Rhizophora*°); Cooper & Record, 1931 (*Anopyxis*, *Cassipourea*, *Rhizophora*); Desch, 1954 (*Anisophyllea*°, *Bruguiera*°, *Carallia*°, *Ceriops*°, *Combretocarpus*°, *Kandelia*, *Gynotroches*°, *Pellacalyx*°, *Rhizophora*°); Geh & Keng, 1974 (*Anisophyllea*); Gerard, 1917 (*Cassipourea*°); Hayashi *et al.*, 1973 (*Bruguiera*°, *Rhizophora*°); Hopkinson, 1912 (*Rhizophora*°); Howard, 1948 (*Anisophyllea*, *Bruguiera*, *Carallia*, *Ceriops*, *Rhizophora*); Jentsch & Appel, 1936 (*Rhizophora*°); Jutte, 1958 (*Gynotroches*); Kanehira, 1921 (*Bruguiera*°, *Ceriops*, *Rhizophora*), 1924 (*Carallia*); Karlstedt, 1971 (*Rhizophora*°); Kribs, 1950 (*Carallia*°); Lecomte, 1925 (*Carallia*°); Lindeman *et al.*, 1963 (*Rhizophora*°); Marco, 1935 (all genera except *Comiphyton* and *Polygonanthus*, many °); Martin, 1953 (*Rhizophora*°); Méniaud, 1931 (*Rhizophora*); Metcalfe, 1952 (*Anisophyllea*, young stem); Metcalfe & Chalk, 1950 (mainly referring to Marco, 1935); Moll & Janssonius, 1918 (*Bruguirea*°, *Carallia*°, *Gynotroches*°, *Rhizophora*°); Normand, 1960 (*Anopyxis*°, *Anisophyllea*°, *Cassipourea*°, *Rhizophora*°); Panshin, 1932 (*Bruguiera*, *Ceriops*°, *Rhizophora*); Pearson & Brown, 1932 (*Bruguiera*°, *Carallia*°, *Rhizophora*°); Perrot, 1921 (*Rhizophora*); Pires & Rodrigues, 1972 (*Anisophyllea*°, *Polygonanthus*°); Rao & Purkayastha, 1972 (*Blepharistemma*°, *Bruguiera*°, *Carallia*°, *Ceriops*°, *Kandelia*°, *Rhizophora*°); Record & Hess, 1943 (*Cassipourea*, *Rhizophora*, *Sterigmapetalum*); Record & Mell, 1924 (*Rhizophora*); Reyes, 1938 (*Bruguiera*°, *Carallia*°, *Ceriops*°, *Rhizophora*°); Riera, 1947 (*Poga*); Sarlin, 1954 (*Bruguiera*, *Crossostylis*); Solereder, 1899 (*Bruguiera*, *Carallia*, *Cassipourea*, *Ceriops*, *Gynotroches*, *Kandelia*, *Macarisia*, *Rhizophora*) and Sprague & Boodle, 1909 (*Anopyxis*, young stem).

Geographical distribution of the Rhizophoraceae

Representatives of the Rhizophoraceae (18 genera, ± 161 species), occur in the tropics of all continents. *Polygonanthus* (2 spec.) and *Sterigmapetalum* (3 spec.) are restricted to tropical S. America. *Anopyxis* (1 spec.), *Comiphyton* (1 spec.), and *Poga* (1 spec.) only occur in Africa. *Macarisia* (± 8 spec.) is restricted to Madagascar. *Combretocarpus* (1 spec.) can only be found in Malesia, *Crossostylis* (± 10 spec.) only in Melanesia. *Gynotroches* (1 spec.), *Pellacalyx* (7 spec.), *Kandelia* (1 spec.), *Carallia* (± 10 spec.), *Ceriops* (2 spec.), and *Bruguiera* (16 spec.) have their distribution in Malesia and adjoining areas, the last three also occur in E. Africa. *Anisophyllea* (± 25 spec.), *Cassipourea* (± 65 spec.), and *Rhizophora* (7 spec.) are pantropical.

MATERIAL AND METHODS

Wood samples were obtained from a number of institutional wood collections. The institutions will be referred to using Stern's (1967) abbreviations; when no wood collection references are given, the samples are from the Rijksherbarium wood collection. The wood collection numbers are given between brackets. Herbarium vouchers are listed when known. Mature wood samples are listed without special indication, immature samples are listed with the branch or stem diameter.

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

For each sample, 25 measurements were made for the vessel member length, vessel diameter, number of bars per perforation plate, and for fibre length. Vessel member length was measured including the tails. Data on vessel frequencies are based on at least 5 counts in each specimen in areas of 1 mm^2; in specimens with a very low vessel frequency (1–3/mm^2) the 5 counts were made in areas of *c.* 7 mm^2. Data on ray frequency are based on at least 4 counts over a tangential distance of 1 mm each.

Specimens marked with an asterisk (*) were studied using macerations only, specimens marked with ° were studied using sections only. Specimens marked with $^+$ were also used for scanning electron microscopy.

When possible, the names of the species were adjusted to revisions and studies by Alston (1925) for *Cassipourea*, by Hou (1957, 1958, 1960) for *Bruguiera*, *Rhizophora*, and the remaining Malesian taxa, by Hutchinson & Dalziel (1954) for *Anopyxis* and *Cassipourea*, and by Lewis (1956) for *Cassipourea*.

DESCRIPTIVE PART

Explanatory notes to the descriptions

The absence of characters is not recorded unless this is important for identification purposes.

For quantitative characters, no size classes are used except for the thickness of the walls of the fibres, as seen in transverse section. For these, the following size classes are used:

Very thin — Lumen wider than three times the thickness of the walls.
Thin — Lumen one to three times the thickness of the walls.
Medium thick — Lumen as wide as the thickness of the walls to half the thickness of the walls.
Thick — Lumen as wide as half the thickness of the walls to ¼ of the thickness of the walls.
Very thick — Lumen narrower than above.

This classification differs from the one proposed by Chattaway (1932) in the presence of a fifth class, that of the medium thick-walled fibres and in the more exact definition of the size classes.

In the descriptions, quantitative values are recorded including extreme values and range of means. In cases where two specimens were studied both means are given connected with &.

If more than two species have been studied, the quantitative characters are given in additional tables, specified for each sample.

Data on specimens present in the slide collections of the Jodrell Laboratory, Kew; the Forest Products Laboratory, Princess Risborough, and the Commonwealth Forestry Institute, Oxford, are briefly mentioned in the notes, only when these refer to specimens not studied here, or when striking differences were observed. Data from literature are also given in the notes.

Descriptions

ANISOPHYLLEA R. Br. ex Sabine

Material studied. A. beccariana Baillon: Borneo, *Jacobs 5245*°. — *A. boehmii* Engl.: Zaire, *Coget 63* (= *IF 21196*, Tervuren); *Malaisse 4* (= *IF 24226*, Tervuren, diam. ±4.5 cm).—*A. cinnamomoides* (Gard. & Champ) Alston: Ceylon, (*MADw 33139**), (*SJRw 48537*)°, (*Hw 22435*); India (*SJRw 22905*).—*A. corneri* Ding Hou: Singapore, *SF 25927* (= *FHOw 7960*).—*A. gossweileri* Engl. & Brehm.: Zaire, *Dechamps*, *Murta & Da Silva 1021*° (= *IF 28526*, Tervuren); (*IF 24378*, Tervuren).—*A. griffithii* Oliver: Malaya, *Kep 84001*°, (= *W.T. 7275*).—*A. laurina* R. Br. ex Sabine: Sierra Leone, *Cons. of For. 86* (= *FHOw 8164*); (*MADw 14138*).—*A. manausensis* Pires & Rodr: Brazil, *Loureiro X-3145* (= *Uw 20754*).—*A. meniaudi* Aubr. & Pellegr.: Liberia, *T.P. 4294–70* (ex RTIw).—*A. obtusifolia* Engl & Brehm.: Tanzania, *Bryce 135* (= *FHOw 20796*). From literature (see note): *A. disticha* (Jack) Baill.; *A. guianense* Sandwith.

Mainly large trees, up to 25(–40) m, in evergreen forests; *A. disticha* and *A. boehmii* are small trees, up to 5(–7)m; the latter inhabits the dry *Brachystegia-Isoberlinia* woodlands.

Growth rings usually absent, rarely faintly present (*A. boehmii*). *Vessels* diffuse, 1 or 2(–5)/mm², solitary and in radial multiples of 2(–4), occasionally in clusters including vascular tracheids, 40–95% solitary, round to oval, tangential diameter (90–)160–270 (–350) μm, radial diameter up to 420 μm, walls 5–10 μm thick. Vessel member length (220–)390–960(–1200) μm. Perforations simple in horizontal to oblique end walls. Inter-vessel pits crowded, alternate, round to polygonal, 4–7 μm, frequently with coalescent apertures. Vessel–ray pits not seen, because the vessels are completely surrounded by axial parenchyma. Vessel–parenchyma pits similar to the inter-vessel pits, but half-bordered, 5–8 μm, sometimes more elongate, up to 11 μm, infrequently with coalescent apertures or unilaterally compound. Solid amorphous contents present in *A. cinnamomoides*, *A. corneri*, *A. meniaudi*, and *A. obtusifolia*. *Vascular tracheids*, with or without perforations fairly frequent and in clusters in *A. boehmii*, infrequent and also solitary in the other species, not seen in *SJRw 22905* of *A. cinnamomoides*, tangential diameter 30–70μm, (420)550–1700(–1800)μm long. Pits between vascular tracheids and parenchyma more elongate than the vessel–parenchyma pits, up to 16 μm, occasionally unilaterally compound. Solid contents with crystal-like surface as seen with SEM noted in vascular tracheids of *A. boehmii*, crystal-like structures not visible with the light microscope. *Fibres* (840–)1270–2590(–3100) μm long, walls thick to very thick, with bordered pits of 3–5 μm. Pits frequent on both radial and tangential walls, but more frequent on radial walls in *A. beccariana*, *A. cinnamomoides*, and *A. griffithii*. Fibres infrequently gelatinous. *Parenchyma* paratracheally banded, completely embedding the vessels, bands more or less continuous, 2–4(–7) cells wide; infrequently in short tangential lines and scanty diffuse; abundant in most species, least so in *MADw 14138* of *A. laurina* where bands are mostly 2 cells wide. Strands of (6–)7–9(–13) cells. *Rays* heterogeneous II, of two distinct sizes; broad multiseriate rays, 1–2/mm, up to 20 cells wide and up to 4–6(–11) mm high, occasionally with sheath cells; uniseriate rays 3–7 /mm, mainly composed of square to erect cells, infrequent with biseriate parts, (2–)4–7(–10) cells high. Solitary *crystals* in axial and ray parenchyma cells, rarely absent. Crystalliferous cells usually chambered and sometimes with thick walls. Globular and amorphous contents in rays and axial parenchyma; 'gelatinous' contents in rays and axial parenchyma noted in *A. obtusifolia*, sometimes attached to the cell walls.

Note. Metcalfe (1952) described the secondary xylem of a twig of *A. guianense* Sandwith from British Guyana and mentioned a great resemblance with the African species *A. laurina*. He recorded an opposite or even almost scalariform arrangement of the vessel wall pits of the first species. Geh & Keng (1974) gave an account of the wood of *A. disticha* (Jack) baillon and *A. corneri*. For these species they mention mixed simple and scalariform perforations. Both these reports of deviations from the description given here may be due to the fact that immature material was used. Unfortunately, Geh & King did not mention the nature of their material, nor did they mention whether

TABLE 2. Quantitative characters of Anisophyllea

Species and/or specimen	2	3	4	5	6	7	10
A. beccariana	1—2	60	140—250—300	320			
A. boehmii							
Coget 63	1—3(—12)	70	90—160—220	245	230—390— 620	420— 550— 750	840—1270—1600
Malasse 4	2—3(—13)	65	95—170—230	250	220—440— 630	630— 645— 710	950—1410—1630
A. cinnamomoides							
SJRw 48537	1—2	50	180—260—330	370			
MADw 33139					630—860—1070	760— 795— 855	1630—2020—2580
Hw 22435	3—4(— 5)	70	90—190—270	310	510—700— 900	690— 760— 830	1680—1970—2130
SJRw 22905	1—2	95	200—250—300	360	580—780— 990		1950—2160—2730
A. corneri	1—2	65	110—180—240	250	510—620— 720	700— 820— 990	1130—1900—2260
A. gossweileri							
IF 28526	1—2	60	120—230—280	310			
IF 24378	1—2	55	110—220—270	320	320—540— 710	510— 690— 840	1340—1730—2080
A. griffithii	2—3	60	190—250—320	400			
A. laurina							
Cons. of For. 86	1—2	60	110—250—350	420	700—960—1200	1210—1450—1760	2070—2590—3100
MADw 14138	1—3	60	120—240—310	360	540—760— 870	820— 970—1210	1660—2190—2710
A. manauensis	1—2	80	90—190—300	320	500—670— 940	550— 940—1340	1370—1800—2180
A. meniaudi	1—2(— 3)	50	190—270—330	420	620—880—1070	970—1210—1420	1790—2570—2870
A. obtusifolia	1—2(— 4)	80	120—260—320	410	450—620— 780	1320—1700—1800	1470—1890—2130

Explanation of the figures in the tables 2—8.

1. Growth rings: + = present; ± = faint; - = absent.
2. Vessel frequency $/mm^2$.
3. Percentage of solitary vessels.
4. Tangential vessel diameter in μm.
5. Maximum radial vessel diameter in μm.
6. Vessel member length in μm.
7. Length of vascular tracheids in μm.
8. Percentage of vessel end walls with scalariform perforations.
9. Number of bars per scalariform perforation plate.
10. Fibre length in μm.
11. m = mature sample (Ø > 10 cm); a figure indicates the diameter of the sample in cm.

the mixed scalariform and simple perforations were present in both species or only in one of the two. I did not find scalariform perforations in the mature wood of *A. corneri*. The growth rings of *A. boehmii* are probably due to the growth conditions of this species in the dry *Brachystegia-Isoberlinia* woodlands, where it is submitted to seasonal drought.

ANOPYXIS Engl.

Material studied. A. klaineana (Pierre) Engl.: Liberia (*SJRw 15743*)+; Gold Coast (*FHOw 843*); Côte d'Ivoire, *Bamps 2242* (=*IF 21850*, Tervuren); Zaire, *Corbisier-Baland 48* (= *IF 711*, Tervuren).

Large tree, up to 30 m. Frequent in evergreen forests.

Growth rings absent. *Vessels* diffuse, (4–)5–11(–14)/mm^2, almost exclusively solitary, round to oval, tangential diameter 110–160—250 μm, radial diameter up to 340 μm, walls 3–6 μm thick. Vessel member length (920–)1260–1765(–2340) μm. Perforations simple in oblique to almost horizontal end walls, very rarely scalariform with 8–14 bars (no scalariform perforations seen in *Bamps 2242*). Inter-vessel pits rarely present, transitional where tails are in contact with succeeding vessel members. Vessel–ray pits more or less opposite to scalariform, half-bordered to almost simple, circular (up to 14 μm) to elongate (up to 78 μm). Vessel–parenchyma pits reticulate to scalariform, up to 53 μm long, occasionally half-bordered and unilaterally compound. Vessel–fibre pits in vertical rows, round, 8–10 μm, rarely paired and with coalescent apertures on the fibre side. Thin-walled tyloses present in two specimens. *Fibres* (1240–)2080–2740(–3390) μm long, with thick to very thick walls and frequent bordered pits of 8–10 μm on both radial and tangential walls. In *FHOw 843* and *SJRw 15743*, with long extending apertures, frequently coalescent in the former, rarely so in the latter. Fibres with bulging, densely pitted ends and 'short' fibres with numerous pits infrequently present. Fibres occasionally gelatinous or with minutely branched tips. *Parenchyma* paratracheal, mostly unilaterally aliform. Strands of (7–)9–11(–14) cells. *Rays* heterogeneous I–II, (5–)6–8(–10)/mm, (1–)3–4(–5)-seriate, rays up to 1.3 mm high, tails composed of (2–)6–7(–14)square to erect cells; uniseriate and biseriate rays infrequent, (2–)4–7(–11) cells high. Solitary *crystals* frequent or infrequent in rays and axial parenchyma. Crystalliferous cells usually chambered and often with thick walls. Solid amorphous or granular contents in rays and axial parenchyma.

Note. Formerly another species was recognized, *A. ealaensis* (de Wild.) Engl., but Hutchinson & Dalziel (1954) reduced it to *A. klaineana*. Wood anatomically, no differences could be found between samples named *A. klaineana* and the sample named *A. ealaensis* (*SJRw 15743*).

BLEPHARISTEMMA Wall. ex Benth.

Material studied. B. membranifolia (Miq.) Ding Hou: India. (*SJRw 22907*), (*Dehra Dun 4584*).

Tree up to 30 m, in evergreen forests.

Growth rings faint. *Vessels* diffuse, (23–)27–35(–41)/mm^2, solitary and in radial or oblique multiples of 2–3 (–4), 60 & 65% solitary, round to oval, tangential diameter (39–) 67 & 80(–105) μm radial diameter up to 108 μm, walls 2–4 μm thick. Vessel member length (760–)1080 & 1175(–1690) μm. Perforations both simple and scalariform in oblique end walls; 2 & 7% of the perforations scalariform with (2–)6 & 7(–11) thin bars, infrequently with some finely reticulate ones. Inter–vessel pits opposite to transitional. Vessel–ray pits opposite to reticulate, usually almost simple, occasionally half-bordered, circular (up to 9 μm) to elongate (up to 26 μm) Vessel–fibre pits in vertical rows, round, 7–9 μm infrequently elongated up to 15 μm, rarely paired and with coalescent apertures on the fibre side. Thin-walled tyloses rarely present in *SJRw 22907*. *Fibres* (960–) 1910 & 2020(–2420) μm long, with thick walls and frequent bordered pits of 7–9 μm on both radial and tangential walls. 'Short' fibres with numerous pits frequently present. Fibres occasionally gelatinous and with minutely branched tips. *Parenchyma* predominantly apotracheally banded, infrequently in contact with some vessels, bands irregular, 1–2(–4) cells wide; also scantily diffuse or diffuse in small aggregates. Strands of (6–)7 & 9(–11) cells. *Rays* heterogeneous I–II, (10–)11 & 13(–15)/mm, 1–2(–3)-seriate, multiseriate rays with short to very long tails of 1–26 square to erect cells; uniseriate rays infrequent, (2–)4 & 7(–12) cells high. Solitary *crystals* infrequent in rays and axial parenchyma.

Note: Rao & Purkayastha (1972) mentioned a vessel frequency of 16–24/mm^2.

BRUGUIERA Lamarck (Fig. 2a; Plate 1/1; Table 3)

Material studied. B. cylindrica (L.) Bl.: C. Java (*SJRw 30813*).—*B. gymnorrhiza* (L.) Savigny: N. Borneo, *SAN A 2672* (= *FHOw 18300*); Australia (*SFCw D 9099*); Philippines (*SJRw 2422*)°; E. Africa, *Schlieben Reinbek 1561* (= *Uw 15521*).—*B. hainesii* C. G. Rogers: Malaya, *KEP 45397* (= *W.T. 5732*)°.—*B. parviflora* (Roxb.) Arn.: British Solomon Isl., *Walker 204* (= *FHOw 18050*); Borneo, *SAN A 2628* (= *FHOw 18302*).—*B. sexangula* (Lour.) Poir.: Burma (*SJRw 13124*); New Caledonia, *Sarlin 180* (= *CTFT 6136*); N. Borneo, *SAN A 2623* (= *FHOw 18298*); *SAN 29761* (= *IF 10644*, Tervuren); Philippines, *For. Serv. 6086*, TS (= *IF 10835*, Tervuren); W. New Guinea, *van Royen 4614*.

Trees up to 30(–40) m; mangrove forests, ascending tidal parts of rivers.

Growth rings absent. *Vessels* diffuse, (6–)11–34(–46)/mm^2, solitary and in radial multiples of 2–3(–4), 25–65% solitary, round to oval, tangential diameter (38–)70–101(–126) μm, radial diameter up to 151 μm, walls 4–10 μm thick. Vessel member length (220–)510–1190(–1660) μm. Perforations scalariform in oblique end walls, with (3–)6–11(–19) thick bars. Inter-vessel pits scalariform, extending over the entire inter-vessel walls, infrequently transitional. Vessel–ray pits almost simple and reticulate to half-bordered and opposite, up to 32 μm long, long axis also vertical; half-bordered pits frequently vertically unilaterally compound, each slender ray pit subtending 2–3(–5) vessel pits (Fig. 2a). Vessel–parenchyma pits predominantly large and simple, uniseriate, scalariform or diffuse, crowded or not, oval to elongate, up to 27 μm; infrequently half-bordered and unilaterally compound. Vessel–fibre pits small, round, diameter 2–4 μm, rarely the fibre pit subtended by a larger, elongated pit, up to 7 μm, in the vessel wall. Thin-walled tyloses frequently present. Solid granular contents infrequently present. *Fibres* (710–) 1015–1790(–2400) μm long, walls thick to very thick, with minutely bordered to almost simple pits of 1–3 μm, frequent on the radial walls. Fibres septate, frequently gelatinous and often with granular contents. *Parenchyma* scanty to very scanty, paratracheal, rarely vasicentric. Strands of (5–)6–8(–10) cells. *Rays* heterogenous II–III, infrequently homogeneous, (5–)6–8(–9)/mm, (1–)3–5(–6) cells wide; multiseriate rays up to 3.7 mm high, with infrequent sheath cells; uniseriate rays very infrequent, 0–1/mm, composed of square to procumbent cells, rarely with a small biseriate part, (2–)4–7(–12) cells high. Solitary *crystals* present in rays. Globular, granular and amorphous contents frequent in rays and axial parenchyma. In *SAN A 2623* of *B. sexangulare* some infrequent groups of ray cells with probably silica-incrusted (optically isotropic) walls.

