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WOOD ANATOMY OF THE COMBRETACEAE

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SUMMARY

The wood anatomy of all genera of the *Combretaceae* (*Meiostemon* excepted) is described in detail on the basis of 120 samples representing 90 species from 19 genera. Additional data from the literature are added. The structural variation of the vestured pits is described and classified. There are two main types, of which the distribution follows the subfamily classification. Considering the overall wood anatomy, the recognition of two subfamilies: *Strephonematoideae* (*Strephonema* only) and *Combretoideae* (all remaining genera) can be supported. *Strephonema* stands out on account of its fibre-tracheids, type of vesturing and parenchyma distribution pattern. Within *Combretoideae*, one group of genera (subtribe *Combretinae sensu* Exell & Stace) stands out markedly on account of their radial vessels, a unique feature not known to occur in any other plant group, and two distinct size classes of vessel elements. The remaining genera, belonging to the tribe *Laguncularieae* and subtribes *Terminaliinae* and *Pteleopsidinae* of tribe *Combreteae* show a wide overlap in wood anatomical features. The *Laguncularieae* differ in the ratio of vessel member to fibre length, *Terminaliinae* and *Pteleopsidinae* cannot be separated wood anatomically.

Although difficult to interpret phylogenetically, arguments are brought forward to consider *Strephonema* as having the most primitive wood structure and the *Combretinae* to have the most derived wood.

Variation in some quantitative characters such as vessel member length is shown to be at least partly correlated with ecological conditions of the taxa involved. Wood anatomical differences between lianas and erect species are discussed. Synoptical keys to the genera of the *Combretaceae* and to the species studied of *Terminalia* are given.

CONTENTS

INTRODUCTION

Aims of this study.

A comprehensive survey of the *Combretaceae*, dealing with the wood anatomy of all genera has never been made. Rao (1972) was the only wood anatomist who discussed the relationships within the family, largely based on quantitative xylem characters of a large part of the genera. The comprehensive taxonomic work by A. W. Exell and C. A. Stace on the *Combretaceae* provides a solid working basis, which makes a wood anatomical study profitable. It is hoped, that the present study of 120 wood samples of 90 species belonging to 19 of the 20 Combretaceous genera may contribute to major points in the classification of the family such as: the separation of the subtribes *Combretinae* and *Terminaliinae;* the relationships between *Combretum* and *Terminalia* and their respective satellite genera; and the position of *Strephonema.*

The genera of the *Combretaceae* and of the other families of the *Myrtales* have vestured pits and a comparative study of the structure of these vestures enables an evaluation of their possible taxonomic and diagnostic value. The results of this study have been published elsewhere (van Vliet, 1978), but a summary of the results as far as *Combretaceae* are concerned is included in this paper.

The position of this family in the order *Myrtales* has never been the subject of much discussion, but deserves more attention from the wood anatomical point of view. It will be discussed more elaborately in a separate paper (van Vliet, in prep.) following further wood anatomical studies in this order. Other papers in this series dealt with *Crypteroniaceae* (van Vliet, 1975), *Rhizophoraceae* (van Vliet, 1976b), *Melastomataceae* (Koek-Noorman & Ter Welle, in prep.; van Vliet in prep.), *Lythraceae* (Baas & Zweypfenning, in prep.) and *Punicaceae* (Bridgwater & Baas, 1978).

Historical

According to Exell & Stace (1966) the *Combretaceae* form a very natural family. The major classification of the genera has not often been discussed. Table 11 summarizes the classification by Exell & Stace and also gives the main geographical distribution of the genera. Engler & Diels (1899) only slightly differed in their opinion on the classification of the family. They treated *Calycopteris* separately as *Calycopterideae*, and included *Pteleopsis* in the *Combretinae*. Exell & Stace (1966) elaborately discussed these differences in classification. The genera of the *Combretaceae* are not always sharply delimited. *Quisqualis* and *Meiostemon* are for instance difficult to separate from *Combretum; Ramatuella* and *Terminaliopsis* are very close to *Terminalia*. The other genera are, however, distinct from each other.

The great number of synonyms in *Combretum* indicates that there is no consensus on the specific delimitation in this genus. Yet three distinct subgenera can be recognized, based on the presence or absence of scales and stalked glands. In these three subgenera of *Combretum*, as well as in the genus *Terminalia*, many sections have been recognized. A world-wide revision of these genera is, however, still needed for a satisfactory delimitation of these numerous sections.

Wood anatomical studies discussing implications for relationships within the *Combretaceae* are few. Initial workers like Solereder (1885), Holtermann (1893) and Lefèvre (1905) studied a restricted number of genera, often using twig or branch material only. Rao (1972) based some disputable phylogenetic considerations on mainly quantitative data such as vessel frequency and diameter, vessel member length and wall thickness, and also on parenchyma distribution. Venkateswarlu & Rao (1971) discussed the position of *Strephonema*. On the basis of wood structure they suggested a family status for this genus. Den Outer & Fundter (1976) included phloem and secondary xylem in their discussion of *Strephonema* and were in favor of the subfamily status, adopted by amongst others Exell & Stace (1966).

A considerable number of published papers deal with the wood anatomy of one or several genera of this family. Many of these refer to the large genus *Terminalia*, because a number of species are of commercial interest. Other genera often referred to are *Anogeissus*, *Combretum*, *Lumnitzera*, *Pteleopsis*, and *Strephonema*. Data on the remaining genera are scanty or even absent. In the following list of papers dealing with the wood structure of *Combretaceae*, those genera of which the woods are illustrated with a plate or figure are indicated with °. These publications, containing microscopical and/or macroscopical data are by: Abbate, 1970 (*Anogeissus*°, *Combretum*°*)*; Alves de Pinho, 1966 (*Terminalia*); Ayensu & Bentum, 1974 (*Terminalia*°); Bargagli-Petrucci, 1902 (*Lumnitzera*); Barreto, 1967 (*Combretum, Pteleopsis, Terminalia*): Benoist, 1931 (*Buchenavia, Terminalia*); Den Berger, 1926 (*Terminalia*); British Honduras Forest Department, 1946 (*Bucida, Terminalia*); Brown, 1922 (*Terminalia*); Burgess, 1966 (*Lumnitzera, Terminalia); B*urgerstein, 1912 (*Terminalia*); Cardoso, 1960 (*Terminalia*°); Cellai, 1967 (*Terminalia*); Chalk *et al.*, 1933 (*Terminalia*°); Chowdhury, 1936 & 1939 (*Terminalia*°); Coode, 1969 (*Terminalia*°, *Lumnitzera*); Cooper & Record, 1931 (*Terminalia, Strephonema*); Coster, 1927 (*Terminalia*); Desch, 1941 (*Lumnitzera*°, *Terminalia*°); Fasolo, 1939 (*Combretum*°); Fouarge & Gerard, 1964 (*Pteleopsis, Terminalia*°); Fouarge *et al.*, 1953 (*Pteleopsis*°); Foxworthy, 1907 (*Terminalia*°); 1909 (*Anogeissus, Lumnizera Terminalia*°); Freitas, 1955 (*Terminalia*); Fundter & Wisse, 1977 (*Terminalia*°);

Furuno, 1977 (*Terminalia*°); Furuno & Saiki, 1974 (*Terminalia*°); Hate, 1911 (*Calycopteris*°); Hayashi *et al.*, 1973 (*Terminalia*,° only); Heiden, 1893 (twigs only; all genera, except *Calopyxis*, *Finetia*, *Meiostemon*, *Pteleopsis*, *Strephonema*, *Terminaliopsis*); Holtermann, 1893 (*Anogeissus*, *Combretum*, *Conocarpus*, *Laguncularia*, *Lumnitzera*, *Quisqualis*, *Terminalia*); Hooks, 1966 (*Terminalia*°); Hopkinson, 1912 (*Terminalia*°); Howard, 1948 (*Anogeissus*); Huber & Schmidt, 1938 (*Terminalia*); Huizzi, 1974 (*Terminalia*°); Jentsch & Appel, 1936 (*Terminalia*°); Jutte, 1959 (*Combretum*°, *Terminalia*°); Kanehira, 1921 (*Lumnitzera*, *Terminalia*°); Kanehira, 1924 (*Lumnitzera*, *Terminalia*); Kanehira, 1926 (*Terminalia*); Kribs, 1950 (*Bucida*°, *Laguncularia*°, *Terminalia*°); Lamb & Ntima, 1971 (*Terminalia*°); Lefèvre, 1905 (mainly leaf anatomical data but also some information on the twigs of *Anogeissus*, *Combretum*, *Guiera*, *Quisqualis*, *Terminalia*); Lindeman *et al.*, 1963 (*Buchenavia*°, *Terminalia*°); Lomibao, 1973 (*Terminalia*°); Méniaud, 1931 (*Terminalia*); Metcalfe & Chalk, 1950; Moll & Janssonius, 1918 (*Lumnitzera*°, *Terminalia*°); Normand, 1960 (*Anogeissus*°, *Laguncularia*°, *Pteleopsis*°, *Strephonema*°, *Terminalia*°); Normand & Paquis, 1976 (*Pteleopsis*°, *Strephonema*°, *Terminalia*°); Obaton, 1960 (*Combretum*); Den Outer & Fundter, 1976 (*Strephonema*); Panshin, 1932 (*Lumnitzera*°); Pearson & Brown, 1932 (*Anogeissus*°, *Terminalia*°); Purkayastha *et al.*, 1976 (*Terminalia*°); Rao & Rao, 1972 (*Terminalia*); Rao, 1972 (all genera except *Calopyxis*, *Finetia*, *Meiostemon*, *Strephonema*, *Terminaliopsis*, *Thiloa*; some °); Rao & Purkayastha, 1972 (*Anogeissus*°, *Calycopteris*°, *Lumnitzera*°, *Terminalia*°); Record & Hess, 1943 (*Buchenavia*, *Bucida*, *Conocarpus*, *Languncularia*, *Ramatuella*, *Terminalia*); Record & Mell, 1924 (*Terminalia*); Reyes, 1938 (*Lumnitzera*, *Terminalia*); Riera, 1947 (*Terminalia*); Seabra & Ferreirinha, 1959 (*Terminalia*); Van der Slooten & Gonzalez, 1971 (*Terminalia*°); Solereder, 1885 (*Anogeissus*, *Buchenavia*, *Calycopteris*, *Combretum*, *Guiera*, *Laguncularia*, *Lumnitzera*, *Terminalia*, *Thiloa*); 1899 (*ibid.*); Stone, 1918 (*Bucida*); Venkateswarlu & Rao, 1971 (*Strephonema*°); Verhoeven & van der Schijff, 1975 (*Combretum*); Wagenführ, 1967 (*Terminalia*); Williams, 1936 (*Terminalia*).

MATERIALS AND METHODS

Wood samples were obtained from several institutional wood collections, and these will be referred to using Stern's (1967) abbreviations, when no wood collection references are given, the samples are from the Rijksherbarium. 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, and fibre length; vessel member length was measured including the tails. Data on vessel frequency are based on at least five counts in each specimen in areas of 1 mm^2; data on ray frequencies are based on at least five counts over tangential distances of 1 mm each.

Specimens marked with $^+$ were also studied with a scanning electron microscope.

When possible, the names of the species and genera were adjusted according to revisions and studies by Exell & Stace, 1966 (generic names mainly); Exell, 1933 (Surinam); Exell, 1954 (Malesia); Bailey, 1900 (Australia); Hutchinson & Dalziel, 1954; Liben, 1968; Exell, 1970; Wickens, 1973 (all Africa); Lecomte, 1969 (S. E.

Asia); Exell, 1953; Engler & Diels, 1899 (*Combretum*); Griffith, 1959, Coode, 1969 (*Terminalia*); Exell, 1964 (*Quisqualis*); Exell & Stace, 1963 (*Buchenavia* and *Ramatuella*). For nomenclature, the more recent publications have been given preference over the earlier ones.

DESCRIPTIVE PART

Explanatory notes to the descriptions.

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

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

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

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

The vesturing is described using the types and forms recognized by me earlier (van Vliet, 1978), only the letters referring to these types are indicated in the descriptions; the various types that are present in this family are briefly dealt with in the discussion of wood anatomical characters.

The genera are arranged in an alphabetical sequence.

ANOGEISSUS (Wall.) Guill. & Perr.

Table 1; Fig. 3: c; 5: b; Plate 2: 7.

Material studied. *A. acuminata* (Roxb. *ex* DC) Wall.: BURMA, (*FHow 1441*$^+$, *FHow 2443*). – *A. latifolia* Wall.: INDIA (*BFA 10837*, *RBHw*). – *A. leiocarpus* Guill. & Perr.: SUDAN (*FHOw 2397*): ETHIOPIA, *H–7–69–22* (*ex RTIw*); NIGERIA, *Marsen s.n.* (*ex K–Jw*), *FHI 14178*$^+$ (= *FPRL 23123*). — *A. pendula* Edgw.: INDIA, *Gamble P 454* (*ex K–Jw*). — *A. sericea* Brandis: INDIA, *C. 4847*$^+$ (*ex K–Jw*).

Small to large trees, up to 30 m. Savannas and open forests, sometimes very dry.

Growth rings faint or distinct. *Vessels* diffuse, sometimes tending to form an oblique pattern, (7–)11–92(–109)/mm^2, solitary and in radial multiples of 2–4(–6), of up to 10 in *A. latifolia*, the multiples often including or terminating with some narrow vessels or even entirely consisting of narrow elements, 25–70% solitary, round to oval, tangential diameter (19–)43–125(–160) μm, radial diameter up to 240 μm, walls 3–6 μm thick. Vessel member length (160–)270–480(–680) μm. Perforations simple in horizontal to oblique end walls. Inter-vessel pits crowded, alternate, round to polygonal, 4–7 μm in diameter, with infrequent coalescent apertures in *A. latifolia*, *A. leiocarpus*, and *A. pendula*. Vestures of type B form 3. Vessel – parenchyma and vessel – ray pits more or less similar, but half-bordered and rarely unilaterally compound; vestures similar to those of the inter-vessel pits. Solid amorphous contents infrequent in the vessels of *Marsen s.n.* of *A. leiocarpus* and *A. pendula*. *Fibres* (550–) 820–1580(–1950) μm long, walls medium thick to very thick, with infrequent simple to minutely bordered pits (1–2 μm), mainly confined to the radial walls, infrequently to frequently septate in *A. latifolia*, *A. leiocarpus*, and *A. pendula*, rarely gelatinous. *Parenchyma* paratracheal, scanty, vasicentric, aliform, and confluent as well as very scantily diffuse and occasionally with thin, interrupted, narrow marginal bands. All or most of these types present within single transverse sections. Parenchyma abundant, and scanty paratracheal parenchyma therefore infrequent in *FHOw 2443* of *A. acuminata* and in *A. sericea*. Strands of (4–)5–7(–9) cells. *Rays* (9–)11–16(–17)/mm, mainly uniseriate, occasionally with a small biseriate portion, but with frequent bi- (and some tri-) seriate rays in *H–7–69–22* of *A. leiocarpus* and in *A sericea*, (1–)7–21(–52) cells high, composed of intermingled square and procumbent cells, rarely including some erect cells or with some erect marginal cells. Large solitary *crystals*, usually completely filling the cells, more or less isodiametric to elongate and with blunt or pointed ends, frequent in ray cells, infrequent in axial parenchyma. Crystalliferous ray cells often in radial series and/or enlarged. Granular and amorphous *contents* in rays and axial parenchyma. *Pith flecks* rarely present (*FHOw 1411* of *A. acuminata* and *A. sericea*).

Table 1. Quantitative characters of Anogeissus

Species and/or specimen	1	2	3	4	5	7	8
A. acuminata							
FHOw 1411	7–11–15	70	93–125–160	240	240–390–530	1080–1400–1780	8
FHOw 2443	11–16–25	50	85–117–160	238	250–430–570	1080–1470–1800	m
A. latifolia	43–44–46	35	65–90–105	133	280–480–680	1080–1580–1950	m
A. leiocarpus							
FHOw 2397	57–72–89	25	27–64–92	118	160–290–470	590–875–1130	6
H–7–69–22	21–27–32	35	42–54–80	115	170–270–410	610–820–990	7
Marsen s.n.	35–55–81	40	53–76–101	118	220–350–440	700–1120–1300	4
FHI 14178	29–32–40	50	40–85–118	158	260–370–440	550–1440–1670	m
A. pendula	72–92–109	55	19–43–68	93	300–400–510	950–1120–1330	m
A. sericea	18–23–29	40	47–69–90	135	160–270–420	690–960–1290	7

Explanation of the figures in the tables
1. Vessel frequency/mm^2
2. Percentage of solitary vessels
3. Tangential vessel diameter in μm
4. Maximum radial vessel diameter in μm
5. Vessel member length in μm
6. Length of very narrow vessels mixed with vascular tracheids, in μm
7. Fibre length in μm
8. m = mature sample (Ø > 10 cm); a figure indicates the diameter of the sample in cm

Note. Data from Abbate (1970), Foxworthy (1907), Holtermann (1893), Howard (1948), Normand (1960), Pearson & Brown (1932), Rao & Purkayastha (1972), and Solereder (1885) agree well with the above description.

The variation in vessel frequency of the species of this genus corresponds well with their ecological preferences (see also the chapter on ecological considerations). The wood anatomical characters of *Anogeissus* overlap with those of *Terminalia* and many other genera of the *Terminaliinae*. *Anogeissus* can, however, be recognized by its type of vestures (only also present in *Buchenavia* and *Terminalia p.p.*) and by the occurrence of very large crystals in the stronly enlarged ray cells (not present in the genera and species referred to above).

BUCHENAVIA Eichl.

Table 2; Fig. 4: d, e; Plate 2: 9; 8: 56.

Material studied. *B. acuminata* Exell & Stace: BRAZIL, *Krukoff 6916* (=Uw 8044). *B. fanshawei* Mag. & Exell: GUYANA, *Cons. of For. 3580* (=*FHOw 17848*). – *B. huberi* Ducke: BRAZIL, *Krukoff* 6472^+ (=*Uw 7754*). — *B. kleinii* Exell: BRAZIL, *Lindeman & de Haas* 2355^+ (=*Uw 13699*). — *B. oxycarpa* (Mart.) Eichl.: BRAZIL, (*FPRL B 6733*).

Fom literature (see note): *B. capitata* Eichl.

Shrubs, small trees or large trees up to 50 m; in wet lowland forests and upland rain forests.

Growth rings faint to distinct. *Vessels* diffuse, (3–)5–37(–45)/mm^2, solitary and in radial muliples of 2–4 (in *B. kleinii* multiples of up to 8), often including some narrow vessels, 9–80% solitary, round to oval in transverse section, tangential diameter (40–)74–192(–270) µm, radial diameter up to 340 µm, walls 3–6 µm thick. Vessel member length (170–)340–620(–890) µm. Perforations simple in horizontal to oblique and walls. Inter-vessel pits alternate, crowded, round to polygonal, 6–8 µm in diameter but in *B. acuminata* 9–12 µm, infrequently elongate (up to 19 µm) and slightly curved, apertures frequently coalescent in *B. huberi*. Vestures of type B, form 3. Vessel–ray and vessel–parenchyma pits more or less similar, but half-bordered and with wider apertures. Pits frequently almost simple and unilaterally compount in *B. huberi* and *B. oxycarpa*, rarely so in *B. acuminata*. Vestures similar to those of the inter-vessel pits but simple pits often without vestures. Delicate wall thickenings, forming a horizontal to oblique, striated pattern, present on the vessel walls and the walls of the axial parenchyma of *B. huberi*. Solid amorphous contents infrequent in the vessels of *B. kleinii*. Thin-walled tyloses infrequent in the vessels of *B. fanshawei*. *Fibres* (750–)1000–1560(–2050) µm long, walls thin to thick in *B. fanshawei* and *B. kleinii*, medium thick to very thick in the other species, with few simple or minutely bordered pits (1–2 µm), mainly confined to the radial walls. Fibres frequently (*B. acuminata* and *B. fanshawei*) or infrequently septate; frequently gelatinous in *B. oxycarpa*. *Parenchyma* predominantly paratracheal (including some marginal), but also scantily diffuse. Paratracheal parenchyma vasicentric to aliform and confluent in *B. kleinii*, aliform and confluent in *B. fanshawei* and *B. huberi*, and aliform to banded in *B. acuminata* and *B. oxycarpa*. Marginal bands of 1—2(–4) cells wide continuous with paratracheal parenchyma; in some species (notably *B. kleinii* and *B. oxycarpa*) not well developed and often interrupted. Strands of (2–)3–5(–6) cells. *Rays* (5–)6–13(–14)/mm, uniseriate, in *B. huberi* infrequently with a biseriate portion; rays (2–)5–9(–21) cells high, composed of square and procumbent cells and with square to erect marginals. Rhomboidal to elongated *crystals* not filling the cell-lumen frequent in the ray cells of *B. huberi*, infrequent in those of *B. fanshawei* and *B. oxycarpa*, rare in the axial parenchyma of *B. oxycarpa*; large solitary crystals, completely filling the cells, more or less isodiametric or elongate, mostly with blunt ends, frequent in chambered axial parenchyma of *B. kleinii*. Crystals not observed in *B. acuminata*. More or less globular *silica grains* with a granular surface (17–28 μm) frequent in the axial parenchyma of *B. acuminata* and *B. fanshawei*, infrequent in the rays of *B. acuminata*. *Vertical canals* arranged in a concentric ring, probably of traumatic origin noted in *B. kleinii*. Granular *contents* frequent in rays and axial parenchyma.

Table 2. Quantitative characters of Buchenavia

(For explanation of the figures see table 1, Anogeissus)

Species and/or specimen	1	2	3	4	5	7	8
B. acuminata	5– 7–10	67	113–145–165	207	360–570–780	1325–1530–2050	m
B. fanshawei	3– 5– 6	80	83–192–270	340	380–620–890	1300–1560–2000	m
B. huberi	5– 8–10	30	85–135–187	232	300–490–760	1050–1330–1700	m
B. kleinii	32–27–45	10	53– 74–100	120	170–340–710	750–1000–1425	m
B. oxycarpa	9–16–19	45	40– 74–105	165	330–500–730	900–1210–1500	m

Note. *B. capitata* Eichl. was studied by Benoist (1931). He recorded 4–8 vessels/mm^2, with a diameter up to 175 μm, parenchyma aliform, confluent and terminal (= marginal), rays uniseriate. These observations agree with those on slides studied from the Kew slide collection (*Yale 1357 & 16308*) which also showed frequently septate, thin-walled fibres, but marginal parenchyma was only scantily present; crystals or silica grains were not observed.

Silica grains were also observed in the axial parenchyma of a sample of *B. acuminata* studied from the Utrecht slide collection (*A. C. Smith 3033*). Ter Welle (1976) did not observe silica in three species of *Buchenavia* (*B. capitata*, *B. macrophylla*, and *B. oxycarpa*, private communication).

The presence of intercellular canals of the vertical traumatic type is also reported by Metcalfe & Chalk (1950).

On wood anatomical characters, all species mentioned in the description and the note can easily be separated from each other.

BUCIDA L.

Fig. 3: a, b.

Material studied. *B. buceras* L.: CENTRAL AMERICA, (*MADw 23133*$^+$). — *B. macrostachya* Standl.: MEXICO, (*FPRL 28162*).

Shrubs or small to medium-sized trees.

Growth rings faint. *Vessels* diffuse, (8–)12(–14)/mm^2 in *B. buceras*, in *B. macrostachya* (34–)42(–46)/mm^2. Solitary and in radial multiples of 2–3(–5) in *B. buceras*, of 2–6(–13) in *B. macrostachya*, multiples infrequently including some very narrow vessels, 50% solitary in *B. buceras*, 10% solitary in *B. macrostachya*, round to oval in transverse section, tangential diameter (68 –)102(– 155) μm in *B. buceras*, (38 –)97(– 128) μm in *B. macrostachya*, radial diameter up to 178 μm thick. Vessel member length (270 –)450(– 810) μm in *B. buceras*, in *B. macrostachya* (280 –)390(– 570) μm. Inter-vessel pits crowded, alternate, round to polygonal, 8 – 11 μm in diameter, apertures very rarely coalescent in *B. buceras*, frequently so in *B. macrostachya*. Vestures of type B, form 2. Vessel – ray and vessel – parenchyma pits ± similar, but half-bordered and rarely unilaterally compound, apertures coalescent in *B. macrostachya*. Vestures similar to those of the inter-vessel pits, but large warts/vestures also present on the apertures. Vessel walls warted. Thin-walled tyloses and solid amorphous contents observed in *B. macrostachya*. *Fibres* (1300 –)1790(– 2180) μm long in *B. bucida*, (360 –) 1120 (– 1330) μm long in *B. macrostachya*, thick-walled, walls with few simple or minutely bordered pits (1 – 2 μm), mainly confined to the radial walls. *Parenchyma* paratracheal and marginal; paratracheal parenchyma aliform to confluent in *B. buceras*, in *B. macrostachya* more scanty, vasicentric to aliform; marginal parenchyma in interrupted bands, 1 – 2 cells wide, partly connected with paratracheal parenchyma. *Rays* 1 – 3-seriate, (12 –)14(– 15)/mm in *B. bucida*, (8 –)9(– 10)/mm in *B. macrostachya*, multiseriate rays composed of procumbent cells but including some crystalliferous, square and erect cells, uniseriate, rays (1 –)3(– 7) cells high, composed of procumbent and infrequent erect marginal cells. Large, solitary *crystals*, completely filling the cells, elongated or isodiametric, usually with blunt ends, frequently present in the rays; crystals of the same type also present in the chambered axial parenchyma of *B. buceras*, rarely so in *B. macrostachya*. Crystalliferous ray cells in radial series and enlarged, in radial and tangential view giving an idioblast-like appearance; however, not extending beyond the outline of the ray in tangential view.

Note. The two species studied differ markedly from each other in general wood anatomical appearance. This is due to the different degrees of vessel grouping and abundance of paratracheal parenchyma. Data and figures presented by Kribs (1950) and Reyes (1938) agree well with the above description of *B. buceras*.

CALOPYXIS Tul.

Material studied. *C. malifolia* Baker: MADAGASCAR, *D'Alleizette s.n.*$^+$ (twig, ∅5 mm)

Shrubs

Secondary xylem of twig.

Growth rings distinct. *Vessels* diffuse, but the narrow band of wood of the latest growth ring strongly suggests a tendency to ring- or semi-ring-porosity, vessels of two distinct sizes; normal vessels solitary or associated with very narrow vessels or vascular tracheids, (23 –)25(– 29)/mm^2. Tangential diameter (35 –)52(– 72) μm, radial diameter up to 78 μm, walls 2 – 3 μm thick, very narrow vessels intermingled with *vascular tracheids*, if not in association with the vessels, in radial multiples of 2 – 4(– 9), tangential diameter 17 – 36 μm, radial diameter up to 45 μm. Vessel member length (180 –)350(– 530) μm, very narrow elements (339)440(– 610) μm long. Perforations simple in horizontal or oblique end walls. Inter-vessel pits crowded, alternate, round to polygonal, 5 – 7 μm in diameter, those of the narrow vessels and vascular tracheids sometimes elongate and up to 11 μm. Vestures of type B, intermediate between form 2 and 3. Vessel–ray and vessel–parenchyma pits similar but half-bordered, infrequently in a more or less alternate–opposite pattern, elongate and up to 19 μm, infrequently with slightly reduced borders. Vestures similar to those of the inter-vessel pits. Vessel walls with finely warted surfaces. *Fibres* (480–)590(–810) μm long, walls thin to very thin with simple or minutely bordered pits, mainly confined to the radial walls, septate, partly gelatinous. *Parenchyma* scanty paratracheal. Strands of (2—)5(–6) cells. *Rays* (13–)16(–17)/mm, uniseriate, rarely with a small biseriate portion, (2–)37(–66) cells high, composed of erect cells. *Radial vessels* frequent, radial vessel members similar to normal ray cells, pits to contiguous ray cells ± alternate 5–7 μm, vestured. *Pith flecks* infrequently present.

Note. Of this genus only very immature material was studied, and differentiating characters with the other genera of the *Combretinae* (to which subtribe this genus undoubtedly belongs because of the occurrence of radial vessels) can therefore not be presented.

CALYCOPTERIS Lam.

Fig. 2; Plate 5: 30; 6: 38; 8: 54.

Material studied. *C. floribunda* (Roxb.) Lam.: INDIA, *Ryan s.n.*+ (*ex K–Jw*).

Liana of 5–10 m; wet forests.

Growth rings distinct. Wood diffuse- to semi-ring-porous. *Vessels* of two distinct sizes; normal vessels (2–)3(–5)/mm^2, exclusively solitary or associated with narrow vessels and vascular tracheids, round to oval, tangential diameter (98–)155(–240) μm, radial diameter up to 330 μm, walls 2–4 μm; very narrow vessels intermingled with *vascular tracheids* if not in association with the vessels, forming clusters of 3–11 and radial multiples of 3–5(–8), the latter usually frequent on growth ring boundaries, tangential diameter (28–)46(–58) μm, radial diameter up to 71 μm. Vessel member length (300–)400(–500) μm; narrow elements (290–)495(–660) μm long. Perforations simple in horizontal to oblique end walls. Pits from vessels to narrow elements crowded, alternate, round to polygonal, 7–9 μm in diameter, pits between the narrow elements similar but also elongate (up to 16 μm). Vestures type B form 2. Vessel – ray and vessel–parenchyma pits ± similar, but half-bordered, apertures infrequently coalescent. Vestures similar to those of inter-vessel pits. Vessel walls with infrequent warts. Large axial strands of *phloem* oval to crescentiform or of irregular shape, usually tangentially flattened (foraminate type), frequent. *Fibres* (490–)665(–850) μm long, walls thin to medium thick with infrequent simple or minutely bordered pits (1–2 μm), mainly confined to the radial walls, frequently septate. *Parenchyma* scanty paratracheal, strands of 2–4 cells. *Rays* 11–12/mm, uniseriate, rarely with a small biseriate portion, composed of procumbent and infrequent square and erect, mainly marginal cells, (4–)25(–49) cells high; ray cells ± cubical in tangential view. *Radial vessels* frequent; radial vessel members similar to normal ray cells, pits to contiguous ray cells alternate, 5–8 μm, vestured. Radial strands of phloem present in some of the rays. Small and large clustered *crystals* frequent in the parenchyma of the axial strands of included phloem; large cluster also infrequent in wood rays.