Note. Vessel frequencies, mentioned in literature by Kanehira (1921), Moll & Janssonius (1918), Panshin (1932), and Reyes (1938) are: 13–40/mm^2 for *B. cylindrica*, 12–35/mm^2

TABLE 3. Quantitative characters of Bruguiera

(For explanation of the figures see table 2, Anisophyllea)

Species and/or specimen	2	4	5	6	9	10
Bruguiera cylindrica	26—29—32	71— 87—105	113	520— 960—1130	6— 8—19	1025—1380—1735
B. gymnorhiza						
SAN A 2672	27—34—43	71— 91—122	151	660—1110—1660	8—11—14	1290—1790—2200
SFCw 9099	6—17—21	75— 91—110	116	920—1190—1470	8—11—15	1530—1810—2160
SJRw 2422	22—27—33	63— 97—110	141			
Schlieben 1561	23—33—46	63— 80— 93	97	630— 930—1210	6—11—13	740—1290—1630
B. hainesii	18—21—24	69— 84—107	121			
B. parviflora						
Walker 204	22—25—27	63— 89—101	121	580— 930—1110	4— 7—10	580— 930—1110
SAN A 2628	23—25—28	76— 91—105	143	450— 800— 890	5— 9—14	920—1250—1600
B. sexangula						
SJRw 13124	18—21—25	76—101—126	130	390— 520— 700	6— 7— 9	710—1015—1315
Sarlin 180	11—16—21	58— 71— 82	113	390— 850—1100	4— 8—14	870—1370—1890
SAN 20761	8—11—15	58— 72—105	127	220— 510— 680	4— 6— 8	850—1090—1290
SAN A 2623	23—27—31	63— 87—121	131	600— 960—1190	6— 8—17	1240—1640—1950
Serv. For. 6086 TS	20—23—25	55— 70—101	131	610— 860—1040	7—10—13	1160—1630—2400
Van Royen 4614	13—17—21	38— 72— 93	109	670— 880—1270	5— 8—10	1000—1430—1790

for *B. gymnorrhiza*, 10–40/mm^2 for *B. parviflora*, and 10–16/mm^2 for *B. sexangulare*. Rao & Purkayastha (1972) recorded for these species together (*B. cylindrica* excepted) a vessel frequency of 8–25/mm^2. No differences could be found when the vessel frequencies of species growing in the outer fringe of the mangrove forest were compared with the frequencies of species growing in the inner, rarely inundated part of the mangroves (see part on ecological aspects). Marco (1935) and Metcalfe & Chalk (1950) did not mention septate fibres nor the minutely bordered fibre pits, but recorded simple pits only. Gonggrijp (1932) studied *B. parviflora*, *B. caryophylloides* (= *B. cylindrica*), and *B. eriopetala* (= *B. sexangula*); he recorded groups of silicious ray cells in the latter species only.

CARALLIA Roxb. (Plate 1/5)

Material studied. C. brachiata (Lour.) Merr.: Pakistan, *Majumbar & Islam 30* (= *MADw 24544*); Malaya, *F.M.S. 34021* (= *FHOw 3801*); Sumatra, *Krukoff 4154* (= *Hw 22438*); Borneo, *SAN A 1547* (WIBw); New Guinea, *van Royen 4557*, *BW 12357°*; Madagascar (*SJRw 12892*); Queensland (*Hw 26635*).—*C. eugenioidea* King; Malaya, *F.M.S. 4045* (= *SJRw 50489*).

Small trees, but *C. brachiata* up to 50 m; rain forests, *C. branchiata* rarely in savannas and edges of swamp forests; *C. eugenioidea* occurs from low altitudes up to 1800 m.

Growth rings absent. *Vessels* diffuse, (3–)5–6(–10)/mm^2 but in *SAN A 1547* and *van Royen 4557* of *C. brachiata* (5–)9 & 13(–18)/mm^2, solitary and in radial or tangential multiples of 2, rarely in multiples and clusters of 3 and 4, 25–60% solitary, round to oval, tangential diameter in *C. branchiata* (90–)130–210(–300), in *C. eugenioidea* (75–)115(–160) μm, radial diameter respectively up to 320 μm and up to 190 μm, walls 6–7 μm thick. Vessel member length in *C. brachiata* (530–)860–1460(–1780) μm, in *C. eugenioidea* (420–)780(–1020) μm. Perforations simple in horizontal to slightly oblique end walls. Inter-vessel pits crowded, alternate, round to polygonal, 5–9 μm. Vessel–ray pits infrequently present, because a great part of the vessels is completely surrounded by axial parenchyma; diffuse to ± alternate, half-bordered and often unilaterally compound, to almost simple, round to oval, up to 16 μm. Vessel–parenchyma pits typically large and simple, infrequently half bordered, uniseriate, biseriate, diffuse or alternate, round (up to 14 μm) to elongate (up to 37 μm). Vessel–fibre pits infrequently present, 5–8 μm. Thin-walled tyloses infrequent in *Majumbar & Islam 30*, *BW 12357*, *F.M.S. 3402* of *C. brachiata*. *Fibres* of *C. brachiata* (1600–)1990–3020(–3480) μm long, of *C. eugenioidea* (1210–)1680(–2320) μm long, walls thick to very thick, thin to medium thick if a fibre is in contact with a vessel, with bordered pits of 5–8 μm, frequent on both radial and tangential walls. *Parenchyma* paratracheally banded, vessels often completely embedded, but on abaxial and/or adaxial side of the vessels the parenchyma ring sometimes interrupted and some fibres then in contact with the vessels; bands (2–)4–6(–7) cells wide, narrower, 1–3(–4) cells wide in *Majumbar & Islam 30* and *Krukoff 4154* of *C. brachiata*, irregularly banded, bands 2–15 cells wide in *C. eugenioidea*, parenchyma infrequently aliform, sometimes slightly confluent in *BW 12357* of *C. brachiata*; parenchyma also infrequently diffuse or diffuse in short apotracheal lines in *C. brachiata*, more frequently so in *C. eugenioidea*. Strands of (6–)7–9(–12) cells. *Rays* heterogeneous II, of two distinct sizes; broad multiseriate rays, 1–2/mm, up to 26 cells wide, up to 3.1 mm high, occasionally with sheath cells; uniseriate rays 4–7(–9)/mm, mainly composed of square to erect cells, infrequently with a small biseriate portion, (3–)6–10(–22) cells high. Solitary *crystals* frequent in rays and axial parenchyma, abundant in *F.M.S. 34021* of *C. brachiata*. Crystalliferous parenchyma cells usually chambered and sometimes with thick walls, one clustered crystal observed in *Hw 26635* of *C. brachiata*. Granular contents infrequent in rays and parenchyma cells.

Note. Geh & Keng (1974) recorded shorter vessel members (620–)680(–1155) and fibres (395–)908(–1105) μm for *C. brachiata* and *C. eugenioidea*. The crystalliferous fibres mentioned by Marco (1935) are parenchyma strands with crystals, scattered among the fibres (Metcalfe & Chalk, 1950). Rao & Purkayastha (1972) reported a vessel frequency of 3–10/mm^2 for *C. lucida* (= *C. brachiata*). Kanehira (1924) mentioned for *C. brachiata* tracheids of 1500–2000 μm long. Possibly he identified the infrequent more thin-walled fibres as tracheids, or he had a sample of an *Anisophyllea* species, which is wood anatomically very much alike. *C. caryoides* Ridley, mentioned by Desch (1954: 470) is very probably a transcription error for *C. euryoides* Ridley. Quantitative data of *C. brachiata*, presented by Reyes (1938) are within the range of the material studied by me.

CASSIPOUREA Aubl.

(Plate 2/12; plate 3/17–19; Plate 4/20, 21, 25; Table 4)

Material studied. C. alba (Sw.) Poir.: Dominica, *Stern & Wasshausen 2479* (= *MADw 24180*) (see below).—*C. afzelii* Alston: Liberia, *Cooper 214* (= *IF 26608*, Tervuren)$^{+}$.—*C. calimensis* Cuatr.: Colombia, *Cuatrecasas 16625* (= *SJRw 43078*)$^{+}$.—*C. congoensis* R. Br. ex DC.: Nigeria, *For. Dept. 15005* (= *FHOw 22039*)$^{+}$; Rwanda, *G. Bouxin 1098* (= *IF 24194*, Tervuren).—*C. elliptica* Poir.: Barro Colorado Isl., *Watmore & Abbe 161* (= *Hw 161*); Panama, *U.S. Nat. Herb. 715714–15* (= *Uw 7043*).—*C. euryoides* Alston: Kenya, *Wormald 13* (= *FHOw 21251*).—*C. firestoneana* Hutch. & Dalz.: Liberia, *C. P. Cooper 96* (= *FHOw 4071*), *Cooper L 214 a* (= *IF 26689*, Tervuren).—*C. gerrardii* Alston: S. Africa, *For. Serv. 13487* (= *IF 26100*, Tervuren).—*C. guianense* Aubl.: Surinam, *Oldenburg Nord Herb. 591* (= *Uw 15637*), *Stahel 255*.—*C. gumiflua* Tul. var. *ugandensis* Stapf.°: Angola, *Dechamps, Murta & Da Silva 1010* (= *IF 28533*, Tervuren).—*C. gumiflua* Tul. var. *verticillata* (R.E. Br.) J. Lewis: Moçambique (*IF 19084*, Tervuren)$^{+}$.—*C. kilipii* Cuatr.: Colombia, *Cuatrecasas 19878* (= *SJRw 44377*).—*C. lasiocalyx* Alston: British Guyana, *For. Dept. 3058* (= *FHOw 13043*), *Maguire 40453* (= *Uw 4881*).—*C. macrodonta* Standl.: Panama, *G. P. Cooper 446* (= *SJRw 12064*).—*C. malosana* (Baker) Alston: Tanzania, *Hughes 329* (= *FHOw 21736*); Kenya, *FPRL (GB) 894* (= wood *22837b*, = *IF 25110*, Tervuren), (*SJRw 50357*).—*C. peruviana* Alston: Brazil, *Krukoff 1023* (= *Uw 19192*).—*C. rotundifolia* (Engl.) Alston: E. Africa, *Schlieben 185* (= *SJRw 27534*).—*C. ruwenzoriensis* (Engl.) Alston: Rwanda, *G. Troupin 14450* (= *IF 14450*, Tervuren); Kenya, *For Dept. 868* (= *FHOw 11140*).

From literature (see note): *C. cooperi* Hutch. & Dalz.; *C. latifolia* Alston; *C. nialatou* Aubr. & Pellegr.; *C. podantha* Standley, and *C. sessiliflora* Alston.

The name *C. alba* (Sw.) Poir. is not present in the Index Kewensis. The authority is probably erroneously cited from the label of the wood sample. The correct name is therefore probably *C. alba* Griseb, which is *C. elliptica* Poir.

Shrubs and small trees, in evergreen forest, dry savannas, and on sandy beaches.

Growth rings absent, faint or distinct. *Vessels* diffuse, (6–)9–125(–138)/mm², solitary and in radial multiples of 2–3, 65–100% of the vessels solitary, round to oval, tangential diameter (21–)39–127(–155) μm, maximum radial diameter ranging from 67 to 214 μm, walls 2–5 μm thick. Vessel member length (400–)650–1540(–2370) μm, immature material of shrubs included. Perforations exclusively simple, exclusively scalariform, and both simple and scalariform in oblique end walls. Perforations with (1–)2–40(–62) fine bars, infrequently finely reticulate, strongly reticulate in *C. elliptica* and *C. kilipii*, in *C. calimensis* some bars perpendicular to the other ones. Inter-vessel pits opposite, infrequently transitional, also transitional where tails are in contact with succeeding vessel members. Vessel–ray pits opposite to reticulate, mostly almost simple, those from the most procumbent ray cells to vessels frequently half-bordered (Plate 3/20), circular (up to 11 μm) to elongated (up to 52 μm), long axis usually horizontal, but also oblique and vertical, infrequently unilaterally compound. Vessel–parenchyma pits mainly large and simple, infrequently half-bordered, 1–2-seriate, diffuse, scalariform, infrequently reticulate, circular (up to 15 μm) to elongated (up to 37 μm). See Fig. 1. Vessel–fibre pits in one to several vertical rows, rounded, 7–10 μm, 3–5 μm in *C. calimensis*, pits infrequently elongated up to 20 μm, rarely with an elongated pit chamber in the vessel wall only. Solid granular contents infrequently present in the vessels. Thin-walled tyloses infrequently present in *SJRw 50357* of *C. malosana* and *C. rotundifolia*, sclerified tyloses present in *C. firestoneana* and *C. rotundifolia*. *Fibres* (680–)1200–2060 (–2680) μm long, walls thick to very thick, thin to medium thick in *C. verticillata*, with distinctly bordered pits of 6–9 μm, in *C. calimensis* 3–4 μm with narrow borders; pits numerous on both radial and tangential walls, in *C. calimensis* mainly on the radial walls. Elongated fibre pits, up to 23 μm (Plate 4/25), frequently present in C. *alba* and C. *gumiflua* var. *verticillata*, infrequent in the other species. 'Short' fibres with numerous pits frequently or infrequently present; in *C. gumiflua* var. *verticillata* all fibres with numerous pits. Intermediate types between fibre-tracheids and vessels with scalariform pits at the tips infrequently present in *C. alba* and *C. gumiflua* var. *verticillata*. Fibres frequently branched, infrequently forked; partly septate in *C. calimensis*; frequently or infrequently gelatinous. Granular contents present in *SJRw 50357* of *C. malosana*. *Parenchyma* very scanty paratracheal (*C. calimensis*) or unilaterally paratracheal, very rarely vasicentric; aliform to confluent, sometimes forming more or less continuous bands of 1–2 cells wide, scanty diffuse and diffuse in small aggregates; in *C. firestoneana* very regularly aliform to confluent, bands of 1–2(–4) cells wide. Strands of (4–)6–9(–11)

TABLE 4. Quantitative characters of Cassipourea

(For explanation of the figures see table 2, Anisophyllea)

Species and/or specimen	1	2	3	4	5	6	8	9	10	11
C. afzelii	+	15—21—34	100	67—80—92	92	550—1030—1450	-		1320—1580—2000	m
C. alba	+	33—35—39	100	53—73—91	121	580—1020—1290	1	11—26—35	850—1490—1870	6.5
C. calimensis	-	78—87—95	65	51—57—70	84	950—1540—2370	100	21—40—62	1240—2060—2680	m
C. congoensis										
For. Dept. 15005	±	111—125—138	87	34—46—71	71	660—990—1290	10	4—8—12	1080—1380—1600	8
G. Bouxin 1098	±	95—110—122	75	38—59—101	119	710—1000—1630	4	3—29—48	1370—1620—1920	9
C. elliptica										
W. & A. 161	-	19—22—26	98	38—66—92	124	710—1340—1660	2	14—29—47	1340—2010—2580	4
US Herb.	-	29—32—55	95	50—71—88	105	730—1050—1370	3	8—19—40	1660—1860—2260	m
C. euryoides	+	95—112—120	92	21—39—50	67	490—815—1190	2	5—6—9	1130—2470—1820	9
C. firestoneana										
Coop. 96	-	17—20—24	92	67—86—105	113	760—1200—1870	10	2—9—31	1420—1770—2180	m
Coop. L 214	-	6—9—18	99	76—123—147	174	730—1050—1370	10	9—26—43	1630—2000—2420	m
C. gerrardii	±	53—62—65	86	38—59—86	105	680—860—1050	few	6	840—1460—2000	m
C. guianense										
Oldenburg 591	+	30—36—47	100	55—66—82	92	890—1220—1580	few	5	1370—1840—2420	5
Stahel 255	+	9—13—17	100	43—92—126	172	1160—1420—1840	few	6—8	1320—1840—2100	m
C. gumiflua										
var. ugandensis	-	11—13—16	88	79—102—131	167		few	27		
var. verticillata	+	14—18—21	100	76—127—155	214	870—1140—1630	-		1130—1630—2290	m
C. kilipii	-	70—73—82	90	39—61—81	103	730—1130—1550	24	1—13—31	1000—1540—2000	6
C. lasiocalyx										
F.D. 3058	+	13—37—46	100	25—67—78	83	870—1230—1740	26	1—20—46	1530—1710—1870	5
Maq. 40543	+	8—16—21	100	44—68—90	115	840—1300—1870	64	1—6—25	1600—2000—2400	8
C. macrodonta	±	59—70—86	100	46—60—71	84	840—1160—1630	100	4—12—49	1260—1720—2030	5
C. malosana										
H. 329	-	42—50—53	70	50—71—98	142	580—1150—1580	6	4—6—7	1050—1990—2470	5
FPRL 849	-	53—56—71	90	39—67—91	140	820—1040—1450	3	1—2—9	1110—1860—2180	7
SJRw 50357	±	47—60—66	89	28—53—78	86	630—880—1160	2	5—6—8	970—1510—1920	7.5
C. peruviana	-	38—44—49	96	46—63—88	113	400—820—1080	47	2—6—11	980—1420—2130	8
C. rotundifolia	-	48—57—101	94	36—51—66	76	470—820—1080	25	1—5—11	680—1200—1680	8
C. ruwensoriensis										
G.T. 14450	+	44—56—79	94	37—56—81	114	420—650—920	11	2—5—8	820—1250—1630	m
F.D. 868	+	81—83—85	83	34—51—66	97	500—1030—1390	21	7—8—11	1260—1710—2160	m

cells. *Rays* heterogeneous I–II, (7–)8–10(–12)/mm, (1–)2–3- or 2–4(–5)-seriate; multiseriate rays composed of central portions of procumbent cells and uniseriate tails of up to 36 erect cells, in *C. calimensis* multiseriate rays 4–5-seriate with infrequent sheath cells, in *C. gumiflua* var. *ugandensis* multiseriate rays up to 6-seriate, and with short, up to 6 cells high, uniseriate tails; uniseriate rays 1–4/mm, composed of erect cells, infrequently with a small biseriate portion of square to procumbent cells, (2–)6–9(–20) cells high. Solitary *crystals* frequent in rays. Amorphous contents frequent in rays and axial parenchyma.

Note. The species of this genus are either shrubs or small trees, so they do not always provide 'mature' wood samples (diameter at least 10 cm). For this reason all quantitative data are recorded in the descriptions. In Table 4 these data are specified and the diameter of the immature samples is given. Benoist (1931) studied *C. guianense* Aubl. Characters he recorded are: growth rings absent, 1–5 vessels/mm², with a diameter up to 170 μm, rays uniseriate, rarely with a small biseriate portion. The specimens of this species, studied by me do have growth rings and 2–3-seriate rays. The vessel frequency of the specimen studied by Benoist is very low when compared with the mature samples of this genus, studied by me. The macromorphological characters, presented by Benoist are not in accordance with those given by Alston (1925), Williams (1932), and Jonker (1942) for this species or for the genus *Cassipourea*. Very probably the wood described by Benoist is therefore not *C. guianense* Aubl. or not even *Cassipourea*. An alternative can, however, not be given. Araujo & Mattos (1973) studied two samples of *C. guianense*, one of which is the Stahel sample included in this study. They mention wider (diameter (90–)100–125(–148) μm) and shorter ((500–)750–875(–1750) μm) vessel members, the other characters agree well with those presented by me. Marco (1935) recorded sclerified tyloses for *C. elliptica*. Record & Hess (1943) gave a general description for *C. alba*, *C. elliptica*, *C. guianense* (studied in this paper), *C. latifolia* Alston, and *C. podantha* Standley. The quantitative characters they mentioned are within the total range of this genus. Normand (1960) reported that the anatomical structure of *C. nialatou* Aubr. & Pellegr. is much like that of *C. firestoneana*, used for this study, with which I agree. Gerard (1917) studied *C. sessiliflora* Alston; wood anatomical characters given by him are: vessels 15–29/mm², solitary, diameter 60–100 μm fibres 1400–1600 μm long, parenchyma rather abundant. Carlquist (1975) reported for *C. elliptica* 2–5 bars per perforation plate, and an average vessel member length of 1000 μm. *C. gumiflua* var. *verticillata*, present in the slide collection of the Jodrell Laboratory, Kew had irregularly banded parenchyma. The specimen described in this paper has unilaterally paratracheal parenchyma, aliform to confluent, sometimes forming a reticulate pattern. *C. cooperi* Hutch. & Dalz. (Liberia, Y1 3746) also present in the Kew slide collection has few scalariform perforations, scanty, unilaterally aliform parenchyma and strongly sclerified tyloses, vessel frequency was not determined and macerations were not available.

CERIOPS Arn. (Plate 4/23; Fig. 2b)

Material studied. C. tagal (Perr.) C. B. Rob.: N. Borneo, *SAN A 2626* (= *FHOw 18319*)$^{+}$; Sabah, *Sab. Herb. Inst. 6* (= *IF 21614*, Tervuren); Philippines, *For. Serv. 6099* (= *IF 10905*, Tervuren); India, *For. Res. Inst. 90015* (= *IF 17715*, Tervuren); E. Africa, *Schlieben 1560* (= *Uw 15520*); Tanzania, *Schlieben 2594* (diam. 7 cm) (= *SJRw 23430*), (*MADw 20957*)$^{\circ}$.

From literature (see note): *C. decandra* (Griff.) Ding Hou.

Small to medium-sized trees, up to 15 m; typical constituents of the inner mangrove.