Note. Hate (1911) presented some photographs of transverse sections of Calycopteris showing the included phloem; he did not record further wood anatomical details.

The wood of *Calycopteris* can be recognized from other *Combretinae* by the crescentiform islands of included phloem and the shape of the ray cells (*cf.* Plate 5/30; 6/38).

Calycopteris and one *Combretum* species (*C. edwardsii*) are the only lianas for which included phloem is recorded. This character is further present in *Guiera* and *Thiloa* and various species of *Combretum*, all with a non-climbing habit.

COMBRETUM Loefl.

Table 3, 4, 14; Fig. 3: d, e; 4: a, b, f; Plate 1: 6; 2: 10, 12; 6: 34 – 37; 8: 50, 51, 53, 55, 58 – 61.

Material studied. *C. celastroides* Engl. & Diels: E. Africa, *Schlieben 6113* (= *BFA 1915, RBHw*). — *C. collinum* Fresen: N. Rhodesia, *For. Dep. 486138*. – *C. collinum* subsp. *binderanum* (Kotschy) Okafor: Uganda, *Entebbe Herb. 1175* (= *FPRL 6718*); Tanzania, *Jefford, Juniper & Newbould 2182*$^+$ (*ex K – Jw*). – *C. collinum* subsp. *suluense* (Engl. & Diels) Okafor: Tanzania, *Cons. of For. 49* (= *FPRL 12147*). — *C. erythrophyllum* (Burch.) Sond.: S. Africa$^+$ (*ex K – Jw*) — *C. fragrans* F. Hoffm.: Sudan, (*FHOw 2385*$^+$). — *C. fruticosum* (Loefl.) Stuntz.: Brazil, *Reitz 23323*$^+$ (= *Uw 6985*). — *C. gallabatense* Schweinf.: Ethiopia, (*FPRL 29479*$^+$). — *C. imberbe* Wawra: S. Africa, (*FPRL 14810*), *TP 222 – 14* (*ex RTIw*), *MacGillivray s.n.* (= *R 936 – 401, SFCw*); S.W. Africa, *Walter 13* (= *BFA 6942, RBHw*). — *C. kraussii* Hoechst: S. Africa, *Pret. For. Prod. Inst. 472*$^+$ (= *BFA 322, RBHw*). – *C. molle* R. Br.: E. Africa, *Deutsch. O. Afrik. Gesellsch.* (= *BFA 1161, RBHw*); Rhodesia (*FPRL 19402*). — *C. nigricans* var. *elliottii* (Engl. & Diels) Aubrév.: Nigeria (*FHOw 14537*). — *C. pyramidatum* Desv.: Surinam, *Lindeman 1861* (= *Uw 1565*). — *C. rotundifolium* Rich.: Surinam, *Lindeman 1873*$^+$ (= *Uw 1574*). — *C. trifoliatum* Vent.: New Guinea. *Van Royen 4608*. — *C. zenkeri* Engl. & Diels: Cameroun, *Breteler 2792* (= *Uw 9412*).

Data on many other species are listed in table 4 or mentioned in the note.

Shrubs and small trees up to 12(– 33) m; also scandent shrubs and lianas Wooded grasslands, *Brachystegia* woodlands, deciduous thickets, rain forests.

Abbreviated generic wood anatomical description.

Growth rings faint to distinct, infrequently of wavy outline. *Vessels* diffuse, but wood infrequently ring-porous or tending to semi-ring-porous, vessels of two distinct sizes: normal vessels 3 – 40/mm^2, solitary, infrequently in radial multiples, average tangential diameter 64 – 302 μm; very narrow vessels intermingled with *vascular tracheids* in association with normal vessels or in clusters of up to 5, average tangential diameter 19 – 31 μm. Average vessel member length 200 – 440 μm. Perforations simple in horizontal to oblique end walls. Inter-vessel pits crowded, alternate, 5 – 7(– 13) μm, infrequently coalescent. Vestures of type B form 2, sometimes intermediate between form 2 and 3; walls and apertures infrequently with warts. Included axial *phloem* of the foraminate type or in concentric bands, present in part of the species. *Fibres* on average 610 – 1140 μm long, with thin to medium thick or very thick walls, and simple or minutely bordered pits (1 – 2 μm) more frequent on radial than on tangential walls, frequently or infrequently septate

Table 3. Quantitative characters of Combretum
(For explanation of the figures see table 1, Anogeissus)

Species and/or specimen	1	2	3	4	5	6	7	8
C. celastroides	32–45–60	95	52–164–328	415	160–290–420	260–380–520	750–1130–1330	7
C. collinum								
For Dept. 486138	2– 3– 5	100	60–165–223	308	170–350–520	280–420–510	1000–1140–1370	7
C. collinum subsp. *binderanum*								
Entebbe Herb 1157	2– 4– 5	100	78–155–225	274	250–340–450	320–410–470	950–1120–1300	m
Jefford et al.	3– 4– 5	100	73–119–159	201	130–270–400	320–440–460	690– 960–1230	m
C. collinum subsp. *suluense*	2– 4– 5	100	103–183–295	370	230–350–460	260–400–530	780–1120–1450	m
C. erythrophyllum	7–11–16	100	43– 64–120	138	240–360–470	140–370–470	600–1130–1440	m
C. fragrans	6– 8–12	95	38– 86–130	214	110–200–340	240–350–430	320– 680– 910	5
C. fruticosum	12–15–17	100	90–115–150	290	150–350–520	300–430–530	430– 680– 830	2
C. gallabatense	2– 5–17	50	43– 89–125	160	170–250–390	310–410–480	580– 700–1010	5
C. imberbe								
FPRL 14810	2– 3– 4	100	128–173–245	275	240–300–380	290–450–510	610– 850–1130	m
TP 222–14	3– 5– 8	100	86–126–166	223	130–310–430	260–310–330	710– 980–1390	m
MacGillivray s.n.	4– 4– 6	100	74–142–205	208	220–290–330	230–310–380	620– 940–1180	m
Walter 13	2– 4– 5	100	108–193–210	335	210–310–490	260–340–460	820– 950–1180	m
C. kraussii	1– 3– 5	100	53– 85–115	142	190–310–400	160–280–340	610– 780– 990	m
C. molle								
BFA 1161	5– 7– 8	85	48– 70–115	158	190–320–470	190–240–380	910–1230–1780	m
FPRL 19402	5– 7–17	95	102–135–228	260	210–330–430	370–410–460	725–1270–1450	m
C. nigricans var. *elliottii*	11–15–22	100	68–120–140	170	160–280–350	220–290–380	875– 950–1125	5
C. pyramidatum	6–11–14	100	42–126–199	252	290–380–480	380–410–480	660– 860–1260	2
C. rotundifolium	12–15–18	100	63–113–187	230				1.5
C. trifoliatum	8– 9–11	100	83–199–260	420	240–350–500	340–430–510	430– 610– 920	8
C. zenkeri	4– 5– 6	100	140–281–360	510	250–370–470	290–410–480	625– 815–1120	4

or all non-septate, frequently gelatinous. *Parenchyma* mainly paratracheal, ranging from scanty vasicentric to abundant and confluent to banded, partly also diffuse. *Rays* heterogeneous III to homogeneous, 1–3-seriate, composed of square to procumbent and infrequent erect marginal cells. *Radial vessels* frequent or infrequent, sometimes rare. Radial *phloem* strands present or absent. *Crystals* of various types and frequencies, rhomboidal to elongate or as large solitary crystals or druses in idioblasts present in rays and/or axial parenchyma, sometimes absent. Sometimes present in fibres of juvenile wood. *Pith flecks* present or absent.

Detailed wood anatomical description

Growth rings faint or distinct, of wavy outline in *C. celastroides*. *Vessels* diffuse in most species, but wood ring-porous in *C. celastroides*, tending to semi-ring-porous in *C. erythrophyllum*, *C. gallabatense*, and *C. nigricans* var. *elliottii*, vessels of two distinct sizes: normal vessels, (1–)3–40(–52)/mm^2, solitary or solitary and in radial multiples, but frequently associated with very narrow vessels and vascular tracheids, 30–100% of the normal vessels solitary, round to oval, tangential diameter (38–)64–302(–360) μm, radial diameter up to 510 μm, walls 3–7(–10) μm thick; very narrow vessels intermingled with *vascular tracheids*, if not in association with vessels, forming clusters of up to 5 (but up to 15 in *C. gallabatense* and *C. zenkeri*) or radial multiples of up to 3(–5), the latter usually frequent on growth ring boundaries, but very infrequent in *C. fruticosum*, *C. pyramidatum*, *C. rotundifolium*, *C. trifoliatum* and *C. zenkeri*, tangential diameter (13–)19–31(–42) μm, radial diameter up to 51 μm. Vessel member length (130–)200–380(–520) μm; narrow elements (140–)240–440(–530) μm long. Perforations simple in horizontal to oblique end walls. Inter-vessel pits crowded, alternate, round to polygonal, 5–7 μm in diameter, those of the very narrow elements infrequently elongate and up to 13 μm, apertures coalescent in *C. molle*, infrequently so in *C. kraussii* and *C. pyramidatum*. Vestures of type B, form 2, but more or less intermediate between form 2 and 3 in the very narrow elements, apertures with infrequent warts/vestures in *C. kraussii*. Vessel–ray and vessel–parechyma pits more or less similar, but half-bordered, infrequently elongate (up to 16 μm), apertures infrequently coalescent in *FPRL 14810* of *C. imberbe* and in *C. gallabatense*, occasionally with reduced borders in *FPRL 14810* of *C. imberbe* and in *C. molle*, vessel–ray pits sometimes arranged in distinct horizontal rows. *Vestures* similar to those of the inter-vessel pits. Vessel walls warted in *C. kraussii*. Solid amorphous contents infrequent in the vessels of *C. celastroides*, *C. collinum* subsp. *suluense*, *C. erythrophyllum*, *C. imberbe* (*TP 222–14*), and *C. pyramidatum*. Axial strands of included *phloem* (foraminate type) present in *C. erythrophyllum*, *C. fragrans*, *C. gallabatense*, *C. molle*, and *C. nigricans* var. *elliottii*; in *C. kraussii* included phloem in concentric bands. *Fibres* (320–)610–1140(–1440) μm long, walls thick to very thick in most species, but thin in *C. fruticosum* and *C. trifoliatum*, thin to medium thick in *C. celastroides*, *C. fragrans*, *C. imberbe*, *C. molle* and *C. pyramidatum*, with simple or minutely bordered pits (1–3 μm), more frequent on the radial than on the tangential walls; septate in *C. celastroides*, *C. collinum* subsp. *suluense*, *C. collinum* subsp. *binderanum p.p.* (*Entebbe Herb. 1175*), *C. fruticosum*, *C. trifoliatum*, and *C. zenkeri*, only partly septate in *C. collinum* subsp. *binderanum p.p.* (Jefford et al.), *C. fragrans* and *C. pyramidatum*; short, thin-walled, septate fibres, in length more or less similar to the axial parenchyma strands, infrequent in *C.*

fragrans, where fibres are bordering the axial parenchyma; septate vascular tracheids rare in *C. collinum* subsp. *binderanum p.p.* (*Entebbe Herb. 1175*); frequently gelatinous; solid to granular contents observed in *C. imberbe*, *C. rotundifolium* , and *C. trifoliatum*. *Parenchyma* paratracheal, marginal and diffuse or diffuse in small aggregates; scanty in *C. fruticosum*, *C. rotundifolium*, and *C. trifoliatum*, abundant in *C. collinum*, *C. fragrans*, and *C. gallabatense;* paratracheal parenchyma predominantly vasicentric-aliform in *TP 222–14*, *FPRL 14810*, and *McGillavray s.n.* of *C. imberbe* and *C. zenkeri*, predominantly aliform-confluent in *C. erythrophyllum* (sometimes in a more or less oblique pattern), *Walter 13* of *C. imberbe*, *C. kraussii*, *C. molle*, *C. nigricans* var. *elliottii*, and *C. pyramidatum* (first formed secondary xylem excepted), predominantly confluent and banded in *C. celastroides*, *C. collinum s.l.* and *C. gallabatense;* bands usually 3 – 6 cells wide, but up to 11 cells wide in *Jefford et al.* of *C. collinum* subsp. *binderanum* and *C. celastroides*, of up to 17 cells wide in *C. collinum s.s.;* narrow (1 – 3 cells wide), often interrupted bands of marginal parenchyma present in *C. celastroides*, *C. collinum*, *C. gallabatense*, *Walker 13* and *McGillavry s.n.* of *C. imberbe*, *C. molle*, and *C. nigricans* var. *elliottii*: diffuse parenchyma comparatively frequent in *C. collinum p.p.* (*For. Dep. 486138*) and *C. erythrophyllum*, in a more or less reticulate pattern in *C. nigricans* var. *elliottii*. Strands of (2 –)4 – 6(– 9) cells; fusiform septate parenchyma cells infrequent in *C. fragrans*, *C. kraussii* and *C. molle* where parenchyma is bordering on the fibres; in *C. celastroides* one cell of the axial parenchyma strands infrequently differentiated into a tracheid with one perforation. *Rays* (9 –)10 – 19(– 21) μm, uniseriate, rarely with a small biseriate portion, but uni- and biseriate in *C. collinum* (*For. Dep. 486138*), *C. collinum* subsp. *binderanum*, and *C. imberbe p.p.* (*FPRL 14810*), uni- to triseriate in the remaining samples of *C. imberbe;* rays composed of square and procumbent cells and erect marginal cells, but sometimes also including some erect cells, especially in the more juvenile samples; in the juvenile wood of *C. fruticosum* composed of erect cells mainly; (2 –)7 – 25(– 39) cells high, in *C. fruticosum* much higher; *radial vessels* frequent or infrequent, rare in *C. fragrans*, radial vessel members similar to normal ray cells, pits from radial vessels to contiguous ray cells and axial parenchyma alternate, slightly smaller than inter-vessel pits, vestured; perforated ray cells infrequent in *C. celastroides* and *C. imberbe p.p.* (*FPRL 14810*); radial phloem strands, sometimes connected with the axial phloem strands, infrequent in the rays of *C. erythrophyllum*, *C. fragrans*, *C. kraussii*, *C. molle p.p.* (*D.O.A.G. s.n.*), and *C. nigricans* var. *elliottii*. Idioblasts containing one large solitary *crystal* each infrequent in the axial parenchyma of *C. celastroides*, frequent in the rays of *C. celastroides*, *C. erythrophyllum*, *C. molle*, *C. nigricans* var. *elliottii*, *C. pyramidatum* and *C. rotundifolium;* rhomboidal to elongated crystals more or less completely filling the cells, frequent in the rays of *C. erythrophyllum*, *C. imberbe*, and *C. molle* and in the axial parenchyma of *C. erythrophyllum* and *C. rotundifolium;* fragmented crystals frequent in the axial parenchyma of *C. erythrophyllum;* small rhomboidal crystals frequent in the chambered axial parenchyma of *C. molle* (several crystals per chamber); idioblasts containing large druses frequent in the axial parenchyma of *C. collinum* subsp. *binderanum*. smaller druses less frequent in the rays of this subspecies; large clustered crystals frequent in the axial parenchyma and infrequent in the rays of *C. gallabatense;* small clustered crystals infrequent in the axial parenchyma of *C. collinum* subsp. *binderanum*, abundant in the parenchyma of the axial strands of included phloem; clustered crystals mixed with solitary crystals present in the diffuse parenchyma strands of *C. fruticosum* and in the chambered fibres of the first formed secondary xylem. Crystals not observed in the secondary xylem of *C. collinum p.p* (*For. Dep. 486138*), *C. collinum* subsp. *suluense*, *C. fragrans*, *C. kraussii*, *C. trifoliatum*, and *C. zenkeri*. Granular to amorphous *contents* often present in ray cells and axial parenchyma. *Pith flecks* present in *C. collinum* subsp. *binderanum (Entebbe Herb. 1157)*, *C. erythrophyllum*, *C. gallabatense*, *C. imberbe (McGillavray s.n., Walter 13, TP 222 – 14)*, *C. molle (FPRL 19402)*, *C. trifoliatum*, and *C. zenkeri*.

Note. Data on the presence or absence of included phloem, obtained from the literature (see introduction) and from the FHOw, FPRL, Uw, and Kew slide collections are listed in table 4. Observations on small twigs obtained from the Rijksherbarium collection are also recorded in this table. Synonyms are not listed. It appears, that the presence of included phloem is restricted to the African species of subgenus *Combretum* (though not present in all species) and that it is absent from all liana species except one (*C. edwardsii*). Schenck (1893) mentioned that Holtermann had found included phloem in Indian *Combretum* species, but Holtermann himself (1893) recorded this character for African species only. Holtermann also recorded distinctly bordered pits in the fibres of *C. decandrum*. A section taken from a twig (*Griffith s.n., E. Indies*) showed simple pits only; Holtermann probably studied a wrongly identified sample, or he mistook the very narrow elements and vascular tracheids for fibres. He also reported crystals in the fibres of *C. extensum* (= *C. latifolium* Bl.) and *C. truncatum* Welw. (*C. imberbe* Wawra), probably in immature samples (like *C. fruticosum* studied by me); a mature sample of *C. fruticosum*, studied from the Uw-slide collection (*A. C. Smith 3105 = Uw 21627*) had no crystals in the fibres. Data provided by Fasolo (1939; *C. triquetum* (= *C. molle*); also illustrating the 'normal' vessels and the very narrow elements mixed with vascular tracheids), by Barreto (1967; *C. molle*), Abbate (1970; *C. gallabatense*), and Jutte (1959; *C. trifoliatum*) agree well with the above description. Quantitative data given by Rao (1972; vessel frequencies excepted, these are not reliable) on *C. aculeatum*, *C. apetalum* Wall., *Poivrea coccinea* = *C. coccinea* (Sonn.) Lamk., and by Obaton (1960) on *C. dolichopetalum* Engl. & Diels are within the range found by me. Idioblasts, containing a large solitary crystal each, are illustrated by Chattaway (1956) and Scurfield *et al.* (1973) for *C. leucanthemum* Engl. & Diels (= *C. nigricans* var. *elliottii*). Scurfield *et al.* also illustrated the large crystals in the rays of *C. verticillatum* Engl. & Diels (= *C. collinum* subsp. *hypopilium* (Diels) Okafor). They did not mention the idioblasts with clustered crystals, so characteristic for subsp. *binderanum*. *C. lamprocarpum* Diels (= probably *C. collinum* subsp. *geitonophyllum*; Okafor, 1967) studied from the FHOw slide collection also had idioblasts with clustered crystals in the axial parenchyma. A more elaborate investigation on the occurrence of this crystal complement may contribute to a better understanding of the relationship and/or taxonomic status of the species and subspecies of the *C. collinum* complex. The occurrence of septate fibres and the ray type may also appear to be valuable characters. When surveying twigs on the occurrence of included phloem, semi-ringporosity was observed in *C. grandieri* Baill. Record (1936) also recorded ringporous woods for *Combretum* but he did not mention any species names.

Obaton (1960) mentioned that in *C. dolichopetalum* septate fibres replaced the paratracheal parenchyma and were arranged in a confluent pattern. Similar features were not observed in the *Combretum* species studied by me. However, in *C. fragrans* (septate fibres bordering the paratracheal parenchyma and of the same length as the parenchyma strands) and in *C. kraussii* (septate, fusisorm parenchyma) a more or less intermediate situation in the replacement of parenchyma by fibres was found.

Table 4. Geographic distribution, habit, and occurrence of included phloem in species of Combretum.

subgenus COMBRETUM	this paper	literature	twigs 1)	Africa	Asia	America	shrub	tree	scandent	liana	included phloem
acuminatum Roxb.			×		As				○		–
acutifolium Exell		×		Af					○	○	–
apiculatum Sond.		×	×	Af			○	○			+
assimile Eichl..			×			Am				○	–
caffrum Kuntze		×		Af			○	○			+
capituliflorum Fenzl.			×	Af					○		–
celastroides Engl. & Diels	×	×		Af			○	○	○		–
collinum Fresen	×	×		Af			○	○			–
cuspidatum Planch.			×	Af						○	–
duarteanum Cambess.			×			Am				○	–
edwardsii Exell		×		Af					○	○	+
engleri Schinz		×		Af			○	○			+
erythrophyllum Sond.	×	×		Af					○		+
fragrans Hoffm.	×			Af				○			+
fruticosum Stuntz.	×		×			Am				○	–
gallabatense Schweinf.	×	×		Af				○			+
glutinosum Guill. & Perr.		×		Af				○			+
hartmannianum Schweinf.		×		Af				○			+
heroense Schinz		×		Af			○	○			–
illairii Engl.			×	Af			○		○	○	–
imberbe Wawra	×	×		Af			○	○			–
kraussii Hochst.	×	×		Af			○	○			+
lamprocarpum Diels		×		Af			○	○			–
lepidotum Rich.		×		Af				○			+
micranthum Don		×		Af			○				+
moggii Exell		×		Af			○	○			+
molle R. Br.	×	×		Af				○			+
nelsonii Dümmer		×		Af			○	○			+
nigricans Aubrév.	×			Af				○			+
padoides Engl. & Diels		×		Af				○	○		–
pyramidatum Desv.	×					Am				○	–
rotundifolium Rich.	×					Am				○	–
salicifolium Engl.	×			Af				○			+
woodii Dümmer		×		Af			○	○			+
yunnanense Exell			×		As				○	○	–
zeyheri Sond.		×		Af			○	○			–

Subgenus CACOUCIA	this paper	literature	twigs¹)	Africa	Asia	America	shrub	tree	scandent	liana	included phloem
aculeatum Vent.		×		Af					○		–
bracteosum Brandis		×		Af			○				–
comosum Don		×		Af					○		–
decandrum Roxb.		×	×		As					○	–
dolichopetalum Engl. & Diels		×		Af					○	○	–
grandidieri Baill.			×	Af						○	–
latifolium Don		×			As					○	–
mossambicense Engl.		×		Af			○	○	○		–
paniculatum Vent.		×		Af					○	○	–
racemosum Beauv.		×		Af					○	○	–
sericeum Don			×	Af			○				–
trifoliatum Vent.		×			As					○	–
zenkeri Engl. & Diels		×		Af					○		–
subgenus APETALANTHUM											
apetalum Wall.			×		As				○	○	–

1) From transverse sections of twigs of herbarium material,
2) + = present; – = absent.

CONOCARPUS L.

Table 5.

Material studied. *C. erectus* L.: FLORIDA, *S. 1477*⁺ (*K–Jw*), *Curtiss s.n.* (*K–Jw*). — *C. lancifolius* Engl.: SUDAN, *Herb. Karthoum VW 16*⁺ (*= BFA 12919, RB Hw*).

Shrub or small erect tree up to 15–20 m. *C. erectus* grows in the littoral formations along the East American and W. African shores; *C. lancifolius* is restricted to the coastal plains of the Red Sea.

Growth rings more or less distinct in *C. erectus*, indistinct in *C. lancifolius*. *Vessels* diffuse, (10–)11–28(–33)/mm², solitary and in radial multiples of 2–3(–5), 60–75% solitary, round to oval in transverse section, tangential diameter (38–)83–92(–120) μm, radial diameter up to 135 μm. Vessel member length (150–)330–540(–770) μm. Perforations simple in horizontal to oblique end walls. Inter-vessel pits crowded, alternate, round to polygonal, 5–8 μm in diameter, apertures infrequently coalescent in *S. 1477* of *C. erectus*. Vestures type B, intermediate between form 2 & 3. Vessel – ray and vessel – parenchyma pits more or less similar, but half-bordered and slightly larger, 5–10 μm, apertures infrequently coalescent in *S. 1477* of *C. erectus*, vessel–parenchyma pits infrequently elongate and up to 26 μm, vessel pits to the procumbent raycells often in distinct horizontal lines. Vestures similar to those of the inter-vessel pits. Solid amorphous contents infrequent in the vessels, but absent from *S. 1477* of *C. erectus*. *Fibres* (490–)830–980(–1240) μm long, walls thin to thick, but thick to very thick in *Curtiss s.n.* of *C. erectus*, with simple or minutely bordered pits (1–3 μm) frequent on the radial walls, frequently septate in *S. 1477* of *C. erectus;* very rarely septate in the other samples. *Parenchyma* paratracheal and infrequently diffuse, abundant in

C. erectus, scarce in *C. lancifolius*; in *C. erectus* paratracheal parenchyma confluent and irregularly banded (bands 3–5 cells wide), completely embedding the vessels, more abundant and with a more or less marginal appearance on growth ring boundaries; in *C. lancifolius* parenchyma aliform, rarely confluent, and scantily diffuse. Strands of (3—)4—5(—8) cells. *Rays* (5—)7(—9)/mm in *C. erectus*, uniseriate, infrequently with a small biseriate portion; (7–)11(–14)/mm in *C. lancifolius*, uni- and biseriate rays ± equally numerous; rays composed of intermingled erect to procumbent cells, (2–)5–10(–24) cells high. Large solitary *crystals*, usually completely filling the cells, isodiametric to elongate, frequent in the rays, also infrequent in the axial parenchyma of *C. lancifolius* (and often fragmented); crystalliferous ray cells in short radial series, enlarged, but in tangential view hardly extending beyond the outline of the normal ray cells.

Note. The two species are different from each other in the abundance of the axial parenchyma, the ray width and the vessel frequency. The occurrence of distinct growth ring boundaries must be very variable in *C. erectus*: Tomlinson & Craighead (1972) reported them to be absent, whilst one of the samples used for this study (*Curtiss s.n.*) showed marked growth rings and the other sample more vague ones.

Table 5. Quantitative characters of Conocarpus.
(For explanation of the figures see table 1, Anogeissus).

Species and/or specimen	1	2	3	4	5	7
C. erectus						
S. 1147	17–25–33	75	67–83–100	113	180–330–480	650–840–1020
Curtiss s.n.	25–28–33	60	38–92–120	135	340–540–770	720–980–2240
C. lancifolius	10–11–14	75	45–86–123	135	150–340–530	490–830–1180

FINETIA Gagnep.

Material studied. *F. rivularis* Gagnep.: THAILAND, *Swat Mahapol s.n.*$^{+}$ (twig, ∅4 mm)

Tree of 5–15 m along rivers.

Secondary xylem of twig.

Growth rings faint to distinct. *Vessels* diffuse, (73–)85(–92)/mm^2, solitary and in radial multiples of 2–3(–6), 55% solitary, round to oval in transverse section, tangential diameter (29–)40(–57) μm, radial diameter up to 65 μm, inter-vessel walls up to 6 μm. Vessel member length (230–)330(–420) μm. Perforations simple in horizontal to oblique end walls. Inter-vessel pits crowded, alternate, round to polygonal, 4–5 μm in diameter, infrequently elongated up to 8 μm. Vestures of type B form 2. Vessel–ray and vessel–parenchyma pits more or less similar, but half-bordered, the latter infrequently elongate and up to 13 μm and also infrequently diffuse; vestured but not studied with SEM. *Fibres* (530–)750(–900) μm, walls of medium thickness with simple or minutely bordered pits (1–2 μm) frequent on both radial and tangential walls; septate; gelatinous fibres in more or less concentric rings. *Parenchyma* paratracheal, scantily aliform, or confluent, wings of 1 – 3 cells wide. Strands of (2 –)4(– 5) cells. *Rays* 16 – 17/mm, uniseriate, very rarely with a small biseriate portion, composed of erect to procumbent cells, (3 –)17(– 29) cells high. Large solitary *crystals* usually completely filling the cells, more or less isodiametric to elongate, frequent in ray cells, crystalliferous ray cells in radial series and enlarged, in tangential section slightly extending beyond the outline of the non-crystalliferous ray cells. *Pith flecks* infrequently present.

Note. Exell & Stace (1966) regarded this species as a separate monotypic genus, but Lecomte (1969) included it in *Anogeissus* under the name *A. rivularis* (Gagnep.) Lecomte. Of *Finetia* only juvenile wood has been studied, of *Anogeissus* only mature wood, and a complete comparison of wood anatomical characters can therefore not be made. The two genera show, however, a marked difference in type of vesturing. *Anogeissus* has the, in this family, infrequent form 3 of the type B, whilst *Finetia* has type B. form 2. The type of vesturing is often constant for a particular pit type (see also chapter on vestured pits), and the difference found here may be used to support Exell & Stace's view point. Similarities as for instance ray type are also found between these and other distinct genera and can therefore not be used as an argument to reduce *Finetia* to *Anogeissus*.

GUIERA Juss.

Plate 5: 33; 6: 39.

Material studied. *G. senegalensis* Lam.: NIGER, *A. Mariaux 508* (= *CTFT 15422*), *A. Mariaux 515*† (= *CTFT 14529*).

Small shrub of sandy wastes and semi-desert areas.