Growth rings absent or faint (*SAN A 2626*, *Schlieben 1560*, *Schlieben 2594*). Vessels diffuse, (14–) 19–63(–68)/mm^2, solitary and in radial multiples of 2–3(–5), ± 50% solitary, 85% in *SAN A 2626*, round to oval, tangential diameter (34–)49–57(–67) μm, radial diameter up to 83 μm, walls 4–10 μm thick. Vessel member length (390–) 520–720 (–890) μm. Perforations scalariform, in oblique end walls, with (3–)5–8(–13) thick bars. Inter-vessel pits scalariform, extending over the entire inter-vessel walls, rarely transitional. Vessel–ray pits half-bordered and opposite, infrequently almost simple and more or less reticulate; frequently vertically unilaterally compound, each oval to round ray pit subtending 2–5(–7) vessel pits, with oval to slit-like apertures (Fig. 2b), sometimes bilaterally compound. Vessel–parenchyma pits large and simple, infrequently half-bordered with slit-like apertures; uniseriate, infrequently biseriate or scalariform and diffuse, oval to elongate, up to 31 μm, long axis also oblique, the half-bordered pits frequently unilaterally compound. Vessel–fibre pits infrequent, round, 2–3 μm. Thin-walled tyloses and granular contents frequently present. *Fibres* (760–) 1075–1410(–2130) μm long, walls thick, with minutely bordered to almost simple pits of 2–3 μm, mainly confined to the radial walls. Fibres frequently with granular contents and often gelatinous. *Parenchyma* scanty; radially or unilaterally paratracheal with small aliform wings and scanty diffuse and diffuse in small aggregates; in *For. Serv. 6099* abundant, frequently in irregular, more or less continuous bands of 2–4 cells wide, part of the vessels completely or partly surrounded by axial parenchyma. Strands of (4–)6–8(–9) cells. *Rays* heterogeneous II–III, (5–)6–10(–11)/mm, (1–)3–4 cells wide, up to 6 cells wide in *SAN A 2626*; multiseriate rays up to 3.4 mm high, with infrequent sheath cells; uniseriate rays infrequent, 0–2/mm, composed of square to erect cells, (4–)6–8(–11) cells high. Solitary *crystals* present in ray cels. Granular and amorphous contents present in rays and axial parenchyma.

Note. In the description quantitative data for the immature wood sample *Schlieben 2594* have been omitted. The vessel frequency is (45–)87(–146)/mm^2, vessel member length is within the range given in the generic description, fibres are slightly shorter and parenchyma is more abundant than in most specimens, but not as abundant as in *For. Serv. 6099*. In qualitative characters this specimen agrees well with the others. Panshin (1932) recorded for *C. tagal* a vessel frequency of 20–25/mm^2. Reyes (1938) mentioned 25–35 vessels/mm^2. Anatomical characters given by Panshin for *C. decandra*

(Griff.) Ding Hou are: growth rings distinct; vessels in multiples of 2–5, 50–70/mm^2, diameter 50–60 μm, 500–800 μm long, scalariform perforation plates with 6–8 bars; parenchyma, abundant, aliform to confluent, scanty diffuse; fibres 850–1400 μm long, thick-walled; rays 1–10-seriate. From the plates Panshin gave in his paper, it appears that the parenchyma distribution of the species he studied is very much like that of *For. Serv. 6099* and *Schlieben 2594* of *C. tagal*, studied by me. Rao & Purkayastha (1972) mentioned for *C. candolleana* (= *C. tagal*) and *C. roxburghiana* (= *C. decandra*) a vessel frequency of 20–36/mm^2. Marco (1935) and Metcalfe & Chalk (1950) did not record the minutely bordered fibre pits, they mentioned only simple pits. Contrary to my observations Metcalfe & Chalk reported moderately abundant uniseriate rays composed of both upright and procumbent cells. Ceriops is the only mangrove genus without septate fibres.

COMBRETOCARPUS Hook. f.

Material studied. C. rotundatus (Miq.) Danser: Borneo, *S 14560* (= *FHOw 19984*), (*SJRw 23777*)$^+$; Malaya, *F.M.S. 37160* (= *FHOw 4172*).

Tree up to 25 m; on sandy soils in peat swamps, in fresh water swamps, along the coast.

Growth rings mostly absent, faint in *SJRw 23777*. *Vessels* diffuse, 2 or 3(–4)/mm^2, solitary and in radial or oblique multiples of 2–3, 65–80% solitary, round to oval, tangential diameter (90–)180–250(–330) μm, radial diameter up to 370 μm, walls 3–7 μm thick. Vessel member length (320–)510–630(–820) μm. Perforations simple in horizontal to slightly oblique end walls. Inter-vessel pits crowded, alternate, round to polygonal, 6–9 μm, apertures frequently coalescent over 2–4 (–7) pits. Vessel–ray pits rarely present, because most of the vessels are completely surrounded by axial parenchyma, alternate to reticulate, half-bordered, rarely almost simple, round to elongate, 6–17 μm, long axis mostly horizontally also oblique to vertical. Vessel–parenchyma pits similar to inter-vessel pits, alternate, half-bordered, round to oval, 7–12 μm, apertures occasionally coalescent, frequently unilaterally compound, up to 57 μm, in *F.M.S. 37160* sometimes only one or two large pits present in the wall of one parenchyma cell. Vessels with solid, granular contents. *Fibres* (1370–)1620–1830(–2130) μm long, walls thick to very thick, but thin to very thin in *SJRw 23777*, with bordered pits of 5–7 μm, mainly confined to the radial walls. Fibres with granular or amorphous contents; infrequently gelatinous, frequently so in *S 14560*. *Parenchyma* paratracheally banded, completely embedding the vessels, bands more or less continuous, 3–6 cells wide; infrequently in short tangential lines, and scanty diffuse. Strands of (6–)7–9(–11) cells. *Rays* heterogeneous II, of two distinct sizes; broad multiseriate rays, 1 or 2/mm, up to 16 cells wide and up to 5 mm high, occasionally with sheath cells; uniseriate rays (3–)5–7(–9)/mm, mainly composed of square to erect cells, infrequently with a small biseriate portion of procumbent cells, (1–)4–7(–10) cells high. Solitary *crystals* (sometimes fragmented) frequent in rays and axial parenchyma. Crystalliferous cells usually chambered and sometimes with thick walls, frequently present in diffuse parenchyma or in banded parenchyma where cells are in contact with fibres. Crystals abundant in *S 14560.* Globular bodies and amorphous contents present in ray and parenchyma cells.

Note. The crystalliferous fibres mentioned by Marco (1935) are crystalliferous parenchyma strands, scattered among the fibres (Metcalfe & Chalk, 1950). Gonggrijp (1932) recorded silica grains in some parenchyma cells of *C. motleyi* (= *C. rotundatus*) (*no. 4411*). He also reported silica plugs or a thin layer of silica on the walls of many fibres of that sample. The silica inclusions were, however, not observed by me, nor by other students of the wood of this genus.

COMIPHYTON J. J. Floret (Plate 2/7; Plate 3/15; Plate 4/26–27)

Material studied. C. gabonense J. J. Floret: Zaire, *C. Donis 3155*$^{+}$. Secondary xylem of twigs: Zaire, *C. Donis 3155* (diam. 3.5 mm); *Evrard 3232*$^{\circ}$, (diam. 6 mm); *Le Testu 5918* (diam. 3.5 mm).

Tree up to 30 m. Everwet forests.

Mature wood

Growth rings faint. *Vessels* diffuse (5–)6(–9)/mm^2, exclusively solitary, round to oval, tangential diameter (71–)139(–176) μm, radial diameter up to 226 μm, walls 3–5 μm thick. Vessel member length (970–)1240(–1600) μm. Perforations both simple and scalariform in oblique end walls; 4% of the perforations scalariform with 12–16 bars. Inter-vessel pits transitonal, where tails are in contact with succeeding vessel members. Vessel-ray pits reticulate to opposite, typically large and simple and infrequently half-bordered, circular (up to 11 μm) to elongated (up to 32 μm), with the long axis mostly horizontal, but also oblique or vertical. Vessel-parenchyma pits uni- or biseriate to reticulate, large and simple, infrequently half-bordered, oval to elongated, up to 24 μm, infrequently unilaterally compound. Vessel-fibre pits frequent in vertical rows, round, 6–9 μm, on tangential walls infrequently elongated, up to 20 μm long. Vessels infrequently with thin-walled tyloses and solid granular contents. *Fibres* (1315–)1910 (–2390) μm long, with medium thick to thick walls and frequent bordered pits of 6–8 μm, on both radial and tangential walls, infrequently elongated up to 21 μm. 'Short' fibres with numerous pits frequently present. Fibres infrequently gelatinous or with branched tips. *Parenchyma* irregularly apotracheally banded and aliform to confluent, partly or completely embedding the vessels; bands more or less continuous, 1, rarely up to 3 cells wide; parenchyma frequently diffuse and diffuse in small aggregates, incidentally in apotracheal bands of 1 cell wide. Strands of (6–)9(–12) cells. *Rays* heterogeneous I–II, (6–)7(–8)/mm, 1–3-seriate; 2–3 seriate rays up to 1.6 mm high, tails composed of

(2–)7(–15) square to erect cells; uniseriate rays 1–3/mm, composed of (2–)6(–12) square to erect cells, infrequently with a small biseriate portion. Amorphous contents infrequent in rays and axial parenchyma.

Secondary xylem of twigs

As in mature wood, but with the following deviations: *vessels* sometimes in radial multiples of 2, 108–135/mm²; vessels much narrower, tangential diameter (29–)39–47 (–59) μm, radial diameter up to 63 μm, vessel member length (320–)555–570(–710) μm, 32 & 60% of the perforations scalariform with (2–)6–7(–14) thick to thin bars. Inter-vessel pits transitional, vessel–parenchyma pits uniseriate (scalariform) up to 16 μm. Thin-walled tyloses infrequent in *Evrard 3232*. *Fibres* (390–)755–780(–1010) μm long, with thin to medium thick walls. In *Le Testu 5918* frequently gelatinous and infrequently branched. Fibres infrequently with granular contents. *Parenchyma* scanty, mainly paratracheal, with infrequent aliform wings; more frequent and unilaterally aliform to confluent in *Evrard 3232*. *Rays* 10–12/mm, 1–2-seriate, mainly composed of square to erect cells, infrequently with a small portion of procumbent cells; in *Evrard 3232* 1–3-seriate and procumbent cells frequently present.

CROSSOSTYLIS J. R. & G. Forst.

(Plate 1/6; Plate 3/16; Plate 4/24; Table 5)

Material studied. C. biflora Forst.: Tahiti, *van Balgooy 1715* (branch, diam. 2–2.5 cm); New Caledonia, *N.C. 17847* (= *SJRw 14175*)$^{+}$.—*C. grandiflora* Brong. & Gris.: New Caledonia, *Sarlin 133* (= *CTFT 6104*).—*C. multiflora* Brong. & Gris.: New Caledonia, *Sarlin 274* (= *CTFT 6190*).—*C. parksii* (Gill.) A. C. Smith: Fiji, (*SJRw 25779*) (branch, diam. ± 3.5 cm).—*C. richii* (A. Gray) A. C. Smith: Fiji, *A. C. Smith 4757* (branch, diam. ± 3.5 cm) (= *Hw 28533*).

Trees, up to 15(–25) m. Evergreen forests.

Growth rings absent. *Vessels* diffuse, (15–)19–24(–29)/mm², solitary and in radial, infrequently tangential, multiples of 2–3(–4), 55% solitary, oval to rounded, tangential diameter (71–)100–129(–168) μm, radial diameter up to 168 μm, walls 2–5 μm. Vessel member length (450–)850–1020(–1260) μm. Perforations mainly simple in horizontal to oblique end walls, in *C. biflora*, *C. parksii*, *C. richii* also infrequently scalariform with 3–24 bars; bars sometimes forked; in case of a low number of bars, these are often restricted to the apical or basal part of the perforation plate. Inter-vessel pits crowded, alternate, round to polygonal, 4–7 μm, infrequently elongate, up to 11 μm; pits from vessel tails to succeeding vessels alternate to opposite. Vessel-ray pits opposite-alternate to reticulate, half-bordered, oval to elongate, up to 32 μm, frequently unilaterally compound, long axis usually horizontal but also oblique and vertical. Vessel–parenchyma pits ± similar, more frequently almost simple, infrequently unilaterally com-

TABLE 5. Quantitative characters of Crossostylis

(For explanation of the figures see table 2, Anisophyllea)

Species and/or specimen	2	3	4	5	6	8	9	10
C. biflora								
N.C. 17847	15—19—23	55	71—100—126	143	680—1020—1260	3 %	5—11—24	1525—1950—2310
Van Balgooy 1715	16—23—30	70	71— 88—105	134	470— 770—1130	few	3—11,	1520—1790—2130
C. grandiflora	15—21—26	55	101—129—168	168	760— 970—1160	-	-	1630—2250—2710
C. multiflora	17—24—29	55	97—116—134	147	450— 850—1260	-	-	1390—1920—2550
C. parksii	38—47—56	80	54— 77—105	126	580— 910—1260	few	3 & 8	1260—1820—2310
C. richii	23—26—29	80	63— 81— 97	130	390— 780—1080	few	8 & 15	1470—1990—2240

pound, also uniseriate or in clusters (Plate 3/16), simple or almost simple, round (up to 12 μm) to elongate (up to 25 μm). *Fibres* (1390–)1920–2250(–2710) μm long, walls thick to very thick, with moderately frequent bordered pits of 5–7 μm, mainly confined to the radial walls; fibres frequently gelatinous. *Parenchyma* aliform to confluent, confluent bands 2–4 cells wide; frequent or infrequent with narrow apotracheal bands of 1(–2) cells wide, infrequently diffuse or diffuse in small aggregates. Strands of (3–)4–7(–11) cells. *Rays* heterogeneous II, of two distinct sizes; broad multiseriate rays, 1–2/mm, up to 21 cells wide, up to 6 mm high, frequently with sheath cells; uniseriate rays 2–4(–6)/mm, composed of square to erect cells, rarely with a biseriate portion of procumbent cells, (2–)4–7(–48) cells high. Exclusively solitary *crystals* observed in *van Balgooy 1715* of *C. biflora*; exclusively clustered crystals observed in *C. grandiflora*; both solitary and clustered crystals observed in the rays of *C. multiflora* and *C. richii*; crystals absent in *N.C. 17847* of *C. biflora* and in *C. parksii*. Globular bodies and amorphous contents present in the rays and axial parenchyma.

Note. In the description, the quantitative data for the immature wood samples of *C. biflora* (*van Balgooy 1715*). *C. parksii*, *C. richii* have been omitted. These are given in Table 5.

Sarlin mentioned for *C. grandiflora* 16 vessels/mm², and for *C. multiflora* 11/mm². Some of the species of this genus are very outstanding in the family, because they have clustered crystals in their rays. These crystals have only been recorded once in a specimen of *Carallia* and are absent from all other genera of the Rhizophoraceae.

GYNOTROCHES Bl. (Plate 3/4)

Material studied. G. axillaris Bl.: Solomon Isl., *Craven & Schodde 533**; New Guinea, *van Royen 3690*; Sumatra, *de Wilde & de Wilde-Duyfjes 14052*⁺; Philippines, *Jacobs 7969* (branch 3.5 cm in diameter).

Tree, up to 30 m; primary and secondary everwet forests.

Growth rings faint or distinct. *Vessels* diffuse, (7–)10–12(–16)/mm², solitary and in radial multiples of 2–3(–4), rarely in clusters, 37–54% solitary, round to oval, tangential diameter (110–)140–150(–180) μm, radial diameter up to 230 μm, walls 3–5 μm. Vessel member length (720–)1060–1280(–1620) μm. Perforations simple or scalariform in oblique end walls, 6–7% of the perforations scalariform with 2 (in the apical or basal part of the perforation) to 48 (over the whole perforation) bars. Inter-vessel pits scalariform, extending over the entire inter-vessel wall, infrequently transitional. Vessel–ray pits infrequent because almost all the vessels are completely surrounded by axial parenchyma, ± similar to the vessel–parenchyma pits, but more often reticulate. Vessel–parenchyma pits typically large and simple, occasionally half-bordered, reticulate, ± scalariform or diffuse, circular (up to 13 μm) to elongate (up to 30 μm), usually with the long axis horizontal but sometimes oblique to almost vertical, occasionally in vertical pairs and unilaterally or bilaterally compound. Solid amorphous contents and thin-walled tyloses infrequently present in *de Wilde & de Wilde-Duyfjes 14052*, and *Jacobs 7969*. *Fibres* (1470–) 1930–2620(–3200) μm long, walls thick, with moderately frequent bordered pits of 6–8 μm, mainly confined to the radial walls. *Parenchyma* aliform to confluent, almost completely embedding the vessels, and apotracheal in narrow bands of 1 (or 2) cells wide, forming a more or less reticulate pattern, and scantily diffuse in aggregates. Strands of (4–)6–8(–10) cells. *Rays* heterogenous II, of two distinct sizes; broad multiseriate rays, 1–2/mm, up to 18 cells wide, up to 5(–7) mm high, frequently with sheath cells; uniseriate rays 3–5/mm, mainly composed of square to erect cells, infrequently with a small biseriate portion, (3–)5–8(–12) cells high. Solitary *crystals* frequent in rays and axial parenchyma. Irregular translucent, optically isotropic bodies, probably *silica* aggregates in some ray and axial parenchyma cells, but absent from *de Wilde & de Wilde-Duyfjes 14052*. Globular bodies and amorphous contents in ray and axial parenchyma cells.

Note. In the description, the quantitative data for the immature wood sample *Jacobs 7969* have been omitted. In woods with both scalariform and simple perforations, the frequency of scalariform perforation plates in the immature wood is usually higher than in the mature wood. In this sample of immature wood, however, 3% of the perforations are scalarfiform, in the mature wood 6–7%. In qualitative data this specimen agrees well with the others. Jutte (1958) gave a description of the wood of *Gynotroches* based on the van Royen specimen included in this study. She recorded simple perforations only, stating that 'the scalariform pitting on the vessel walls sometimes gives the incorrect impression of scalariform perforation plates.' This in indeed so, but the actual perforations reported here differ widely from the the scalariform inter-vessel pits. Scurfield *et al.* (1974) succeeded in isolating the silica bodies from the ray parenchyma cells. They reported and illustrated that marks of the parenchyma pits are visible on the silica body.

KANDELIA W. & A. (Plate 1/2)

Material studied. K. candel (L.) Druce: Sumatra, *b.b. 8884* (= *RTIw 8427*), *b.b. 17338* (= *RTIw 18248*); Malaya, *KEP 29229* (= *W.T. 2071*).

Tree up to 7 m; on banks of tidal rivers in the mangrove forest.

Growth rings absent or present (*KEP 29229*). *Vessels* diffuse, (23–)27–35(–42)/mm², solitary and in radial multiples of 2–4, 22–66% solitary, round to oval, tangential diameter (36–)52–62(–78) μm, radial diameter up to 82 μm, walls 4–7 μm thick. Vessel member length (230–)470–550(–670) μm. Perforations scalariform in oblique end walls with (4–)7(–11) thick bars. Inter-vessel pits scalariform, extending over the entire inter-vessel walls, infrequently transitional. Vessel–ray pits half-bordered and opposite, less often almost simple and more or less reticulate; frequently vertically unilaterally compound, each slender to oval ray pit subtending 2 or 3(–5) vessel pits (cf. Fig. 2a). Vessel–parenchyma pits half-bordered to almost simple, uniseriate, bisseriate, scalariform or diffuse, round to elongate, up to 26 μm long, frequently unilaterally compound. *Fibres* (820–)1040–1080(–1230) μm long, walls thin to medium thick, in *KEP 29229* thick-walled fibres near growth ring, with minutely bordered to almost simple pits of 2–4 μm, mainly confined to the radial walls. Fibres frequently or infrequently (*KEP 29229*) septate. *Parenchyma* irregularly banded, the vessels partly or completely surrounded by axial parenchyma, bands (1–)2–4(–5) cells wide. Strands of 6 or 7(–10) cells. *Rays* heterogeneous II, (6–)7–8(–10)/mm, (1–)4–6 cells wide; multiseriate rays up to 3 mm high, with infrequent sheath cells; uniseriate rays very infrequent, 0–1/mm, composed of 2–4 erect cells. *Crystals* absent. *Silica bodies* present in ray cells. Globular and amorphous contents present in rays and axial parenchyma.

Note. Rao & Purkayastha (1972) mentioned a vessel frequency of 15–24/mm². Marco (1935) did not record septate fibres for *Kandelia*, nor the minutely bordered fibre pits. Metcalfe & Chalk (1950) did observe septa in a specimen of *K. rheedii* (= *K. candel*), but recorded simple fibre pits only. This is the only one of the mangrove genera of this family with thin-walled fibres. Only one inland genus, *Poga*, has thin-walled fibres too. Marco (1935) did not record thin-walled fibres; he presented a photograph of a transverse section of *Kandelia*, showing thick-walled fibres.

MACARISIA Thou. (Plate 2/9, 13)

Material studied. M. pyramidata Thou.: Madagascar (*SJRw 22758*)⁺.–*M.* spec.: Madagascar (*R. 933–24*).

Small to medium-sized trees, up to 16 m; wet forests.

Growth rings absent. *Vessels* diffuse, (20–)23 & 25(–27)/mm^2, solitary and in radial multiples of 2–3, 86 & 95% solitary, tangential diameter (54–)109 & 114(–139) μm, radial diameter up to 168 μm, walls 3–5 μm thick. Vessel member length (550–)1110(–1525) in *M. pyramidata*, (740–)1560(–1970) in *M.* spec. Perforations both simple and scalariform in oblique end walls, 43% of the perforations in *M.* spec. scalariform with (1–)8(–25) bars, 4% in *M. pyramidata* with (3–)5(–6) bars, infrequently with some forked and vestigial bars. Inter-vessel pits rarely present, alternate to opposite, pits from tails to succeeding vessel elements transitional. Vessel–ray pits opposite to reticulate, half-bordered to almost simple, oval to elongate, up to 37 μm, long axis usually horizontal, but also oblique or vertical, frequently unilaterally compound. Vessel–parenchyma pits uniseriate to alternate–opposite, half-bordered, rarely almost simple, oval to elongate, up to 16 μm, rarely up to 21 μm, infrequently unilaterally compound. Vessel–fibre pits in vertical rows, round, 5–8 μm, infrequently elongated, infrequently paired, in *M.* spec. rarely with a coalescent aperture on the fibre side. *Fibres* (970–)1810(–2710) μm long in *M. pyramidata*, (1580–)2220(–2550) μm long in *M.* spec., with thick to very thick walls, some thin-walled fibres infrequently present; distinctly bordered pits frequently present on radial and tangential walls. 'Short' fibres with numerous pits frequently present in *M. pyramidata*, infrequent in *M.* spec. Fibres frequently branched. *Parenchyma* unilaterally paratracheal, aliform to confluent, bands 1–2(–3) cells wide; infrequently diffuse and scantily diffuse in small aggregates. Strands of (6–)7–8(–10) cells, in *M. pyramidata* with infrequent branched terminal cells; frequently the terminal cells and less frequently so some cells from the middle of strands with thick walls (more or less of the same thickness as the 'short' fibres) and numerous bordered pits. *Rays* heterogenous II, (6–)7(–8/mm, (1–)2–3-seriate; 2–3-seriate rays up to 0.9 mm high, tails composed of (1–)2–3(–8) square to erect cells; uniseriate rays very rare, 0–2/mm, composed of (3–)6(–8) square to erect cells, rarely with a small biseriate portion. Solitary *crystals* present in rays. Solid amorphous contents present in rays and axial parenchyma.

PELLACALYX Korth. (Plate 2/11; Table 6)

Material studied. P. axillaris Korth.: E. Indies, (= *SJRw 15451*); Indonesia (*RTIw 1569*).—*P. lobbii* (Hook. f.) Schimp.: Borneo, *Kostermans 7038°*; Sumatra, *Krukoff 4284* (= *Hw 22437*).—*P. parkensonii* Fisher: Burma, *Bur. For. Dept. 2051* (= *FHOw 3040*)$^+$.—*P. saccardianus* Scort.: Malaya, *Flora of Malaya 2600* (branch, diameter ± 2 cm); Java, (? *4292*) (= *SJRw 22631*)$^+$.

Note. According to Hou (1958) *P. saccardianus* is restricted to the Malay Peninsula. Therefore, it is possible that the *SJRw 22631* sample from Java has not been correctly identified.

Trees up to 24 m high, *P. lobbii* up to 35(–45) m; primary and secondary forests up to 2250 m.

Growth rings absent. *Vessels* diffuse, (6–)8–19(–21)/mm^2, solitary and in tagential to oblique clusters or multiples of 2–3(–5), infrequently in some radial multiples, 32–50%

of the vessels solitary, oval to round, tangential diameter (74–)120–196(–264) μm, radial diameter up to 302 μm, walls 3–6 μm, in *P. parkensonii* up to 8 μm. Vessel member length (630–)980–1370(–1790) μm. Perforations in oblique to almost horizontal end walls; simple in *P. axillaris*; 8% of the perforations scalariform in *P. saccardianus* (*Fl. of Malaya 2600*) with (0.5–1)1–16(–39) rather delicate bars, rarely more or less reticulate. In the other specimens and species scalariform perforation plates are rarely present, with (3–)9(–39) thin bars. Inter-vessel pits opposite, infrequently or frequently transitional, almost scalariform in the narrowest vessels of *P. saccardianus* (*Fl. of Malaya 2600*) and *P. parkensonii*. Vessel–ray pits not common, because a great part of the vessels is surrounded by axial parenchyma, half-bordered, opposite to reticulate, infrequently unilaterally compound. Vessel-parenchyma pits typically large and simple, occasionally half-bordered, reticulate, ± scalariform, biseriate or diffuse, circular (up to 12 μm) to elongate (up to 33 μm), usually with the long axis horizontal, but sometimes oblique to vertical; in *P. parkensonii* and *P. saccardianus* (*SJRw 22631*) more frequently half-bordered, more often opposite or biseriate; in the latter species infrequently vertically or obliquely unilaterally compound, the slender parenchyma pits subtending 2–3 vessel pits. *Fibres* (1480–)1960–2470(–3230) μm long, walls thick to medium thick, with bordered pits of 5–8 μm present on both radial and tangential walls. *Parenchyma* aliform to confluent, frequently completely embedding the vessels, confluent bands 2–5 cells wide, infrequently with some apotracheal bands of 1–2 cells wide, also infrequently diffuse and diffuse in small aggregates. Strands of (6–)7–9(–11) cells. *Rays* heterogeneous II, of two distinct sizes; broad multiseriate rays, 1–2/mm, up to 32 cells wide, up to 4.5(–7) mm high, occasionally with sheath cells; uniseriate rays 1–4/mm, mainly composed of square to erect cells, rarely with a small biseriate portion of procumbent cells, (2–)5–9(–14) cells high. Granular and amorphous contents frequently present in rays and axial parenchyma.

TABLE 6. Quantitative characters of Pellacalyx

(For explanation of the figures see table 2, Anisophyllea)

Species and/or specimen	2	3	4	5	6	8	9	10
P. axillaris								
SJRw 15451	7—8—10	32	164—191—231	302	610—980—1210	-		1480—1960—2390
RTIw 1569	6—10—11	34	105—192—248	285	630—980—1140	-		1600—2170—2580
P. lobbii	16—19—21	33	80—138—197	277		few	19—21	
P. parkensonii	6—10—17	36	75—120—206	269	740—1160—1360	few	7—21	1600—2470—3230
P. saccardianus								
SJRw 22631	8—10—11	57	147—196—264	274	890—1370—1790	few	18—39	2000—2440—2920
Fl. of Malaya 2600	14—20—25	50	68—104—130	137	270—570—1050	8	1—16—39	1000—1470—1790
Krukoff 4284	9—10—11	47	126—150—168	172	820—1070—1470	few	3—19	1500—2470—3020

Note. In the description quantitative data for the immature wood sample of *P. saccardianus* (*Fl. of Malaya 2600*) have been omitted. These are recorded in Table 6. In qualitative data this specimen agrees well with the others. Marco (1935) studied *P. saccardianus* and *P. axillaris*, then the only two species known. He recorded predominantly scalariform vessel–ray pits, parenchyma in bands of 6–12 cells wide, extremely large and conspicuous fibre-tracheid pits, commonly 30 μm high (Marco very probably meant the length of the apertures), apertures broad and lenticular in *P. axillaris*, slit-like in *P. saccardianus*. These differences in the shape of the apertures were not observed by me. Gonggrijp (1932) mentioned for *P.* spec. and *P. axillaris* (*no. 1569*) glass-like silica plugs in the fibres and thin silica layers on the walls of the fibres. These plugs or silica layers were not observed by me.

POGA Pierre (Plate 1/3)

Material studied. P. oleosa Pierre: Africa (*SJRw 14954*)°+; Gabon, *Reinbek BFA 33* (*Uw 6447*); Zaire, *Sargos 673* (= *FHOw 13702*).

Tree, up to 50 m, wet forests.

Growth rings absent. *Vessels* diffuse, 1 or 2/mm², solitary, rarely in radial multiples of 2(–3), round to oval, tangential diameter (110–)200–340(–430) μm, radial diameter up to 450 μm, walls 4–7 μm thick. Vessel member length (550–)960–980(–1320) μm. Perforations simple in horizontal to slightly oblique end walls. Inter-vessel pits crowded, alternate, round to polygonal, 6–8 μm in diameter, apertures frequently coalescent over 2–6 pits. Vessel–ray pits not seen, because all the vessels are completely surrounded by parenchyma. Vessel–parenchyma pits similar to the inter-vessel pits, but half-bordered, round to elongated, up to 12 μm, frequently with coalescent apertures, and unilaterally compound. *Fibres* (1660–)2340–2420(–3220) μm long, walls thin to very thin, with few bordered pits, diameter 4–6 μm, mainly confined to the radial walls. *Parenchyma* aliform, infrequently confluent, completely embedding the vessels, infrequently with some narrow apotracheal bands. Strands of (5–)6–8(–11) cells. *Rays* heterogeneous II, of two distinct sizes; broad multiseriate rays, 1–2/mm, up to 16 cells wide and up to 5 mm high, occasionally with sheath cells; uni- or biseriate rays 2–5/mm, (2–)6(–11) cells high. Globular bodies present in ray and parenchyma cells.

Note. Of all the inland genera this is the only one with thin-walled fibres. *Kandelia*, one of the mangrove genera has thin-walled fibres too. Marco (1935) mentioned very large (27 μm) intervascular pit-pairs (see p. 70), and widely spaced, narrow bands of confluent paratracheal parenchyma, which is more like the parenchyma distribution in the other genera of the Anisophylleae.

POLYGONANTHUS Ducke (Plate 1/4)

Material studied. P. amazonicus Ducke: BRAZIL, *J. M. Pires 53*, diameter 6 cm.

Tree up to 25 m; very wet forest.

Growth rings absent. *Vessels* diffuse, (3–)6(–12)/mm^2, mainly solitary, infrequently in radial multiples of 2–3, round to oval, tangential diameter (84–)121(–168) µm, radial diameter up to 189 µm, walls 4–7 µm thick. Vessel member length (280–)460(–600) µm. Perforations simple in horizontal to oblique end walls. Inter-vessel pits crowded, alternate, round to polygonal, 5–7 µm, apertures frequently coalescent over 2–3(–4) pits. Vessel—ray pits rarely present, because almost all the vessels are completely surrounded by axial parenchyma, half-bordered, alternate, but sometimes elongated, 6–21 µm. Vessel—parenchyma pits ± similar, but rarely elongated, apertures infrequently coalescent, sometimes unilaterally compound, *Vascular tracheids* with or without perforations infrequently present in association with the vessels, tangential diameter 50–70 µm, length 670–780 µm. *Fibres* (680–)1320(–1630) µm long, medium thick to thick, with bordered pits of 4–7 µm; pits frequent on the radial walls. *Parenchyma* paratracheally banded, completely embedding the vessels, bands more or less continuous, 2–3(–5) cells wide; infrequently apotracheal in short tangential lines and scantily diffuse. Strands of (5–)7(–9) cells. *Rays* heterogeneous II, of two distinct sizes; broad multiseriate rays, 1–2/mm, up to 20 cells wide and up to 3 mm high, occasionally with sheath cells; uniseriate rays 3–8/mm, mainly composed of square to erect cells, rarely with a small biseriate part, (1–)4(–12) cells high. Solitary *crystals* in axial and ray parenchyma. Crystalliferous cells usually chambered and sometimes with thick walls. Globular bodies and amorphous contents in axial and ray parenchyma.

Note, Pires & Rodrigues (1971) studied a wood sample of the same collection; they found a vessel frequency of 3–5/mm^2. This is one of the two genera not studied by Marco (1935). The first publication dealing with this genus is from 1932, when it was treated as a member of the Euphorbiaceae. Later *Polygonanthus* was transferred to the Rhizophoraceae. See also the section on the taxonomic position of *Comiphyton* and *Polygonanthus*.

RHIZOPHORA L (Table 7)

Material studied. R. apiculata Blume: Philippines (*Hw 23414*)$^{+}$; Malaya (*KEPw 1938*).—*R. harrisonii* Leechm.: Colombia, *Cuatrecasas 16016* (= *MADw 17559*); Venezuela, *Breteler 5185* (= *Uw 22426*).—*R. mangle* L.: Peru, *J. Vargas A. 35* (= *MADw 22561*); Cuba, *J. G. Jack 4941* (= *Hw 22434*); Haiti (*SJRw 19583*); Gabon (*SJRw 12863*).—*R. mucronata* Lamk.: N. Borneo (*FHOw 18533*); India, *Gamble s.n.* (= *FHOw 10002*).—*R. racemosa* G. F. W. Mey.: Surinam, *Stahel 108*; Fr. W. Africa (*SJRw 44686*); Gabon, *BFA 37* (= *Uw 6451*).—*R. stylosa* Griff.: Indonesia, *b.b. 3690* (= *RTIw 3665*).

Trees up to 25(–30) m; in coastal swamps and along tidal streams; the most widespread of all mangrove genera.

Growth rings absent. *Vessels* diffuse, (9–) 12–30(–38)/mm^2, solitary and in radial multiples of 2–3, 50–85% solitary, round to oval, tangential diameter (63–) 74–115(–130) μm, radial diameter up to 172 μm, walls 4–10 μm thick, up to 14 μm in *KEPw 1938* of *R. apiculata*. Vessel member length (390–) 620–1120(–1420) μm. Perforations scalariform in oblique end walls, with (4–) 5–11(–15) thick bars. Inter-vessel pits scalariform, extending over the entire inter-vessel walls, infrequently transitional, more frequently so in *R. harrisonii* (*Cuatrecasas 16016*). Vessel—ray pits half-bordered to almost simple, opposite to reticulate, round to elongate, 5–39 μm, long axis also oblique; opposite pits frequently unilaterally compound in a vertical pattern, each slender ray pit subtending 2–4(–5) vessel pits (cf. Fig. 2a). Vessel—parenchyma pits large and almost simple, infrequently half-bordered, uniseriate, biseriate, scalariform, or diffuse, oval to elongated, up to 31 μm, infrequently unilaterally compound. Seemingly vestured pits infrequent in *Hw 23414* of *R. apiculata*. Vessel—fibre pits infrequently present, 2–3 μm. Solid granular contents frequently present in the vessels. Thin-walled tyloses frequently present, some sclerified tyloses present in *R. harrisonii* (*Cuatrecasas 16016*). *Fibres*

TABLE 7. Quantitative characters of Rhizophora

(For explanation of the figures see table 2, Anisophyllea)

Species and/or specimen	2	4	5	6	9	10
R. apiculata						
Hw 23414	16—17—18	101—110—122	130	660— 930—1180	4— 6— 7	1630—1950—2370
KEP 1938	23—30—38	72— 91—101	104			
R. harrisonii						
Cuatrecasas 16016	27—29—32	75— 90— 97	105	450— 800—1050	4— 5— 6	1020—1220—1660
Breteler 5185	13—17—18	92—115—130	142	450— 660— 900	4— 5— 6	840—1240—1440
R. mangle						
Vargas A. 35	16—20—23	58— 84— 98	118	420— 760— 920	5— 6— 8	1160—1380—1790
Jack 4941	18—20—21	63— 83—102	116	630— 790—1000	4— 6— 8	940—1370—1630
SJRw 19583	21—22—24	67— 74— 88	118	660— 800—1050	4— 5— 8	820—1370—1660
SJRw 12863	20—22—24	78— 92—118	118	660— 870—1100	4— 5— 6	1180—1590—1920
R. mucronata						
FHOw 18533	14—15—16	63— 80— 97	113	550— 820—1160	4— 6—7	1130—1530—1840
Gamble s.n.	24—26—29	80— 94—101	126	950—1100—1420	8—11—15	1130—1650—2000
R. racemosa						
Stahel 108	14—16—21	88—102—130	172	685— 800—1050	5— 6— 8	1100—1460—1870
SJRw 44686	9—14—15	94—106—119	145	810—1090—1290	5— 7— 8	1340—1810—2070
BFA 37	10—12—15	91—111—121	153	950—1120—1320	4— 5— 8	1550—1950—2230
R. stylosa	15—17—19	63— 74— 92	105	320— 620— 840	4— 6— 8	1020—1450—1680

(820–)1220–1950(–2370) μm long, walls thick to very thick, with minutely bordered to almost simple pits of 2–3 μm, frequent on the radial walls. Fibres frequently septate, but infrequently septate in *R. apiculata*, *R. mucronata*, and *R. stylosa*, frequently gelatinous and with granular or amorphous contents. *Parenchyma* very scanty, radially or unilaterally paratracheal, with infrequent, small, aliform wings, parenchyma more abundant, rarely confluent in *R. mucronata* (*Gamble s.n.*). Strands of (4–)5–7(–9) cells. *Rays* heterogeneous III to homogeneous, (5–)6–8(–10) /mm, (1–)3–6(–7)-seriate; multiseriate rays up to 4.3 mm high and with infrequent sheath cells; uniseriate rays very infrequent, 0–1/mm, composed of square to procumbent cells, (3–)5–7(–18) cells high, rarely with a small biseriate part. Solitary *crystals* present in rays. Globular, granular, and solid amorphous contents frequent in rays and axial parenchyma.

Note. Araujo & Mattos (1973) studied two samples of *R. mangle*, one of which appeared to be the *Stahel 108* sample, which should correctly be named *R. racemosa*; they did not record septate fibres but all other characters are within the range reported in the above description. Vessel frequencies, mentioned in the literature by Karlstedt (1971), Kanehira (1921), Martin (1953), Moll & Jonssonius (1918), Panshin (1932), Pearson & Brown (1932), and Reyes (1938) are: 20–25/mm^2 for *R. apiculata*, 18/mm^2 for *R. harrisonii*, 18–25/mm^2 for *R. mangle*, 14–40/mm^2 for *R. mucronata* (Moll & Janssonius mentioned 45–50 vessels/mm^2 in an immature wood sample of ±5 cm diameter), 16/mm^2 for *R. racemosa*. Kárlstedt recorded crystals in sclerified tyloses of *R.* spec. from Brazil. Karlstedt also found that *R. harrisonii*, *R. mangle*, and *R. racemosa* had often 5, 3, and 1 septa per fibre respectively. Marco (1935) and Metcalfe & Chalk (1950) did not mention septate fibres for this genus, nor did they record the minute borders to the fibre pits. Metcalfe & Chalk also mentioned that the rays may be up to 10 cells wide. Pearson & Brown too did not observe septate fibres.

STERIGMAPETALUM Kuhlm. Plate 2/8; Plate 4/22; Table 8)

Material studied. S. colombianum Monachina: Colombia, *Espina & Giacometto A 90* (= *SJRw 20865*) and *A 142* (= *SJRw 20917*).—*S. guianense* Steyerm.: Surinam, *Maguire 24737* (= *Uw 2602*) and *24780* (= *Uw 2605*)$^+$.—*S. obovatum* Kuhlm.: Brazil, *Krukoff 7021* (= *FHOw 20675*), (*I.N.P.A. X-3845* = *Uw 18830*).

Trees, up to 15–20(–25) m; in everwet forests.

Growth rings absent. *Vessels* diffuse (8–)9–13(–15)/mm^2, almost exclusively solitary, oval, tangential diameter (67–)107–126(–168) μm, radial diameter up to 179 μm, walls 5–7 μm thick. Vessel member length (520–)1000–1250(–1730) μm, in *S. guianense* (1230–)1750–1780(–2210) μm. Perforations both simple and scalariform in oblique end walls; 4–29% of the perforations scalariform with (6–)16–31(–36) mostly delicate bars, infrequently forked. Inter-vessel pits rarely present, transitional where tails are in contact with succeeding vessel members. Vessel–ray pits more or less opposite to scalariform, half-bordered to almost simple, circular (up to 15 μm) to elongate (up to 69 μm) infrequently unilaterally compound. Vessel–parenchyma pits reticulate to scalariform, up to 51 μm long, occasionally half-bordered and unilaterally compound. Vessel–fibre pits in vertical rows, pit chambers in the fibre-wall rounded, 8–10 μm, rarely elongated up to 18 μm, pit chambers in the vessel-wall more frequently elongated. *Fibres* (970–)1330–2030(–2440) μm long, with thick to very thick walls with frequent bordered pits of 8–10 μm, rarely elongated, up to 17 μm, frequent on both radial and tangential walls. 'Short' fibres with numerous pits infrequently present. Fibres with a large diameter up to 55 μm and thin walls infrequently present, frequently so in *S. colombianum*. Fibres occasionally gelatinous. *Parenchyma* paratracheal, mostly unilaterally aliform, infrequently unilaterally confluent, wings and bands 1–2(–3) cells wide. Strands of (6–)7–9(–13) cells. *Rays* heterogeneous I–II, (5–)7–8(–10)/mm, 1–3-seriate, 2–3-seriate rays up to 1.6 mm high, tails composed of (1–)3–5(–8) square to erect cells. Uniseriate rays infrequent, 0–3/mm, composed of (1–)4–6(–13) square to erect cells, infrequently with a small biseriate portion. Solitary *crystals* present in rays and axial parenchyma. Globular bodies and amorphous contents present in rays and axial parenchyma.

Note. Araujo & Mattos (1974) studied two samples of *S. obovatum*, one of which is the Krukoff sample, included in this study. Characters recorded by them are: vessels (7–)9–11(–15)/mm^2, diameter (125–)162–187(–212) μm, vessel member length (625–) 750–1500(–1650) μm, deposits present in the vessel elements, fibre length (1375–) 1750–2125(–2457) μm, rays (5–)7–8–10(–12)/mm, parenchyma unilaterally paratracheal, aliform to confluent.

TABLE 8. Quantitative characters of Sterigmapetalum

(For explanation of the figures see table 2, Anisophyllea)

Species and/or specimen	2	4	5	6	8	9	10
S. colombianum							
E. & G. A 142	8—11—13	67—108—130	173	520—1000—1290	21	11—19—25	970—1330—2000
E. & G. A 90	8— 9—11	67—107—155	176	870—1250—1600	14	16—22—31	970—1765—2440
S. guianense							
B. & S. 24780	11—13—14	71—117—168	176	1230—1750—2210	14	22—30—36	1820—2500—3130
B. & S. 24737	10—12—14	80—126—147	172	1340—1780—2210	29	20—28—34	1630—2615—3130
S. obovatum							
Krukoff 7021	12—13—15	69—109—128	167	870—1210—1630	4	23—31—34	1740—2030—2320
I.N.P.A. X-3845	9—11—14	73—116—151	171	870—1240—1730	17	6—16—25	1180—1830—2390

DISCUSSION OF SOME OF THE WOOD ANATOMICAL CHARACTERS

A scanning electron miscroscopical study of material representing almost all the genera revealed that none of these had vestured pits. In one of the specimens of *Rhizophora* seemingly vestured pits were observed. However, these structures were absent in slides with bleached sections, so these contents probably consisted of soluble protoplasmic remains.