Growth rings faint. *Vessels* diffuse, of two distinct sizes; large vessels (21 –)23 & 25(– 27)/mm^2, exclusively solitary or associated with narrow vessels and vascular tracheids, round to oval in transverse section, tangential diameter (37 –)57 & 62(– 82) μm, radial diameter up to 125 μm, very narrow vessels intermingled with *vascular tracheids*, if not in association with the vessels, in clusters of up to 12 or in radial multiples of up to 5, multiples frequent on growth ring boundaries; in *Mariaux 508* in very large clusters connecting 2 or 3 large vessels, tangential diameter (19 –)22 & 27(– 36) μm, radial diameter up to 51 μm; walls of all elements 2 – 5 μm thick. Vessel member length (130 –)180 & 190(– 260) μm, very narrow elements (140 –)200 & 210(– 270) μm. Perforations simple in horizontal to oblique end walls. Pits from vessels to narrow elements crowded, alternate, round to polygonal, 5 – 8 μm in diameter, pits between narrow elements also elongate (up to 17 μm). Vestures of type B form 2. Vessel – ray and vessel – parenchyma pits ± similar but half-bordered. Vestures similar to those of the inter – vessel pits, but vesture-like warts present on the apertures. Vessel walls warted. Axial strands of included *phloem* (foraminate type) frequent. *Fibres* (310 –)500 & 520(– 660) μm long, walls medium thick to very thick with simple or minutely bordered pits (1 – 3 μm), mainly confined to the radial walls, fibres bordering on vessel elements with more frequent pits, fibres frequently gelatinous in *Mariaux 515*. *Parenchyma* scanty paratracheal, also very scantily diffuse. Strands of 1 – 3 cells. *Rays* (7 –)9 & 10(– 12)/mm, uni- and biseriate, rarely triseriate; multiseriate rays composed of procumbent cells mainly, but also containing some erect marginals, (80–)160–175(–330) μm high, uniseriate rays 2–4/mm, composed of erect, square or infrequent procumbent cells, (1–)2 & 3(–6) cells high. *Radial vessels* frequent, radial vessel members similar to the normal ray cells, pits to contiguous ray cells ± alternate, 5–7 μm, vestured. Radial strands of phloem present in the multiseriate rays. Large idioblasts containing a solitary *crystal* each frequent in the rays. In *Mariaux 508*, together with more than one per cell, infrequent in the axial parenchyma. *Pith flecks* present in *Mariaux 508.*

Note. *Guiera* grows under very dry conditions, which is reflected in some of the wood anatomical characters. Following the tendency that is commonly found (cf. Carlquist, 1975; Baas 1976) *Guiera* has shorter vessel members than the other relatives of the *Combretinae* that grow under more moist conditions, even shorter than all other *Combretaceae* (see Fig. 8, arrows). It is also one of the genera with relatively narrow vessel elements but not in very high frequencies, as might be expected. It must, however, be mentioned that the very narrow vessels mixed with vascular tracheids (characteristic for the *Combretinae*) are most abundant in this genus.

LAGUNCULARIA Gaertn.

Plate 7: 41, 44.

Material studied. *L. racemosa* (L.) Gaertn.: GUYANA, *For. Dep. 5096*⁺ (= *FHOw 14634*); *Stahel 94a*⁺.

Shrubs or small trees from the mangrove formations of tropical America and W. Africa.

Growth rings not observed. *Vessels* diffuse, (9–)12 & 19(–23)/mm², solitary and in radial multiples or infrequent clusters (*Stahel 94a)* of 2–3(–6), infrequently including some very narrow elements, 30 & 65% solitary, tangential diameter (41–)108 & 126(–152) μm, walls 4–8 μm. Vessel member length (270–)440 & 470(–700) μm. Perforations simple in horizontal or oblique end walls. Inter-vessel pits crowded, alternate, round to polygonal, 6–9 μm in diameter in *For. Dep. 5096* infrequently elongate (up to 11 μm). Vestures of type B form 2. Vessel–ray and vessel–parenchyma pits more or less similar, infrequently tending to be arranged in horizontal rows, vessel–parenchyma pits infrequently elongate (up to 14 μm). Vestures similar to those of the inter-vessel pits, solid amorphous contents abundant. *Fibres* (580–)880 & 950(–1250) μm long, walls thin to medium thick with simple or minutely bordered pits (1–3 μm) mainly confined to the radial walls; rarely with solid amorphous contents. *Parenchyma* abundant paratracheal and scantily diffuse, paratracheal parenchyma aliform to confluent, completely embedding the vessels, in *Stahel 94a* also irregularly banded, bands 2–5 cells wide. Strands of (3–)4 & 5(–7) cells. *Rays* (9–)10(–12)/mm, uniseriate, very rarely with a biseriate portion, composed of square to erect and weakly procumbent cells, (1–)5 & 9(–15) cells high. Solitary, sometimes elongate *crystals* with blunt or pointed ends in erect ray cells. Granular *contents* frequent in rays and axial parenchyma.

Note. Data recorded by Kribs (1950) agree with the above description. Contrary to what would be expected, the vessel frequencies of this mangrove inhabiting species are low, when compared with other genera from the mangrove (*Conocarpus* and *Lumnitzera*), which even grow under less saline conditions. Vessel frequencies are also not higher than in inland species of comparable tree size (see also Ecological considerations).

LUMNITZERA Willd.

Table 6; Plate 2: 8; 7: 42, 45.

Material studied. *L. littorea* (Jack) Voigt: BURMA, (*FHOw 2747*); SOLOMON ISL., *Walker 290*$^+$ (=*FPRL 19837*); N. BORNEO, *SAN A 4079* (=*FHOw 18048*). – *L. racemosa* Willd.: E. AFRICA, *Schlieben 2593*$^+$ (=*BFA 1559, RBHw;* Ø3.5 cm).

Shrubs or small evergreen trees up to 18 m; in mangrove swamps.

Growth rings faint or indistinct. *Vessels* diffuse, (22–)24–69(–107)/mm^2, solitary and in radial multiples of 2–5(–10) in *L. littorea*, or of 2–3(–8) in *L. racemosa*, 10–20% solitary, round to oval in transverse section, tangential diameter (32–)42–96(–122) μm, radial diameter up to 160 μm, walls 4–8 μm. Vessel member length (290–)540–570(–950) μm. Perforations simple in horizontal to strongly oblique end walls. Inter-vessel pits crowded, alternate, round to polygonal, 5–7 μm in diameter, in *L. littorea* apertures frequently coalescent over 2–3 pits, infrequently so in *L. racemosa*. Vestures of type B intermediate between form 1 and 2, in *L. littorea* apertures with mostly unbranched bead-like vestures on the apertures, in *L. racemosa* with frequently branched ± filamentous vestures on the apertures. Vessel–ray pits alternate to opposite, half-bordered, round to oval (5–9 μm), infrequently elongate (up to 27 μm), long axis horizontal, oblique or vertical, frequently unilaterally compound, frequently with coalescent apertures, in *SAN A 4079* of *L. littorea* occasionally with reduced borders. Vessel–parenchyma pits diffuse, oval to elongate (9–22 μm), infrequently unilaterally compound. Vestures similar to those of the inter-vessel pits, but apertures completely covered with vestures, more abundant over vessel-parenchyma than over vessel-ray pits. Vessel walls warted, warts also present in the pit canal. Solid amorphous contents frequent in the vessels of *L. racemosa*. *Fibres* (540–)840–1110(–1400) μm long, thin- to medium thick-walled, partly thick-walled in *L. racemosa* with infrequent simple or minutely bordered pits (1–4 μm), mainly confined to the radial walls; partly gelatinous in *L. racemosa*. *Parenchyma* scanty paratracheal, in *L. racemosa* in some infrequent confluent bands of 1(–2) cells wide, in *SAN A 4079* of *L. littorea* one growth ring with an irregular band of marginal parenchyma of 1(–2) cells wide. Strands of (3–)4–5(–7) cells. *Rays* (9–)11–14(–17)/mm, uniseriate, infrequently with a small biseriate portion, composed of procumbent cells and square to erect marginals, in the more or less immature sample of *L. racemosa* composed of erect cells only, rays (1–)4–7(–16) cells high. Solid amorphous *contents* frequent in rays and axial parenchyma.

Note. Data provided by Bargagli-Petrucci (1902), Burgess (1966), Coode (1969), Kanehira (1924), Moll & Janssonius (1918), Rao & Purkayastha (1972), and Reyes (1938) agree well with the above description. Silica grains, not observed in the samples studied by me, were reported to be sporadically present in one sample (out of three) studied by Gonggrijp (1932). Although growing in less frequently inundated, hence physiologically less dry parts of the mangrove vegetation than *Laguncalaria*, *Lumnitzera* has a much higher vessel frequency. The high percentage of vessels in fairly long multiples is reminiscent of *Macropteranthus* (however, vessels in much higher, ± 150/mm^2, frequencies) and some *Anogeissus* species (which differ in the occurrence of large crystals, completely filling the ray cells, the strongly procumbent ray cells, and the type of vesturing of the vessel pits).

6. Quantitative characters of Lumnitzera.
(For explanation of the figures see table 1, Anogeissus.)

species and/or specimen	1	2	3	4	5	7
L. littorea						
FHOw 2747	34–38–40	15	58–77–113	118	430–570–770	830–1110–1400
Walker 290	22–24–28	15	48–96–122	160	290–540–950	800–1090–1280
San A 4079	43–47–59	15	51–83–102	117	340–570–760	700–1080–1350
L. racemosa	46–69–107	15	43–42–60	75	380–560–670	540–840–1060

MACROPTERANTHUS F. v. M.

Plate 7: 43, 46.

Material studied. *M. fitzalanii* F. v. M.: AUSTRALIA, *R. 977–204*$^+$ (*SFCw*), *Dep. of For. 164 A*$^+$ (= *FPRL 28640*).

Small tree of inland forests, along rivers.

Growth rings indistinct. *Vessels* diffuse, (138–)152 & 164(–191)/mm^2, solitary and in radial multiples of 2–6(–10), 10 & 35% solitary, mostly round (rarely oval) in transverse section, tangential diameter (23–)45 & 48(–63) μm, radial diameter up to 63 μm, walls 4–7 μm. Mean vessel member length (250–)500 & 550(–650) μm. Perforations simple in oblique end walls. Inter-vessel pits crowded, alternate, round to polygonal, 4–7 μm in diameter, very rarely with some coalescent apertures. Vestures of type B, form 2. Vessel–ray and vessel–parenchyma pits more or less similar but half-bordered. Vestures similar to those of the inter-vessel pits, but vestures present on the apertures of vessel-parenchyma pits. Solid amorphous contents frequent in the vessels of *Dep. of For. 164 A*. *Fibres* (600–)930 & 960(–1230) μm long, walls thick to very thick with simple or minutely bordered pits (1–3 μm), mainly confined to the radial walls. *Parenchyma* very scanty paratracheal. Strands of (4–)5(–7) cells. *Rays* (6–)8 & 10(–12)/mm, uniseriate, very rarely with a small biseriate portion, composed of square to procumbent cells with some infrequent erect marginal cells, (1–)4 & 6(–9) cells high. Large solitary *crystals* infrequent in chambered axial parenchyma.

Note. The high vessel frequency with a high percentage of fairly long radial multiples, and scanty parenchyma is characteristic for this genus. A more or less similar wood anatomical appearance (though with a lower vessel frequency) can only be found in some samples of *Lumnitzera*. Rao (1972) mentioned a distinctly higher vessel frequency (330 – 400)/mm^2; he probably made an error when calculating the vessel frequencies.

PTELEOPSIS Engl.

Table 6; Plate 1: 2; 4: 23, 24.

Material studied. *P. anisoptera* (Welw. *ex* Laws.) Engl. & Diels: ZAMBIA, *Milne-Redhead 4599* (*K – Jw*). – *P. hylodendron* Wildbr: GOLD COAST, *C. Vigne* 1812^+ (*= FHOw 5870*); CAMEROUN, *Gottwald s.n.* (*= BFA 13541, RBHw*). – *P. myrtifolia* (Laws.) Engl. & Diels: E. AFRICA, *Schlieben* 200^+ (*= BFA 12978, RBHw*). – *P. suberosa* Engl. & Diels: NIGERIA, (*FHOw 21707*).

Shrubs and small trees of savannas (*P. anisoptera*, *P. myrtifolia* and *P. suberosa*), and rain forests (*P. hylodendron*).

Growth rings faint or distinct. *Vessels* diffuse, (15 –)17 – 46(– 61)/mm^2, solitary and in radial multiples of 2 – 3(– 5), in *P. myrtifolia* more often of 3 – 4(– 6), in *P. suberosa* some multiples of up to 16 and including some very narrow vessels, 15 – 55% solitary, round to oval, tangential diameter (22 –)74 – 117(– 187) μm, radial diameter up to 195 μm, walls 3 – 7 μm thick. Vessel member length (200 –)320 – 500(– 660) μm. Perforations simple in horizontal to oblique end walls. Inter-vessel pits crowded, alternate, round to polygonal, 7 – 10 μm in diameter, in *C. Vigne 1812* of *P. hylodendron* infrequently elongate (up to 37 μm) apertures infrequently coalescent, most frequently so in *P. suberosa*. Vestures of type B, intermediate between form 2 & 3. Vessel – ray and vessel – parenchyma pits more or less similar, but half-bordered, infrequently elongate up to 16 μm, vessel – ray pits sometimes arranged in horizontal rows, vessel – parenchyma pits infrequently diffuse, apertures rarely coalescent. Vestures similar to those of the inter-vessel pits. Vessel walls with warted surfaces in *P. hylodendron* (*C. Vigne 1812*). Thin-walled tyloses and solid amorphous contents infrequent in *P. anisoptera*, solid amorphous contents also in *P. hylodendron*. *Fibres* (780 –)1130 – 1250(– 1650) μm long, walls medium thick to thick, with simple or minutely bordered pits (1 – 3 μm), mainly confined to the radial walls, but in *P. anisoptera* more or less equally numerous on both radial and tangential walls, frequently septate, in *P. myrtifolia* partly gelatinous. *Parenchyma* paratracheal, scantily diffuse and marginal: in most species paratracheal parenchyma aliform to confluent and infrequently banded (bands 1 – 3 cells wide), mostly completely embedding the vessels (not so in *P. anisoptera*), in *P. suberosa* parenchyma mainly banded, bands 3 – 5(– 7) cells wide; marginal parenchyma present in most species, frequently continuous with paratracheal parenchyma. Strands of (3 –)5(– 7) cells. *Rays* (6 –)8 – 12(– 14)/mm, uniseriate, infrequently with a biseriate portion, but 1 – 3-seriate in *P. hylodendron*, composed of procumbent cells, rarely with some square marginal cells, (3 –)7 – 13(– 22) cells high. Large solitary *crystals*, more or less cubical or infrequently elongate with blunt or pointed ends, usually completely filling the cells, frequent in the axial parenchyma, but scarce in *P. anisoptera*. Crystalliferous cells chambered and slightly enlarged. Longitudinal, intercellular canals, probably of traumatic origin, present in one growth ring of *P. suberosa.*

Note. Data on *P. myrtifolia,* recorded by Barreto (1967) and Rao (1972) agree well with the above description. Fouarge *et al.* (1953) mentioned a slightly lower vessel frequency (8 – 10/mm^2) for *P. hylodendron.*

P. hylodendron stands out in this genus because of its broader rays; *P. suberosa* is slightly aberrant on account of its abundantly banded parenchyma and long radial pore chains.

The different vegetations favoured by the species studied here are reflected in the quantitative data, which follow the commonly found tendency that species growing under moist conditions have longer and wider vessel members in lower frequencies than their relatives growing under more dry conditions (*cf.* Carlquist, 1975; Baas, 1976): *P. hylodendron,* growing in the rain forest, has longer and wider vessel members in lower frequency than the other species growing in more dry savannas (see table 7).

Table 7. Quantitative characters of Pteleopsis.
(For explanation of the figures see table 1, Anogeissus).

Species and/or specimen	1	2	3	4	5	7	8
P. anisoptera	34 – 36 – 39	50	22 – 76 – 105	140	200 – 420 – 630	780 – 1050 – 1180	m
P. hylodendron							
C. Vigne 1812	17 – 20 – 25	55	65 – 107 – 138	170	290 – 500 – 660	950 – 1240 – 1650	m
Gottwald s.n.	15 – 17 – 22	45	52 – 117 – 187	195	240 – 450 – 640	950 – 1250 – 1580	m
P. myrtifolia	32 – 46 – 61	20	38 – 74 – 95	118	220 – 415 – 520	950 – 1135 – 1525	8
P. suberosa	21 – 28 – 46	15(–27)	55 – 108 – 155	155	220 – 320 – 510	800 – 1130 – 1530	4

QUISQUALIS L.

Plate 1: 5.

Material studied. *Q. indica* L.: CAMEROUN, *Metcalfe 166* (ex. *K–Jw* Ø1.5 cm). – *Q. latialata* (Engl.) Exell: CAMEROUN, *Breteler 1408*$^+$ (= *Uw 9323,* Ø3 cm).

Woody climbers; bushlands, hill slopes and along stream banks. *Q. indica* is native in Asia, now widely cultivated and in the tropics often naturalized.

Growth rings faint to distinct, in *Q. latialata* the third and later rings very narrow and with wavy boundaries. *Vessels* diffuse in *Q. latialata,* but wood tending to semi-ring-porous in *Q. indica. Vessels* of two distinct sizes; normal vessels (12–)14(–18)/mm^2 in *Q. indica,* (2–)6(–9)/mm^2 in *Q. latialata,* exclusively solitary or associated with very narrow vessels and vascular tracheids, round to oval in transverse section, tangential diameter (45–)71(–108) μm and (150–)232(–340) μm, respectively, radial diameter up to 380 μm, walls 3–7 μm thick; very narrow vessels intermingled with *vascular tracheids* if not associated with the normal vessels forming clusters or radial multiples of up to 4, radial multiples more frequent in *Q. latialata*, usually frequent on growth ring boundaries, tangential diameter (19–)23 & 27(–36) μm, radial diameter up to 53 μm. Mean vessel member length (200–)350 & 370(–510) μm, narrow elements (230–)420 & 430(–640) μm long. Perforations simple in horizontal to oblique end walls. Pits between large vessels and narrow elements crowded, round to polygonal, alternate, 4–7 μm in diameter, infrequently elongate and up to 11 μm. Vestures of type B form 2. Vessel–ray and vessel–parenchyma pits similar but half-bordered, vessel–ray pits infrequently unilaterally compound. Vestures similar to those of the inter-vessel pits, but small vestures are present on the apertures of vessel–ray and vessel–parenchyma pits, sometimes completely covering the aperture. Vessel walls warted. Solid amorphous contents infrequent in the vessels of *Q. latialata*. *Fibres* (420–)580 & 690(–890) μm long, walls thin to very thin, with few simple or minutely bordered pits, (1–3 μm), on both radial and tangential walls, septate. *Parenchyma* scanty paratracheal. Strands of (3–)4 & 6(–8) cells. *Rays* (9–)10(–12)/mm in *Q. latialata*, (16–)19(–21)/mm in *Q. indica*, uniseriate, rarely with a small biseriate portion, composed of erect to square and infrequent procumbent cells in *Q. latialata*, and of erect cells in *Q. indica*, (4–)21 & 44(–88) cells high. *Radial vessels* frequent, radial vessel members similar to normal ray cells, pits ± alternate, 5–7 μm, vestured, apertures also with vestures. Clustered *crystals* present in the traumatic parenchyma (pith flecks) in *Q. latialata*.

Note. *Quisqualis* is very closely related to *Combretum* subgenus *Cacoucia* Exell, 1964. This is not only reflected in the liana habit, but also in the absence of included phloem in both taxa.

RAMATUELLA Kunth.

Plate 4: 22; 5: 29.

Material studied. *R. argentea* Kunth.: Venezuala, *Maguire 41879*⁺ (= *USw 25029*). – *R. virens* Spruce *ex* Eichl.: Venezuela, *Maguire 41493*⁺ (= *USw 24902*, ⌀2.5 cm).

Small to medium-sized evergreen trees of riverine forests.

Growth rings distinct (*R. argentea*) or faint (*R. virens*). *Vessels* diffuse, (9–)12(–20)/mm^2 in *R. argentea*, (14–)18(–24)/mm^2 in *R. virens*, solitary and in radial multiples of 2–3, of up to 9 in *R. argentea* and often including some very narrow vessels, 7% (*R. argentea*) or 70% (*R. virens*) solitary, round to oval in transverse section, tangential diameter (40–)109(–175) μm in *R. argentea*, (68–)89(–115) μm in *R. virens*, radial diameter resp. up to 217 μm and 187 μm, walls 3–5 μm. Vessel member length (300–)620(–840) μm in *R. argentea*, (230–)440(–620) μm in *R. virens*. Perforations simple in horizontal to oblique end walls. Inter-vessel pits crowded, alternate, in *R. argentea* round to polygonal, 7–10 μm, infrequently elongate and up to 16 μm, in *R. virens* more or less oval, 8–12 μm. Vestures of type B form 2. Vessel–ray and vessel–parenchyma pits more or less similar, but half-bordered, vessel–parenchyma pits infrequently diffuse, more often elongate (up to 18 μm). Vestures similar to those of the inter-vessel pits, but in *R. virens* vessel–ray and vessel–parenchyma pits with vestures on the apertures, in *R. argentea* apertures are free of vestures. Vessel walls with densely warted surface. Thin-walled tyloses infrequent in *R. virens*, granular contents usually lining the vessel walls. *Fibres* (930–)1290(–1530) μm long in *R. argentea*, (830–)1080(–1300) μm long in *R. virens*, walls thick to very thick, with few simple or minutely bordered pits (1–3 μm), mainly confined to the radial walls; gelatinous fibres usually intergrading with narrow bands of non-gelatinous fibres in each growth ring of *R. argentea;* in *R. virens* is the distribution of gelatinous fibres more irregular. *Parenchyma* mainly paratracheal and also scantily diffuse; in *R. argentea* parenchyma only scantily present, aliform and infrequently confluent, in *R. virens* parenchyma abundant, confluent to irregularly banded, only rarely aliform, bands 3–5(–7) cells wide. Strands of (4–)6(–9) cells. *Rays* in *R. argentea* (10–)12(–14)/mm, uniseriate, rarely with a small biseriate portion, composed of square to weakly procumbent cells and 1–2 rows of erect marginals, (3–)9(–23) cells high; in *R. virens* (7–)9(–10)/mm, 1–3-seriate, uniseriate rays only 1–3/mm, composed of erect and square cells, multiseriate rays composed of square to procumbent central cells and 1–3 rows of erect marginals. Longitudinal intercellular canals, probably of traumatic origin present in *R. virens.*

Note. The woods of the two species studied differ rather markedly from each other. This is due to differences in the rays, in the abundance of axial parenchyma, and in the grouping of vessels. The intergrading gelatinous and non-gelatinous fibres are found in one species of this genus only.

STREPHONEMA Hook. *f.*

Plate 1: 1; 7: 47–49.

Material studied. *S. pseudocola* A. Chev.: Gold Coast, *C. Vigne 3090*⁺ (=*FHOw 8514*); Ivory Coast, *Min. de Col. Paris s.n.*⁺ (=*BFA 2226, RBHw*).

Forest trees up to 22 m.

Growth rings indistinct. *Vessels* diffuse, of two distinct sizes: normal vessels, (1–)2(–3)/mm^2, exclusively solitary, rarely associated with a very narrow vessel or vascular tracheids; round to oval in transverse section, tangential diameter (150–)255 & 270(–330) μm, radial diameter up to 470 μm, walls 4–7 μm, very narrow vessels, intermingled with *vascular tracheids* very infrequent, if not in association with the vessels forming small clusters of 2–3. Vessel member length (450–)620 & 750(–1020) μm, narrow elements 330–1280 μm long. Perforations simple in horizontal to oblique end walls. Pits between vessels and very narrow elements or between contiguous narrow elements alternate, round to oval, 8–11 μm, slightly elongate up to 16 μm. Vestures of type A. Vessel–ray and vessel–parenchyma pits alternate, 6–9 μm, half-bordered. Vestures similar to those of the inter-vessel pits. Vessel walls with frequent warts, warty layer continuous into the pit cavities. Solid amorphous contents infrequent. *Fibres* (1250–)1760 & 2190(–2660) μm long, medium thick- to thick-walled, with frequent bordered pits (8–10 μm) on both radial and tangential walls. Small bead-like vestures present in the pit chambers. *Parenchyma* abundant paratracheal and apotracheal; paratracheal parenchyma aliform to confluent, completely embedding the vessels, confluent bands up to 5 cells wide; apotracheal parenchyma in short tangential bands of 3–5 cells wide, infrequently diffuse or diffuse in small aggregates. Strands of (5–)7 & 8(–10) cells. *Rays* heterogeneous II–III, (6–)8 & 10(–12)/mm, 1–3-seriate; uniseriate rays 2–5/mm, (2–)5 & 6(–11) cells high, composed of procumbent to erect cells, multiseriate rays with central portions of procumenbent cells and short tails (1–4 cells high) of square to erect marginal cells. Optically isotropic *opaque contents*, probably silica, present in some fibres and axial parenchyma cells of *C. Vigne 3090.*

Note. Venkateswarlu & Rao (1971) described the fibre tissue to consist of libriform fibres with only a small percentage of fibre-tracheids. The samples I studied had fibre tracheids only, and this was also recorded by Den Outer & Fundter (1976).

In this family *Strephonema* is very outstanding because of the fibre-tracheids, the parenchyma distribution, the heterogeneous II–III rays, and the type of vesturing; characters which are found in no other genus of the *Combretaceae*. The taxonomic position has been the subject of several publications and will more elaborately be discussed in a separate chapter. The above mentioned wood anatomical differences with the other genera are so great that a separate taxonomic (subfamily) status for *Strephonema* must be favoured.

TERMINALIA L.

Table 8, 9b; Fig. 3: f–h; 4: g, h, j; 5: a; Plate 1: 3, 4; 2: 11; 3: 13–18; 4: 19–21; 5: 25–28; 8: 52, 57.

Material studied. *T. acuminata* Eichl.: Brazil, *Bot. Inst. Fir. 795*$^+$ (*= FPRL 28555*). – *T. alata* Heyne *ex* Roth.: India, (*FHOw 355*). – *T. amazonia* (F. J. Gmel.) Exell: Panama, (*USw 107 = FPRL 25054*); Venezuela, *Steyermark 86314*$^+$ (*= Uw 17611*). – *T. arbuscula* Sw. var. *xanthice* Gomez: Jamaica, *FPL Costa Rica AJA–1*$^+$ – *T. arjuna* Bedd.: Egypt, *Graham Sch. B. 690 A* (*= FPRL 16527*); Sri Lanka *Cons. of For. s.n.*$^+$ (*FPRL 386*). – *T. arostrata* Ewart & Davies: N. Australia, *Perry 2074*$^+$. – *T. bialata* Steud.: India, (*FHOw 359*)$^+$ – *T. brassii* Exell: Solomon Isl., *Walker S.I. 73*$^+$ (*= FPRL 19697*). – *T. brownii* Fresen: Sudan, (*FHOw 2390*$^+$). – *T. burseriana* F. v. M.: Queensland, *C. T. White Q 161a*$^+$ (*= FPRL 17645*). – *T. calamansanai* (Blanco) Rolf.: Burma, (*FHOw 1665*$^+$, *FHOw 2432*). – *T. catappa* L.: Cameroun, *Maitland s.n.*$^+$ (*FHOw 3871*); Sri Lanka, (*FHOw 703*$^+$); Philippines, (*FHOw 1913*); Jamaica$^+$, (*K–Jw*); Florida, *Stern & Brizicky 340* (*= Uw 6187*); Netherlands (Cult.), (*UN 482*$^+$, *UN 551*$^+$,). – *T. chebula* Reitz.: Thailand, *v. Beusekom & Geesink 3827*$^+$. – *T. chiriquensis* Pittier: Panama, *Stern, Eyde & Ayensu 1826*$^+$ (*= Uw 14796*). – *T. complanata* K. Schum.: Papua New Guinea, *Hoogland 8909*$^+$. – *T. copelandii* Elmer: Philippines, *FPRI 467*$^+$ (*= Uw 10740*). – *T. corticosa* Pierre *ex* Lanessan: Thailand (*Uw 15675*). – *T. dichotoma* G. F. W. Mey.: Surinam, *Lindeman 5522*$^+$ (*Uw 3819*). – *T. edulis* F. v. M.: Florida, *Milton s.n.*$^+$ (*= FPRL 20617*). – *T. foetida* Griff.[1]): Malaya, (*KEPw 6955*). – *T. glaucescens* Planch. *ex* Benth.: Uganda, *F. D. 214*$^+$ (*= FHOw 8252*). – *T. grandiflora* Benth.: N. Australia, *Perry 2587*$^+$. – *T. impediens* Coode: New Guinea, *Schodde & Craven 4310*$^+$ – *T. ivorensis* Chev.: Nigeria, *Mitchell s.n.*$^+$ (*= FHOw 5179*). – *T. kilimanscharica* Engl.: Tanzania, *Cons. of For. T. T. 329*$^+$ (*= FPRL 15259*). – *T. laxiflora* Engl.: Gold Coast, *C. Vigne 2013*$^+$ (*= FHOw 5934*). *W. T. S. Brown s.n.* (*= FHOw 6594*). – *T. lucida* Hoffmans: Costa Rica, *ECO 28*$^+$ (*= UW 25695*). – *T. macroptera* Guill. & Perr.: Cameroun, *Breteler 311*$^+$ (*= Uw 9249*, ∅4 cm). – *T. manii* King: India, (*USw 8643*$^+$ *= Uw 8477*). – *T. mollis* Laws.: Tanzania, *Hoyle 1036*$^+$ (*= FHOw 3190*). – *T. nigrovenulosa* Pierre *ex* Lanessan: Thailand, *v. Beusekom & Geesink 3727*. – *T. nitens* Presl: Philippines. *FPRI 106*$^+$ (*= Uw 10690*). – *T. orbicularis* Engl. & Diels: Somalia, *Bot. Inst. Fir. 92* (*= FPRL 26468*). – *T. papuana* Exell: Papua New Guinea, *Reid s.n.*$^+$ (*= FPRL 17757*). – *T. platyphylla* F. v. M. *ex* Benth.: Queensland, *C. T. White Q 163 b*$^+$ (*= FPRL 17520*). – *T. polyantha* Presl: Sri Lanka, *Gamble s.n.* (*= FHOw 702*). – *T. porphyrocarpa* F. v. M. *ex* Benth.: Queensland, *C. T. White*

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[1]) *T. foetida* Griff., a name not listed in the *Index Kewensis*, may be an erroneous spelling of *T. foetidissima* Griff.