In most of the genera, the vessel–parenchyma pits are typically large and simple, infrequently half-bordered. Their distribution is described as 1–2-seriate, scalariform or diffuse for the mangrove genera and *Blepharistemma* (Fig. 1a–e); uniseriate to reticulate for *Comphyton* (Fig. 1a–f); reticulate to scalariform for *Anopyxis*, *Gynotroches*,

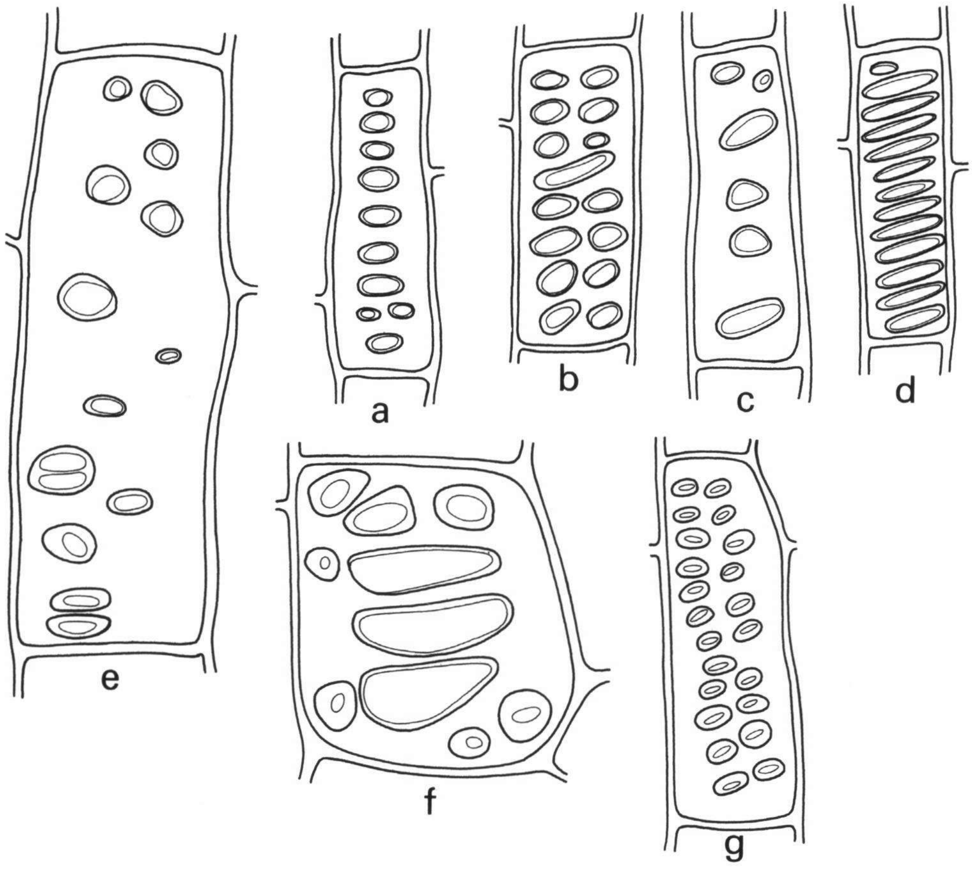

Fig. 1 Camera lucida drawings of the distribution patterns of vessel–parenchyma pits. (All × 650.)—a. uniseriate.—b. biseriate.—c. diffuse.—d. scalariform.—e. diffuse.—f. reticulate.—g. alternate–opposite.

Pellacalyx, and *Sterigmapetalum* (Fig. 1d and f). These distribution types are useful for identification purposes, but may, however, be closely related to each other. Scalariform is a term used, when a parenchyma cell is crowded with one row of elongated pits (Fig. 1f), but uniseriate (Fig. 1a), is used when these pits are round to oval. Uni- to biseriate distributions are found only in narrow, axial parenchyma cells (mostly in species with narrow vessels), and one can easily believe that if there had been room for a third row, this distribution would have been described as opposite. That these apparently different patterns are mutually related is supported by the vessel–parenchyma distribution within the single genus *Cassipourea*. In this genus these pits are frequently arranged in a uni–biseriate pattern (e.g. *C. calimensis*, Plate 3/7), but a predominantly scalariform pattern can be found as well (e.g. *C. verticillata*, Plate 3/18); intermediate forms are present too. Part of this range is sometimes found in a single section. From the large group of genera with typically large and simple pits transitions can be found to the remaining genera. In *Carallia* and *Crossostylis* the vessel–parenchyma pits are besides large and simple, often half-bordered, smaller, in an alternate, alternate–opposite (Fig. 1g) to reticulate pattern, a transition to the half-bordered, alternate vessel–parenchyma pits of the genera which are listed under Anisophylleae in Table 9. *Macarisia* also has alternate–opposite, half-bordered vessel–parenchyma pits, but, as will be discussed in a later chapter, these can be regarded as a more specialized form within the group of the Macarisieae, rather than as a link with the Anisophylleae.

The distribution patterns of the vessel–ray pits do not require such elaborate description, and are rather constant within the several groups, Only in the Gynotrocheae some different patterns can be recognized, varying from alternate-opposite to opposite and reticulate. In the Macarisieae the vessel–ray pits are frequently almost simple, in the other groups they are often to very often half-bordered.

In the woods of the Rhizophoraceae the two main fibre types are present; fibres with minutely bordered or simple pits (libriform fibres) in the Rhizophoreae and, in the other genera, fibres with distinctly bordered pits (fibre-tracheids). Besides the 'common type' of fibre-tracheids, some deviating types occur in the genera grouped in the Macarisieae (see Table 9). Relatively short fibres with numerous bordered pits in several rows, resembling true tacheids, are infrequent to frequent (e.g. *Cassipourea*) in all Macarisieae and, in the descriptions, they are referred to as 'short' fibres with numerous pits. A portion of these fibres have elongated pits, mostly near the tips, but, occasionally, also in the middle part of the fibres (Plate 4/26). The most extreme case is found in *Cassipourea alba* and *C. verticillata*, where the bulging fibre tips have scalariform pits (Plate 4/25). In *Anopyxis*, a few of the fibres also have bulging tips, which bear numerous pits, but these are not elongated. Although the bulging fibres should be called tracheids, according to the Multilingual Glossary of Terms used in Wood Anatomy (I.A.W.A., 1964), this terminology has not been used here in view of the numerous transitions between this type of cell and the 'common' type of fibre-tracheids found in the woods concerned.

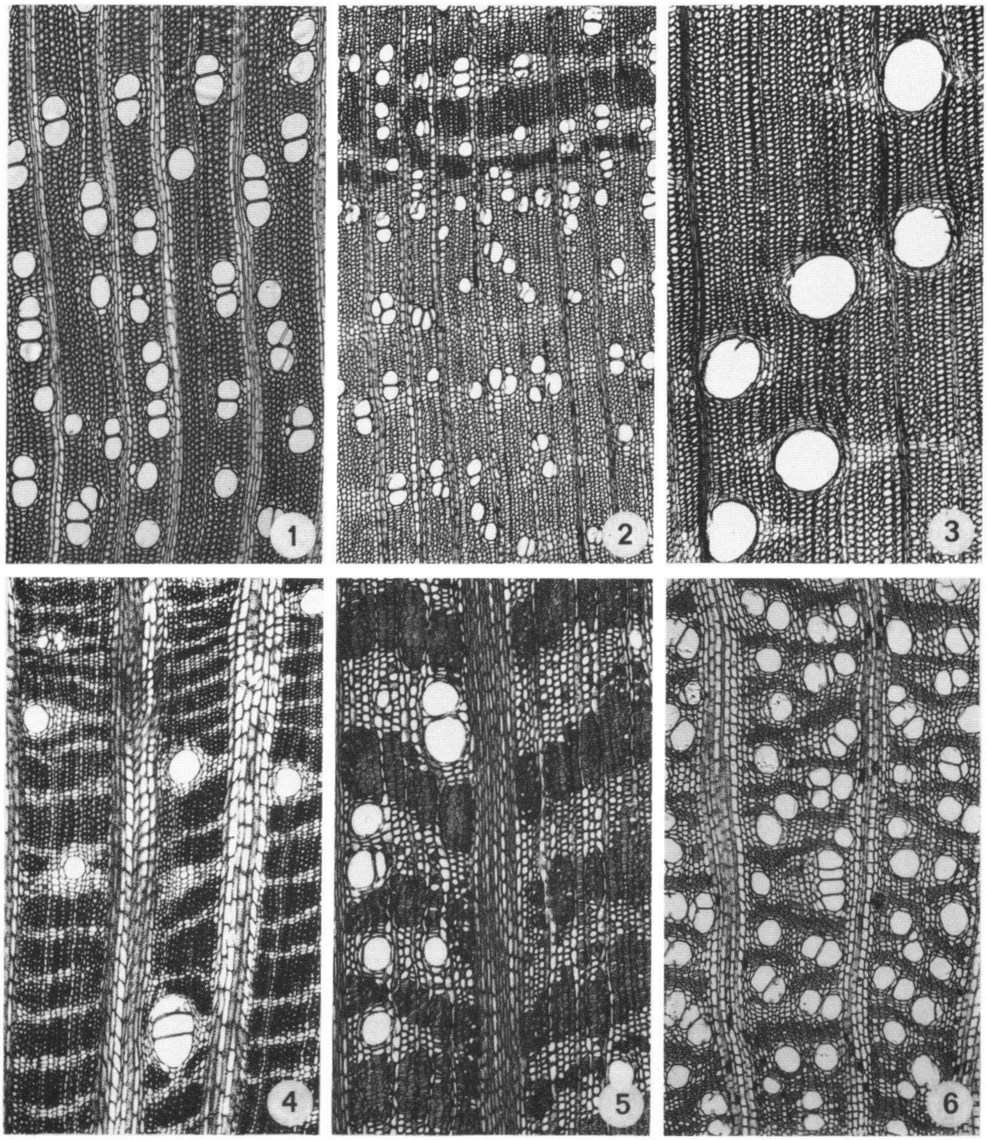

Plate 1. Rhizophoraceae. Transverse sections. (Fig. 3 × 21, others × 31.)—1. *Bruguiera parviflora* (*SAN A 2628*).—2. *Kandelia candel* (*KEP 29229*).—3. *Poga oleosa* (*FHOw 13702*).—4. *Polygonanthus amazonicus* (*J. M. Pires 53*).—5. *Carallia eugenioidea* (*F.M.S. 4045*).—6. *Crossostylis parksii* (*SJRw 25779*).

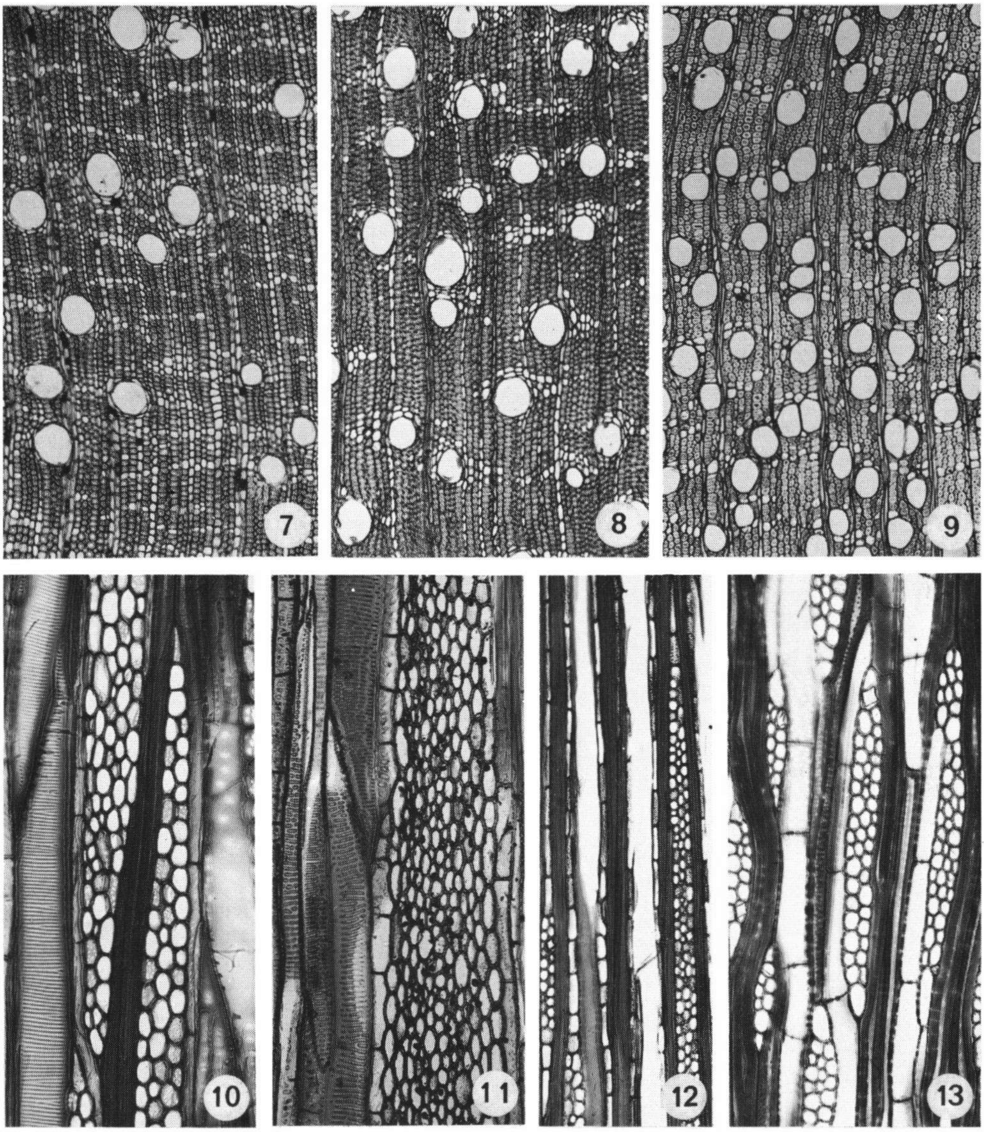

Plate 2. Rhizophoraceae. Figs. 7–9, transverse sections. Figs. 10–13 tangential sections.—7. *Comiphyton gabonense* (*C. Donis 3158*), × 31.—8. *Sterigmapetalum colombianum* (*SJRw 20917*), × 31.—9. *Macarisia* sp. (*R 932–24*), × 31.—10. *Bruguiera gymnorhiza* (*SFCw D 9099*), scalariform inter-vessel pits (left) and diffuse vessel–parenchyma pits (right), × 80.—11. *Pellacalyx lobbii* (*Kostermans 7038*), transitional inter-vessel pits (left), × 80.—12. *Cassipourea calimensis* (*Cuatrecasas 16625*), heterogeneous I rays, × 47.—13. *Macarisia pyramidata* (*SJRw 22758*), heterogeneous II rays and opposite–alternate vessel–parenchyma pits (left, top), × 80.

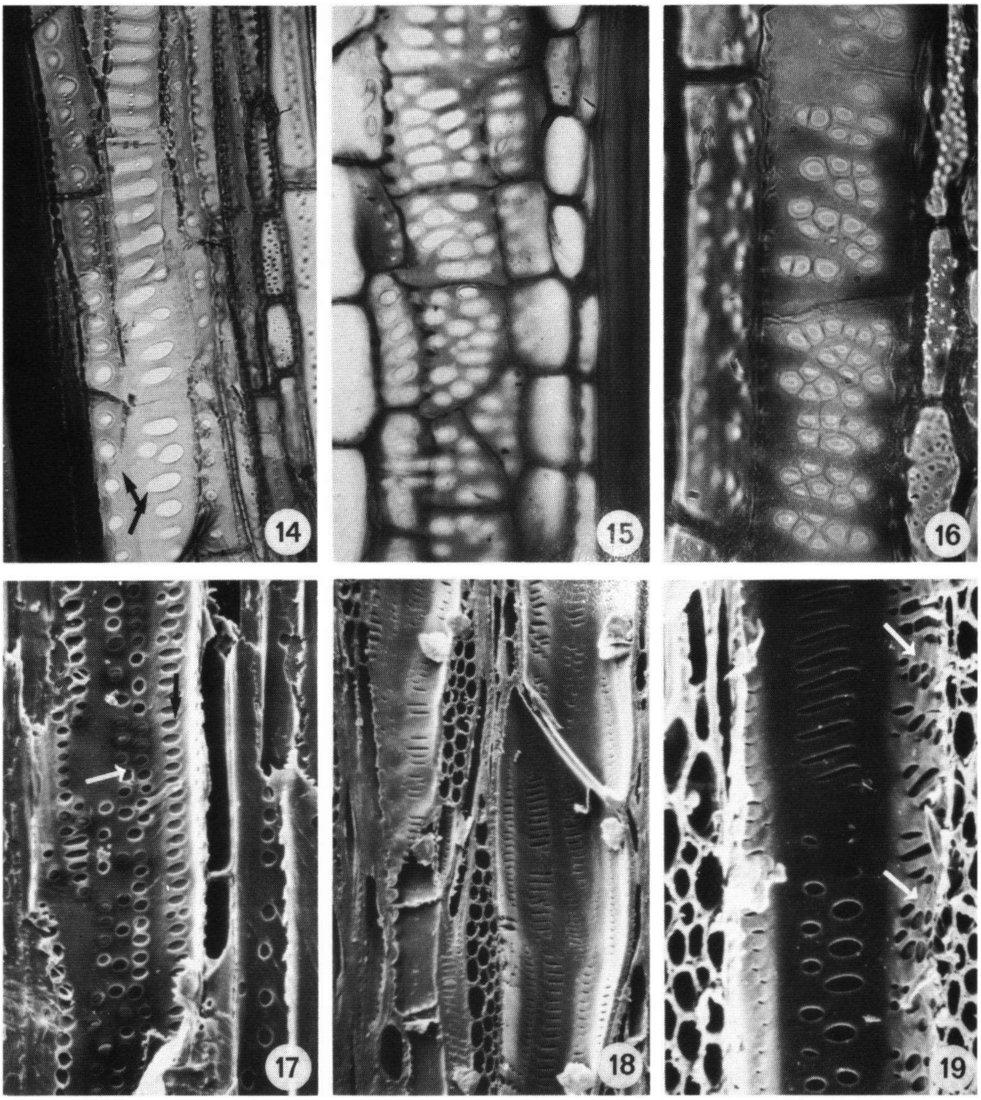

Plate 3. Rhizophoraceae. Figs. 14–19, tangential sections, showing vessel–parenchyma pit distribution; Figs. 17–19 SEM photographs.—14. *Gynotroches axillaris* (*de Wilde & de Wilde-Duyfjes 14052*), scalariform (top); uniseriate and uni-biseriate (bottom-arrows), × 200.—15. *Comiphyton gabonense* (*C. Donis 3158*), reticulate, × 200.—16. *Crossostylis multiflora* (*Sarlin 274*), in clusters, × 310.—17. *Cassipourea congoensis* (*FHOw 22039*), uniseriate (black arrow) and biseriate (white arrow), × 400.—18 & 19. *Cassipourea gumiflua* var. *verticillata* (*IF 19084*, Tervuren).—18. scalariform, × 150.—19. scalariform (top), biseriate (bottom), and some reticulate vessel–ray pits (arrow), × 365.