Q 163 c$^+$ (=*FPRL 17521*). – *T. reitzii* Exell: BRAZIL, *Reitz & Klein 31113*$^+$ (=*Uw 14580*). – *T. samoensis* Rechinger: MARSHALL ISL., (*MADw 15714*)$^+$. – *T. scutifera* Planch. *ex* Laws.: SIERRA LEONE, *Cons. of For. R. D. 119*$^+$ (=*FHOw 8167*). – *T. sepicana* Diels: NEW GUINEA, (*FPRL 28584*$^+$). – *T. superba* Engl.: NIGERIA, *Mitchell FUO 18*$^+$ (*FHOw 6092*). – *T. volucris* R. Br.: N. AUSTRALIA, *Perry 2236*$^+$. For species mentioned in the literature see table 14.

Evergreen and deciduous trees of rain forests, swamp forests, wet or dry deciduous forests, and savannas; also along sandy coasts.

Abbreviated generic wood anatomical description.

Growth rings absent to distinct. *Vessels* diffuse, 2–75/mm^2, solitary and in radial multiples of 2–3(–11), rarely exclusively solitary, average tangential diameter 65–315 µm. Average vessel member length 270–665 µm. Perforations simple in horizontal to oblique end walls. Inter-vessel pits crowded, alternate (4–)9–11(–21 µm) µm, sometimes with coalescent apertures. Vestures of type B, form 2 or 3, or intermediate. Vessel-ray and vessel-parenchyma pits more or less similar but half-bordered; slightly deviating in pattern in some species, rarely unilaterally compound or with reduced borders. Thin-walled tyloses or amorphous to granular contents in some species only. Vessel walls infrequently warted.*Fibres* on average 820–1960 µm long, with thin to medium thick walls in most species, walls sometimes very thin or thick to very thick, with simple or minutely bordered pits (1–3 µm), mainly confined to the radial walls, frequently to infrequently septate or all non-septate, rarely gelatinous or with gelatinous contents. *Parenchyma* mainly paratracheal, ranging from scanty vasicentric to abundant and in paratracheal bands, partly also diffuse and marginal; strands usually of 5–7 cells. *Rays* heterogeneous (II–)III to homogeneous, exclusively uniseriate to 1–6-seriate, mainly composed of procumbent cells with infrequent square to erect marginal cells; in some species with a higher proportion of square and erect cells. *Crystals* of various types and frequencies, and sometimes occurring in several combinations, large and rhomboidal, elongated rod- to styloid-like, or as isodiametric to elongated druses in ray- and/or axial parenchyma cells, sometimes absent. Longitudinal *intercellular canals* of the traumatic type and *pith flecks* in some species only.

Detailed description

Growth rings faint in most species, but distinct in *T. bialata*, *T. calamansanai*. *T. catappa p.p.* (*UN 482*), *T. copelandii*, *T. corticosa*, *T. dichotoma*, *T. foetida*, *T. impediens* (boundaries marked by longitudinal intercellular canals in this species). *T. nitens*, *T. reitzii*, and *T. scutifera;* not observed in *T. brassii* and *T. edulis*. *Vessels* diffuse, (1–)2–75(–82)/mm^2, exclusively solitary or solitary and in radial multiples of 2 & 3, larger multiples sometimes including some very narrow elements, especially in woods with wide vessels (tangential diameter 120 µm or more), multiples of up to 5 & 6 in *T. arjuna p.p.* (*Graham Sch. B. 690 A*), *T. calamansanai*, *T. catappa p.p.* (*UN 552*), *T. glaucescens*, *T. nigrovenulosa* and *T. polyanthe*, multiples of up to 7 & 8 in *T. acuminata*, *T. amazonia p.p.* (*Steyermark 86314*), *T. brownii*, *T. burseriana*, *T. catappa p.p.* (*Maitland s.n.*), *T. manii*, *T. platyphylla*, *T. polyantha*, *T. porphyrocarpa*, and *T. reitzii*, of up to 11 in *T. corticosa;* infrequently in some

Species and/or specimen	1	2	3	4	5	7	8
T. acuminata	10–19–29	5	107–244–205	260	360–450–540	1075–1420–1700	m
T. alata	7–9–14	80	118–175–227	286	330–420–530	1030–1310–1740	m
T. amazonia	7–11–15	45	55–124–180	242	380–500–630	1125–1450–1800	m
Steyermark 86314 USw 107	15–18–23	75	78–123–175	233	240–460–610	850–1170–1530	
T. arbuscula var. *xanthice*	4–8–10	20	70–108–132	168	200–350–460	750–980–1275	m
T. arjuna	5–8–10	35	78–169–255	260	130–325–480	700–1280–1625	8
Graham Sch. B. 690A Cons. of For. s.n.	4–6–11	40	65–156–205	280	230–290–330	1080–1480–1780	m
T. arostrata	4–5–6	85	95–110–128	145	340–460–760	1050–1870–2200	m
T. bialata	4–5–6	70	155–226–302	352	340–560–720	1100–1410–1850	m
T. brassii	1 & 2	100	280–315–410	430	380–665–1030	1350–1890–2275	m
T. brownii	34–37–40	25	58–83–105	111	190–270–390	660–980–1160	m
T. burseriana	67–75–82	10	45–69–95	107	190–280–380	540–820–1010	m
T. calamansanai							
FHOw 1665	3–6–11	45	130–175–214	294	390–510–690	1290–1790–2160	?
FHOw 2432	2–4–6	36	151–202–244	320	350–480–690	1370–1690–2050	?
T. catappa							
Maitland s.n.	2–4–8	60	95–142–217	231	190–310–490	770–870–1100	m
FHOw 703	4–6–10	65	74–143–200	228	170–400–630	850–1180–1370	8
FHOw 1913	4–7–9	80	95–173–243	313	180–280–370	620–900–1120	m
K-Jw	3–4–5	70	90–127–163	215	180–340–530	680–890–1090	m
Stern & Brizicky 340	8–11–13	65	75–145–180	213	320–430–630	780–1120–1500	7
UN 482	7–9–12	45	70–126–188	203	340–530–740	720–1050–1310	5
UN 551	9–12–16	55	85–108–155	203	280–400–480	620–915–1130	5
T. chebula	19–29–37	20	75–95–138	155	350–450–660	750–1400–1700	4.5
T. chiriquensis	10–12–15	35	83–122–170	243	230–405–630	1050–1460–1780	?
T. complanata	3–4–6	50	140–188–232	347	260–460–630	975–1280–1550	m
T. copelandii	2–3–4	40	120–250–320	490	330–525–640	1020–1280–1550	m
T. corticosa	13–26–41	35	52–65–120	137	360–540–710	1025–1440–1750	4.5
T. dichotoma	3–4–5	50	85–125–165	217	320–540–730	1600–1960–2375	m
T. edulis	6–8–11	70	115–168–215	278	340–470–540	1050–1350–1680	m
T. foetida	6–7–9	65	145–225–240	308			?
T. glaucescens	5–11–16	15	58–120–203	298	220–350–530	1000–1290–1530	m
T. grandiflora	11–15–19	35	53–114–175	210	200–320–500	700–1040–1330	7
T. impediens	3–7–12	30	133–205–247	310	310–620–750	1000–1440–1880	m
T. ivorensis	5–7–9	85	135–172–215	283	290–420–520	1050–1360–2050	m
T. kilimanscharica	17–21–27	40	80–121–182	252	200–360–530	975–1175–1325	?
T. laxiflora	6–7–8	75	110–152–180	230	280–390–510	1025–1300–1600	m
C. Vigne 2013 Brown s.n.	4–6–7	85	105–140–195	272	280–380–520	980–1420–1720	m
T. lucida	7–11–14	50	95–171–207	298	320–395–540	950–1190–1570	
T. macroptera	12–22–35	50	65–101–158	172	190–280–390	610–820–1060	2.5
T. manii	28–33–43	10	75–117–170	212	310–490–640	1080–1310–1700	?
T. mollis	6–7–9	30	80–173–223	312	280–450–720	930–1430–1875	?
T. nigrovenulosa	42–46–49	30	47–75–102	120	310–390–520	825–1070–1280	?
T. nitens	6–7–9	60	110–161–207	257	230–470–670	1100–1410–1825	?
T. orbicularis	6–7–8	30	58–128–170	257	320–550–690	900–1250–1650	m
T. papuana	1–2–3	60	102–189–277	327	330–440–630	980–1330–1550	m
T. platyphylla	8–11–13	50	105–142–180	255	230–360–470	925–1130–1350	?
T. polyantha	12–13–14	50	88–123–157	177	310–470–640	975–1240–1515	m
T. porphyrocarpa	19–28–37	30	65–100–151	176	360–480–740	800–1150–1525	?
T. reitzii	19–28–37	30	45–75–105	115	310–450–850	780–1130–1400	8
T. samoensis	6–9–13	75	90–122–155	177	230–380–580	800–1000–1280	m
T. scutifera	3–4–6	85	160–202–260	310	320–480–630	1030–1280–1600	m
T. sepicana	3–6–11	40	90–163–205	307	260–470–710	925–1290–1720	m
T. superba	2–3–5	70	154–206–240	370	380–510–580	900–1250–1700	m
T. volucris	21–28–34	30	58–81–98	118	210–340–430	680–930–1180	m

Table 8. Quantitative characters of Terminalia
(For explanation of the figures see table 1 Anogeissus).

tangential multiples, rarely tending to be arranged in oblique patterns, 5 – 100% of the vessels solitary; vessels round to oval in transverse section, tangential diameter (40 –)65 – 315(– 410) µm, maximum radial diameter 107 – 490 µm, walls 3 – 7 µm, inter-vessel walls sometimes up to 11 µm. Vessel member length (130 –)270 – 665(– 1030) µm. Perforations simple in horizontal or oblique end walls. Inter-vessel pits crowded, alternate, 9 – 11 µm in most species, but 4 – 6 µm in *T. burseriana*, 6 – 8(– 9) µm in *T. catappa*, *T. chebula*, *T. foetida*, *T. kilimanscharica*, *T. laxiflora*, *T. lucida*, *T. macroptera*, *T. nitens*, *T. platyphylla*, *T. polyantha*, *T. porphyrocarpa*, and *T. samoensis*, 11 – 14 µm in *T. acuminata*, *T. bialata*, *T. orbicularis* (infrequently elongate and up to 21 µm) and *T. superba*; apertures frequently coalescent in *T. catappa p.p.* (*FHOw 1913*), *T. corticosa*, *T. grandiflora*, *T. kilimanscharica*, *T. impediens*, and *T. nitens*, less frequently so in *T. alata*, *T. arostrata*, *T. catappa* (remaining samples), *T. glaucescens*, *T. ivorensis*, *T. manii*, *T. mollis*, *T. papuana*, *T. platyphylla*, and *T. volucris*, only rarely so in *T. complanata*, *T. copelandii*, and *T. porphyrocarpa*. Vestures of type B, forms 2, 3, and intermediate forms. Vessel wall warted in *T. catappa* (*UN 482*, *UN 551*, *FHOw 703*, *K-Jw*), *T. chiriquensis*, *T. laxiflora* (*C. Vigne 2013*), *T. lucida*, *T. nitens*, *T. papuana*, *T. platyphylla*, *T. reitzii*, *T. superba*, and *T. volucris*. Vessel – ray and vessel – parenchyma pits more or less similar, but half-bordered, vessel-parenchyma pits also diffuse or slightly elongate, vessel – ray pits tending to be arranged in distinct horizontal rows in most species; some slightly different vessel-parenchyma pit patterns (more or less transitional to scalariform or uniseriate, and pits elongate and up to 24 µm) present in *T. acuminata*, *T. amazonia p.p.* (*Steyermark 86314*), *T. glaucescens*, *T. macroptera*, *T. nitens*, *T. papuana*, and *T. reitzii;* pit borders reduced in *T. acuminata*, *T. arjuna*, *T. brownii*, *T. chiriquensis*, *T. glaucescens*, *T. macroptera*, *T. platyphylla*, *T. reitzii*, and *T. sepicana*; infrequent unilaterally compound pits observed in *T. calamansanai*, *T. complanata*, *T. laxiflora*, *T. macroptera*, and *T. superba*. Vestures similar to those of inter-vessel pits; apertures with more frequent warts in *T. catappa* (*K – Jw*), *T. chiriquensis*, *T. platyphylla*, and *T. reitzii;* pits with reduced borders show a reduced quantity of vestures in the pit chamber, almost simple pits sometimes without vestures. Delicate wall thickenings, forming an oblique, striated pattern, present on the walls of vessels and axial parenchyma of *T. papuana*. Thin-walled tyloses infrequent in *T. alata*, *T. acuminata*, *T. bialata*, *T. catappa p.p.* (*FHOw 703*, *UN 482*), *T. copelandii*, and *T. dichotoma*, frequent in *T. orbicularis*. Solid amorphous contents frequent in *T. alata* and *T. catappa p.p.* (*UN 482*), infrequent in *T. acuminata*, *T. arostrata*, *T. bialata*, *T. catappa p.p.* (*FHOw 703*), *T. glaucescens*, *T. impediens*, *T. laxiflora*, *T. reitzii*, *T. samoensis*, and *T. scutifera*, granular contents infrequent in *T. catappa p.p.* (*UN 482*), *T. nitens* and *T. porphyrocarpa*. *Fibres* (540 –)820 – 1960(– 2375) µm long; walls thin to medium thick in many of the species but thin to very thin in *T. amazonia p.p.* (*USw 107*), *T. brassii*, *T. catappa p.p.* (*K-Jw*, *FHOw 703*, *UN 482*, *UN 551*), *T. complanata*, *T. copelandii*, *T. edulis*, *T. foetida*, *T. impediens*, *T. orbicularis*, *T. sepicana*, *T. superba*, thin to thick in *T. bialata*, *T. nitens*, and *T. papuana*, medium thick to thick in *T. amazonia p.p.* (*Steyermark 68134*), *T. grandiflora*, *T. macroptera*, *T. manii*, and *T. platyphylla*, thick to very thick in *T. alata*, *T. arbuscula*, *T. arostrata*, *T. brownii*, *T. burseriana*, *T. catappa p.p.* (*Stern & Brizicky 340*), *T. chebula*, *T. glaucescens*, *T. laxiflora*, *T. lucida*, *T. mollis*, and *T. volucris;* pits simple or minutely bordered, 1 – 3 µm, mainly confined to the radial walls, but in *T. manii* and *T. orbicularis* frequent on both radial and tangential walls; very frequently septate in *T. alata*, *T.*

amazonia, *T. arjuna*, *T. brassii*, *T. chebula*, *T. ivorensis*, *T. nigrovenulosa*, *T. orbicularis*,' *T. papuana*, *T. platyphylla*, and *T. polyantha;* infrequently so in *T. acuminata*, *T. brownii*, *T. grandiflora*, and *T. sepicana;* in *T. bialata* septa only in the late wood fibres of each growth ring; fibres non-septate in other species; granular contents frequent in the fibres of *T. alata;* fibres gelatinous in *T. dichotoma*, some infrequent gelatinous fibres present in most of the species. *Parenchyma* paratracheal, in many species also marginal and scantily diffuse or diffuse in small aggregates; paratracheal parenchyma in most species completely embedding the vessels, abundant in *T. acuminata*, *T. glaucescens*, and *T. volucris*, scanty in *T. brassii*, *T. brownii*, *T. burseriana*, *T. impediens*, *T. kilimanscharica*, *T. manii*, *T. nigrovenulosa*, and *T. polyantha;* vasicentric to aliform in *T. brassii*, *T. brownii* (infrequently confluent), *T. burseriana*, *T. catappa p.p.* (*UN 482*, infrequently confluent), *T. impediens*, and *T. kilimanscharica* (infrequently confluent); aliform to confluent in *T. amazonia* (*USw 107* also infrequently vasicentric), *T. arjuna* (*Cons. of For. s.n.* also infrequently banded), *T. arostrata*, *T. catappa p.p.* (*Stern & Brizicky 340*, *K-Jw*, *FHOw 1913*, *FHOw 703*, *Maitland s.n.*) *T. chebula*, *T. copelandii*, *T. foetida*, *T. grandiflora*, *T. ivorensis*, *T. macroptera* (mainly aliform), *T. manii*, *T. mollis*, *T. nitens*, *T. platyphylla*, *T. polyanthe*, *T. samoensis* (infrequently banded), *T. scutifera*, *T. sepicana*, and *T. superba;* aliform to banded in *T. alata*, *T. bialata*, *T. dichotoma*, *T. laxiflora*, *T. papuana*, and *T. porphyrocarpa* (bands irregular), confluent to banded in *T. acuminata*, *T. catappa p.p.* (*UN 551*), *T. chiriquensis* (bands irregular), *T. corticosa* (bands ± anostomosing), *T. lucida* (bands ± anostomosing), *T. orbicularis*, and *T. volucris* (bands ± anostomosing); typically banded in *T. arbuscula*, *T. calamansanai* (bands ± anostomosing), and *T. glaucescens;* parenchyma bands mostly 2–4(–6) cells wide, but 1–2(–3) in *T. corticosa*, up to 11 cells wide in *T. glaucescens* and up to 15 cells in *T. acuminata;* narrow marginal bands of 1–3 cells wide, continuous with paratracheal parenchyma present in *T. acuminata*, *T. alata*, *T. amazonia*, *T. arostrata*, *T. bialata*, *T. brassii*, *T. burseriana*, *T. calamansanai* (interrupted in *FHOw 2432)*, *T. catappa p.p.* (*UN 551*, *Stern & Brizicky 340*, *Maitland s.n.*, *FHOw 1913*, in *FHOw 703* frequently interrupted), *T. chebula*, *T. chiriquensis* (not on all growth ring boundaris), *T. copelandii*, *T. dichotoma*, *T. grandiflora*, *T. ivorensis*, *T. kilimanscharica*, *T. lucida*, *T. macroptera*, *T. manii*, *T. nitens*, *T. orbicularis*, *T. platyphylla*, *T. samoensis*, and *T. sepicana;* marginal bands up to 11 cells wide in *T. glaucescens*, up to 14 cells wide in *T. arjuna p.p.* (*Graham Sch. B 690 A*); apotracheal marginal parenchyma in short tangential aggregates of 2–4 cells wide in *T. bialata* and *T. dichotoma;* diffuse parenchyma frequent in *T. kilimanscharica*, *T. laxiflora*, *T. mollis*, and *T. porphyrocarpa*. Strands of (3–)5–7(–8) cells. *Rays* heterogeneous (II–)III to homogeneous, (5–)7–18(–24)/mm, uniseriate, infrequently with a small biseriate portion in most species, uni- and biseriate in *T. arjuna p.p.* (*USw 107*), *T. catappa p.p.* (*FHOw 703*), and *T. macroptera* (also with some rare triseriate rays), 1 to 3-seriate in *T. brownii*, *T. burseriana*, *T. catappa p.p.* (*UN 551*, *Stern & Brizicky 340*, *Maitland s.n.*, *K-Jw*), *T. edulis*, *T. foetida*, *T. grandiflora*, *T. impediens*, *T. kilimanscharica*, *T. laxiflora*, *T. mollis*, *T. nitens*, *T. porphyrocarpa*, *T. samoensis*, *T. scutifera* and *T. sepicana;* 1- to 4-seriate in *T. arostrata* and *T. copelandii;* 1- to 5-seriate in *T. catappa p.p.* (*FHOw 1913*); 1- to 6-seriate in *T. complanata* and *T. platyphylla;* uniseriate rays (1–)3–12(–50) cells high, multiseriate rays 120–600 μm high; in many of the species rays composed of strongly procumbent cells and 1(–2) infrequent rows of square to erect marginal cells (Heterogeneous III – Homogeneous), in *T.*

arostrata, *T. nitens* and *T. platyphylla* uniseriate rays composed of erect and square cells, in *T. platyphylla* marginal cells in uniseriate tails of 1–4(–7) cells high (Heterogeneous II – III), multiseriate rays hardly with sheath cells; rays composed of weakly procumbent and square to erect cells in *T. alata*, *T. acuminata*, *T. amazonia*, *T. brassii*, *T. chebula*, *T. macroptera*, *T. manii*, *T. nigrovenulosa*, *T. orbicularis*, *T. polyantha*, *T. porphyrocarpa* (also with some strongly procumbent cells). *T. reitzii*, *T. samoensis* and *T. volucris*. Conspicuous radial intercellular spaces, sometimes completely separating the ray cells, present in *T. brassii*, *T. calamansanai*, *T. chiriquensis*, *T. papuana*, and *T. superba*. *Crystals* large and rhomboidal, elongated rod- to styloid-like, or regularly clustered (druses) in greatly varying frequencies in ray- and/or axial parenchyma, or absent. Very large solitary, isodiametric crystals, completely filling tangentially enlarged, radial series of ray cells in *T. rostrata;* large rod-like crystals with blunt or pointed ends, more or less completely filling radial series of tangentially hardly enlarged ray cells frequent in *T. nigrovenulosa* and *T. orbicularis*, infrequent in *T. acuminata*, *T. amazonia*, and *T. corticosa;* similar crystals abundant in the axial parenchyma of *T. alata*, *T. arbuscula*, *T. arjuna p.p.* (*Graham Sch. B 690 A*), *T. chebula*, and *T. reitzii*, infrequent to rare in axial parenchyma of *T. amazonia p.p.* (*USw 107*), *T. bialata*, *T. corticosa*, *T. dichotoma*, and *T. nigrovenulosa;* cubical to rod-like crystals completely filling the chambers of chambered axial parenchyma strands, abundant in *T. burseriana*, less frequent in *T. chiriquensis* and *T. lucida;* crystals rhomboidal to elongated with pointed ends, 1 or 2 per cell frequent in normal ray cells of *T. manii* and *T. polyantha;* elongated to styloid-like crystals in non-chambered axial parenchyma of *T. burseriana* and *T. papuana* and in septate (± chambered) fibres of *T. reitzii.*

Isodiametric druses to clustered crystals completely filling large idioblasts frequent in the axial paranchyma of *T. catappa p.p.* (all specimens except cultivated ones from the Netherlands), *T. grandiflora*, *T. impediens*, and *T. platyphylla*, infrequent to scanty in the axial parenchyma of *T. catappa* (*UN 482 & UN 551*) *T. complanata*, *T. glaucescens*, *T. porphyrocarpa*, *T. samoensis* and *T. sepicana;* similar druses in *T. impediens* restricted to parenchyma around traumatic intercellular canals; axially elongated druses to clustered crystals frequent in axial parenchyma of *T. catappa p.p.* (*K-Jw*, *UN 482*) and *T. kilimanscharica*, rare in axial parenchyma of *T. complanata*, *T. platyphylla*, *T. samoensis* and *T. sepicana;* similar crystals rare in ray cells of *T. glaucescens* and *T. samoensis*. Crystals not observed in *T. brassii*, *T. copelandii*, *T. edulis*, *T. foetida*, *T. ivorensis*, *T. laxiflora*, *T. macroptera*, *T. nitens* and *T. scutifera*. Longitudinal *intercellular canals* of the traumatic type present in concentric rings in *T. acuminata*, *T. burseriana*, *T. impediens*, *T. laxiflora*, *T. macroptera*, and *pith flecks* present in *T. glaucescens* and *T. laxiflora p.p.* (*Brown s.n.*).

Note. The wood anatomy of the *Terminalia* species studied here shows a considerable variation, overlapping with all genera of the subtribe *Terminaliinae* as well as with some from other taxa. Using combinations of characters the latter can in most instances be separated from the *Terminalia* species. The wide amplitude of vessel member length can largely be explained from ecological influences (see Ecological considerations).

Keys to a limted number of species have been presented by Hooks (1966), Lomibao (1973), and Pearson & Brown (1933). From these, together with the present results and a great number of other publications (see introduction) a vast amount of wood anatomical data on 73 species could be accumulated. Those of the species studied for this paper are presented in a synoptical key at the end of this paper; comparatively incomplete wood anatomical data on the remaining 30 species are presented separately (Table 14). In the literature, intercellular canals, probably of traumatic origin, are reported for a great number of species. Some of these have been studied by me although the intercellular canals were not always observed, indicating that the presence of such canals is not a stable species character.

Burgess (1966) recorded 'definitely ring-porous' wood for *T. copelandii* (studied by me but not ring-porous) and *T. citrina*. Other records on ring-porous wood are not found for these two species or for other species of *Terminalia*. They are only mentioned for *Combretum* (Record, 1936; this paper). The possibility must therefore be considered that Burgess studied wrongly identified samples.

Of the many samples studied of *T. catappa* the two samples taken from cultivated trees (*UN 482 & 551*) are markedly different in having only scarce idioblasts with one clustered crystal and thin-walled fibres. The only other sample of probably cultivated origin (*K-Jw*, Jamaica) had thin-walled fibres too, but more abundant crystals. These differences may be caused by a different habitat.

Furuno (1977) mentioned bordered fibre pits for *T. complanata*, *T. oreadum*, and (infrequently present) in *T. archipelagii* and *T. microcarpa*. He probably incorrectly referred to the often minutely bordered (2 – 3 μm) fibre – ray pits, clearly visible in radial sections.

Amorphous silica is of very rare occurrence and was found in one sample of *T. dichotoma* from the Uw slide-collection only, but was not present in two other samples of this species. Apart from the species studied by me silica, has been reported to be absent from *T. coriacea*, *T. crenulata*, *T. myriocarpa*, and *T. paniculata* (Gonggrijp, 1932; Hirata *et al.;* 1972; Sharma & Rao, 1970).

TERMINALIOPSIS Danguy

Material studied. *T. tetrandra* Danguy: Madagascar, *Rotavoarison SF 1959* (= *CTFT 12063*), *Rotavoarison SF 25603*⁺ (= *CTFT 17026*).

Medium-sized trees from moist forests.

Growth rings faint. *Vessels* diffuse, (6 –)11 & 13(– 15)/mm², solitary and in radial multiples of 2 – 3, 50 & 70% solitary, round to oval, tangential diameter (58 –)93 & 98(– 140) μm, radial diameter up to 170 μm, walls 2 – 3 μm, in *SF 25630* up to 6 μm. Vessel member length (220 –)430 & 540(– 720) μm. Perforations simple in horizontal or oblique end walls. Inter-vessel pits crowded, alternate, round to polygonal, 6 – 8 μm. Vestures of type B, form 2. Vessel – ray and vessel – parenchyma pits more or less similar, but half-bordered, vessel – parenchyma pits infrequently elongate and up to 17 μm, vessel – ray pits infrequently unilaterally compound. Vestures similar to those of the inter-vessel pits. Solid granular contents frequent in the vessels of *SF 25630*. *Fibres* (950 –)1210 & 1300(– 1600) μm long, walls thin to medium thick with frequent simple or minutely bordered pits (1 – 3 μm) mainly confined to the radial walls. *Parenchyma* paratracheal, completely embedding the vessels, marginal and diffuse or diffuse in small aggregates; paratracheal parenchyma confluent to banded and infrequently aliform in *SF 1959*, aliform and confluent in *SF 25630*, bands of 2–4(–7) cells wide; marginal parenchyma with paratracheal parenchyma, forming interrupted bands of 1–3 cells wide. *Rays* heterogeneous (II–)III, (7–)8 & 9(–11)/mm, 1–3-seriate, uniseriate rays 1–3/mm, composed of square and erect cells, (1–)4 & 5(–7) cells high, multiseriate rays up to 1 mm high composed of central portions of procumbent cells and short uniseriate tails (1–4 cells high) of square and erect cells. *Crystals* absent.

Note. *Terminaliopsis* shares all of its characters with *Terminalia*. Strongest resemblance is with *T. macroptera*, from which it differs in ray width and composition only.

THILOA Eichl.

Plate 5: 31–32; 6: 40.

Material studied. *T. glaucocarpa* (Mart.) Eichl.: Brazil (*JPT 11052*⁺, *BCTw*).

Growth rings faint. *Vessels* diffuse or with a tendency to form oblique patterns, of two distinct sizes: normal vessels, (33–)45(–80)/mm^2, predominantly solitary, infrequently in radial multiples of 2 or 3 or associated with very narrow vessels and vascular tracheids, tangential diameter (49–)61(–73) μm, radial diameter up to 98 μm, walls 4–7 μm; very narrow vessels intermingled with *vascular tracheids* if not in association with the vessels, forming clusters or radial multiples of up to 5, the latter usually frequent on the growth ring boundaries, tangential diameter (15–)23(–32) μm, radial diameter up to 33 μm. Vessel member length (180–)300(–420) μm, narrow elements (260–)340(–460) μm long. Inter-vessel pits crowded, alternate, round to polygonal, 5–7 μm in diameter, infrequently elongate and up to 10 μm. Vestures of type B, intermediate between form 2 & 3. Vessel–ray and vessel–parenchyma pits more or less similar, infrequently elongate and up to 15 μm. Vestures similar to those of the inter-vessel pits. Axial strands of *phloem* (foraminate type) frequent. Thin-walled tyloses and solid amorphous contents infrequent in the vessels. *Fibres* (640–)870(–990) μm long, walls very thick with simple or minutely bordered pits (1–2 μm), mainly confined to the radial walls, frequently gelatinous. *Parenchyma* very scanty paratracheal, strands of 5 & 6 cells. *Rays* (11–)13(–15)/mm, uniseriate and infrequently biseriate, composed of procumbent, thick-walled cells, (4–)14(–22) cells high. *Radial vessels* frequent, radial vessel members similar to normal ray cells, pits to contiguous ray cells ± alternate, 5 μm, vestured. Radial phloem strands present in some of the broader rays. Frequent small clusters and infrequent large clustered (to more or less solitary) *crystals* present in the parenchyma of the included axial phloem strands.

Note. Included phloem was also reported for *T. stigmaria* Eichl. (Solereder, 1885). *Thiloa paraquariensis* Eichl. (Brazil, *Prance et al. 156617*, twig ⌀5 mm) studied for comparison, also showed axial phloem strands and radial vessels; vessels frequently in radial multiples; the vessel–ray and vessel–parenchyma pits were more often elongate and occasionally with coalescent apertures, and the rays were composed of erect cells only. *Thiloa* is outstanding in the *Combretinae* because of its thick-walled ray cells.

DISCUSSION OF SOME OF THE WOOD ANATOMICAL CHARACTERS

Growth rings

Irregular or undulating growth rings were found in some liana species of *Combretum* and in *Quisqualis* (also lianas) only. A tendency to ring- or semi-ring-porous woods is found in several genera (table 12) but only in one species of *Combretum* (*C. celastroides*) distinctly ring-porous wood was observed. All other genera have diffuse-porous woods. An observation of ring-porous wood in *Terminalia*, mentioned in the literature (Burgess, 1966) is probably based on wrongly identified samples (see description and note of *Terminalia*).

Vessels

In most genera of the *Combretaceae* vessels have a diffuse distribution but there are a few exceptions in which the wood is ring-porous (*Combretum p.p.;* Plate 6/35) or tending to semi-ringporous (*Combretum p.p.*, *Calopyxis*, *Calycopteris*, *Quisqualis*). *Calycopteris* and *Quisqualis* are lianas, the others trees are shrubs; the occurrence of semi-ring-porosity is therefore not restricted to a special type of habit in the *Combretaceae*, nor is there a distinct correlation with habitat or deciduousness.

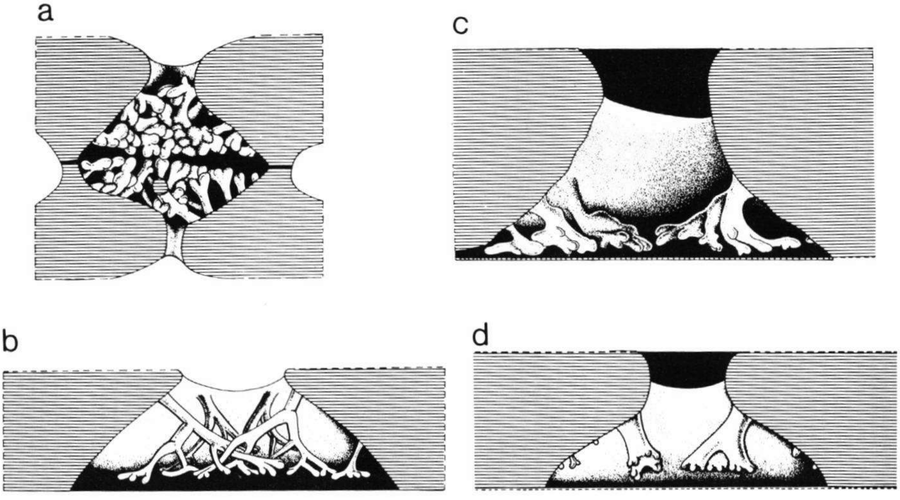

Fig. 1. Drawings of transverse sections of bordered pits illustrating different types of vesturing. a: type A; b: type B form 1; c: type B form 2; d: type B form 3.

There is a considerable variation in vessel diameter and vessel member length. Differences in frequency, diameter and member length due to different habitats will be discussed in a separate chapter.

In the genera of the *Combretinae*, and to a lesser extent also in *Strephonema*, two distinct types of vessels can be recognized; the 'normal' type of vessel elements and very narrow ones (Plate 5/30 – 33). These very narrow elements form a grading series from vessel members with two (or three) perforations to vascular tracheids with one or without perforations (Fig. 2) all of more or less the same length. These are present in association with the normal vessels or in clusters and radial multiples wholly consisting of such elements. In the genera of the *Combretum* group they occur often in radial multiples on the growth ring boundaries (Plate 5/31 – 33). Some very narrow elements are occasionally also present in other genera, mostly in those with fairly long vessel multiples and associated with those multiples.

Vestured pits

The vestured pits of the *Combretaceae* (together with those of some allied families) are comprehensively dealt with in a separate publication (van Vliet, 1978). Of *Combretaceae* 73 samples of 67 species, covering all genera (*Meiostemon* excepted) were studied.

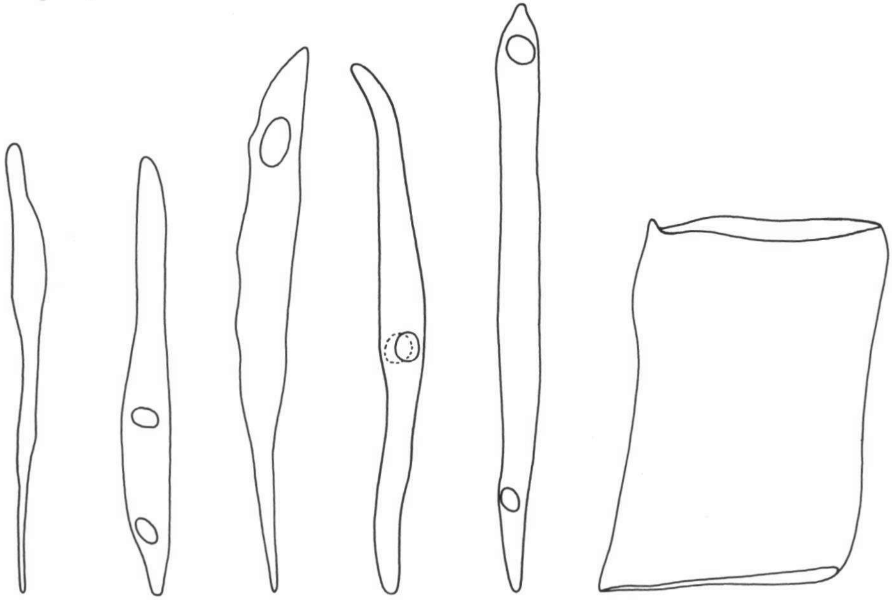

Fig. 2. Camera lucida drawings of vessel elements of *Calycopteris floribunda*, showing a normal vessel and grading series of very narrow vessels and vascular tracheids.

The presence of morphological intermediates between vestures and warts are suggestive for homology of these two structures. It makes it also impossible to present definitions of vestures and warts that are of general application. The definitions used here are based on the localisation of the structures involved, but cannot always be rigidly applied because of the occurrence of intermediates.

Vestures are defined as mostly branched structures present in, or distinctly associated with, any part of a bordered pit (pit chamber, pit canal, or pit aperture). In bordered fibre pits, however, and rarely also in vessels pits, unbranched vestures can be found as well.

Warts are defined as unbranched structures present on the vessel wall. Sometimes warts can be found on pit apertures, and rarely they may be branched as well.

In *Combretaceae* two major types of vesturing are recognized in the pit chamber.

Type A. The vestures are attached to all parts of the roof of the pit chamber, and branch into a compact mass of vestures of equal thickness. (Fig. 1a; Plate 1/1). Viewed from the pit floor into the pit chamber the result of this branching is a compact mass of bead-like endings of terminal branches.

Type B. To the roof of the pit chamber, nearby the pit canal, trunk-like vestures are attached, pointing into the pit chamber and dichotomizing to various extents into thinner branches; on lower parts of the roof much thinner, partly unbranched vestures may be infrequently present in various densities (Fig. 1b – d; Plate 1/2 – 5). Viewed from the pit floor the result of this branching is a compact to loose or very open mat of vestures of ± equal thickness. (Plate 1/6; 2/7) Vestures were always found in dintinctly bordered vessel pits. The vesturing was often reduced or absent from pits with reduced borders (Plate 2/9).

In *Combretaceae* the type A vesturing is found in *Strephonema* only, the other genera have type B vesturing in their vessel pits. This distribution of vesture types parallels the subfamily classifications of this family into *Strephonematoideae* (*Strephonema* only) and *Combretoideae* (*sensu* Exell & Stace, 1966).

Comparing type B vesturing in *Combretaceae* and *Melastomataceae* there appeared to be a substantial variation in the degree of branching and in thickness of the vestures, which could be classified into three forms of which two are present in *Combretaceae*.

These forms are:

Form 1. The trunk-like bases of the vestures are of ± the same thickness as the branches (Fig. 1b; not represented in *Combretaceae*).

Form 2. Most of the basal trunks are thick and branch elaborately into the pit chamber (Fig. 1c; Plate 1/4, 5).

Form 3. The trunk-like vestures are hardly branched, viewed from the pit floor

Form 1. The trunk-like bases of the vestures are of … the same thickness as the branches (Fig. 1b; not represented in *Combretaceae*).

The distribution of these forms in the subfamily *Combretoideae* (table 9a) corresponds in no way with any proposed classification of the genera. Within *Terminalia* (37 species studied) both forms and their intermediates were found (table 9b), thus strongly limiting the taxonomic and diagnostic value of this character.

Vestures on pit apertures were found in a few genera only (table 8c), mostly on vessel – ray and vessel – parenchyma pit apertures, in one genus also on inter-vessel pit apertures, but not on all of them. In *Ramatuella* they were observed in only one of the two species studied. In *Lumnitzera* vestures were less abundant on pit apertures in *L. racemosa* than in *L. littorea*.

In fibres of the *Combretaceae* vestures were only observed in the bordered pits of the fibre-tracheids of *Strephonema*.

Warts were found in most genera (see descriptions) though not in all samples or species studied of one genus and not of constant abundance. They may be present or not on pit apertures and are then hardly distinct from vestures on apertures (Plate 2/8). In *Quisqualis latialata* a wide variation was found in this respect: on some heavily warted vessel walls vestures appear to be absent from the apertures, whilst in other vessel elements with less frequent warts on their walls they were concentrated around the apertures which then had a more dense vesturing. The variation in distribution and prominence of warts together with the variation in the occurrence of vestures on apertures (*cf.* table 9c) not only strengthens the view that they are homologous structures, but also implies that they are of little diagnostic and taxonomic value.

Table 9a. Distribution of the types and forms of vesturing in the pit chamber in the genera of the Combretaceae.

Type A.	Strephonema
Type B, form 2	Bucida, Calycopteris, Combretum, Finetia, Laguncularia, Lumnitzera, Quisqualis, Ramatuella, Terminalia p.p., Terminaliopsis.
Type B, intermediate between form 2 & 3.	Calopyxis, Conocarpus, Guiera, Macropteranthus, Pteleopsis, Terminalia p.p.
Type B, form 3	Anogeissus, Buchenavia, Terminalia p.p., Thiloa.

Table 9b. Distribution of the various forms of type B vesturing in the genus Terminalia

Form 2.	T. acuminata, T. arbuscula, T. arjuna, T. bialata, T. brassii, T. catappa, T. chiriquensis, T. complanata, T. copelandii, T. dichotoma, T. edulis, T. impediens, T. ivorensis, T. kilimanscharica, T. laxiflora, T. lucida, T. manii, T. mollis, T. papuana, T. platyphylla, T. reitzii, T. samoensis, T. scutifera, T. sepicana, T. superba (24 sp.)
Intermediate between 2 and 3	T. amazonia, T. arostrata, T. brownii, T. chebula, T. glaucescens, T. grandiflora, T. macroptera, T. nitens (8 sp.)
Form 3.	T. burseriana, T. calamansanai, T. porphyrocarpa, T. volucris. (4 sp.)

Table 9c. Distribution of vestures on pit apertures in Combretaceae.

Vestures over inter-vessel pits	Lumnitzera littorea, L. racemosa
Vestures over vessel-ray and vessel-parenchyma pits	Lumnitzera littorea, L. racemosa Quisqualis latialata Ramatuella virens (absent from R. argentea)

Radial vessels

In an earlier paper (van Vliet, 1976a) I have reported on the presence of a special type of element in the rays of some genera of the *Combretaceae.* These ray cells have perforations in their tangential walls and the terminal cells of a radial series of such elements are connected with a very narrow axial vessel or vascular tracheid through a perforation (Plate 8/54 & 55). These elements are called radial vessels and are found in uniseriate rays and uniseriate tails of multiseriate rays only. The shape of these radial vessel members is not different from a normal ray cell, but they also have some characters that are typical for vessel members, like bordered vestured pits to contiguous parenchyma cells in an alternate pattern. They have been found now in all species of the genera belonging to the subtribe *Combretinae* (*Calopyxis*, *Calycopteris*, *Combretum*, *Guiera*, *Quisqualis*, and *Thiloa*).

Although stated differently earlier (van Vliet, 1976a) they also appeared to be infrequently present in *Combretum fragrans;* the *Combretum apiculatum* sample, referred to in my previous paper, was wrongly identified.

This type of ray cell has not been recorded before although ray cells with perforations in the radial walls only, referred to as perforated ray cells (Plate 8/50) are recorded for several families (*cf.* Chalk & Chattaway, 1933; McLean and Richardson, 1973). Such perforated ray cells were found in *Combretum* only (*C. celastroides* and one sample of *C. molle*). Only once it was found that two superimposed perforated ray cells were connected by a perforation (Plate 8/50). Perforated ray cells were not found during the SEM surveys, and it could not be established whether these possess vestured pits.

In the literature vessel elements in rays have been reported by Chattaway (1948a & b) for *Banksia* and *Duandra* of the *Proteaceae*. In these woods bundles of narrow vessels and tracheids run radially in broad rays, and are also connected with axial elements. The vessel members and tracheids of these bundles are morphologically very different from ray cells. Almost all of the bundles arise at a more or less fixed distance from the pits and are continuous from their site of initiation towards the cambium; the elements even show some elongation.

The radial vessels present in the *Combretaceae* do not form bundles, are not continuous to the cambium and are of similar size as the ray cells. They are therefore different from the vessel elements arranged in bundles in the rays of the two genera of the *Proteaceae*.

The presence of radial vessels in the *Combretaceae* is not correlated with habit — they are present in lianas as well as in shrubs or trees — nor with habitat — they occur in species growing in the relatively dry savannas as well as in species growing in the rain forest.

Included phloem

Included phloem of the foraminate type occurs in a restricted number of genera (*Calycopteris*, *Combretum*, *Guiera*, *Thiloa*; Plate 6/26 – 40). Included phloem of the concentric type is only incidentally present in *Combretum*. In this genus, included phloem is restricted to species with a shrub or tree habit (though not present in all of them) and absent from the lianas (except for one species, *C. edwardsii*, which according to Verhoeven & van der Schijff (1975) shows included phloem). See also the chapter on lianas. Pfeiffer (1926) mentioned included phloem for many other genera of the *Combretaceae* (*Ramatuella*, *Terminalia*, *Anogeissus*, *Conocarpus*, *Pteleopsis*, *Quisqualis*, and 'leicht zu übersehen bei *Laguncularia* und *Lumnitzera*') in which it does not occur. Het probably wrongly quoted Heiden (1893) and Holtermann (1893) who studied all these genera and who mentioned difficulties in finding bicollateral vascular bundles in young twigs of *Laguncularia* and *Lumnitzera*.

Radial strands of phloem are less frequently found, and only in species that have axial ones as well. Connections between radial and axial strands were also observed (Plate 8/61).

Fibres

Many of the woods have septate fibres, and in a number of genera this character is present (or absent) in all samples studied (*cf.* Table 12). In other genera there is a great variation in the frequency of septate fibres, varying from all fibres septate to none of the fibres septate. The fibre length (like vessel member length) of all genera strongly overlaps. Comparing average values only (Fig. 7), *Strephonema* has the longest fibres, only with a small overlap with *Terminalia.* Although tending to have longer vessel members, the liana species from the *Combretum* group have comparatively short fibres. (Table 10, see also the chapter on lianas).

Parenchyma

The parenchyma distribution in the woods of the *Combretaceae* can easily be described with the widely accepted terminology. Only the parenchyma on the growth ring boundaries is difficult to classify. Chowdhury (1936) has demonstrated that in *T. tomentosa* the parenchyma on the growth ring boundary is initial parenchyma. In a number of species it was not possible to determine, whether such parenchyma is initial or terminal.According to the Multilingual Glossary of Terms used in Wood Anatomy (I.A.W.A., 1964) both initial and terminal parenchyma is apotracheal parenchyma. However, in many species of *Terminalia*, the apotracheal parenchyma, delimiting the growth rings, is often continuous with the paratracheal parenchyma. In the descriptions the term marginal parenchyma (Laming & Mennega, 1972), with the additions paratracheal or apotracheal, has been used therefore to describe the parenchyma on the growth ring boundaries.

Rays

In *Combretaceae*, ray width can vary from uniseriate (very rarely with a small biseriate portion) to 6-seriate (*cf.* table 13 and descriptions, Plate 5/25 – 30). In the juvenile woods of some genera, rays are entirely composed of erect cells. In most genera, however, rays are composed of procumbent or square to procumbent cells with, sometimes infrequent, erect marginal cells. (According to Kribs' (1950) definitions ± uniseriate heterogeneous to uniseriate homogeneous or intermediate between heterogeneous III (with erect marginals) and homogeneous). Only in *Strephonema* rays are typically heterogeneous II – III, with uniseriate rays composed of erect cells only. In a number of genera (*e.g. Anogeissus, Terminalia p.p.*) the rays contain radial series of sometimes strongly enlarged crystalliferous cells, completely filled with a solitary crystal (see also the following part on crystals). In the determination of the type of ray according to Kribs the deviating shape of these crystalliferous cells has not been taken into account.

Crystals

Crystals mainly occur in parenchymatous tissues. In the first formed secondary xylem of *C. fruticosum* crystals (both solitary and clustered) were also observed in the fibres (Fig. 4b; Plate 8/58). In the literature (Holtermann, 1883) these crystals are also mentioned for *C. latifolium* and *C. imberbe*, probably also in young twigs, because they were not observed in the mature samples of *C. imberbe* studied by me.

In many genera, solitary crystals are frequently present and the shape of the crystals as well as their localisation offers a wide variety of types, which may be of considerable diagnostic value, especially on the specific level. This variety is illustrated in Fig. 3 for the ray parenchyma and in Fig. 4 for the axial parenchyma. The solitary crystals can be divided into two groups: relatively small, more or less rhomboidal or elongated crystals, easily visible with the light microscope, and large to very large, isodiametric to elongated crystals with blunt or pointed ends, completely or almost completely filling the ray cells, and of which the shapes correspond with the shape of the enlarged cells (*cf.* Fig. 3c, f, g; 4d; Plate 8/57). When using the light microscope these crystals are sometimes difficult to find because their outline completely coincides with the wall of the enlarged cells (Fig. 3c).

These enlarged crystalliferous cells are not randomly distributed in the rays, but are arranged in radial series. Even in woods where they are only infrequently present they are always found in short series of at least three or four cells. Viewed in tangential sections the crystalliferous ray cells of these radial series have an idioblast-like appearance (Fig. 3b; see also Kribs, 1950, Fig. 101) although they do not extend beyond the outline of the uni- or multiseriate ray. This may cause a nomenclatural problem. In the Multilingual Glossary of Terms Used in Wood Anatomy (I.A.W.A., 1964) an idioblast is defined as a cell 'differing markedly in form and contents from the other constituents of the same tissue', and this seems applicable to the enlarged crystalliferous cells, especially when seen in tangential section in multi-seriate rays. Their arrangement in continuous series and their regular shape when seen in radial sections, makes them, however, not so different from the other ray tissue. The term idioblast will here only be used when referring to large, rounded, isolated (or sometimes in short series, as in axial parenchyma) cells (*cf.* Fig. 3d; Plate 8/59 & 60) and which do extent beyond the ray outline (Fig. 3e).

Large solitary crystals, completely filling the cell can also be present in axial parenchyma, being cube-like, rod-like or more or less elongated in shape, depending on the number of chambers in the parenchyma cell (Fig. 4d, e, & h). The smaller crystals can conveniently be described using two categories recognized by Chattaway (1955, 1956). These are: rod-like to elongated crystals (2 – 4 times as long as broad) with blunt or pointed ends (Plate 8/52) and rhomboidal or diamond-shaped crystals. Styloids (not mentioned by her, at least four times longer than broad, Fig. 4j) are infrequently found in the axial parenchyma of some species of *Terminalia*.

Hooks (1966) described for *Terminalia* a type of idioblast in the axial parenchyma containing a small rhomboidal crystal, that was not found by me (Fig. 4i).

Clustered crystals are in the *Combretaceae* less frequently present than solitary crystals. Small crystals (Plate 2/10) are abundant in the chambered parenchyma of the included phloem (see table 13). In xylem parenchyma clustered crystals are rare or frequent in various species of *Combretum* and *Terminalia* and rare (2 crystals per cell) in the rays of *Calycopteris*. Mostly the clustered crystals are large and present in idioblasts in the axial parenchyma (Fig. 4g; Plate 3/18); but large crystals may also be present in unmodified cells of the axial parenchyma and are then often asymetrically elongated (Fig. 4c).

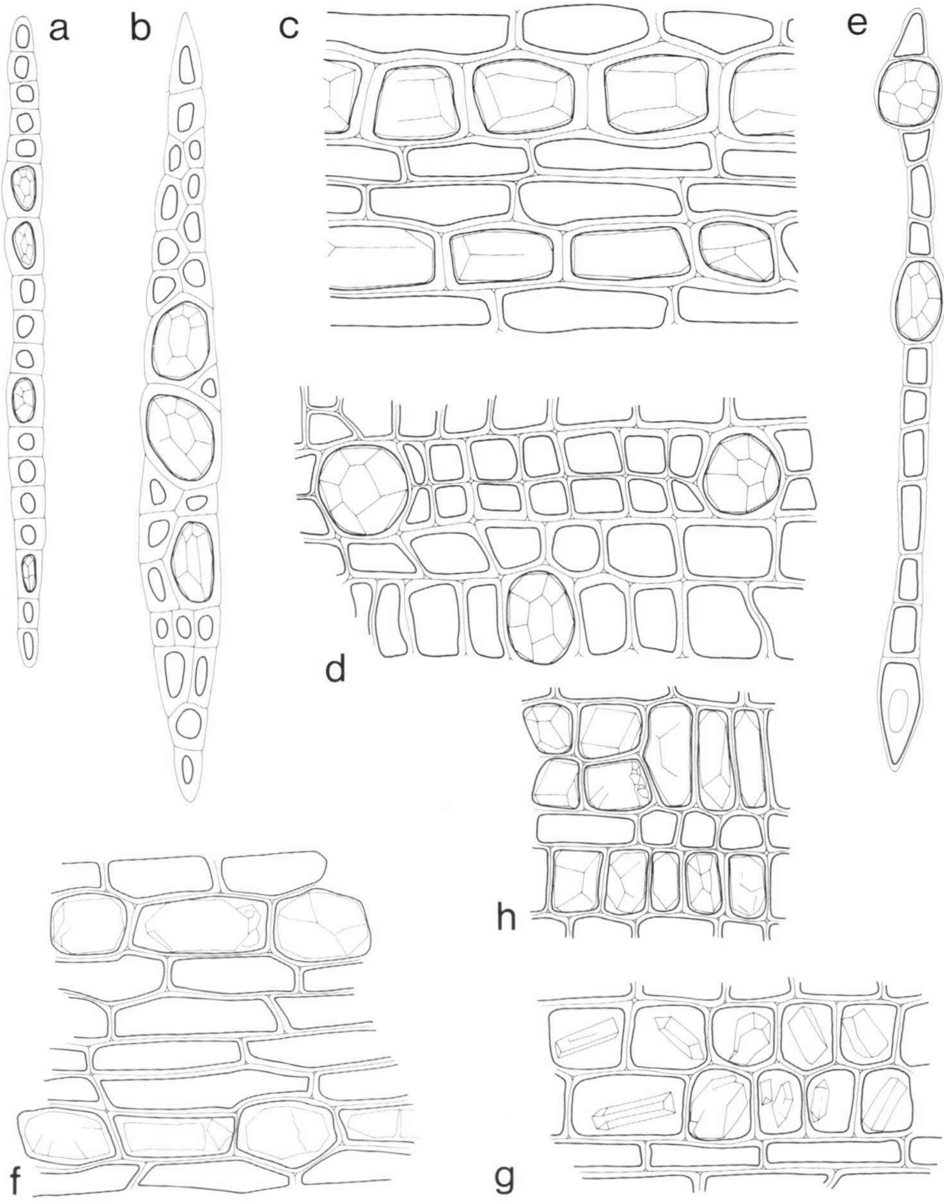

Fig. 3. Camera lucida drawings of solitary crystals in rays of some *Combretaceae*, all × 250. – a. b, e, tangential sections; c, d, f – h, radial sections. – a – c, f, g, very large crystals, completely filling the ray cells, crystalliferous cells enlarged, but in tangential view not, or hardly extending beyond the outline of the rays. – d & e, idioblast, containing a large solitary crystal; note the perforation of a radial vessel member in the bottom cell of e. – h. Small, more or less rhomboidal crystals to elongate crystals with blunt or pointed ends. – a. *Bucida macrostachya*. – b. *Bucida buceras*. – c. *Anogeissus acuminata*. – d & e. *Combretum celastroides*. – f. *Terminalia orbicularis*. – g. *Terminalia nigrovenulosa*. – h. *Terminalia polyantha*.

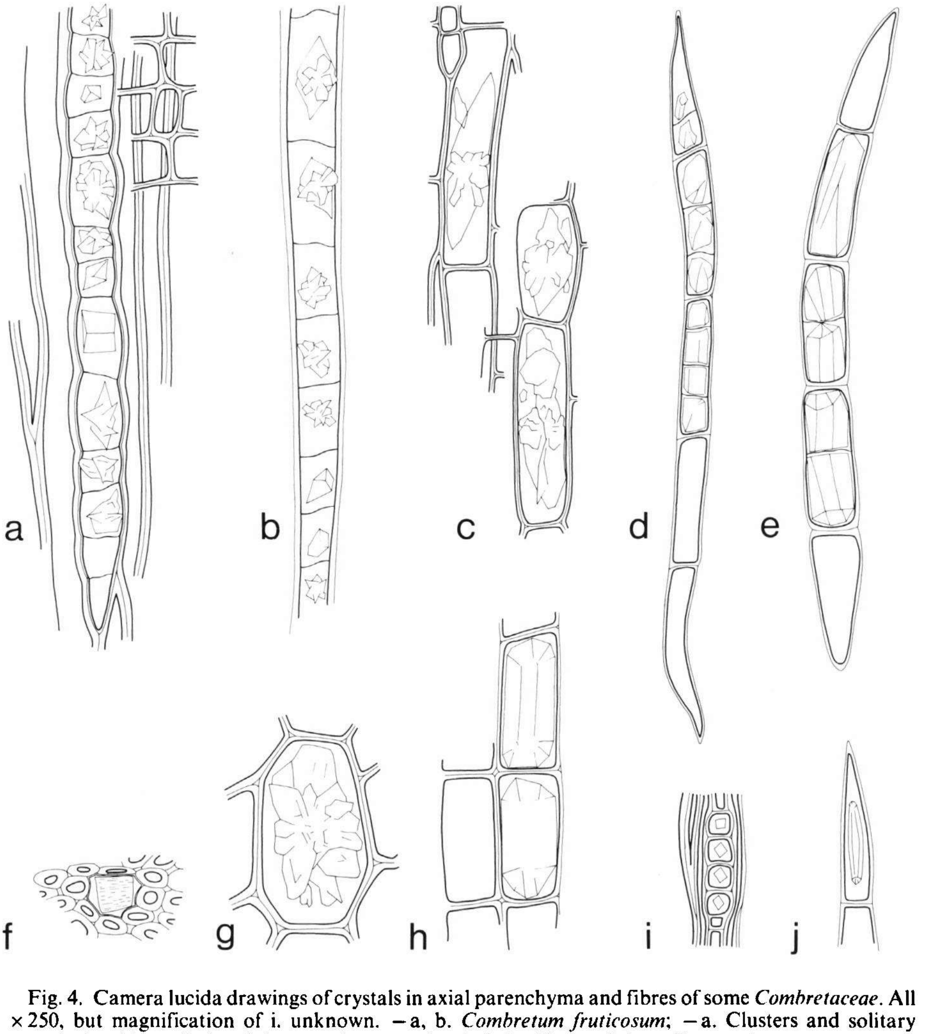

Fig. 4. Camera lucida drawings of crystals in axial parenchyma and fibres of some *Combretaceae*. All ×250, but magnification of i. unknown. —a, b. *Combretum fruticosum*; —a. Clusters and solitary crystals in thin-walled axial parenchyma. —b. *ibid.* in fibres of juvenile wood. —c. *Terminalia complanata;* asymmetrically elongated clustered crystal. —d & e. *Buchenavia kleinii*; solitary crystals, partly or completely filling chambers of chambered axial parenchyma. —f. *Combretum fruticosum;* transverse section of very thin-walled axial parenchyma with solitary crystal. —g. *Terminalia catappa*; idioblast with clustered crystal. —h. *Terminalia arbuscula;* large solitary crystal, completely filling nonchambered axial parenchyma cell. —i. *Terminalia prunoides*; rhomboidal crystals in idioblasts in axial parenchyma (from: Hooks, 1966). —j. *Terminalia papuana*; styloid.

Silica

Silica is only rarely found in this family, and it is therefore not surprising that several authors (Amos, 1952; Sharma & Rao, 1970; Hirata *et al.*, 1972; Ter Welle, 1976) mention in their surveys that silica is absent from the *Combretaceae.* Only Gonggrijp (1952) recorded a few silica grains in only one of several samples of *Lumnitzera.* Silica was not found in the Lumnitzera samples studied by me. More or less globular silica grains with a granular surface were only found in the axial parenchyma of *Buchenavia acuminata* (Plate 8/56) and *B. fanshawi.* Amorphous silica was present in one out of three samples of *Terminalia dichotoma* and in one sample out of two of *Strephonema pseudocola.*

Intercellular longitudinal canals

Intercellular longitudinal canals, containing a solid amorphous ('gummy') contents are reported for a varying number of species in some genera of this family (*Anogeissus, Bucida, Combretum, Ramatuella* and *Terminalia*, Plate 3/14). In *Anogeissus*, the gum canals are formed as a result of some injury to the bark and/or to the cambium and xylem (Gosh & Purkayastha, 1959). The gum canals in the other genera are probably of a similar traumatic origin, This may explain why these canals were not observed in a number of samples studied by me, although they were mentioned in the literature for the species concerned. The gummy products (at least of *Anogeissus* and *Terminalia*) are of good quality (Anderson & Bell, 1974; Gosh & Purkayastha, 1959; Lefèvre, 1905) and are in small amounts harvested in India. Large scale exploitation however, appears unprofitable.