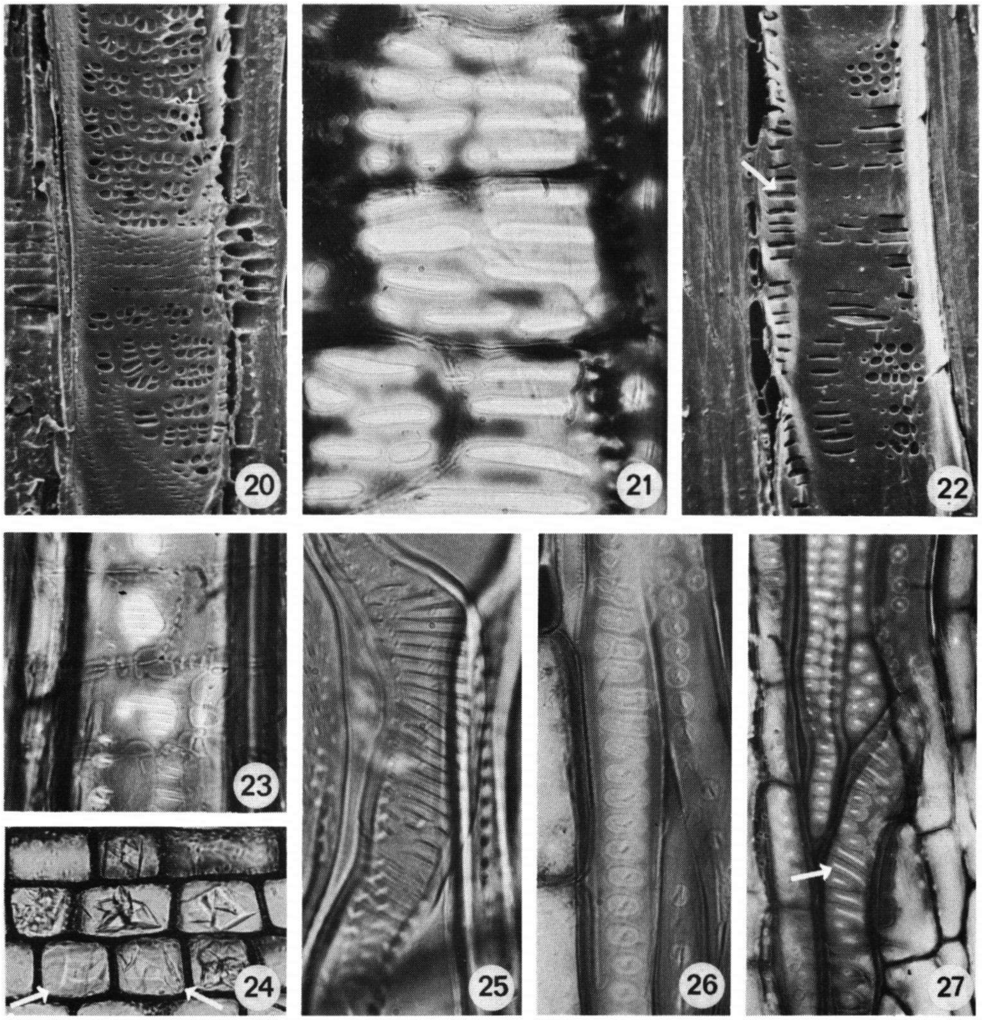

Plate 4. Rhizophoraceae. Figs. 20–24, radial sections, Fig. 25 maceration. Figs. 26, 27, tangential sections. Figs. 20, 22, SEM photographs.—20. *Cassipourea gumiflua* var. *verticillata* (*IF 19084*, Tervuren), vessel–ray pits, those in the erect ray cells simple, those in the procumbent ray cells half-bordered, × 150.—21, 22. *Sterigmapetalum guianense* (*Uw 2665*).—21. Opposite to transitional vessel–ray pits, × 310.—22. Scalariform-transitional, and opposite vessel–ray pits, on the left (arrow) some scalariform vessel–parenchyma pits, × 150.—23. *Ceriops tagal* (*Schlieben 2594*), vertically unilaterally compound vessel–ray pits with oval to round ray pits and coalescent apertures, × 310.—24. *Crossostylis richii* (*A. C. Smith 4757*), clustered and solitary (arrow) crystals in ray, × 200.—25. *Cassipourea gumiflua* var. *verticillata* (*IF 19084*, Tervuren), fibre with elongated, ± scalariform pits near the tip, × 310.—26, 27. *Comiphyton gabonense* (*C. Donis 3158*). —26. Round and elongate fibre pits in the middle of the fibre, × 310.—27. Fibres with numerous pits, and with elongated ones near the tip (arrow), × 200.

In *Anisophyllea* and *Polygonanthus* the frequent or infrequent vasicentric tracheids are not linked with the fibre tissue trough intermediates.

For the descriptions of the rays, the terms given by Kribs (1950) have been used. This can give rise to some confusion with terms present in earlier literature, because a number of authors have used the terms, Kribs gave in an earlier paper (1935) and which are, in some cases, different from the ones he presented in his 1950-paper. In the woods of the Rhizophoraceae, most of the rays are heterogeneous I or II, or intermediate. Only in the genera *Rhizophora* and *Bruguiera* this is different. Here, the rays are very often heterogeneous III, in *Rhizophora* frequently shifting to homogeneous; this latter type is more infrequent in *Bruguiera*. In the woods of the Rhizophoraceae, the uniseriate rays are rather frequent to infrequent, in the genera *Rhizophora* and *Bruguiera* they are very rare. Marco (1935) recorded only 1 uniseriate ray in an area of 2 cm^2 in *R. mucronata*.

VARIABILITY AND DIAGNOSTIC VALUE

A number of wood anatomical characters have a good diagnostic value on the generic or supra-generic level (cf. Table 10), and in some limited cases, on the specific level too. However, other anatomical characters are rather variable and are not or only rarely diagnostic.

A character like the presence (or absence) of growth rings has, for a number of genera (*Ceriops*, *Combretocarpus*, *Kandelia*), no diagnostic value, since these rings were not always present in all the samples studied. In the genus *Anisophyllea*, however, growth rings were observed in the two samples studied of one species (*A. boehmii*) only, and in *Cassipourea*, in most cases where more than one sample per species was studied, growth rings were constantly absent, or present, or faint. In these two cases, the presence or absence of growth rings might have diagnostic value on the species level.

In the woods of this family, the vessel frequencies vary from 1–2 to 129/mm^2 and, in most genera and species, these frequencies are not very constant (cf. Tables 3–8). Only in the genera with the very low vessel frequencies (up to 5/mm^2) there appears to be very little variation. The thickness of the vessel walls does not show much variation, and mostly ranges from 3–7 μm. Very thick walls, up to 13 μm, were observed only in the mangrove genera. Exclusively scalariform perforation plates were observed in the mangrove genera and in some species of *Cassipourea*. In the latter genus the number of bars varies considerably (Table 4), while in the mangrove genera there were mostly 5–8 bars per perforation, rarely up to 11. The genera which have both simple and scalariform perforations have the same variation in the number of bars as was observed for the species of *Cassipourea* mentioned before. As is illustrated in Table 9, the presence of exclusively scalariform perforations with a constant number of bars is characteristic for the mangrove genera, while mixed perforations with a variable number of bars is characteristic for another group of genera. The total range of vessel member length of a species or genus has a strong overlap with other species or genera. However, when comparing the ranges of the average values some genera (Table 10) or species (Table 2) can be told apart. This is, however, hardly justified, since only a restricted number of species was studied, and the individual specific or generic variation is hardly known. In this family, all the main types of intervascular pitting (scalariform, opposite, and alternate) are present, as well as the intermediates, and the type of inter-vessel pits is a good diagnostic character on the suprageneric level. Only one individual genus (*Macarisia*) can easily be recognized, because it is the only one with alternate–opposite inter-vessel pits. The distribution patterns of the vessel–ray pits show some variation within the species of a given genus, but these variations (e.g. opposite to alternate) are rather constant within the genus. This character has a rather good diagnostic value on the suprageneric level. Vertically unilaterally compound vessel–ray pits (Fig. 2) are characteristic for the Rhizophoreae (mangrove-genera) and the shape of the ray pit pair makes one of the four genera (*Ceriops*, Fig. 2b) easily recognizable. There is a great variety in vessel–parenchyma pit patterns, within one species as well as within one specimen. As shown in Table•10, it is possible to arrange the patterns in such a way that groups of genera can be recognized. Only one genus (*Macarisia*) has such a characteristic pattern that it can be recognized immediately. The presence (or absence) of vessel contents and tyloses is not constant for a species or genus. Only in *Combretocarpus* vessel contents were observed in all studied specimens.

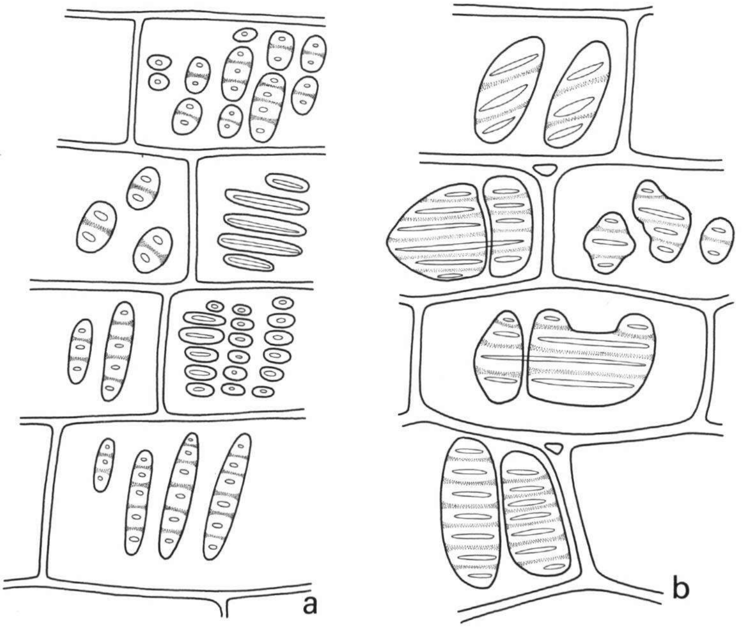

Fig. 2. Camera lucida drawings of vessel–ray pits. (All × 500.)—a. vertically unilaterally compound vessel–ray pits with slender ray pits. Present in *Bruguiera*, *Kandelia*, and *Rhizophora*.—b. vertically unilaterally compound vessel–ray pits with ± oval ray pit, characteristic for *Ceriops*.

For reasons, that were already mentioned above for vessel member length, fibre length does not have a diagnostic value. The fibres have thick or very thick walls, except in two genera (*Kandelia* and *Poga*) where the walls are usually thin. However, these genera cannot reliably be identified by this character. Marco (1935, Plate 1) illustrated that *Kandelia* can have very thick-walled fibres as well. In the previous chapter the different fibre types were already discussed and because of the variation in fibre type a number of groups of genera can be recognized.

Fibres with septa were observed in three of the four mangrove genera, being absent in *Ceriops*. According to Karlstedt (1971) there are some specific characteristics in the number of septa in the fibres of *Rhizophora*. He observed for *R. racemosa*, *R. mangle*, and *R. harrisonii* respectively 1, 3, and 5 septa per fibre. The number of septa I observed in *R. racemosa* and *R. mangle* was the same as the number mentioned by Karlstedt. In *R. harrisonii*, however, I observed 3–5 septa per fibre, and when the other species are taken in account (1 septum, in *R. mucronata* rarely 2 septa) this character holds little specific diagnostic value.

For most of the genera the main type of parenchyma distribution (unilaterally paratracheal, paratracheally banded, scantily paratracheal) is rather constant, although some species or genera are variable in this respect. The variation is rather considerable in the genus *Ceriops* (from scanty to ± banded) and *Cassipourea* (absent to frequent, scanty unilaterally paratracheal to unilaterally paratracheally banded). Yet it is very well possible to recognize some groups of genera using parenchyma distribution.

The rays of the Rhizophoraceae vary from heterogeneous I to III, and are in some cases even homogeneous (mangrove genera). Yet, the ray type is typical for certain groups of genera, either with heterogeneous I–II (narrow) rays, heterogeneous II (wide), or heterogeneous II–III.

Solitary crystals were observed in almost all genera, but can be absent from some species or specimens. Therefore they have a restricted diagnostic value. Clustered crystals were frequently observed in some species of *Crossostylis*, but in one specimen of *Carallia* a clustered crystal was found as well. The intraspecific variability of *Crossostylis* is moreover insufficiently known, so that the diagnostic value could not be determined. Silica is present in a number of genera. Only in *Kandelia* it is of diagnostic value, since silica bodies were present in the ray cells of all samples studied. In *Gynotroches* siliceous inclusions were observed in the ray parenchyma, but these were not present in all samples studied. In the other genera silica is too scantily present to be of diagnostic value.

SYSTEMATIC VALUE OF THE CHARACTERS

From the previous chapter it is clear, that a great number of wood anatomical characters are very useful for identification purposes. Their systematic value is, however, much more difficult to evaluate. The best method to establish the relationships between the several genera of this family is to search for good overall similarities. However, not all wood anatomical characters are suitable for such a comparison. The presence or absence of growth rings and the length of vessel elements and fibres are in this family of no use for this purpose. Vessel frequency and vessel diameter are characters which must be used with appropriate care, because the genera involved may grow under different ecological conditions. The subject of ecological correlations will be discussed at greater length in another chapter. The different patterns of vessel–parenchyma pitting are of important diagnostic value, but as has already been discussed in a previous chapter, most types of pitting are linked by the presence of numerous intermediate types. The vertically unilaterally compound vessel–ray pits can be used to support the close, mutual relationship of the genera growing in the mangroves, because this typical structure is restricted to these four genera alone, and not known to be common in any other family. Other characters which are useful to establish the relationship between the several genera are: the type of vessel perforation, the type of inter-vessel pits, the type of fibres and the ray type. The last character must, however, be used with caution, because the ray type can change during the ontogenetic development of the secondary xylem (Barghoorn, 1940, 1941). Because of their restricted diagnostic value and the distribution over the genera the type of crystals and the presence or absence of siliceous inclusions cannot be used in the discussion of the relationships within the family.

Quantitative characters must also be treated carefully, since apparent differences or similarities may be caused by different ecological conditions or by the fact that mature samples were compared with immature ones.

Another point that should be kept in mind is that characters may differ and yet do not exclude close affinity. The type of inter-vessel pit arrangement may serve as an example. In the specialization series scalariform–transitional–opposite–alternate, the occurrence of scalariform pits in one genus may well indicate affinity with another genus, showing transitional to opposite inter-vessel pits. Such speculations are, however, valid only if a number of other characters, also indicate a relationship between these genera.

ECOLOGICAL CONSIDERATIONS

The presence or absence of growth rings may or may not be related to climatic conditions in the tropical and subtropical regions (cf. Tomlinson & Craighead, 1972). For those few species or specimens in which growth rings were observed, ecological data were insufficient to allow an analysis of ecological influences. For the mangrove species, varying salinity, due to seasonal rainfall, may be a controlling factor according to Holterman (1907). Growth rings in *Anisophyllea boehmii*—absent from other *Anisophyllea* species studied—may be due to the seasonally dry climate of the Brachystegia-Isoberlinia woodlands in which it grows, as opposed to the mesic forest conditions of most other species.

Comparison of the wood anatomical characters of the four mangrove-inhabiting genera with those of the other genera, gives interesting results (cf. Table 10), although it is self-evident that not all characters of the Rhizophoreae can be explained in terms of adaptations to the mangrove environment. In this paper, only explanations for the wood anatomical differences between the mangrove and non-mangrove genera of the Rhizophoraceae as suggested in literature will be discussed. In a future paper it is intended to discuss this subject for mangrove inhabitants and non-mangroves of several other families.

In his study on Philippine mangrove species, Panshin (1932) already mentioned that the extreme and specialized site of the mangrove has failed to produce identical structural convergence in the inhabiting genera. Yet, he critically studied the anatomical data he obtained, in order to determine which anatomical changes could be interpreted as adaptations to the saline, and hence physiologically dry, habitat. He observed that most species showed a high to very high vessel frequency (30–200/mm^2), with a diameter rarely exceeding 150 μm, mostly smaller than 100 μm. The data on vessel diameters as given in the present paper correspond very well (49–115 μm), as do the vessel frequen-

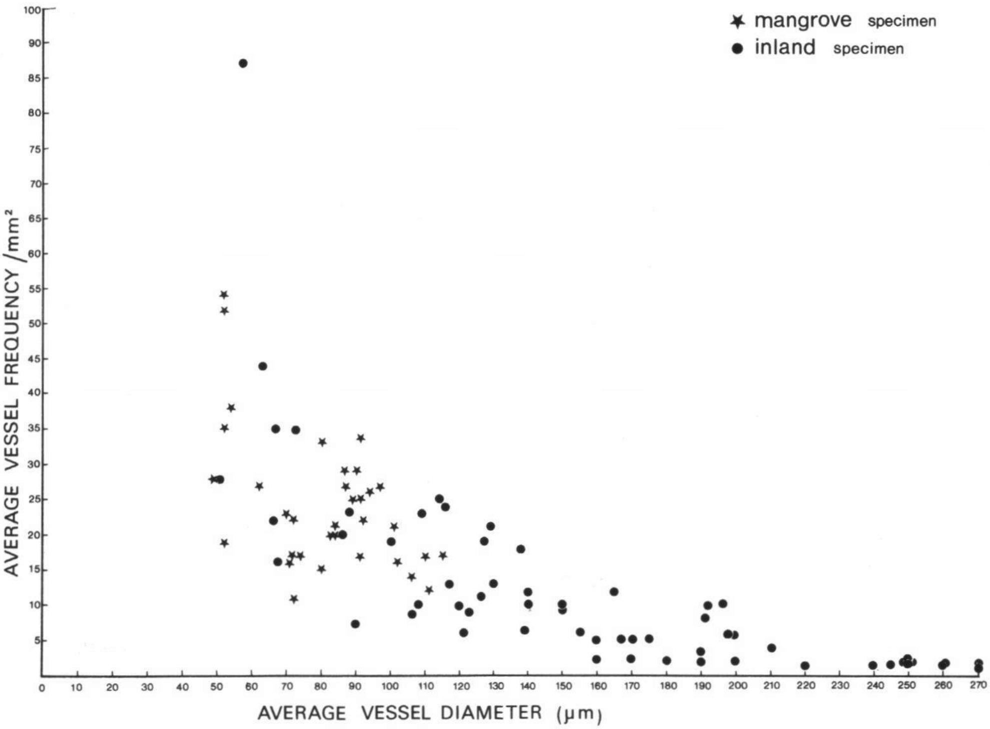

Fig. 3. Relation between the average vessel diameter and the average vessel frequency of the mature wood samples of the Rhizophoraceae.

cies of *Ceriops* and *Kandelia*. The vessel frequency values for *Bruguiera* and *Rhizophora*, however, (an average of 11–34/mm^2), are partly outside the range given by Panshin. Quantitative characters which Panshin himself gave for the Rhizophoraceae species studied by him also fall partly beyond that range.

Janssonius (1950) used the data from his 'Mikrographie des Holzes etc.' (1906–1936) to compare mangrove and non-mangrove representatives of several families. He concluded that the mangroves had a much higher vessel–frequency and narrower vessels that their non-mangrove allies. Fig. 3 represents the relation between the average vessel frequencies and their average diameters for the Rhizophoraceae, studied by me. Only mature wood samples are included, the mangrove specimens indicated by *, the non-mangroves by •. The tendency for the mangroves to have narrow vessels in high frequencies is clear, but there is an overlap with the inland genera, in particular with the genera of the Macarisieae (*Belpharistemma*, *Cassipourea*, *Macarisia*, and *Sterigmapetalum*). Most of these are shrubs or small trees, up to 12 m. The other inland species are mostly larger trees, up to 40–45 m. So, for the inland representatives, there is a trend running from large trees with few vessels/mm^2 to small trees or shrubs with high vessel frequencies. *Bruguiera* and *Rhizophora* are usually rather large trees up to 25(–40) m, *Ceriops* is a rather small tree, and in this genus the highest vessel frequencies are present (19–68/mm^2). Unfortunately, the size of the tree from which the wood samples were taken is not known. However, regarding their size, one can say that there is a tendency for the mangrove genera to have higher vessel frequencies with narrower vessels than their comparable inland relatives.

Janssonius also discussed a correlation between vessel frequency and vessel diameter in relation to the position of the mangrove species in the tidal forest. He concluded that the species growing in the outer fringe of the mangrove forest have higher vessel frequencies than those growing in the more inward parts, where the trees are less often inundated. In Table 9, vessel frequencies and inundation frequencies of the zones

TABLE 9

Species	Frequency of monthly inundation	Vessels /mm^2 according to Janssonius 1950	Vessels /mm^2 from this study	Vessels /mm^2 from literature
BRUGUIERA				
B. parviflora	10—20(—40) times	30—40	21—25	10—40
B. gymnorhiza	c. 10 times	25	17—34	12—35
B. cylindrica	rarely	25	29	13—40
B. sexangula	rarely		11—27	12—16
RHIZOPHORA				
R. mucronata	20—40 times	40—50[1]	15—26	9—30
R. apiculata	2—20 times	20—25	17	20—25

[1] immature sample

where the species commonly grow are given; the latter values were taken from van Steenis in Hou (1958). From Table 9, it is clear that there is no tendency for the frequently inundated species to have more vessels/mm^2 than the species that are less frequently inundated.

Carlquist (1975) suggested that the mangrove genera of the Rhizophoraceae have retained their scalariform perforation plates as a support to prevent their vessels from collapsing when they are submitted to high negative pressure. It is hard to accept this functional explanation. I know of no other mangrove genera with scalariform perforation plates (cf. Panshin, 1932) and, from the purely physical point of view, one would not expect bars of a perforation plate to play an important role in the prevention of collapse of vessel members in such a coherent and thick walled tissue as that of the wood of the mangrove Rhizophoraceae.

Panshin (1932) mentioned that the vessel member length of mangrove inhabitants does not differ considerably from the inland representatives. In the Rhizophoraceae, the mangroves have an average vessel member length of 470–1140 μm, and this is within the range of vessel member lengths of the whole family, thus supporting Panshin's observations.

Correlations of vessel member length with latitude (Baas, 1973) could not be established. Practically all representatives of this family occur between 10° N and 10° S. Only few samples outside this region were studied. Comparison of element length with altitude could not be made because of lack of sufficient data.

RELATIONSHIPS WITHIN THE RHIZOPHORACEAE

Subdivision of the family

A complete classification of all the genera of the Rhizophoraceae in its present delimitation, based on external morphological characters has never been proposed. In reviewing the taxonomic literature (cf. Table 1) there is, however, a strong tendency for the grouping of genera as given below. The names used for the suprageneric taxa follow Melchior (1964).

Rhizophoreae:	*Bruguiera*, *Ceriops*, *Kandelia*, *Rhizophora*.
Gynotrocheae:	*Carallia*, *Crossostylis*, *Gynotroches*, *Pellacalyx*.
Anisophylleae:	*Anisophyllea*, *Combretocarpus*, *Poga*, *Polygonanthus*.
Macarisieae:	*Anopyxis*, *Blepharistemma*, *Cassipourea*, *Comiphyton*, *Macarisia*, *Sterigmapetalum*.

Schimper's completely different classification (1893) hardly needs comment, since earlier wood anatomists and taxonomists have already criticized his sytem, which wood anatomically definitely does not make sense.

Using wood anatomical characters only, it is possible to recognize different groups (see Table 10). The mangrove genera, assembled in the Rhizophoreae, differ in many

TABLE 10. Some wood anatomical characters of Rhizophoraceae

	— RHIZOPHOREAE —				— GYNOTROCHEAE —				— ANISOPHYLLEAE —				— MACARISIEAE —					
	BRUGUIERA	CERIOPS	KANDELIA	RHIZOPHORA	GYNOTROCHES	PELLACALYX	CROSSOSTYLIS	CARALLIA	ANISOPHYLLEA	COMBRETOCARPUS	POGA	POLYGONANTHUS	ANOPYXIS	BLEPHARISTEMMA	CASSIPOUREA	COMIPHYTON	MACARISIA	STERIGMAPETALUM
Vessels:																		
sol	-	-	-	-	-	-	-	-	-	-	-	-	x	-	o	x	-	-
sol and in mult	x	x	x	x	x	x	x	x	x	x	x	x	-	x	o	-	x	x
frequency [1]	11-34	19-63	27-35	12-30	10-12	8-20	19-24	5-13	1-3	1-3	1-2	6	5-11	27-35	13-87	6	23-87	9-13
Perforations:																		
excl. scal	x	x	x	x	-	-	-	-	-	-	-	-	-	-	o	-	-	-
excl. simple	-	-	-	-	-	o	o	x	x	x	x	x	-	-	o	-	-	-
mixed	-	-	-	-	x	o	o	-	-	-	-	-	x	x	o	x	x	x
no. of bars	6-11	5-8	7	5-11	2-48	1-39	3-24	-	-	-	-	-	7-8	6-7	1-62	12-16	1-25	18-30
Inter-vessel pits:																		
scal	x	x	x	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-
opp-trans	-	-	-	-	-	x	-	-	-	-	-	-	x	x	x	x	-	x
alt-opp	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-
alt	-	-	-	-	-	-	x	x	x	x	x	x	-	-	-	-	-	-
Vessel—parenchyma pits:																		
alt; half-bordered	-	-	-	-	-	-	x	x	x	x	x	x	-	-	-	-	-	-
alt-opp; half-bordered	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	x	-
simple; 1-2-ser, diff, scal	x	x	x	x	-	x[2]	x	x	-	-	-	-	-	x	o	-	-	-
simple; ret, scal, diff	-	-	-	-	x	-	-	-	-	-	-	-	x	-	o	x	-	x
Vessel—ray pits:																		
half-bordered; alt	-	-	-	-	-	-	-	x	(x)	(x)	(x)	x	-	-	-	-	-	-
half-bordered; alt-ret	-	-	-	-	-	(x)	(x)	-	-	-	-	-	-	-	-	-	-	-
,, (simple); opp-ret	x	x	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
almost simple (half-bordered) opp-scal-ret	-	-	-	-	(x)	-	-	-	-	-	-	-	x	-	-	-	x	x
simple; opp-ret	-	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	-	-
vertically unilaterally compound. 3)	x	x	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
vascular tracheids	-	-	-	-	-	-	-	-	(x)	-	-	(x)	-	-	-	-	-	-
fibre tracheids	-	-	-	-	x	x	x	x	x	x	x	x	x	x	x	x	x	x
intermediates between tracheids and fibre tracheids	-	-	-	-	-	-	-	-	-	-	-	-	x	x	x	x	x	x
libriform fibres	x	x	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
septate fibres	x	-	x	x	-	-	-	-	-	-	-	-	-	-	(o)	-	-	-
Parenchyma:																		
scanty paratracheal	x	o	-	x	-	-	-	-	-	-	-	-	-	-	(o)	-	-	-
unilaterally paratracheal	-	-	-	-	-	-	-	-	-	-	-	-	x	(x)	o	x	x	x
aliform-confluent	-	(o)	-	-	-	-	-	-	-	-	x	-	x	-	o	x	x	x
paratracheally banded	-	-	x	-	x	x	x	x	x	x	-	x	-	-	-	-	-	-
apotracheally banded	-	-	-	-	-	-	-	-	-	-	-	-	-	x	(o)	x	-	-
Rays: [4]																		
heterogeneous I-II (narrow)	-	-	-	-	-	-	-	-	-	-	-	-	x	x	o	x	-	-
heterogeneous II ,,	-	-	-	-	-	-	-	-	-	-	-	-	-	-	o	-	x	x
heterogeneous II (wide)	-	-	-	-	x	x	x	x	x	x	x	x	-	-	-	-	-	-
heterogeneous II-III	x	x	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-
homogeneous	(x)	-	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-

alt = alternate
diff = diffuse
mult = multiples
opp = opposite
ret = reticulate
scal = scalariform
ser = seriate
sol = solitary
trans= transitional

x = character present in the genus.
o = character present in part of the species only.
( ) = character infrequently present.
\- = character absent.

1) Only the range of the average vessel frequencies is given.
2) Also reticulate.
3) In Ceriops with an oval to rounded ray pit, in the other genera with a slender ray pit.
4) According to Kribs (1950).

respects from the other members of the family, and stand out through the following combination of characters: Perforation plates exclusively scalariform with thick bars, inter-vessel pits scalariform, vessel–parenchyma pits simple, vessel–ray pits frequently vertically unilaterally compound, fibres with minutely bordered to simple pits, and rays heterogeneous II–III, mostly 3–5-seriate with scanty uniseriates. According to Marco (1935) this character-complex distinguishes the Rhizophoreae from any other dicotyledonous family, which may well be true. The genera of the Macarisieae also form a homogeneous group. Their distinctive characters are: perforation plates both simple and scalariform (in *Cassipourea* some species have either exclusively simple or exclusively scalariform perforation plates, cf. Table 4), fibres with distinctly bordered pits, part of the fibres with very frequent pits (tracheid-like), typically unilaterally paratracheal parenchyma, either aliform, confluent, or banded, and rays heterogeneous I–II, mostly 2–3(–5)-seriate with infrequent uniseriates. The vessel–parenchyma pits are large and simple and their distribution pattern varies within fairly narrow limits (see p. 50); the inter-vessel pits, if present, are opposite to transitional. Only *Macarisia* stands out slightly from this homogeneous group because of its vessel wall pitting (see Table 10).

The Rhizophoraceae and the Macarisieae are thus easily recognizable wood anatomically and correspond exactly with the groups adopted by most taxonomists. The eight remaining genera have some wood anatomical features in common, viz.: broad (up to 30 cells wide) heterogeneous II rays with frequent uniseriates, fibres with large bordered pits and aliform to confluent or banded parenchyma, almost always completely embedding the vessels. Within this group, *Anisophyllea*, *Combretocarpus*, *Poga*, and *Polygonanthus* are outstanding because of their alternate, half-bordered vessel–parenchyma pits, and alternate inter-vessel pits with coalescent apertures. They also tend to have large vessels (the smaller vessels in *Polygonanthus* are probably due to the sample being from a young branch or stem). Wood anatomically, one can therefore support the recognition of a suprageneric taxon, the Anisophylleae, consisting of these four genera.

Carallia, *Crossostylis*, *Gynotroches*, and *Pellacalyx* bear much resemblance to the Anisophylleae but are distinguished by mostly large and simple vessel–parenchyma pits in a diffuse, uni- or biseriate, scalariform or reticulate arrangement. Their inter-vessel pits if alternate, do not have coalescent apertures. However, in some other wood anatomical characters, these four genera do not constitute a very homogeneous group. *Carallia* and *Crossostylis* have alternate inter-vessel pits, whilst in *Pellacalyx* they are opposite, and in *Gynotroches* scalariform. Vessel–ray contacts are frequent in *Crossostylis*, but infrequent in the other genera. In *Carallia* the vessels are not completely embedded in axial parenchyma, which is the case in the other three genera. In *Pellacalyx* the vessel arrangement stands out because of the frequent occurrence of radial multiples. Minor patterns of diversity are moreover evidenced in the sporadic occurrence of scalariform perforation plates in *Gynotroches*, *Crossostylis* p.p., and *Pellacalyx* p.p., and in the presence of clustered, as well as solitary crystals in some species of *Crossostylis*.

Wood anatomically, the distinction of the Gynotrocheae from the Anisophylleae is not firmly based. In view of the macromorphological evidence (Anisophylleae with alternate, ex-stipulate leaves; Gynotrocheae and other Rhizophoreae with stipulate, decussate leaves), the distinction must be upheld and the wood anatomical heterogeneity in the small group Gynotrocheae has to be accepted.

It appears to be possible to arrange most of the wood anatomical diversity of the Gynotrocheae in a morphological series, in accordance with the major trends of xylem evolution as established by I. W. Bailey and his students (cf. Tippo, 1946; Carlquist, 1961). Diversity in perforation plates and inter-vessel pits can thus be explained. *Carallia* appears to have the most specialized (exclusively simple) vessel perforations; the other genera have simple and scalariform perforations, but the latter are rare and may be absent in some species or specimens. The inter-vessel pits range from scalariform to alternate; *Gynotroches* is most primitive in this respect with scalariform pits; *Carallia* and *Crossostylis* are most specialized with alternate pits; *Pellacalyx* is intermediate with opposite pits. Other characters in which the Gynotrocheae show wood anatomical diversity, such as vessel–parenchyma pitting and mineral inclusions, cannot be interpreted according to the major trends, but it seems justified on the basis of vessel perforation and inter-vessel pit arrangement to place the genera of the Gynotrocheae in a series reflecting progressive specialization, as follows: *Gynotroches*—*Pellacalyx*—*Crossostylis*—*Carallia*. This possibility of constructing a more or less continuous morphological series does support the validity of the suprageneric taxon Gynotrocheae. Outside the Rhizophoreae, *Gynotroches* is the only genus with scalariform inter-vessel pits in the family of the Rhizophoraceae. It is tempting to interprete this resemblance in one important character as evidence of mutual relationship between *Gynotroches* and the mangrove genera, and hence of the mangrove genera and the other inland genera of the Gynotrocheae. *Kandelia* would seem to be closest to *Gynotroches* because of the abundant parenchyma. However, these similarities are outweighed by many important differences in the wood, so that more evidence from other structures (flowers, pollen, leaves) would be required to evaluate this suggestion.

Before discussing the mutual relationships of the Rhizophoreae, Macarisieae, Anisophylleae, and Gynotrocheae, it should be pointed out that, from the foregoing, one may conclude, that wood anatomy strongly supports the classification of genera as advocated by most students of the Rhizophoraceae. This is partly thanks to the influence of Marco's wood anatomical work (1935) on subsequent classifications, but, in part, these are based on independently reached conclusions. As will be discussed later in this chapter, some of Marco's suggestions considerably deviated from my conclusions.

The taxonomic position of Comiphyton and Polygonanthus

Comiphyton has very recently been described by Floret (1974) as a member of the Rhizophoraceae–Macarisieae, intermediate between *Macarisia* and *Cassipourea*. The genus shares all of its wood anatomical characters with *Anopyxis*, *Cassipourea*, *Sterigmapetalum*, and *Blepharistemma* (see Table 10). From *Macarisia* it differs in the arrangement of the inter-vessel and vessel–parenchyma pits. Wood anatomically, no position in this family can be favoured other than in the Macarisieae, and this is supported by nodal anatomy. The node of *Comiphyton* is characterised by two common gaps from which split laterals enter the opposite leaves together with one median trace for each leaf (for terminology see van Vliet & Baas, 1975). This nodal type has also been recorded for three species of *Cassipourea* (Howard, 1970). The common gaps with split laterals and extra traces between these laterals and the median trace are characteristic for the other Rhizophoraceae species studied by Howard.

The taxonomic position of *Polygonanthus* has been the subject of several publications, in which a number of families were proposed to accomodate this genus. Croizat (1943) regarded it distinct enough to form a family of its own, the Polygonanthaceae. Families, suggested for *Polygonanthus* are: Euphorbiaceae, Olacaceae, Saxifragaceae (cf. Pires & Rodrigues, 1971), Escalloniaceae (Hutchinson, 1973), and Rhizophoraceae. All authors who linked *Polygonanthus* with the Rhizophoraceae, placed the genus in one group with *Anisophyllea*, giving this group the rank of either family (Anisophylleaceae, Airy Shaw, 1973; Takhtajan, 1969), subfamily (Anisophylleoideae, Kuhlman, 1944), or a section (Anisophylleae, Pires & Rodrigues, 1971). In all of the above circumscriptions the *Anisophyllea* group comprises *Combretocarpus* and *Poga* as well. Erdtmann (1952) placed *Polygonanthus* in the Saxifragaceae, and later (in Pires & Rodrigues, 1971) he stated that: 'According to the pollen morphological data it is quite impossible to refer *Polygonanthus* to the Olacaceae and Proteaceae. Nor is there any similarity to the Rhizophoraceae. On the other hand, pollen morphology does not contradict the reference of this genus to the Euphorbiaceae or the Saxifragaceae'.

The wood anatomy of *Polygonanthus* is very unlike that of the woody representatives of the Saxifragaceae-complex (Cunoniaceae, Escaloniaceae, Eucryphiaceae, and Hydrangeaceae) nor is there any resemblance with the wood of the Euphorbiaceae (cf. Metcalfe & Chalk, 1950). Resemblance with the wood of the Proteaceae is present, but pollen morphological as well as macromorphological characters are strongly conflicting with such a position. Wood anatomically *Polygonanthus* perfectly resembles the genera of the Anisophylleae, and its wood is very difficult to tell apart from that of *Anisophyllea* (see the descriptions and the key). A position in this group is also in agreement with macromorphological characters (cf. Pires & Rodrigues, 1971). The pollen morphological objections of Erdtman against affinities with Rhizophoraceae seem invalid if one compares his description (Erdtman, 1952) of *Polygonanthus* pollen with the pollen type of the Rhizophoraceae (J. Muller, personal communication).

Phylogenetic considerations

As was done above for the Gynotrocheae, one can approach the wood anatomical diversity of the whole family from the angle of progressive xylem evolution. Perforation plate characters, inter-vessel pit arrangement, vessel grouping and arrangement, type of fibres, parenchyma distribution, and ray type lend themselves well to such an approach within this family. Vessel member length, and vessel–parenchyma and vessel–ray pits are less suitable, because the variability is either too small, or the different patterns are difficult to interprete unambiguously in a unidirectional specialization series.

Considering the variation in the above mentioned characters relevant for the determination of the specialization level of each genus or group of genera, one can establish the most primitive condition of each individual character present in the family. Accepting the Rhizophoraceae as a natural monophyletic taxon it is possible to picture the most important characteristics of the wood of the hypothetical 'Protorhizophoraceae'

> Vessels diffuse and solitary with scalariform perforation plates and scalariform inter-vessel pits. Fibre-tracheids with frequent bordered pits. Parenchyma at least partly paratracheal, probably scanty. Rays heterogeneous, of two distinct sizes.

Not surprisingly, the resulting picture is that of a primitive type of secondary xylem, still occurring in extant representatives of a number of quite unrelated dicotyledonous families. It provides us, however, with a useful starting point to discuss the position of the different groups within the Rhizophoraceae. It appears, that one must assume independent diverging phylogenetic specialization for the different groups, because it is impossible to juxtapose all groups according to an increasingly high level of xylem specialization.

In Rhizophoreae the perforation plates remained scalariform, but the low number of widely spaced bars is suggestive of some degree of specialization here. The inter-vessel pits conform to the ancestral scalariform type. The fibre tissue, on the other hand is highly specialized with few minutely bordered to simple pits. The paucity of uniseriate rays may be interpreted as a reduction (cf. Barghoorn, 1941), and the heterogeneous II–III multiseriate rays constitute an example of specialization in themselves. Within the Rhizophoreae some of the genera show signs of further specialization; e.g. *Kandelia* has abundant parenchyma; the occurrence of septate fibres in 3 genera, but not in *Ceriops* also suggests further specialization of the former genera.

The Macarisieae also show a mixture of advanced and primitive characters, but specialization has gone a different direction here. Of the 'ancestral' characters they retained the fibre-tracheids and the heterogeneous rays. The perforation plates are partly simple, thus reflecting specialization. The same applies to the transitional to opposite inter-vessel pits. The low frequency of uniseriate rays may be interpreted as a reduction. Some of the genera or species (*Cassipourea* p.p.) have retained the 'ancestral' feature of exclusively solitary vessels and there are some differences amongst and within the genera with regard to the perforation plate specialization: scalariform plates are rare in *Anopyxis*, *Comiphyton*, and *Sterigmapetalum*; in *Cassipourea* they are occasionally the only type present, yet, in other species, they are completely lacking.

The Anisophylleae are more specialized than the two previous groups if all wood anatomical characters are considered. Yet, they represent another diverging line with as 'ancestral' characters: fibre-tracheids and heterogeneous rays of two distinct sizes, and as specialized characters: exclusively simple perforations, alternate inter-vessel pits and abundant parenchyma.

The Gynotrocheae share the 'ancestral' characters of the Anisophylleae, with in addition the occurrence of the sporadic scalariform perforations in *Crossostylis*, *Gynotroches*, and *Pellacalyx*. They also share the specialized parenchyma but the inter-vessel pits show the diversity from scalariform to alternate discussed before.

In attempting to reconstruct a phylogenetic tree for the Rhizophoraceae, it seems therefore plausible to view the Gynotrocheae as an offshoot from the line leading to the Anisophylleae. The genus of the Gynotrocheae with the most primitive xylem, *Gynotroches*, should be placed in the most basal position (see Fig. 4). *Carallia* with the most specialized xylem of the Gynotrocheae resembles the Anisophylleae very closely in its secondary xylem (differences are in vessel–parenchyma pits and apertures of the inter-vessel pits only) but must be viewed as a member of the Gynotrocheae on grounds of macromorphological considerations (leaf arrangement, stipules). Fig. 4 illustrates the phylogenetic conclusions reached above. In a two dimensional diagram, one cannot avoid creating the false impression that the Macarisieae are closer to the Anisophylleae than to the Rhizophoreae. It should, however, be pointed out that the three major lines must be thought to be at about equal distance to each other. *Gynotroches* is intentionally drawn close to the Rhizophoreae, because of the shared inter-vessel pits, as discussed above. Depending on the differences between the individual genera within the major groups, some genera are presented as conspicuous or inconspicuous bulges of the branches of the phylogenetic tree. Fig. 4 and the above phylogenetic considerations are of course fully hypothetical and entirely based on the assumption of irreversibility of the major trends of xylem specialization as claimed by Bailey and many of his students. Baas (1973) and van der Graaff & Baas (1974) have, however, challenged this belief, and although these authors were mainly concerned with vessel member length, a character which has not been used here, I do not exclude the possibility of reversibility. The suggestions made from the wood anatomical point of view should therefore be tested by future workers on other aspects of diversity and evolution in the Rhizophoraceae.

Discussion of suggestions by previous authors

Marco's conclusion (1935) with regard to the wood anatomical homogeneity of the Rhizophoreae and the Macarisieae is supported by the analysis presented here. However, the Gynotrocheae were differently delimited by Marco and included *Anisophyllea*, *Combretocarpus*, *Carallia*, *Crossostylis*, and *Gynotroches* (cf. Table 1). Moreover, *Poga*, and *Pellacalyx* were left unclassified because they 'are two distinct genera that have been included with the Rhizophoraceae, although they appear decidedly out of place in this family' (p. 13). Metcalfe & Chalk (1950), Desch (1954), and Geh & Keng (1974) have already discussed this curious conclusion of Marco. These authors pointed out

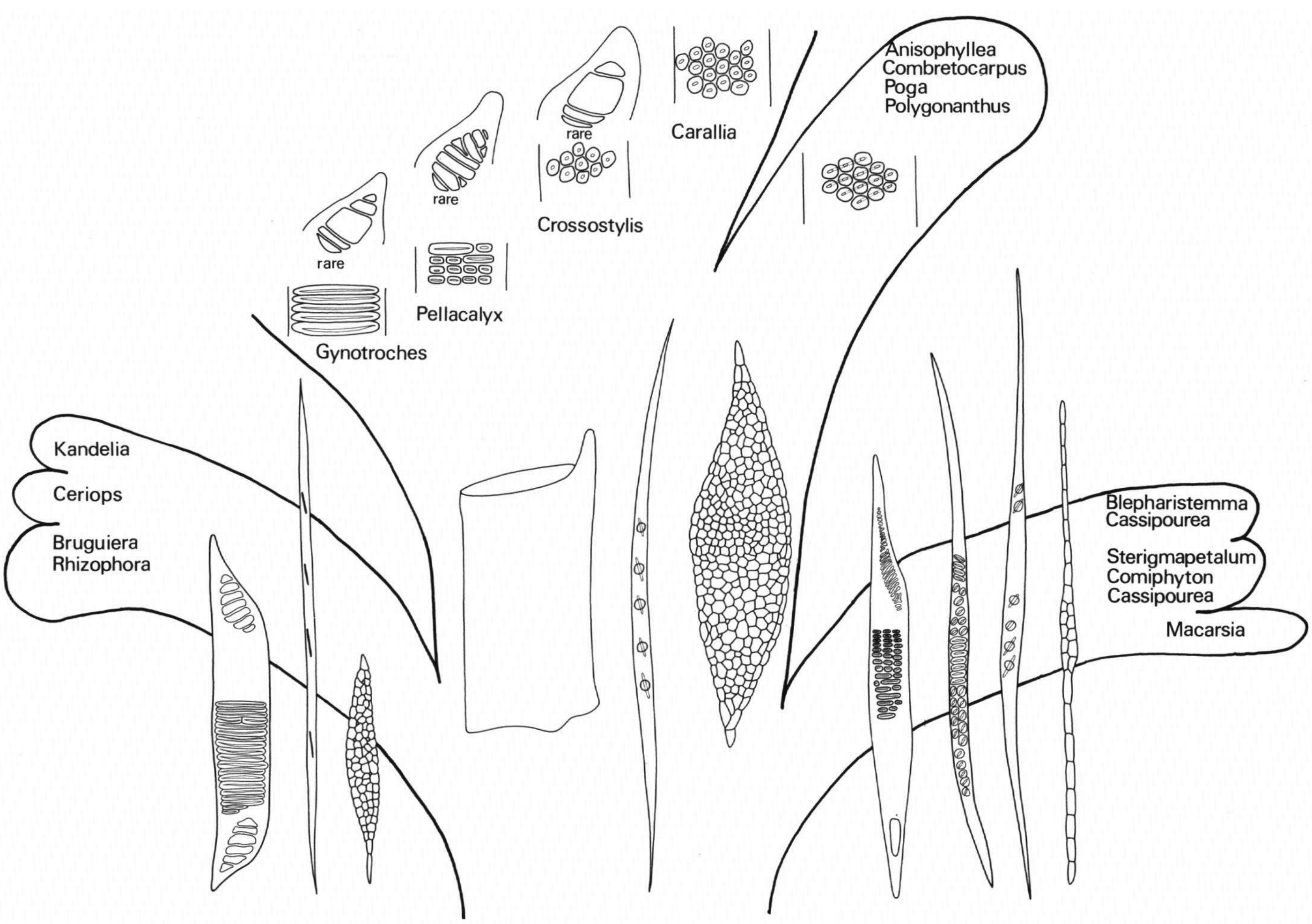

Fig. 4 Phylogenetic tree for the genera of the Rhizophoraceae. The main wood anatomical characters of the several groups are illustrated in the corresponding branches.

the high degree of similarity of *Poga* and *Pellacalyx* with various representatives of the Gynotrocheae sensu Marco. My own results fully support this. Marco himself did not substantiate his decision to leave the two genera unclassified and, from his description, the only reason to keep *Poga* from his Gynotrocheae seems to be the large inter-vessel pits of 27 μm he recorded. This size is, however, obviously wrong: in the three samples studied by me, these pits measure 6–8 μm. Perhaps Marco measured the length of the coalescent apertures instead of the diameter of the pit chambers. In the case of *Pellacalyx* Marco must have overweighed the taxonomic value of the tangential vessel pattern in this genus. Rejecting these weaknesses in Marco's classification, one is faced with his inclusion of representatives of Anisophylleae and Gynotrocheae in one group. Arguments I have given above, and which are based on wood anatomy give evidence for the affinities of these two groups, but also support their distinction. The macromorphological differences are, however, most decisive in this respect.