VARIABILITY AND DIAGNOSTIC VALUE OF THE CHARACTERS

Part of the wood anatomical variation in the *Combretaceae* is listed in table 12. From this table it is clear, that a few characters are constant within a genus, and are therefore of diagnostic value on the generic level. Other characters (like the crystal type) show a great variation within a genus, but can be of considerable value on the species level. The fact that many characters have very little diagnostic value at the genus level is mainly caused by the wood anatomical variation present within the genus *Terminalia* – and to a lesser extent also in *Combretum* – which largely covers the wood antomical variation of the whole family. The presence of certain characters (like vestures on apertures or type of crystals) may be helpful as a positive diagnostic character, but their absence cannot be used for diagnostic purposes. The variation and diagnostic value of the individual wood anatomical characters will be elaborately discussed below.

The presence or absence of growth rings has in many genera not or only a restricted diagnostic value, because they were often only present in part of the samples of a single species (*e.g.* of *Lumnitzera*). In *Conocarpus erectus* growth rings were present in all samples studied by me, but they were absent from *C. lancifolius.* However, Tomlinson & Craighead (1972) mentioned that growth rings were absent from *C. erectus*, thus proving that in this species too growth rings are of no absolute diagnostic value. In *Terminalia* the occurrence of growth rings may be a differentiating character on the species level, but only a limited number of specimens was studied per species, and the infra-specific variation is therefore insufficiently known.

The vessel frequencies of the woods studied here vary from 1 – 2 to 164/mm^2. In most genera (and several species) these frequencies are not very constant and there is a great deal of overlapping in values between the genera.

Data on vessel frequencies recorded in the literature agree well with the values I found. Only Rao (1972) found excessively higher values (4 – 7 times the values I found), and he very probably made an error when calculating the vessel frequencies.

Vessels are mostly arranged in multiples of 2 and 3. Only in a few genera multiples often constist of 4 or 5 elements (*Anogeissus*, *Lumnitzera*, *Macropteranthus*) and in these high to very high vessel frequencies (over 50/mm^2) are commonly found.

Vessel member lengths of the various species and genera strongly overlap with each other (*cf.* Fig. 7) and are hardly of diagnostic value.

Inter-vessel pits are mainly alternate as are the vessel – ray and vessel – parenchyma pits and there is little variation. Apertures may be coalescent in some species, but when more samples of a species were studied, presence or absence and frequency of coalescent apertures often appeared variable below the species level. The diameter of the inter-vessel pits and the occurrence of infrequently unilaterally compound pits or of simple vessel – parenchyma pits (*Buchenavia*) may be of diagnostic value on the species level, not on the generic level.

Two distinct types of vessels (normal ones and very narrow vessel elements, intermingled with vascular tracheids) are present in all samples of the genera of the *Combretinae*. In a few other genera with frequent rather narrow vessels in multiples of 3 – 5 (*e.g. Anogeissus*, *Lumnitzera*) some very narrow elements may incidentally be present, but because of the presence of some intermediate forms, two distinct types cannot be recognized in these genera. Vascular tracheids are also infrequently present in *Strephonema*, but always in association with the very wide vessel elements.

The two main types of vesturing in the pit chamber are of value for separating the two subfamilies, *i.e.* for recognizing *Strephonema*. The variation within the type B recorded in *Terminalia* (Table 9b) makes this character of a doubtful diagnostic value, although the variation was not found in other genera, *cf.* table 9a. The occurrence of vestures on apertures may be a helpful character, but their absence cannot be used for diagnostic purposes.

Radial vessels are frequently or infrequently present in all samples studied of the genera of the *Combretinae*. Because of their uniqueness – until now never recorded for any other family – they are of important diagnostic value to recognize these genera. Yet it must be mentioned that the radial vessels are sometimes very infrequent and difficult to find.

The occurrence of vessel contents or tyloses is of no diagnostic value. Fibre length, like vessel member length, strongly overlaps in most genera. However, the ratio of vessel member length to fibre length provides a useful and significant diagnostic character for the separation of the *Laguncularieae* (*Laguncularia*, *Lumnitzera*, *Macropteranthus*) from the other genera of the family (see Fig. 8).

Distinctly bordered fibre pits (8 – 10 µm) are found in one genus only (*Strephonema*). All other genera have fibres with simple or minutely bordered pits (1 – 3 µm).

The thickness of the fibre walls in some species is rather constant, but may in others and in most genera show a sometimes considerable variation. When used as an additional character of minor importance it may have some diagnostic value on the species level. The presence of septa in fibres is of restricted diagnostic value, and then only on the specific level. They are present in several genera, but not always in all species or in all samples of one species.

In the smaller genera, the main type of parenchyma distribution (aliform, confluent, etc.) is rather constant. In genera of which more species have been studied, the range of variation increases and in *Terminalia* all possible types can be found. Yet this character may have some diagnostic value on the specific level, but only in cases where distinctly different types (*e.g.* aliform and banded) are compared. Transitions from aliform to confluent or from confluent to banded can easily be found within one species or sometimes one specimen. Marginal parenchyma (either apotracheal or paratracheal) is found in a few genera but is not always clearly present on each growth ring boundary and is therefore only of restricted value on the species level.

Ray width is rather constant in some genera, but may be very variable in others (see table 12) and also in some species (*cf. Combretum* and *Terminalia*). Rays of juvenile woods are composed of erect cells only, those of mature woods of procumbent, square and erect cells in varying frequency. Crystalliferous ray cells are frequently enlarged and should not be taken in account when comparing ray types. Typically heterogeneous II (Kribs, 1950) rays are present in the wood of *Strephonema* only. In the other woods rays are more or less intermediate between uniseriate heterogeneous and uniseriate homogeneous or between heterogeneous III and homogeneous and do not always provide a reliable character for diagnostic purposes.

Crystals of various types can be found in rays and axial parenchyma. Although their occurrence can be of considerable diagnostic value on the species level (*Terminalia*, *Combretum*) it can hardly be used on the generic level.

Silica grains are found in one genus (*Buchenavia*, though in two species only). Amorphous silica is found in one sample out of two or three (*Strephonema*, *Terminalia dichotoma*) and is of no diagnostic value here.

Longitudinal intercellular canals are recorded for part of the species of some genera all belonging to the *Terminalia* group, and were not present in all samples studied. Although these canals are of traumatic origin, their presence may be used as a character to designate a sample to this group of genera.

TAXONOMIC VALUE OF THE WOOD ANATOMICAL CHARACTERS

The taxonomic value of the individual woord anatomical characters is largely determined by their diagnostic value (see above) and by the degree of correlation with other micro- or macromorphological characters. Characters of which the diagnostic value is limited because of the occurrence of intermediate character states, may still be of taxonomic value, because they witness mutual affinity. On the other hand, characters which have little diagnostic value because of a strong influence of ecological factors on their expression (most quantitative characters and distinctness of growth ring boundaries) are obviously of no taxonomic value.

In search for overall similarities or dissimilarities of genera or suprageneric taxa in *Combretaceae* the following characters appeared to be of special taxonomic value: fibre type (fibre-tracheids *versus* libriform fibres with simple or minutely bordered pits); the occurrence of two size-classes of vessels; presence or absence of radial vessels; the ratio of vessel member to fibre length; and the main type of vesturing of the vessel wall pits. (Type A *versus* type B).

Included phloem is present in a few genera only, all belonging to the *Combretinae;* however, not in all genera of this group and in *Combretum* restricted to part of the species only (in particular absent from the lianas). The irregular distribution of this character limits its taxonomic value on the supra-generic level. Within *Combretum,* there is some correlation with infra-generic classification. Included phloem is not strictly correlated with habit, because *Calycopteris* has a climbing habit and included phloem.

The great variation in parenchyma distribution within the large genera *Terminalia* and *Combretum* strongly limits the taxonomic value of this character on and above the generic level. In some genera or groups of genera the variation is such that the parenchyma distribution can hardly be used to characterize the wood of these taxa; in other groups a similar variation is caused by a few exceptions. In the latter case the parenchyma distribution may still be used as a complementary taxonomic character.

Although the ray type is rather variable within the *Combretaceae*, it is a useful character for separating *Strephonema* (heterogeneous II – III) from the other genera (heterogeneous uniseriate and heterogeneous III – homogeneous rays).

The taxonomic value of the crystal complement within Combretaceous woods is mostly limited to the specific level.

WOOD ANATOMY OF LIANAS COMPARED TO ERECT SHRUBS AND TREES

Lianas usually have long, thin, pliable stems of which the internal structure is sometimes aberrant as compared with that of straight, erect stems. Many types of 'anomalous structures' have been recognized, especially for species with a climbing habit (*cf.* Schenck, 1893; Obaton, 1960).

In the Combretaceae two genera contain lianas only, *viz. Calycopteris* (1 species) and *Quisqualis* (*c.* 20 species), whilst in the genus *Combretum* part of the species are of climbing habit and many others are shrubs or trees (see table 4). These three genera belong to the subtribe *Combretinae* (also including *Calopyxis, Guiera* and *Thiloa*: shrubs or small trees). In comparing the wood anatomical characters, listed in table 12, of the climbing members of the *Combretaceae* with the erect shrubs and trees of this group, it appears that there are no obvious qualitative differences between these representatives with these widely differing habits. Yet some differences exist, which will be discussed below.

It seems remarkable that the qualitative feature of included phloem, one of the anomalous characters often recorded for lianas of other families, is not related to habit in the *Combretaceae*: trees and shrubs belonging to the genera *Guiera* and *Thiloa* have included phloem and also the lianas belonging to *Calycopteris.* In *Combretum* the occurrence of included phloem is largely restricted to erect species from Africa belonging to the subgenus *Combretum* (see table 4 and taxonomic discussion) but also occurs in the climbing species *C. edwardsii.*

Ayensu & Stern (1964) found in Passifloraceae that lianas have wider elements than their erect relatives; Carlquist (1975) reported similar trends in his general comparison of the wood structure of plants in different habitas and with different habit. From table 10 it appears that in *Combretinae* the lianas also have wider vessels, occurring in a lower frequency than in the erect taxa of the same group. In

	Liana, scandent shrub	Tree, shrub
Vessel frequency /mm^2	(2–)3–9(–11)	(1–)3–45(–80)
Vessel diameter in μm	(54–)156–283(–400)	(26–)54–193(–246)
Vessel member length in μm	(160–)350–430(–600)	(130–)180–350(–520)
Fibre length in μm	(430–)610–815(–1120)	(310–)550–1140(–1440)

Table 10. Quantitative data of lianas of the subtribe *Combretinae* compared with their erect relatives. Data are presented as range of means, with the extremes between brackets.

this table immature samples (diameter less than 4 cm) are omitted for trees and shrubs but have been included for lianas, thus showing that even for immature samples this tendency holds true. According to Carlquist (1975) lianas tend to have shorter vessel members than their erect relatives, in order to offer a better resistance against collapse through high negative pressures. In *Combretaceae* this tendency is reversed: lianas have the longer vessel elements (table 10). Here habitat factors may have played a dominant role: the tree and shrub species of the *Combretinae* studied by me, mainly grow under relatively dry conditions (deciduous thickets, wooded grassland, dry savannas and sandy wastes), whilst the lianas prefer more mesic conditions (wooded grasslands with high rainfall to rainforests). This difference in ecological preference might result in shorter vessel members for the more xeric species (*cf.* Carlquist, 1975 and the next chapter on ecological considerations). For fibre length there is no correlation with either the mesic-xeric gradient nor with the climbing or erect habit. The fact that the lianas with their longer vessel members do not show longer fibres than the erect relatives can be tentatively explained by the wide diameter of the vessels in lianas, which in spite of the low frequency, allows little space for intrusive growth by the fibres.

From the functionally adaptive point of view it seems that lianas are better fit for the conduction of large volumes of water with wide vessels offering little resistance to flow. Other differences may be secondary effects (*e.g.* relatively short fibre length), or may be due to differences in ecological preference (longer vessel members in mesic lianas). The difference in vessel diameter between climbing and erect species may have been accentuated by this difference in ecological preference (*cf.* Carlquist, 1975, who has suggested that xeric conditions induce narrower vessels).

ECOLOGICAL CONSIDERATIONS

In the previous chapter ecological considerations have already entered the discussion when comparing *Combretaceae* of climbing or erect habit. In this part the possible correlations between wood anatomy and the physical environment will be further explored, for as far this is possible with the scanty ecological data. Emphasis is put on moisture availability. Altitudinal and latidudinal trends in the wood anatomy (as discussed by Baas, 1973, 1976; van der Graaff & Baas, 1974) are of little interest here, since most Combretaceae grow at rather low altitudes in the tropical zone.

Most of the ecological data had to be gleaned from the literature, since collecting data accompanying the wood samples studied here were usually insufficient.

For *Terminalia* 38 of the species could roughly be arranged into five groups of decreasing moisture availability.

1. Rain-forests and fresh-water swamps (*T. amazonia, T. belerica, T. bialata, T. brassii, T. complanata, T. copelandii, T. darlingii, T. dichotoma, T. foetidissima, T. impediens, T. microcarpa, T. nitens, T. papuana, T. reitzii, T. sepicana*).
2. Drier parts of rain-forest and moist deciduous forests (*T. alata, T. calamansanai, T. citrina, T. ivorensis, T. manii, T. pellucida, T. scutifera, T. superba*).
3. Dry deciduous forests, dry zone river banks, dry thickets & secondary forest (*T. arjuna, T. chebula, T. laxiflora, T. macroptera, T. oliverii, T. paniculata, T. polyantha*).
4. Savannas (*T. brownii, T. glaucescens, T. kilimanscharica, T. mollis, T. orbicularis*).
5. Coastal species and mangroves, *i.e.* saline environments resulting in physiological drought (*T. catappa, T. samoensis*; the former species is recorded to occur naturally in saline habitats, it is now widely cultivated outside this environment; on the samples studied, data were insufficient to know whether they were from cultivated or native trees).

Fig. 5a clearly demonstrates that the decrease in moisture availability corresponds with a decrease in vessel member length, thus supporting general trends postulated by Carlquist (1975) and others.

In the *Combretinae* (*cf.* Fig. 7) these trends are also present: the longest vessel elements are found in the genera growing under the most mesic conditions (*Calycopteris, Quisqualis*, and *Thiloa*), whilst the more xeric species of *Combretum* and *Guiera* have the shorter vessel members. (For the differences in habit within this group and vessel member length see the previous chapter).

Pteleopsis hylodendron, a rain-forest species, also has longer vessel members than most of the other species studied from this genus, all from savannas (see table 7). However, for *Anogeissus* (table 1, compare legend of Fig. 5b) no correlation between ecological preference and vessel member length is evident.

In *Anogeissus* (Fig. 5b) and *Pteleopsis* another mesic-xeric trend in wood structure is evident, *viz.* that species growing under dry conditions have narrower vessels in higher frequencies than species with a more mesic ecology. This tendency can also be demonstrated when comparing all species from the wood anatomically closely related subtribes *Pteleopsidinae* and *Terminaliinae* (Fig. 6), although somewhat obscured here by the existence of a very strong overlap between the representatives from different ecological categories. This can also partly be accounted for by considering the different tree sizes (*cf.* van Vliet, 1976b). In Fig. 6, *Terminalia catappa* from the landside parts of the mangroves takes a more or less intermediate position in the overlapping range of xeric and mesic taxa. It is tentative, though rather far-fetched, to 'explain' this in terms of the mildly saline conditions of the environment of *T. catappa* and of the possibility that the root system of this species reaches down to the fresh ground water. *Conocarpus* (*Terminaliinae*) and *Laguncularia* and *Lumnitzera* (*Languncularieae*) are also from mangrove vegatations and have fairly high vessel frequencies and narrow vessels as is shown in Fig. 6. However, *Languncularia*, of these three genera growing under the most saline conditions, has the widest vessel elements in the lowest frequencies. The genus *Macropteranthus* also belonging to the *Laguncularieae* and growing along streams in rather dry vegetations in Australia, has very narrow vessel elements in the highest

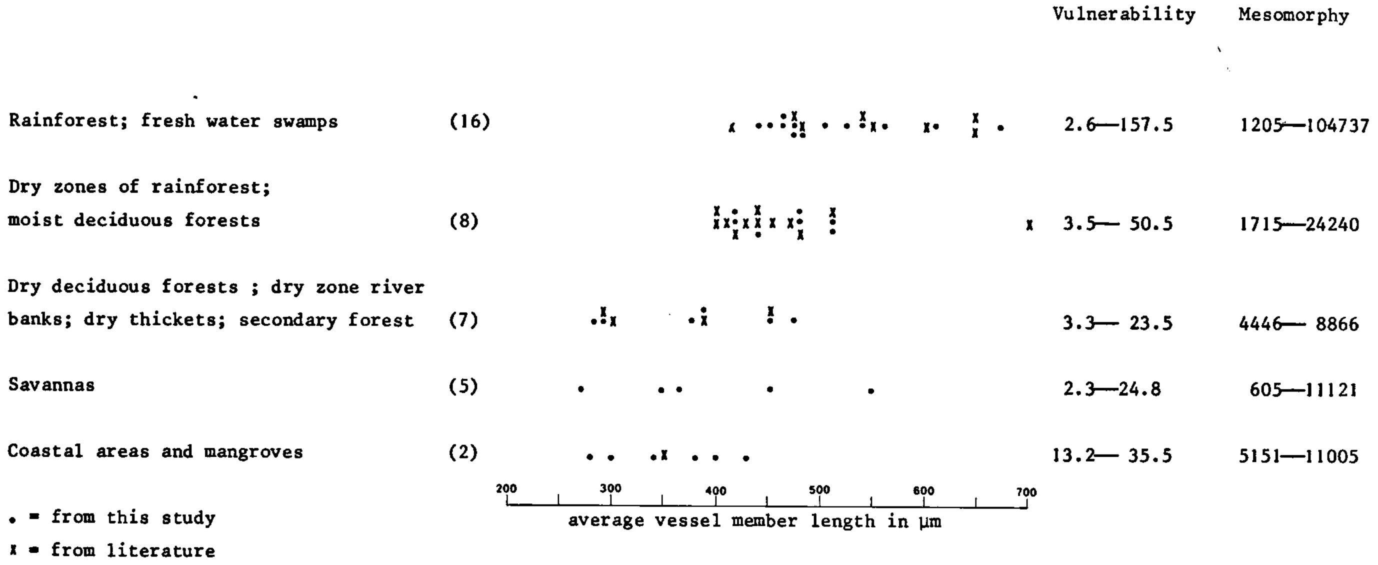

Fig. 5a. Average vessel member length of samples from species of Terminalia growing in five different ecological conditions. Number of species in each group is given between brackets. For Vulnerability and Mesomorphy sensu Carlquist (1977) see text.

frequency for this family. Tree size in *Macropteranthus* is about similar to that in Laguncularia and the range of values for vessel diameter and vessel frequency in *Lagunculariеae* are therefore not to be used as a strong support for tendencies found in other groups where mangrove species have more narrow and more frequent vessels than their inland relatives (*cf.* Panshin, 1932; Janssonius, 1950; van Vliet, 1976b).

In this analysis the *Combretinae* have not been considered on account of the occurrence of two size classes of vessels, which complicates any comparison.

Although within the *Combretaceae* much of the quantitative variation in vessel characters (length, frequency, diameter) can be explained by considering the environmental conditions to which the species are subjected, one cannot generalize the ecological tendencies and apply them to all representatives, as is demonstrated by the deviating values found in the *Lagunculariеae*. This is not at all surprising when one considers that the waterbalance is not only governed by the transport efficiency of the secondary xylem but also by functional components in other plant parts (notably leaf size and indumentum).

Carlquist (1977) has recently introduced two terms in ecological wood anatomy: '*vulnerability*' (= mean vessel diameter, divided by mean vessel frequency) and '*mesomorphy*' (= vulnerability multiplied by the mean vessel member length). Low vulnerability values were said to indicate the capacity of a species to resist water stress or freezing (narrow vessels decrease the risk of air embolism, high vessel frequencies compensate the effect of local air embolism), and high mesomorphy values were said to be indicative of a mesic ecology of the species, thus making special adaptations to water stress and high negative pressure superfluous. In table 5a the vulnerability and mesomorphy values *sensu* Carlquist have been calculated

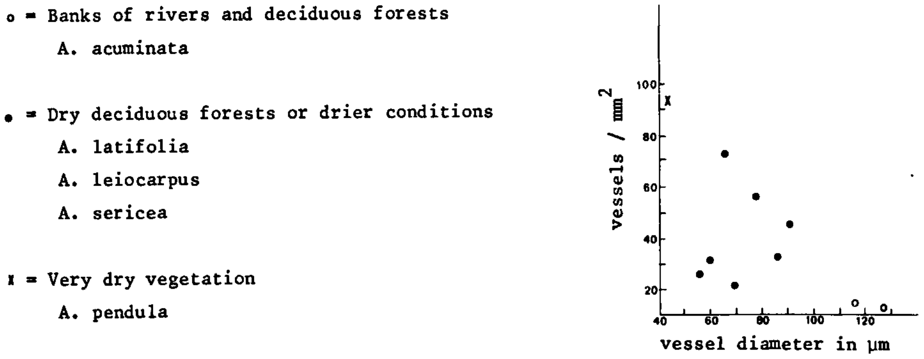

Fig. 5b. Average vessel frequencies and vessel diameters of species of Anogeissus growing in three different ecological conditions.

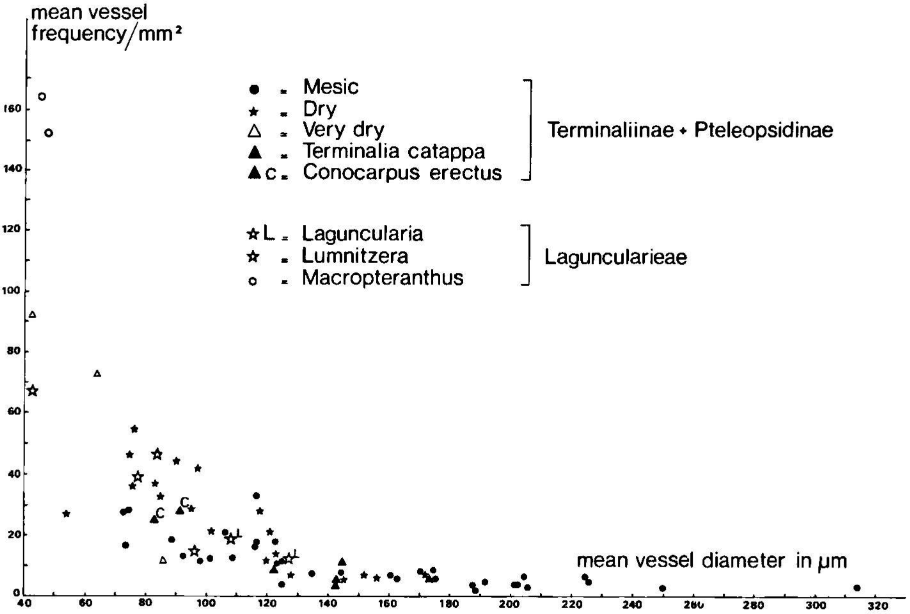

Fig. 6. Vessel frequency plotted against vessel diameter of some *Combretaceae* (see Ecological considerations).

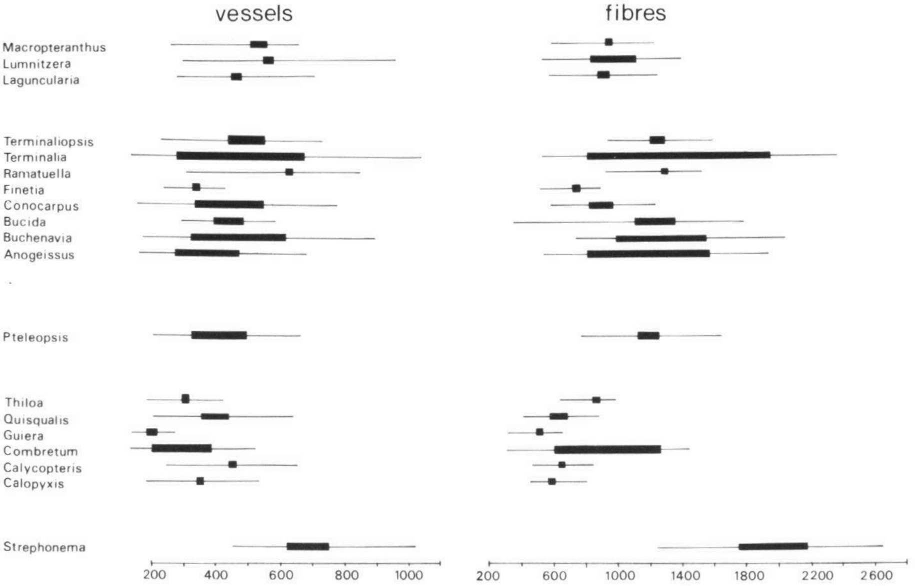

Fig. 7. Range of vessel member and fibre length of the genera of the *Combretaceae* (——— range of extreme values; ▬▬ range of average values).

for the *Terminalia* species used in the ecological analysis of vessel member length. It appears that in all ecological categories except the mangrove vegetation, very low vulnerability values occur (2–4). The absence of such low values in the coastal species and the mangroves is in conflict with Carlquist's hypothesis, because mangroves are known to be subjected to high water stresses and strong negative pressures. The occurrence of the highest vulnerability values in rain-forest species agrees with the hypothesis but for the remainder the ranges of the vulnerability and especially for mesomorphy values make no sense whatsoever. This is not very surprising in view of the fact that vessel frequency, vessel diameter and vessel member length are incomparable units if interpreted functionally. Moreover the relative importance of these characters for water conduction in all its complexity remains to be assessed; especially the role of vessel member length remains completely speculative (*cf.* Carlquist, 1975, *versus* Baas, 1976). Even the data presented by Carlquist himself (1977) lend little support to the relevance of the artificial units 'vulnerability' and 'mesomorphy': the values he presented for different vegetation types in Australia are obviously not significantly different because of the wide range in variation found within each vegetation type.

RELATIONSHIPS WITHIN THE COMBRETACEAE

The *Combretaceae* have been the subject of extensive taxonomic studies, mainly by A. W. Exell and C. A. Stace. Their work, dealing with external morphological as well as leaf anatomical characters, has resulted in a complete classification of all genera and in an understanding of their mutual affinities. Their classification (table 11) will be followed in this paper, when discussing the taxonomic implications of the wood anatomical diversity.

Subdivision of the family.

Wood anatomically the *Combretaceae* can be divided into four groups, two of which (coinciding with the subfamily *Strephonematoideae* and subtribe *Combretinae* respectively) are very distinct.

Strephonema, constituting one of Exell & Stace's (1966) two subfamilies, can be recognized by its fibre-tracheids, the distinctly heterogeneous II–III rays, the parenchyma distribution of large apotracheal aggregates in addition to the more common aliform to confluent type, and the vesturing of type A. All other genera have libriform fibres, heterogeneous III to homogeneous rays, vestures of type B and they lack large apotracheal parenchyma aggregates.

The second distinct group is formed by the genera *Calopyxis*, *Calycopteris*, *Combretum*, *Guiera*, *Quisqualis and Thiloa*. These genera constitute, together with the genus *Meiostemon*, of which no material could be obtained for this study, the subtribe *Combretinae* of the tribe *Combreteae* in Exell & Stace's subfamily *Combretoideae*. Wood anatomically they are characterized by radial vessels and two distinct types of axial vessels: normal ones and very narrow ones mixed with vascular tracheids. Included phloem is encountered in genera of this subtribe only, though not in all of them. Parenchyma is predominantly scanty but in several species of *Combretum* it is abundant.

					a	b
Subfamily STREPHONEMATOIDEAE						
Strephonema			Af		5	1
Subfamily COMBRETOIDEAE						
Tribe COMBRETEAE						
Subtribe COMBRETINAE						
Combretum		Am	Af	As	200	14
Quisqualis			Af	As	16	2
Calopyxis			Af (M)		22	1
Meiostemon			As (M)		2	–
Thiloa		Am			3	1
Guiera			Af		1	1
Calycopteris				As	1	1
Subtribe PTELEOPSIDINAE						
Pteleopsis			Af		10	4
Subtribe TERMINALIINAE						
Terminalia	Au	Am	Af	As	150	43
Ramatuella		Am			6	2
Terminaliopsis			Af (M)		2	1
Bucida		Am			9	2
Buchenavia		Am			22	5
Anogeissus			Af	As	14	5
Finetia				As	1	1
Conocarpus		Am				
Tribe LAGUNCULARIEAE						
Laguncularia		Am	Af		2	2
Lumnitzera	Au		Af	As	2	2
Macropteranthus	Au				4	1
					475	93

Table 11. Classification of the Combretaceae according to Exell & Stace (1966), including geographical range (Au = Australia, Am = America, Af = Africa, Af (M) = Madagascar only, As = Asia), the estimated number of species in each genus (a), and the number of species studied for this paper (b).

The remaining genera are rather heterogeneous in their wood anatomy (*cf.* table 12), but three of them, constituting the tribe *Laguncularieae* of subfamily *Combretoideae* can be separated on the basis of a quantitative wood anatomical character which is seldomly used: the ratio of vessel member to fibre length is significantly lower in the *Laguncularieae* than in the remainder (a few *Combretinae* excepted, but these differ strongly in qualitative characters – see above). In Fig. 8 the differences in fibre length to vessel member length ratio are shown. If compared with genera with which they overlap in qualitative characters (from the subtribe *Terminaliinae* and *Pteleopsidinae* of the tribe *Combreteae*) the Student T-test (*cf.* Zijp, 1964) gives a T. value of 2.08; $p < 0.5$ for the difference in this element length ratio (0.5 – 0.67 for *Laguncularieae*; 0.2 – 0.43 (– 0.57) for the other genera). The *Laguncularieae* show in the genera *Lumnitzera* and *Macropteranthus* the highest values for vessel frequency, thus providing a subsidiary feature for the characterization of (part of) this tribe.

The remaining genera, though very heterogeneous in many of their characters, can be kept together because they lack the features typical for the *Strephonematoideae*, the *Laguncularieae* and the *Combretinae*. The wide wood anatomical range is completely covered by the variation in the large genus *Terminalia*. They constitute the subtribes *Terminaliinae* (*Terminalia*, and 7 other genera) and *Pteleopsidinae* (*Pteleopsis* only), both belonging to the tribe *Combreteae*. The fact that one large genus covers the entire range of variation of all these genera may be taken as an indication of their close mutual affinities.

From the above it is clear that the wood anatomical subdivision of the *Combretaceae* closely follows Exell & Stace's classification. The taxonomic status of the individual groups and the raltionship patterns between their constituents will be discussed more elaborately below.

Subfamily Strephonematoideae. Strephonema

The outstanding wood anatomical characters of this genus fully justify a special taxonomic status for it. Venkateswarlu & Rao (1970) placed it in a family of its own, but Exell & Stace (1966) were of the opinion that *Strephonema* should be included in *Combretaceae*, as a separate subfamily, mainly because of the occurrence of characteristic '*Combretaceae*-hairs' (Stace, 1965) in some of its species. Den Outer & Fundter (1976) found differences as well as shared features in the phloem of *Strephonema* as compared to a limited number of other *Combretaceae* and also supported the subfamily status. Accommodation of *Strephonema* in another family has only been proposed by Bentham & Hooker (1867) who treated the genus in *Lythraceae*, but this position has never been supported by other workers on these families and is certainly in conflict with wood anatomical evidence (*cf.* Baas & Zweypfenning, in prep.).

If judged by its wood anatomy alone, *Strephonema* would probably never be linked with *Combretaceae*. However, in view of the evidence from other plant parts the subfamily status can be accepted as sufficiently emphasizing the aberrant position within the whole family. Similar situations are fairly common in other families where doubtless members may yet show an aberrant wood anatomy (*cf.* the wood anatomical heterogeneity of the *Rhizophoraceae*, van Vliet, 1976).

Subfamily Combretoideae, tribe Laguncularieae

The three genera constituting this tribe are only distinct from the tribe *Combreteae* (*Terminaliinae* and *Pteleopsidinae*) in the vessel member to fibre length ratio. Similarities in other characters with genera of the two subtribes referred to above (especially with *Terminalia*) may be used to indicate affinity (*cf.* table 12). Considering the subtle differences of *Laguncularieae* with part of the tribe *Combreteae* one would, from the wood anatomical point of view, be inclined to disagree with the tribal status of Laguncularieae and prefer a taxonomic status of lower rank.

Table 12. Some wood anatomical characters of the Combretaceae.

	Strephonema	Combretum	Quisqualis	Guiera	Thiloa	Calopyxis	Calycopteris	Pteleopsis	Terminalia	Conocarpus	Bucida	Ramatuella	Terminaliopsis	Buchenavia	Anogeissus	Finetia	Laguncularia	Lumnitzera	Macropteranthus
liana	–	O	×	–	–	–	×	–	–	–	–	–	–	–	–	–	–	–	–
VESSELS																			
diffuse	×	O	×	×	×$^{1)}$	×	×	×	×	×	×	×	×	×	×	×	×	×	×
ring- or semi- ring-porous	–	O	×	–	–	(×)	×	–	–	–	–	–	–	–	–	–	–	–	–
two types of vessel elements	(×)	×	×	×	×	×	×	–	–	–	–	–	–	–	–	–	–	–	–
radial vessels	–	×	×	×	×	×	×	–	–	–	–	–	–	–	–	–	–	–	–
included phloem	–	O	–	×	×	–	×	–	–	–	–	–	–	–	–	–	–	–	–
FIBRES																			
FIBRE-TRACHEIDS	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
libriform fibres	–	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
septate fibres	–	O	×	–	–	×	×	–	O	×	–	–	–	×	O	×	–	–	–
PARENCHYMA																			
scanty	–	O	×	×	×	×	×	–	O	O	–	O	–	–	O	×	–	×	×
vasicentric-aliform	–	O	–	–	–	–	–	–	O	–	O	–	–	O	O	–	–	–	–
aliform-confluent	×	O	–	–	–	–	–	O	O	O	O	O	O	O	O	×	×	(O)	–
confluent-banded	–	O	–	–	–	–	–	O	O	O	–	O	O	O	–	–	–	–	–
banded	–	–	–	–	–	–	–	O	O	–	–	–	–	–	–	–	(O)	–	–
marginal$^{8)}$	–	O	–	–	–	–	–	(O)	O	O	×	–	×	O	×	–	–	(O)	–
apotracheal aggregates	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
RAYS																			
uniseriate$^{10)}$	–	O	×	–	×	×	×	O	O	O	–	O	–	O	O	×	×	×	×
1- & 2-seriate	–	O	–	×	–	–	–	–	O	O	–	–	–	O	O	–	–	–	–
1–3-seriate	×	O	–	–	–	–	–	O	O	–	×	O	×	–	–	–	–	–	–
1- & 4- or more-seriate	–	–	–	–	–	–	–	–	O	–	–	–	–	–	–	–	–	–	–

erect cells only	–	O[2]	O[2]	–	–	x[2]	–	–	–	–	–	–	–	–	–	x[2]	–	O[2]	–
square, erect & weakly procumbent cells	–	–	–	–	–	–	–	–	O	×	–	O	–	–	–	–	×	–	×
procumbent and infr. square cells	–	O	×	×	×	–	×	×	O	×	×	O	O	×	×	–	–	O[9]	–
heterogeneous II – III	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
intercellular spaces	–	–	–	–	–	–	–	–	O	–	–	–	–	–	–	–	–	–	–
CRYSTALS[7]																			
idioblasts with sol. cryst. in rays	–	O	–	×	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
large cryst. filling parenchyma cells	–	O	–	(×)	–	–	–	×[4]	O	(O)	×	–	–	O[4]	×	×	(×)	–	×
rhomboidal to elongated	–	O	–	–	–	–	–	–	O	–	–	–	–	O	–	–	–	–	–
large clusters in indioblasts	–	O	–	–	–	–	–	–	O	–	–	–	–	–	–	–	–	–	–
clusters in normal cells	–	O	O[3]	–	–	–	(×)	–	O	–	–	–	–	–	–	–	–	–	–
crystals in fibres	–	O	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
no crystals observed	–	O[11]	–	–	×	×	–	–	O	–	–	×	×	O	–	–	–	×	–
silica	O[5]	–	–	–	–	–	–	–	–	–	–	–	–	O[6]	–	–	–	–	–

═══ = subfamily boundary; ═══ = tribal boundary; ─── = subtribal boundary; according to Exell & Stace (1966).
× = character present in all samples studied; O = character present in only part of the samples studied; ( ) = character weakly developed; – = character absent from all samples studied.

[1] tending to form oblique patterns
[2] immature sample
[3] only in traumatic parenchyma
[4] axial parenchyma frequently septate
[5] amorphous, in axial parenchyma
[6] ± globular grains
[7] see for a more elaborate account of the distribution of the crystals the key to the genera
[8] mainly continuous with paratracheal parenchyma
[9] frequent square marginal cells
[10] infrequently with a biseriate portion
[11] small druses always present in the parenchyma of the included phloem

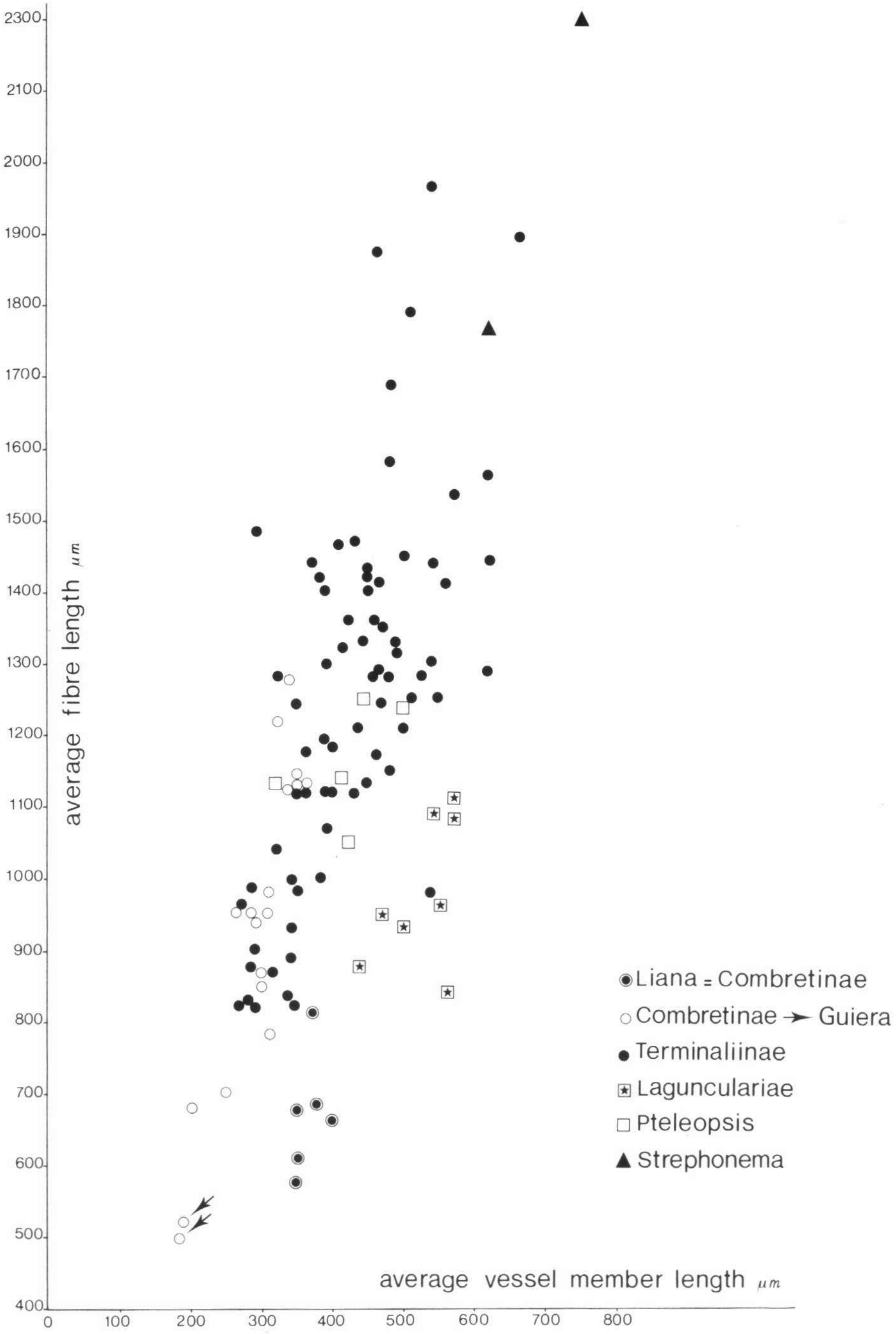

Fig. 8. Relationship between the average vessel member length and average fibre length of suprageneric taxa of *Combretaceae*.

Subfamily Combretoideae, tribe Combreteae, subtribe Combretinae

The genera of this subtribe are wood anatomically very distinct, mainly because of the occurrence of radial vessels and two distinct size classes of axial vessels (see also table 12 for other wood anatomical features, which tend to characterize this subtribe, such as scanty parenchyma and predominantly solitary 'normal' vessels). The wood anatomical distinctness of the subtribe is of slightly lower level than that of *Strephonema*, but the subtribal status hardly reflects the wood anatomical facts and seems too low a rank, especially when compared to the other subtribes *Terminaliinae* and *Pteleopsidinae* and the tribe *Laguncularieae* (see above).

Combretum is the largest genus of this subtribe (±200 species) and its wood anatomical diversity covers that of most other genera. The group is obviously a closely knit one, also from the wood anatomical point of view. This also applies to *Calycopteris* which wood anatomically fits well into this group (*cf.* table 12), although it was placed in a separate taxon by Engler & Diels (1899). Exell & Stace (1966) preferred to place it in *Combretinae* although they mention that it also shares some characters with the *Terminaliinae.*

Exell & Stace (1966) based the presumed relationship patterns in this subtribe on the occurrence of petals and the leaf indumentum. The presence of included phloem tends to be correlated with the occurrence of scales (*Combretum* subgen. *Combretum*, *Thiloa*, *Guiera; Calycopteris* has in this respect a slightly aberrant position, as mentioned above) instead of stalked glands.

Within *Combretum*, Exell & Stace (1966) recognized three subgenera: two large ones, *Combretum* and *Cacoucia*, differing in the presence of either scales or glands on the leaves; and the small subgenus *Apetalanthum*, composed of two species only, both lacking petals. Most species studied by me and described in the literature belong to the subgenus *Combretum*. Of subgenus *Cacoucia* I studied only two species (*C. trifoliatum* and *C. zenkeri*). Species of subgenus *Apetalanthum* have never been the subject of wood anatomical investigations. I briefly studied a twig of *C. apetalum* Wall., searching for included phloem only.

Although radial vessels were found in varying frequencies in all specimens studied, they have never been recorded before and were first described by me in an earlier paper (van Vliet, 1976a). This is most surprising in view of the fairly high number of *Combretum* species described in the wood anatomical literature.

Intraxylary or included phloem is found in part of the species, all belonging to subgenus *Combretum* (*cf.* table 10). As discussed before included phloem has only been found in one climbing species, *C. edwardsii*. Bearing this in mind, it is not surprising that included phloem is absent from the subgenus *Cacoucia* because most species belonging to this subgenus are lianas or scandent shrubs. Taxonomists working on *Combretum* have also recognized several sections in the subgenus *Combretum*. A world-wide revision has, however, never been made and it is therefore difficult to assign each species to its proper section. For an analysis of a possible correlation of the wood anatomical diversity and taxonomic subdivision of genus *Combretum*, an attempt has yet been made to arrange all species studied in sections following Wickens (1973), Stace (1969), Exell (1954, 1970), and Engler & Diels (1900) in that sequence of preference. Table 13 shows the result of this sectional classification and it appears that the occurrence of included phloem is restricted to a limited number of sections and serves as a good sectional character for those sections of which more than one species were studied (sections *Glabri-*

COMBRETUM

Subgenus Combretum	
Section	
Hypocrateropsis	C. celastroides, C. imberbe, C. padoides
Combretastrum	C. pyramidatum, C. cuspidatum
Macrostigmata	*C. engleri*
Metallicum	C. collinum, C. lemprocarpum
Glabripetala	*C. fragrans, C. gallabatense, C. glutinosum, C. hartmannianum, C. lepidotum*
Spathulipetala	C. zeyheri
Ciliapetala	C. acutifolium, *C. apiculataum, C. edwardsii, C. moggii, C. molle, C. nigricans*
Brevirama	C. hereroense
Chionanthoidea	C. capituliflorum, C. illairii
Angustomarginata	*C. erythrophyllum, C. kraussii, C. salicifolium, C. caffrum*
Combretum	C. fruticosum, C. rotundifolium, C. assimile
Paucinervis	*C. micranthum*
Monetariae	C. duarteanum

Table 13. Sectional classification of Combretum subgenus Combretum.
Taken from Wickens (1973), Stace (1969), Exell (1953, 1970), and Engler & Diels (1899), in that sequence of preference. ——— = liana; – – – – = scandent shrub; no underlining = shrub or tree.
Species with wood with included phloem are given in italics.

petala, Ciliapetala, and *Angustomarginata*). *C. acutifolium* forms the only exception in section *Ciliapetala.* In this section *C. edwardsii* is aberrant because it is the only climber in *Combretum* with included phloem. Stace (1969) stressed that this section *Ciliapetala* is in need of revision because it is heterogeneous in its scale characters. My wood anatomical results confirm part of this heterogeneity and support the need for revision. A careful analysis of all wood anatomical characters revealed no further correlation with the sectional subdivision of *Combretum.*

The occurrence of idioblasts containing large druses in the axial parenchyma of the species or subspecies of the *C. collinum* complex may prove to be of taxonomic importance if more material is studied.

Subfamily Combretoideae, tribe Combreteae, subtribes Terminaliinae and Pteleopsidinae

Pteleopsis, the only genus constituting the *Pteleopsidinae,* has been placed by Exell & Stace (1966) between the *Terminaliinae* and the *Combretinae* because it appears exactly intermediate between the two in its external characters. They also mentioned, however, that 'although the number of characters listed seems to indicate a relationship rather nearer to *Terminaliinae* than to *Combretinae*, great weight must be given to the presence of petals' (absent from *Terminaliinae*). Wood anatomy strongly points to a very close relationship of *Pteleopsis* with *Terminaliinae* or even an inclusion into the subtribe because its wood anatomy is completely within the range of variation found in *Terminaliinae* (*cq. Terminalia*). An inclusion in *Combretinae* as proposed by Engler & Diels (1899) is ruled out by wood anatomy because *Pteleopsis* lacks the characters so typical for the subtribe.

The considerable variation in subtribes *Terminaliinae* plus *Pteleopsidinae* is largely covered by the variation within the genus *Terminalia*, making it difficult to key out genera or to draw conclusions on relationship patterns in this group. The lack of a world-wide taxonomic revision of *Terminalia* (over 150 species) moreover makes it impossible to evaluate the taxonomic significance of the wood anatomical variation within that genus. In spite of much overlap, some genera (the marcromorphological distinct ones according to Exell & Stace, 1966) are wood anatomically more or less distinct: *viz. Anogeissus* and *Bucida* with their very large solitary crystals in strongly enlarged ray cells, and *Buchenavia* with silica grains in part of its species and simple vessel – parenchyma pits. However, *Finetia*, which according to Exell & Stace (1966) is a distinct genus but which was included in *Anogeissus* by Lecomte (1969), does not differ from *Anogeissus* in its wood anatomy.

PHYLOGENETIC CONSIDERATIONS

Wood anatomical specialization trends have been convincingly demonstrated for Dicotyledons in general. However, the wood anatomical variation within the *Combretaceae* hardly lends itself for phylogenetic interpretations, mainly because all representatives have a rather advanced wood anatomy. Characters such as vessel member length and vessel diameter, which figure in the Baileyan concepts as important parameters for specialization, have been shown to be largely correlated with environmental factors, in *Combretaceae* as well as in many other families, thus offering possibilities for reversibility (*cf.* Baas, 1973, 1976; van der Graaff & Baas, 1974). This makes them unsuitable for phylogenetic considerations. In my opinion Rao (1972) put too much weight on these characters in his phylogenetic interpretations of the wood anatomy of individual genera in *Combretaceae*.

Parenchyma distribution in *Combretaceae* varies within very wide limits, but cannot be unambiguously interpreted in terms of primitiveness or specialization: scanty parenchyma may be equally well interpreted as a starting point or as a reduction (Carlquist, 1961).

Strephonema forms a notable exception to the rule that wood anatomy can contribute little to the understanding of the derived or ancestral affinity of Combretaceous taxa. In its outstanding characters: fibre-tracheids and distinctly heterogeneous rays of type II – III (Kribs, 1950) it is clearly more primitive than the other *Combretaceae*. In this case this is also supported by vessel member length which is longest for the whole family (Fig. 7) and cannot be accounted for by ecology alone. Bark characters also support the primitive nature of *Strephonema* (Den Outer & Fundter, 1976).

The only other conclusion one can draw in this field can only be tentative. Radial vessels must probably be interpreted as specializations and this may also be true for the occurrence of axial vessels of different size classes. This implies that subtribe *Combretinae* shows the most derived wood anatomy in this family.

CONCLUSIONS

The wood anatomical diversity within the *Combretaceae* lends strong support to a subdivision of the family as proposed by Exell & Stace (1966). Based on wood anatomy alone, one would prefer a classification in which the hierarchical rank of their different groups would be slightly different. A division into two subfamilies, the *Strephonematoideae* and the *Combretoideae*, can be supported because of the significant wood anatomical differences between *Strephonema* and all other genera of the *Combretaceae*. Within *Combretoideae*, the wood anatomical distinctness of the group of genera Exell & Stace placed in subtribe *Combretinae* is such that one would prefer a tribal status for this group in contrast with the remainder of genera of this subfamily; the latter can be divided into two anatomically slightly different groups: the *Laguncularieae* (tribal status *sensu* Exell & Stace) and the *Terminaliinae* plus *Pteleopsidiinae* (subtribal status).

I fully realize, that wood anatomy alone cannot determine a classification, but when comparing the grouping of the genera using wood anatomical characters only with a grouping based on external morphological characters there appears to be a remarkable similarity between the two.

A combination of the more traditional morphological characters with wood anatomical characters will result in the following classification of the *Combretaceae*, differing (*Pteleopsis* excepted) from the one presented by Exell & Stace (1966) in the taxonomic rank of the taxa.

Subfamily *Strephonematoideae* (*Strephonema* only)
Subfamily *Combretoideae*
  Tribe *Combreteae* (*Combretum*, *Quisqualis*, *Calopyxis*, *Thiloa*, *Guiera*, and *Calycopteris*)
  Tribe *Terminalieae*
    Subtribe *Terminaliinae* (*Terminalia*, *Pteleopsis*, *Anogeissus*, *Finetia*, *Conocarpus*, *Ramatuella*, *Terminaliopsis*, *Bucida*, and *Buchenavia*)
    Subtribe *Lagunculariinae* (*Laguncularia*, *Lumnitzera*, *Macropteranthus*)

An analysis of the wood anatomical diversity in connection with ecological preference of the species and genera involved has shown that much of the variation in vessel member length, vessel diameter, and vessel frequency can be accounted for by the trend that mesic species tend to have longer vessel members and fewer and wider vessels than xeric species, although these characters do not always follow these trends. The observation that lianas in *Combretinae* have wider vessels than their relatives of erect habit fits trends postulated for woody climbers; in *Combretaceae* this may also partly be influenced by the mesic ecology of the lianas and the more xeric ecology of their erect close relatives.

Although all *Combretaceae* show a rather specialized wood anatomy, arguments can be brought forward to consider *Strephonema* as the most primitive representative and the *Combretinae* as the most specialized group within the *Combretaceae*.

KEYS TO THE GENERA OF THE COMBRETACEAE AND TO SPECIES OF TERMINALIA

Explanatory notes

Because of the strong overlap in wood anatomical characters between several genera of the *Combretaceae* it appeared impossible to present a functioning analytical key, and preference was therefore given to a synoptical one. In this key the various characters are followed by numbers representing the genera in which they occur. The first items in the first key represent the best differentiating characters (1 – 3). The other features are listed following the sequence in which they appear in the wood anatomical descriptions.

With the use of an increasing number of items, irrespective of the sequence one adopts, the number of genera one can eliminate increases until one is left with few or preferably one possibility.

In the generic key it is not always possible to descriminate between two or more genera, but when consulting the descriptions it will be possible to narrow down the possibilities even further. In many cases *Terminalia* (17) will be one of the alternatives. For easy reference a synoptical key to the species of this genus studies by me is presented, together with table 14, giving a summary of data from the literature on *Terminalia* species not studied by me. This table can, in a way, also be used as a synoptical key, although one should bear in mind that the wood anatomical data in this key are far from complete.

In the keys, numbers printed in italics indicate that the genus or species posesses one or several alternative character states for the character involved. If of a certain character only two states are known (presence or absence for instance), than only one of them is listed and the alternative character state (mentioned between brackets) is present in all genera not listed for that item.

Synoptical key to the woods of the genera of the Combretaceae

1. *Anogeissus*
2. *Buchenavia*
3. *Bucida*
4. *Calopyxis*a)
5. *Calycopteris*
6. *Combretum*
7. *Conocarpus*
8. *Finetia*a)
9. *Guiera*
10. *Laguncularia*
11. *Lumnitzera*
12. *Macropteranthus*
13. *Pteleopsis*
14. *Quisqualis*
15. *Ramatuella*
16. *Strephonema*
17. *Terminalia*
18. *Terminaliopsis*
19. *Thiloa*.

1. Fibres with distinctly bordered pits and rays heterogeneous II – III; (*versus* libriform fibres with simple or minutely bordered pits, rays different): 16.
2. Radial vessels and two distinct sizes of vessel elements; Plate 5/30 – 33; 6; (*versus* radial vessels absent and only one size class of vessel elements although some very narrow elements or vascular tracheids may occasionally be present): 4, 5, 6, 9, 14, 19.
3. Axial included phloem present; Plate 6/36 – 40 (*versus* absent): 5, *6*, 9, 19.

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a) Immature sample
b) Either paratracheal or apotracheal
c) Crystalliferous ray cells excluded
d) Very rare.

4. Vessel solitary, 95 – 100% very narrow vessels and vascular tracheids not included (*versus* vessels also in radial multiples): 5, *6*, 14, 16, 17.
5. Wood.
   a. semi-ring-porous to ring-porous; Plate 6/35: *6*.
   b. diffuse-porous to semi-ring-porous: 4[a]), 5, *6*, *14*.
   c. diffuse-porous: 1, 2, 3, *6*, 7, 8, 9, 10, 11, 12, 13, *14*, 15, 16, 17.
6. Average vessel frequency.
   a. 0 – 5 /mm^2: *2*, 5, *6*, 16, *17*.
   b. 6 – 10 /mm^2: *2*, *6*, *14*, *17*.
   c. 11 – 25 /mm^2: *1*, *2*, *3*, 4[a]), *6*, *7*, 9, 10, *11*, *13*, *14*, 15, *17*, 18.
   d. 16 – 50 /mm^2: *1*, *2*, *3*, *6*, *7*, *11*, *13*, *17*, 19.
   e. 51 – 100/mm^2: *1*, 8[a]), *11*, *17*.
   f. more than 100/mm^2: 12.
7. Vessel – ray and vessel – parenchyma pits also almost simple (*versus* vessel – ray and vessel – parenchyma pits always half-bordered): *2*, *6*, *17*.
8. Vestures (*cf.* Fig. 1.)
   a. Type A: 16.
   b. Type B, form 2: 3, 5, *6*, 8, 9, 11, 12, 13, 14, 15, *17*, 18.
   c. Type B, form 2 – 3: 4, *6*, 7, *17*.
   d. Type B, form 3: 1, 2, *17*.
9. Vessel walls with warted surfaces (*versus* vessel walls not warted): 3, 4, 5, *6*, 11, *13*, 16, *17*.
10. Non-gelatinous fibres intergrading with gelatinous fibres; Plate 4/22 (*versus* these fibres not intergrading): 15.
11. Fibres septate (*versus* non-septate): *1*, *2*, 4, 5, *6*, 7, 8, 13, 14, *17*.
12. Parenchyma.
   a. scanty paratracheal only; Plate 6/34, 35, 38 – 40: *1*, 4, 5, *6*, 9, *11*, 12, 14, *15*, *17*, 19.
   b. frequent to abundant and vasicentric to aliform; Plate 3/17: *1*, *2*, *3*, *6*, *7*, *11*, *15*, *17*.
   c. frequent to abundant and aliform to confluent; Plate 3/13: *1*, *2*, *3*, *6*, *7*, *8*, *10*, *11*, *13*, 16, *17*, *18*.
   d. frequent to abundant and confluent to banded; Plate 3/16, 18: *2*, *6*, *10*, *13*, *15*, *17*, 18.
   e. also marginal; Plate 3/15; 4/19 – 21: *1*, *2*, *3*, *6*, *7*, *11*, 13, *17*, 18.
   f. also with large apotracheal aggregates; Plate 7/47, 49: 16.
13. Crystalliferous parenchyma cells chambered: *2*, *3*, *6*, *13*, *17*.
14. Rays
   a. uniseriate, infrequently with a biseriate portion; Plate 5/25; 7/44 – 46: *1*, 2, 4[a]), 5, *6*, *7*, 8[a]), 10, 11, 12, *13*, 14, *15*, *17*.
   b. 1 – 2-seriate: *6*, 7, 9, *17*.
   c. 1 – 3-seriate; Plate 5/26: *1*, 3, *6*, *13*, *15*, 16, *17*, *18*
   d. 1 – 4(– 6)-seriate; Plate 5/27: *17*.
15. Rays composed of
   a. erect cells only: 4[a]), *6*[a]), 8[a]), *14*[a]).
   b. square to erect and weakly procumbent cells[c]): 1, *11*, *12*, *17*.
   c. central portions of procumbent cells and erect marginal cells: 16, *17*.
   d. procumbent cells and infrequent square marginal cells[c]): 3, 5, 9, 13, *17*, 19.
   e. thick-walled cells (*versus* cells with normal walls): *1*, *3*, 19.

16. Intercellular radial canals present (*versus* absent): *17.*
17. Crystals.
    a. solitary crystals in idioblasts in rays; Plate 8/59–61; Fig. 3/d–e: *6*, 8, 9.
    b. solitary crystals in idioblasts in axial parenchyma cells; Fig. 4/c, h: 1, *2*, 3, *6*, *7*, 12, 13, *17*.
    c. very large solitary crystals in strongly or slightly enlarged ray cells; Plate 2/11; 8/57; Fig. 3/a–c: 1, 3, *6*, 7, *17*.
    d. very large solitary crystals in strongly or slightly enlarged axial parenchyma cells; Fig. 4/h: 1, *2*, 3, *6*, *7*, 12, *13*, *17*.
    e. rhomboidal to elongated crystals in rays; Fig. 3/g: *2*, *10*, *17*.
    f. rhomboidal to elongated crystals in axial parenchyma cells; Fig. 4/a, d: *2*d), *6*, *10*, *17*.
    g. styloids in axial parenchyma; Fig. 4/i: *6*, *17*.
    h. styloid-like crystals in fibres: *17*.
    i. solitary crystals mixed with clustered crystals in fibres; Fig. 4/b; Plate 8/50: *6*a).
    j. solitary crystals mixed with clustered crystals in axial parenchyma; Fig. 4a: *6*.
    k. clustered crystals in idioblasts in axial parenchyma; Plate 2/12, 3/18; Fig. 4/h: *6*, *17*.
    l. clustered crystals in rays: 5, *6*, *17*.
    m. clustered crystals in axial parenchyma; Plate 8/53; Fig. 4/c: *6*, *17*.
    n. clustered crystals in traumatic parenchyma only; *14*, *17*.
    o. clustered crystals in the parenchyma of the included phloem; Plate 2/10: 5, 6, 9, 19.
18. Silica
    a. grains; Plate 8/56: 2
    b. amorphous: *16*, *17*
19. No inclusions present in ray or axial parenchyma cells: *4*, *6*, 11, 15, *17*, 18.