In the past several authors have suggested a family status for groups of genera (see Table 1). These suggestions were mainly based on macromorphological characters, such as the viviparous fruits of the mangrove genera or the different leaf arrangement of the Anisophylleae. Moll & Janssonius (1914–8) were the first to introduce wood anatomical arguments into this discussion. Commenting on the differences between the Javanese species of the mangrove genera, *Bruguiera* and *Rhizophora*, and of the inland genera, *Carallia* and *Gynotroches*, they noted that these two groups are not only more distinct than is usual between genera of one family, but that the differences are greater than those that often occur between two separate families. Marco (1935) suggested a family status for the Rhizophoreae because of their distinctive macromorphological and wood anatomical characters. The macromorphological characters are, however, not so different from those of the inland groups as was suggested by Marco (Geh & Keng, 1974; Hou, 1958).

Some authors favour the recognition of the family Anisophylleaceae, because of their alternate exstipulate leaves (e.g. Takhtajan, 1964). Wood anatomically this group fits in well with the Rhizophoraceae through resemblance with the Gynotrocheae which no student of the family wants to remove from it.

In my opinion, the very diverse pattern of wood anatomical variation cannot be used to advocate the exclusion of some groups of genera to form separate families. The strongly divergent evolution of the wood anatomical characters is perhaps unusual for natural families. There are, however, indications of mutual affinities of all groups, if one considers the macromorphological similarities and the wood anatomical links between Anisophylleae and Gynotrocheae on the one hand, and the suggestion of affinity between *Gynotroches* and the Rhizophoreae through their shared scalariform inter-vessel pits on the other.

Position of the family

The position of the Rhizophoraceae in the natural system for Dicotyledons will not be elaborately discussed here. Their traditional placement in the Myrtales will be assessed after more families of this order have been examined. Preliminary comparisons, however, suggest that Rhizophoraceae do not belong to this order, because they lack vestured pits and internal phloem. The 'reconstruction' of the ancestral type of Rhizophoraceous woods seems to support Thorne's classification (1968) of this family in the Cornales.

CONCLUSIONS

The wood anatomical heterogeneity of the Rhizophoraceae (Table 10) is clearly illustrated by the fact that there are no wood anatomical characters common to all genera of the family. On the basis of wood anatomical characters, three distinct groups of genera can be recognized: the Rhizophoreae with the four mangrove genera *Bruguiera*, *Ceriops*, *Kandelia*, and *Rhizophora*; the Anisophylleae with the inland genera *Anisophyllea*, *Combretocarpus*, *Poga*, and *Polygonanthus*, and the Macarisieae with the inland genera *Anopyxis*, *Blepharistemma*, *Cassipourea*, *Comiphyton*, *Macarisia*, and *Sterigmapetalum*. A fourth group, the Gynotrocheae with the inland genera *Carallia*, *Crossostylis*, *Pellacalyx*, and *Gynotroches* is wood anatomically more heterogeneous, but this wood anatomical variation, as well as that of the whole family, can be arranged in a phylogenetic sequence in accordance with the major trends of wood anatomical specialization.

The recently described genus *Comiphyton* (Floret, 1974) belongs wood anatomically to the Macarisieae. The genus *Polygonanthus* has been placed in several families, but belongs also to this family, as was recently suggested by Pires & Rodrigues (1971).

Although the family in its present delimitation has never received a complete taxonomic treatment, a classification can more or less be deduced from the suggestions of several taxonomists. The wood anatomical classification into four groups is completely in accordance with such a classification on macromorphological characters. This classification is, however, partly not in accordance with the one given by Marco (1935) who also studied this family using wood anatomical characters only. Part of this discrepancy can be explained because since Marco's time more material has become available, and large parts of the family have been taxonomically revised, thus providing a better working base for the anatomist. However, a part of the discrepancy in the conclusions is caused by the fact, that Marco—in my opinion—did not always correctly interprete the wood anatomical evidence.

In the literature, some suggestions have been given to explain the wood anatomical differences between the genera growing in the mangroves and those growing in the inland forests. Although some distinct wood anatomical differences are correlated with the difference in habitat, there is no reason to assume that these differences are caused by that difference in habitat. Hopefully, the results of intended future studies on families with both inland and mangrove representatives (Combretaceae, Sonneratiaceae), will offer the opportunity to deal with this subject more extensively.

KEY TO THE WOODS OF THE RHIZOPHORACEAE

1a. Fibres with minutely bordered or simple pits; perforations exclusively scalariform (Rhizophoreae) 2
b. Fibres with distinctly bordered pits; perforations simple or mixed, very rarely exclusively scalariform 4
2a. Silica bodies present in ray cells . . . . **Kandelia**
b. Silica bodies absent, but ray cells with silicified walls sometimes present . 3
3a. Fibres not septate; vertically unilaterally compound vessel–ray pit pairs with oval to rounded ray pit (Fig. 2b) . . . . **Ceriops**
b. Fibres septate; vertically unilaterally compound vessel–ray pit pairs with slender ray pit (Fig. 2a): Pantropical . . . . **Rhizophora**
Malesia, E. Africa . . . . **Bruguiera**
4a. Multiseriate rays very broad (6–30 cells wide); uniseriate rays frequent . 5
b. Multiseriate rays 2–5(–6) cells wide; uniseriate rays infrequent (Macarisieae) 10
5a. Inter-vessel pits alternate 6
b. Inter-vessel pits scalariform or opposite (Gynotrocheae p.p.) 9
6a. Vessel–parenchyma pits typically simple, or only partly half-bordered, simple pits uni- to biseriate, diffuse, scalariform or reticulate (Gynotrocheae p.p.) . . 8
b. Vessel–parenchyma pits half-bordered, always alternate (Anisophylleae) 7
7a. Parenchyma aliform to confluent, never forming continuous bands; fibres thin-walled . . . . **Poga**
b. Parenchyma forming continuous bands; fibres thick-walled:
Pantropical . . . . **Anisophyllea**
Malesia . . . . **Combretocarpus**
S. America . . . . **Polygonanthus**
8a. Parenchyma paratracheally banded; vessel–ray pits infrequent, alternate or diffuse; perforations exclusively simple . . . . **Carallia**
b. Parenchyma aliform to confluent in a reticulate pattern; vessel–ray pits frequent, opposite–alternate to reticulate; scalariform perforations infrequent in some species . . . . **Crossostylis**
9a. Inter-vessel pits opposite to transitional, in first formed secondary xylem sometimes scalariform; vessels frequently in tangential multiples . . . . **Pellacalyx**
b. Inter-vessel pits always scalariform; vessels partly in radial multiples . . . . **Gynotroches**
10a. Inter-vessel pits alternate–opposite; vessel–parenchyma pits half-bordered, alternate to opposite . . . . **Macarisia**
b. Inter-vessel pits or pits in tails to succeeding vessel elements opposite to transitional; vessel–parenchyma pits typically almost simple 11
11a. Average vessel frequency 5–7/mm^2; vessels exclusively solitary 12
b. Average vessel frequency 8 or more/mm^2; vessels exclusively solitary or solitary and in radial multiples 13

12a. Parenchyma unilaterally aliform . . . . **Anopyxis**

b. Parenchyma irregularly banded . . . . **Comiphyton**

13a. Vessels large, average tangential vessel diameter 160–220 μm; rays mostly 4–5-seriate . . . . **Anopyxis**

b. Vessels smaller, average tangential diameter up to 130 μm, maximum tangential diameter rarely exceeding 150 μm; rays mostly 2–3-seriate, rarely 4–5-seriate:

India . . . . **Blepharistemma**

Ceylon, Africa, S. America . . . . **Cassipourea**

S. America . . . . **Sterigmapetalum**

ACKNOWLEDGEMENTS

I wish to express my sincere thanks for the stimulating and critical, very pleasant support and coaching by Dr. P. Baas, who was of great help in the preparation of the English manuscript. I also wish to thank my supervisor Professor Dr. C. Kalkman who critically read the manuscript. Thanks are due to the curators of the wood collections of Forest Products Research Laboratory, Madison; Commonwealth Forestry Institute, Oxford; Instituut voor Systematische Plantkunde, Utrecht; Harvard University Herbarium, Cambridge, U.S.A.; Koninklijk Museum voor Midden Afrika, Tervuren; Forestry Commission of New South Wales, Sydney; Koninklijk Instituut voor de Tropen, Amsterdam; Landbouw hogeschool, Wageningen; C.S.I.R.O., Melbourne; Pusat Penyelidekan Hutan, Kepong who provided many of the wood samples studied. Dr. A. M. W. Mennega is acknowledged for providing samples of the genus *Polyganthus*, Dr. J. J. Floret kindly sent samples of *Comiphyton*. Mr. J. Muller is acknowledged for his comment on pollen morphological data. The access to the slide collections of the Jodrell Laboratory, Kew; the Commonwealth Forestry Institute, Oxford, and the Forest Products Laboratory, Princes Risborough is gratefully acknowledged. The director of the Institute for Geology and Mineralogy kindly gave access to the scanning electron microscope which was operated by Mr. H. Kammeraat. Miss A. Kuenen is thanked for her share in the microtechnical work; Messrs B. N. Kieft and C. L. Marks prepared the plates; Mr. J. van Os prepared the drawings. Miss M. van Zoelen diligently typed the manuscript.

This study, as well as the visit to the above mentioned slide collections in England was made possible through financial support of the Netherlands Organization for the Advancement of Pure Research (Z.W.O.).

REFERENCES

ALSTON, A. H. G. 1925. Revision of the genus *Cassipourea*. Kew Bull. 1925: 241–276.

AIRY SHAW, H. K. 1973. *In*: J. C. Willis, A dictionary of flowering plants and ferns.

ARAUJO, P. A. M. & A. MATTOS FILHO. 1973. Estrutura das madeiras de Rhizophoraceae. Archos Jard. bot., Rio de J. 19: 133–147.

BAAS, P. 1973. The wood anatomical range in *Ilex* (Aquifoliaceae) and its ecological and phylogenetic significance. Blumea 21: 193–258.

BARGHOORN, E. S. 1940. The ontogenetic development and phylogenetic specialisation of rays in the xylem of Dicotyledons I: The primitive ray structure. Am. J. Bot. 27: 918–928.

BARGHOORN, E. S. 1941. The ontogenetic development and phylogenetic specialisation of rays in the xylem of Dicotyledons II: Modification of the multiseriate and uniseriate rays. Am. J. Bot. 28: 273–282.

BAILLON, H. 1876. Histoire des Plantes. Vol. 6.

BECKING, J. H., L. G. DEN BERGER, & H. W. MEINDERSMA. 1922. Vloed- of Mangrovebosschen in Ned.-Indië. Tectona 15: 561–611.

BENOIST, R. 1931. Les bois de Guyane Française. Archs Bot. Mém. 5: 1–292.

BENTHAM, G. 1859. Synopsis of Legnotidae, a tribe of the Rhizophoraceae. J. Proc. Linn. Soc. 3: 65–80.

BENTHAM, G. & J. D. HOOKER. 1865. Genera Plantarum 1 (2): 677–683.

BERGER, L. G. DEN. 1926. Houtsoorten der cultuurgebieden van Java en Sumatra's oostkust. Meded. Proefstn Boschw., Batavia 13.

BLUME, C. L. 1849. Museum Botanicum: 126–131.

CARLQUIST, S. 1961. Comparative Plant Anatomy.

CARLQUIST, S. 1975. Ecological strategies of xylem evolution.

CHATTAWAY, M. M. 1932. Proposed standards for numerical values, used in describing woods. Trop. Woods 29: 20–28.

COOPER, C. P. & S. J. RECORD. 1931. The evergreen forests of Liberia. Bull. Yale Sch. For. No. 31.

CORNER, E. J. H. 1951. Wayside trees of Malaya.

CROIZAT, L. M. C. 1943. Polygonanthaceae. Cactus Succ. J., Los Ang. 15: 64.

DESCH, H. E. 1954. Manual of Malayan timbers. Malay. For. Rec. 15.

ENDLICHER, S. 1836–1840. Genera Plantarum.

ENGLER, A. 1900. *In*: Engler, A. & K. Prantl. Natürl. PflFam., Nachtr. 2: 49.

ERDTMANN, G. 1952. Pollen morphology and plant taxonomy. Angiosperms.

FLORET, J. J. 1974. *Comiphyton*, genre nouveau gabonais. Rhizophoraceae–Macarisieae. Adansonia 14: 499–506.

GEH, S. Y. & H. KENG. 1974. Morphological studies on some inland Rhizophoraceae. Gdns' Bull., Singapore 28: 183–220.

GERARD, A. 1917. Recherches sur la spéciation histologique de différents bois de Madagascar, avec étude comparative des principaux bois industrielles d'Europe. Trav. Lab. Matière méd., Paris 11 (1920), 1.

GONGGRIJP, J. W. 1932. Gegevens betreffende een onderzoek naar Nederlandsch-Indische houtsoorten welke tegen de paalworm bestand zijn. Meded. Proefstatn Boschw., Batavia No. 25.

GRAAFF, N. A. VAN DER & P. BAAS. 1974. Wood anatomical variation in relation to latitude and altitude. Blumea 22: 101–121.

HAYASHI, S., T. KISHIMA, L. L. CHAU, W. T. MENG, & B. MELON. 1973. Micrographic atlas of South East Asian timbers.

HOLTERMAN, C. 1907. Der Einfluss des Klimas auf den Bau der Pflanzengewebe.

HOPKINSON, A. D. 1912. Beitrage zur Mikrographie tropischer Hölzer. Beih. bot. Zbl. 29: 441–456.

HOU, D. 1957. A conspectus of the genus *Bruguiera* (Rhizophoraceae). Nova Guinea, N.S., 8: 163–171.

HOU, D. 1958. Rhizophoraceae. *In* Flora Malesiana I (5): 429–493.

HOU, D. 1960. A review of the genus *Rhizophora*. Blumea 10: 625–634.

HOWARD, A. L. 1948. Timbers of the world.

HOWARD, R. A. 1970. Some observations on the nodes of woody plants with special reference to the problem of 'split-lateral' versus the 'common-gap'. *In*: New research in plant anatomy (eds. N. K. B. Robson, D. F. Cutler, & M. Gregory). Bot. J. Linn. Soc. 63, Suppl. 1: 194–214.

HUTCHINSON, J. 1973. The families of flowering plants.

HUTCHINSON, J. & J. M. DALZIEL. 1954. Flora of West Tropical Africa 1.

I.A.W.A. 1964. Multilingual glossary of terms used in wood anatomy.

JANSSONIUS, H. H. 1950. The vessels in the woods of Javan mangrove trees. Blumea 6: 465–469.

JENTSCH, F. & E. APPEL. 1936. Beschreibung tropischer Hölzer aus dem Urwalde Kameruns. Weltforstwirtschaft 3: 331–341.

JONKER, F. P. 1942. Flora of Surinam. Vol. III (2): 40–41.

JUTTE, S. M. 1958. Hardwoods of Netherlands New Guinea I. Nova Guinea, N.S., 9: 347–367.

KANEHIRA, B. 1921. Anatomical characters and identification of Formosan woods.

KANEHIRA, B. 1924. Identification of Philippine woods by anatomical characters.

KARLSTEDT, P. 1971. Untersuchungen über Eigenschaften der Sprossachsen von atlantischen Mangrovenarten, mit Berücksichtigung ihrer Verwendung.

KRIBS, D. A. 1935. Salient lines of structural specialisation in the wood rays of Dicotyledons. Bot. Gaz. 96: 547–557.

KRIBS, D. A. 1950. Commercial foreign woods on the American market.

KUHLMAN, J. G. 1925. Contribução para o conhecimento de algumas plantas novas contendo tambem umtrabalho de critica e novas cominações. Archos Jard. bot. Rio de J. 4: 359.

KUHLMAN, J. G. 1944. Nota Prévia. Rodriguesia 8: 65.

LECOMTE, H. 1925. Les bois d'Indochine.

LEWIS, L. 1956. Flora of tropical East Africa; Rhizophoraceae.

LINDEMAN, J. C., A. M. W. MENNEGA, & W. H. A. HEKKING. 1963. Bomenboek voor Suriname.

MARCO, H. F. 1935. Systematic anatomy of the woods of the Rhizophoraceae. Trop. Woods 44: 1–20.

MARTIN, L. G. 1953. Primera contribución al conocimiento de las maderas de la Guinea continental espánola.

MELCHIOR, H. 1964. *In*: Engler, Syllabus PflFam. 12 Aufl. Band II.

MENIAUD, J. 1931. Nos bois coloniaux.

METCALFE, C. R. 1952. Notes on the anatomy of leaf and stem of *Anisophyllea guianense* Sandwith. Kew Bull. 1952: 291–294.

METCALFE, C. R. & L. CHALK, 1950. Anatomy of the Dicotyledons.

MIQUEL, F. A. W. 1855. Flora Indiae Batavae. Vol. I.

MOLL, J. W. & H. H. JANSSONIUS. 1906–1936. Mikrographie des Holzes der auf Java vorkommenden Baumarten.

NORMAND, D. 1960. Atlas des bois de la Côte d'Ivoire.

PANSHIN, A. J. 1932. An anatomical study of the woods of the Philippine mangrove swamps. Philipp. J. Sci. 48: 143–207.

PEARSON, R. S. & H. P. BROWN. 1932. Commercial Timbers of India.

PERROT, E. 1921. Les bois de Gabon. Trav. Lab. Matière méd., Paris 13.

PIRES, J. H. & W. A. RODRIGUES. 1971. Notas sôbres os gêneros *Polygonanthus* e *Anisophyllea*. Acta Amazonica 1: 7–15.

RAO, K. R. & S. K. PURKAYASTHA. 1972. Indian Woods 3: 165–175.

RECORD, S. J. & R. W. HESS. 1943. Timbers of the New World.

RECORD, S. J. & C. D. MELL. 1924. Timbers of tropical America.

REYES, L. J. 1938. Philippine woods.

RIERA, P. F. 1947. Primera contribución al conocimiento de las maderas de la Guinea continental espánola.

RIDLEY, H. N. 1922. The flora of the Malay Peninsula I: 692–703.

SARLIN, P. 1954. Bois et forêts de la Nouvelle Calédonie.

SCHIMPER, A. F. W. 1893. *In*: Engler, A. &. K. Prantl. Natürl. PflFam. 3 (7): 42–56.

SCURFIELD, G., A. ANDERSON, & E. R. SEGNIT. 1974. Silica in woody stems. Aust. J. Bot. 22: 211–229.

SOLEREDER, H. 1899. Systematische Anatomy der Dicotyledonen.

SPRAGUE, T. A. & L. A. BOODLE. 1909. Kokoti (*Anopyxis ealaensis* Sprague). Kew Bull. 1909: 309–312.

STERN, W. L. 1967. Index xylariorum. Regnum veg. 49.

TAKHTAJAN, A. 1969. Flowering plants, origin and dispersal.

THORNE, R. E. 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. Aliso 6: 57–66.

TIPPO, O. 1946. The role of wood anatomy in phylogeny. Am. Midl. Nat. 36: 362–372.

TOMLINSON, P. B. & F. C. CRAIGHEAD. 1972. Growth ring studies on the native trees of subtropical Florida. *In*: Research trends in plant anatomy (eds. A. K. M. Ghouse & M. Yunus): 39–51.

VLIET, G. J. C. M. VAN, 1975. Wood anatomy of Crypteroniaceae sensu lato. J. Micr. 104: 65–82.

VLIET, G. J. C. M. VAN & P. BAAS, 1975. Comparative anatomy of the Crypteroniaceae sensu lato. Blumea 22: 175–195.

WILLIAMS, R. O. 1932. Flora of Trinidad and Tobago. Vol. 1: 322.