Synoptical key to the woods of some species of Terminalia

Data on species, described in the literature and not studied by me are presented in table 14.

1. *T. acuminata*
2. *T. alata*
3. *T. amazonia*
4. *T. arbuscula* var. *xanthice*
5. *T. arjuna*
6. *T. arostrata*
7. *T. bialata*
8. *T. brassii*
9. *T. brownii*
10. *T. burseriana*
11. *T. calamansanai*
12. *T. catappa*
13. *T. chebula*
14. *T. chiriquensis*
15. *T. complanata*
16. *T. copelandii*
17. *T. corticosa*
18. *T. dichotoma*
19. *T. edulis*
20. *T. foetida*1)
21. *T. glaucescens*
22. *T. grandiflora*
23. *T. impediens*
24. *T. ivorensis*
25. *T. kilimanscharica*
26. *T. laxiflora*
27. *T. lucida*
28. *T. macroptera*
29. *T. manii*

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1) *T. foetida* Griff., not mentioned in Index Kewensis, may be an erroneous spelling of *T. foetidissima* Griff.

Table 14. Wood anatomical data from the literature on species of Terminalia not studied for this paper.

		vessels					fibres		
	growth rings a)	vessel frequency /mm	vessel diameter in µm	diameter intervessel pits in µm	coalescent apertures	mean vessel member length in µm	fibre walls	fibres septate	scanty
T. archboldiana Exell		[illegible]	d)						–
T. archepelagi Coode	±	5–7	e)		×		h)		×
T. argentea Mart. & Zucc.		6–30	30–90	6–9					
T. avicennioides Guil. & Perr.	+							(×)	
T. belerica Roxb.	+	0–15	300–335k)	7–11	×	470	thin		
T. citrina Roxb.	±	6–16	59–147	5–8		420	thin	×	×
T. darlingii Merr.	–	5–13	130–170	3–5		640			
T. foetidissima Griff.	–	8–15	130–180	6–9		640	thin		
T. hypargyrea Sch. & Laut.	+	5	160						
T. januarensis DC.	±			8–10				×	
T. kaiserana Hoffm.	+	9	100–200						
T. macadamii Exell		4–6	f)						–
T. megalocarpa Exell						340			
T. microcarpa Decn.	+	2–13	150–170	5–8		620	thinh)		
T. myriocarpa H. & M.	+	1–11	300–550k)	10–13		420			
T. oliveri Brandis	±	85–115	75–85	6–7		390		×	
T. oreadum Diels		4–6	d)				h)		×
T. paniculata Roth	–	4–19	225–250k)	8–11		450	thin	x	
T. pellucida Presl	+	6–16	95–160	5–8	×	480	thin		
T. procera Roxb.	±	3–16	300–326k)	8–11	(×)	450	thick	×	
T. prunoides Laws.	+	6	100				thin	(×)	
T. sericea Burch.	+	9–11	109	4–8					
T. solomonensis Exell	+	3–5	f)						
T. spinosa Engl.	+	6	200				thick	×	
T. steenisiana Exell		11–18	c)						×
T. stenostachya Engl. & Diels	+ & –	5	300–400						
T. stuhlmannii Engl.	±	10	100				thick	×	×
T. subspathulata King									×
T. tanibauca Sw.									
T. triflora Griseb.									

× = character present; – = character absent; O = character variable when comparing several publications; no indication = presence or absence of character not mentioned in the literature.

a) + = growth ring distinct; └ = growth ring faint; – = growth ring absent
b) small and inconspicuous
c) small to very small (cf. Coode, 1969)
d) intermediate to small (cf. Coode, 1969)
e) intermediate (cf. Coode, 1969)

parenchyma						rays				crystals						distribution				
vasicentric to confluer	aliform to confluent	confluent to banded	banded	marginal	diffuse	uniseriate	1 – & 2 – seriate	1 – 3-seriate	4-seriate	idioblast with sol. cryst. in ax. par.	sol. cryst. in ax. par.	sol. cryst. in rays	isioblast with druses in ax. par.	druses in ax. par.	absent	S. America	Africa	Asia	Malesia i)	vertical intercellular canals
×	×	–	–	–	–	–	–	–	×	–	–	–	× b)	–	–	–	–	–	×	–
×	×	–	–	–	–	–	–	×	–	–	×	–	×	–	–	–	–	–	×	×
–	×	–	–	–	–	×	(×)	–	–	–	×	–	–	–	–	×	–	–	–	
×				×	×	–	–	×								–	×	–	–	
–	–	×	×	×	–	×	–	×	–	–	×	×	–	–	–	–	–	×	×	
×	×	–	–		×	×	–	–	–	–	×	×	–	–	–	–	–	×	×	
–	×	–	–		–	×	–	–	–	–	–	–	×	–	–	–	–	–	×	
–	×	–	–		×	–	–	×	×	–	×	–	×	–	–	–	–	–	×	
–	×	–	–			–	×	–	–	–	–	–	×	–	–	–	–	–	×	
–	×	–	–							–	×	–	–	–	–	×	–	–	–	
–	×	–	–	(×)		–	–	×	–	–	–	–	–	–	×	–	×	–	–	
×	–	–	–	–	–	–	–	×	–	–	×	–	×	–	–	–	–	×	×	
–	–	×	–													–	–	–	×	
–	×	–	–	×	×	–	–	×	×	–	–	–	×	–	–	–	–	–	×	
–	×	–	–	×		×	–	–	–	–	×	×	–	–	–	–	–	×	–	×
×	×	–	–							–	×	×	–	–	–	–	–	×	–	
×	–	–	–	–	–	–	–	×	–	–	–	–	○	–	×	–	–	–	×	○
–	×	–	–			×	–	–	–	–	×	×	–	–	–	–	–	×	–	
–	×	–	–			–	–	×	×	–	–	–	×	–	–	–	–	–	×	
–	×	–	–	×		–	–	×	×	–	–	–	×	–	–	–	–	×	–	×
–	×	–	×	×	×	×	–	–	–	×	–	–	–	–	–	–	×	–	–	
○	○	–	○	○		–	×	–	–	–	–	–	×	–	–	–	×	–	–	
×	–	–	–	–		–	–	×	–	–	–	–	○	–	–	–	–	–	×	○
–	×	–	–	×		–	×	–	–	×	–	–	–	–	–	–	×	–	–	
–	×	–	–			–	–	–	×	–	–	–	×	–	–	–	–	–	×	
×	×	–	–		× f)	–	–	×	–	–	–	–	×	–	–	–	×	–	–	
×	–	–	–	○	×	–	×	–	–	×	–	–	–	–	–	–	×	–	–	
–	×	–	–			–		×	–							–	–	–	×	
×	×	×	–			×	–	–	–							×	–	–	–	
×						×	–	–	–	–	×	–	–	–	–	×	–	–	–	

f) intermediate to large (cf. Coode, 1969)
g) frequent
h) Furuno (1977) mentioned bordered fibre pits, see also description and note of Terminalia
i) including Australia and Melanesia
k) maximum diameter

30. *T. mollis*
31. *T. nigrovenulosa*
32. *T. nitens*
33. *T. orbicularis*
34. *T. papuana*
35. *T. platyphylla*
36. *T. polyantha*
27. *T. porphyrocarpa*
38. *T. reitzii*
39. *T. samoensis*
40. *T. scutifera*
41. *T. sepicana*
42. *T. superba*
43. *T. volucris*

1. Growth rings
   a. absent: 8, 19.
   b. distinct: 7, 11, *12*, 16, 17, 18, 20, 23, 32, 38, 40.
   c. faint: 1, 2, 3, 4, 5, 6, 10, *12*, 13, 14, 15, 19, 21, 22, 24, 25, 26, 27, 28, 29, 30, 31 33, 34, 35, 36, 37, 39, 41, 42, 43.
2. Vessel frequency
   a. 0–10/mm^2: 2, 4, 5, 6, 7, 8, *11*, *12*, 15, 16, 18, 19, 20, 23, 24, 26, 30, 32, 33, 34, 39, 40, 41, 42.
   b. 11–30/mm^2: 1, 3, *12*, 17, 21, 22, 25, 27, 28, 35, 36, 43.
   c. more than 30/mm^2: 9, 10, 29, 31.
3. Vessels
   a. exclusively solitary (95–100%): 8.
   b. frequently solitary (50–95%): 2, *3*, 6, 7, *12*, 15, 18, 19, 20, 24, 26, 27, 28, 32, 34, 35, 36, 39, 40, 42.
   c. infrequently solitary (less than 50%): 1, *3*, 4, 5, 9, 10, 11, *12*, 13, 14, 16, 17, 21, 22, 23, 25, 29, 30, 31, 33, 37, 38, 41, 43.
4. Diameter of inter-vessel pits
   a. 4–6 μm: 10.
   b. 6–8(–9) μm: 12, 13, 20, 25, 26, 27, 28, 32, 35, 36, 37, 39.
   c. 9–11 μm: 2, 3, 4, 5, 6, 8, 9, 11, 14, 15, 16, 17, 18, 19, 21, 22, 23, 24, 29, 30, 31 34, 38, 40, 41, 43.
   d. 11–14 μm: 1, 7, 33, 42.
5. Apertures of inter-vessel pits frequently or infrequently coalescent: (*versus* not coalescent) 2, 6, 12, 17, 21, 22, 23, 24, 25, 29, 30, 32, 34, 35, 43.
6. Vestures: see table 9.
7. Vessel–parenchyma pits
   a. ± transitional to scalariform or uniseriate, elongated up to 24 μm: *3*, 21, 28, 32, 34, 38.
   b. with reduced borders: 1, 5, 9, 14, 21, 28, 35, 38, 41
   c. similar to inter-vessel pits: 2, *3*, 4, 6, 7, 8, 10, 11, 12, 13, 15, 16, 17, 18, 19, 20, 22, 23, 24, 25, 26, 27, 29, 30, 31, 33, 36, 37, 39, 40, 42, 43.
8. Fibre walls
   a. thin to very thin: *3*, 8, *12*, 15, 16, 19, 20, 23, 33, 41, 42.
   b. thin to very thick: 7, 32, 34.
   c. thin to medium thick: 1, 5, 7, 11, *12*, 14, 17, 18, 24, 25, 31, 36, 37, 38, 39, 40.
   d. medium thick to thick: *3*, 22, 28, 29, 35.
   e. thick to very thick: 2, 4, 6, 9, 10, *12*, 13, 21, 26, 27, 30, 43.
9. a. fibres very frequently septate: 2, 3, 5, 8, 13, 24, 31, 33, 34, 35, 36.
   b. fibres infrequently septate: 1, 7, 9, 22, 41.
   c. fibres non-septate: 4, 6, 10, 11, 12, 14, 15, 16, 17, 18, 19, 20, 21, 23, 25, 26, 27, 28, 29, 30, 32, 37, 38, 39, 40, 42, 43.
10. Parenchyma
   a. scanty paratracheal: 8, 9, 10, 23, 25, 29, 31, 36.

b. very abundant: 1, 21, 43.
c. predominantly vasicentric to aliform: 8, 9, 10, *12*, 15, 19, 23, 25.
d. predominantly aliform to confluent: 3, *5*, 6, *12*, 13, 16, 20, 22, 24, 28, 29, 30, 32, 35, 36, 39, 40, 41, 42.
e. aliform to banded: 2, *5*, 7, 18, 26, 34, 37.
f. confluent to banded: 1, *12*, 14, 17, 27, 33, 42.
g. typically banded: 4, 11, 21
h. also apotracheally marginal: *7*, *18*.
i. also marginal and continuous with paratracheal parenchyma: 1, 2, 3, 6, *7*, 8, 10, 11, *12*, 13, 14, 16, *18*, 22, 24, 25, 27, 28, 29, 32, 33, 35, 39, 41,
k. also diffuse: 25, 26, 30, 37.

11. Rays
    a. uniseriate, infrequently with a small biseriate portion: 1, 2, 3, 4, *5*, 7, 8, *9*, 11, 13, 14, 17, 18, 21, 24, 27, 29, 31, 33, 34, 36, 38, 42, 43.
    b. 1- & 2-seriate: *5*, *12*, 28.
    c. up to 3-seriate: *9*, 10, *12*, 19, 20, 22, 23, 25, 26, 30, 32, 37, 39, 40, 41
    d. up to 4-seriate and wider: 6, *12*, 15, 16, 35.
12. Rays with conspicuous radial intercellular spaces (*versus* intercellular spaces absent): 8, 11, 14, 34, 42.
13. Crystals (* crystals of rare occurrence).
    a. absent: 8, 16, 19, 20, 24, 26, 28, 32, 40.
    b. solitary, very large, completely filling tangentially enlarged radial series of ray cells: 6.
    c. solitary, large, rod-like, completely filling radial series of hardly deviating ray cells: 1*, 3*, 17*, 31, 33.
    d. solitary, large rod-like, ± filling axial parenchyma cells: 2, *3**, 4, *5*, 7*, 13, 17*, 18*, 31*, 38.
    e. solitary, cubical to rod-like, completely filling chambers of chambered axial parenchyma: 10, 14, 27.
    f. rhomboidal to elongated with pointed ends in rays: 29, 36.
    g. elongated to styloid-like in unchambered axial parenchyma: 10, 34.
    h. elongated to styloid-like in septate fibres: 38.
    i. clustered, completely filling large idioblasts in axial parenchyma: 12* (p.p.), 15*, 21*, 22, 23, 35, 37*, 39*, 41*.
    j. clustered and infrequently axially elongated, present in the axial parenchyma: 12, 15*, 25, 35*, 39*, 41*.
    k. clustered, present in rays: 21*, 39*.
14. Geographical distribution:
    a. Asia: 2, 5, 7, 11, *12*, 13, 17, 29, 31, 36.
    b. Malesia: *12*, 15, 16, 20, 23, 32, 34, 41.
    c. Australia (incl. Melanesia): 6, 8, 10, 22, 35, 37, 39, 43.
    d. Africa: 9, *12*, 21, 24, 25, 26, 28, 30, 33, 40, 42.
    e. S. America: 1, 3, 4, *12*, 14, 18, 19, 27, 38.

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EXPLANATION OF PLATES

Plate 1. – 1. *Strephonema pseudocola.* Longitudinal section of vessel – parenchyma pit; vesturing of type A. × 7600. – 2. *Pteleopsis hylodendron.* Inter-vessel pit viewed from the lumen side, showing vesturing of type B, intermediate between form 2 & 3. × 7600. – 3. *Terminalia grandiflora.* Longitudinal section through inter-vessel pit pair, showing vesturing of type B, intermediate between form 2 & 3. × 7500. – 4. *Terminalia catappa.* Longitudinal section through inter-vessel pit pair, showing vesturing of type B, form 2. × 7700. – 5. *Quisqualis latialata.* Oblique section through vessel wall with inter-vessel pits, showing basel parts of trunk-like vestures, the first branching, and branch-endings. × 3500. – 6. *Combretum kraussii.* Inter-vessel pits viewed into the pit chamber, after removal of the pit floor (p), showing a compact mat of small branch-endings. Vesturing of type B, form 2. × 4400.

Plate 2. – 7. *Anogeissus schimperi.* Inter-vessel pits viewed into the pit chamber after removal of the pit floor. Vesturing of type B, form 3. Note rim (r) free of vesturing, on the lowest part of the pit chamber wall. × 6000. – 8. *Lumnitzera littorea.* Vessel – parenchyma pits; vestures completely covering apertures and grading into the dense warty layer, covering the vessel wall. × 6500. – 9. *Buchenavia huberi.* Vessel – parenchyma pits with strongly reduced, partly coalescent apertures on the vessel wall; vesturing almost completely absent. × 3900. – 10. *Combretum gallabatense.* Clustered crystals in the axial parenchyma of the intraxylary phloem strands. × 1750. – 11. *Terminalia manii.* Large solitary crystal in uniseriate ray, tangential view. × 1800. – 12. *Combretum fruticosum.* Large clustered crystal in idioblast in axial parenchyma. × 1750.

Plate 3. Transverse sections, illustrating the variation in vessel frequency, vessel diameter, thickness of fibre walls and patterns of parenchyma distribution in *Terminalia.* All × 33. – 13. *T. amazonia* (*FPRL 25054*); parenchyma aliform to confluent. – 14. *T. burseriana*; parenchyma scanty paratracheal, rarely completely surrounding the vessel. Note the traumatic gum ducts. – 15. *T. mollis*; parenchyma aliform to

confluent, infrequently diffuse in small aggregates, some marginal parenchyma continuous with paratracheal parenchyma (arrow). – 16. *T. dichotoma*; parenchyma banded. – 17. *T. brownii*; parenchyma scanty paratracheal, vasicentric to aliform. – 18. *T. glaucescens*; parenchyma abundant, confluent to banded, bands in an anostomosing pattern.

Plate 4. Transverse sections. All × 33, but 21 × 85. – 19. *Terminalia mollis;* note the apotracheal, marginal parenchyma. – 20 & 21. *Terminalia bialata*; note the marginal parenchyma, continuous with the paratracheal parenchyma. – 22. *Ramatuella argentea;* showing intergrading zones of gelatinous (dark) and non-gelatinous fibres. – 23. *Pteleopsis hylodendron* (*C. Vigne 1812*); note the difference in vessel frequency and vessel diameter between this species, growing in the rain-forest and *P. myrtifolia* (24), inhabiting more xeric vegetations.

Plate 5. – 25 – 30. Tangential sections; – 31 – 33. Transverse sections. – 25. *Terminalia reitzii*; rays uni- and biseriate, mainly homogeneous, but marginal cells infrequently square to erect. × 85. – 26. *Terminalia impediens*; rays 1 – 3-seriate, composed of square to procumbent cells and with one to several rows of square marginal cells. × 85. – 27. *Terminalia copelandii*; rays 1 – 6-seriate, composed of procumbent cells but with one row of erect marginal cells (Heterogeneous III). × 85. – 28. *Terminalia superba*, uniseriate rays, note the wide intercellular spaces separating the ray cells (arrows). × 200. – 29. *Ramatuella argentea;* rays uniseriate, composed of square and weakly procumbent cells. × 85. – 30. *Calycopteris floribunda*; rays uniseriate, infrequently biseriate, composed of procumbent cells, note the very narrow vessels mixed with vascular tracheids, showing abundant alternate pitting. – 31 – 33. Radial multiples of very narrow vessels mixed with vascular tracheids, in 31 & 32 present on growth ring boundaries (arrows). – 31. *Thiloa glaucocarpa*. × 200. *– 32. Ibid.* × 350. – 33. *Guiera senegalensis*. × 125.

Plate 6. Transverse sections of several genera of the subtribe *Combretinae*, illustrating parenchyma distribution, vessel frequency and vessel diameter and occurrence of included phloem. All × 33. – 34. *Combretum fruticosum*; parenchyma very scanty, note the very narrow vessels and vascular tracheids (arrows) and the pith fleck, included phloem absent. – 35. *Combretum celastroides*; wood ring-porous, parenchyma very scanty, very narrow vessels difficult to observe at this magnification, included phloem absent. – 36. *Combretum gallabatense*; parenchyma confluent to banded, infrequently aliform, narrow axial elements difficult to observe at this magnification, included phloem present. – 37. *Combretum nigricans* var. *elliottii*; parenchyma aliform to confluent, narrow axial vessels difficult to observe at this magnification, included phloem present, note the idioblasts with solitary crystals in the rays (arrows). – 38. *Calycopteris floribunda*; parenchyma scanty paratracheal, very narrow vessels in association with vessels and on growth ring boundaries (arrows), included phloem present. – 39. *Guiera senegalensis*; parenchyma scanty, very narrow vessels in large clusters in association with the vessels and on growth ring boundaries (arrows, see also Plate 5/31 & 32), included phloem present. – 40. *Thiloa glaucocarpa*; parenchyma very scanty, very narrow vessels frequent on growth ring boundary (arrow, see also Plate 5/33), included phloem present.

Plate 7. – 41 – 46. Transverse and tangential sections of the three genera of the *Languncularieae sensu* Exell & Stace (1966), illustrating differences in vessel frequency and vessel diameter; rays are always uniseriate, infrequently biseriate and are composed of weakly procumbent to square and infrequent erect cells. – 41 – 43 × 33. 44 & 46 × 85. – 45 × 50. – 41 & 44. *Laguncularia racemosa*. – 42 & 45. *Lumnitzera littorea*. – 43 & 46. *Macropteranthus fitzalanii* (R 977 – 204). – 47 – 49 *Strephonema pseudocola*, illustrating aliform parenchyma and large apotracheal aggregates (47 & 49. × 33) and 1 – 3-seriate rays which are heterogeneous II – III (48. × 85).

Plate 8. – 50. *Combretum molle* (*PFRL 6714*), tangential section showing perforated ray cells (PC) with perforations (arrows) to adjacent very narrow vessels, two superimposed perforated ray cells are also connected with a perforation. × 200. – 51. *Combretum fruticosum* (*A. C. Smith 3105*); tangential section showing diffuse, very thin-walled axial parenchyma, containing large solitary crystals, or crystals tending to be clustered (arrow). × 200. – 52. *Terminalia superba*; radial section, showing elongated crystal (arrow) in axial parenchyma. × 85. – 53. *Combretum gallabatense*; radial section, showing large solitary to clustered crystals in axial parenchyma. × 200. – 54. *Calycopteris floribunda;* radial section, showing series of three radial vessel members connected with perforations (p) in tangential walls, and terminal cells with also a perforation in the radial wall, probally leading to a very narrow vessel. × 200. – 55. *Combretum erythrophyllum;* tangential section (scanning electron micrograph), showing perforation in the tangential wall of a radial vessel element (P), and large solitary crystals in rays (arrows). × 400. – 56. *Buchenavia acuminata;* radial section, showing silica grains in axial parenchyma. × 200.

— 57. *Terminalia nigrovenulosa*; radial section, showing solitary crystals completely filling the ray cells, crystalliferous cells in radial series. × 85. — 58. *Combretum fruticosum;* radial section, showing clustered crystals, tending to solitary crystals (arrow) in the fibres of juvenile wood. × 200. — 59. *Combretum rotundifolium*: radial section (scanning electron micrograph), showing idioblasts with large solitary crystals in uniseriate rays. × 175. — 60. *Combretum nigricans* var. *elliottii;* radial section, showing idioblasts with one large solitary crystal, in uniseriate rays. × 85. — 61. *Combretum molle* (*FPRL 6714*); radial section, showing connection between axial and radial strands of included phloem. × 33.

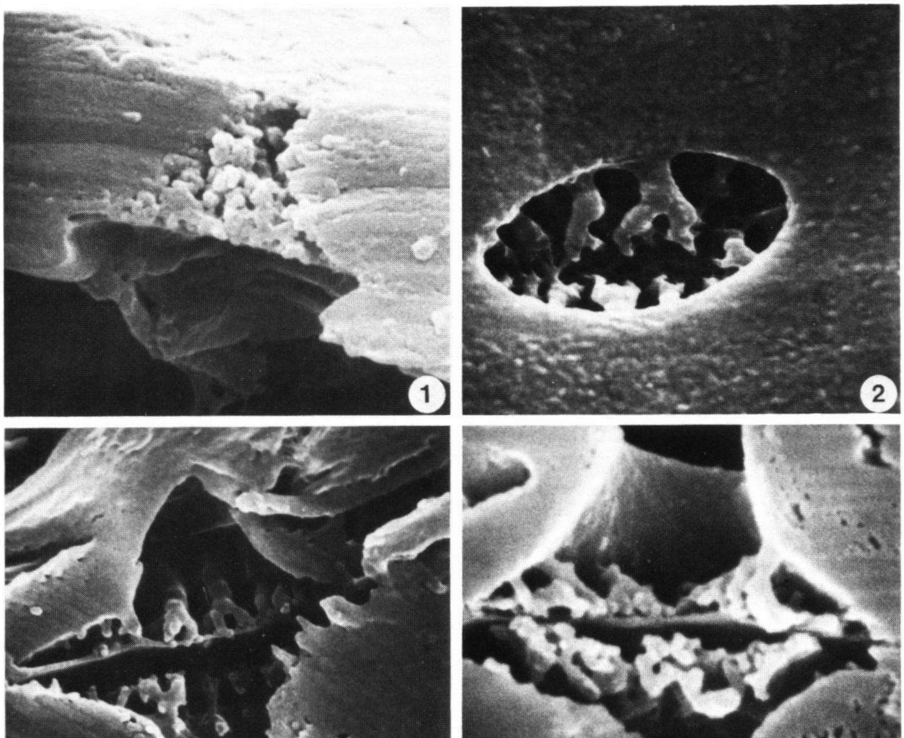
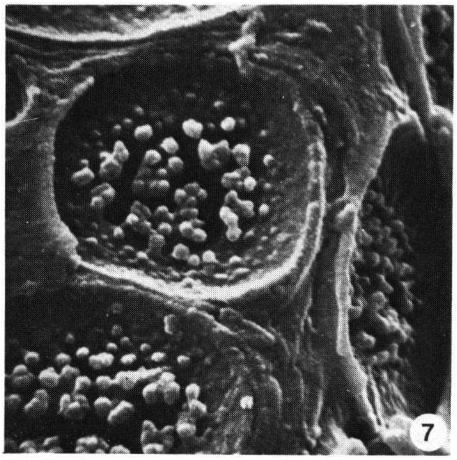


PLATE 1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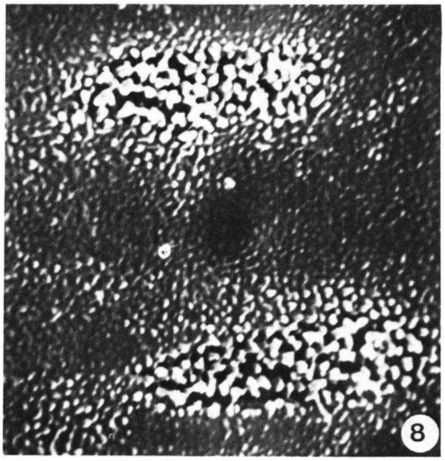
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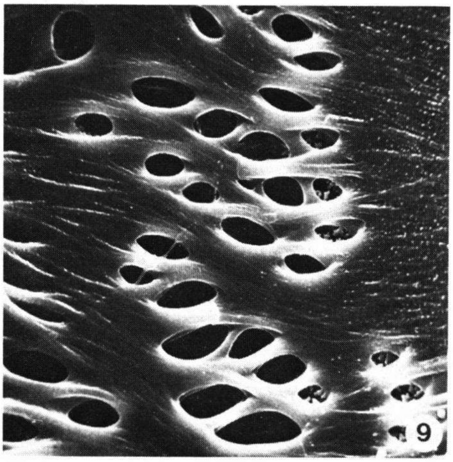
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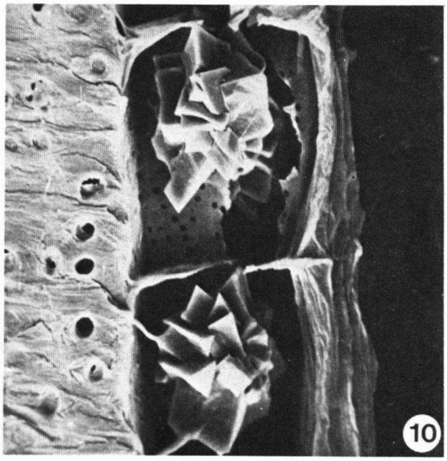
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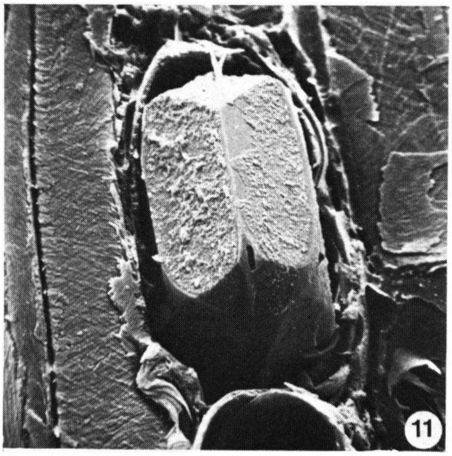
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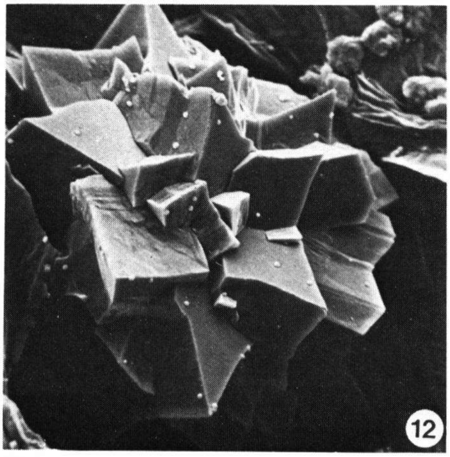
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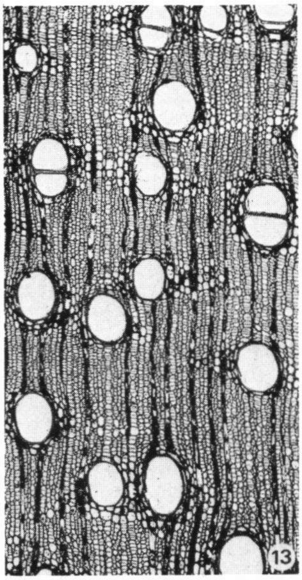

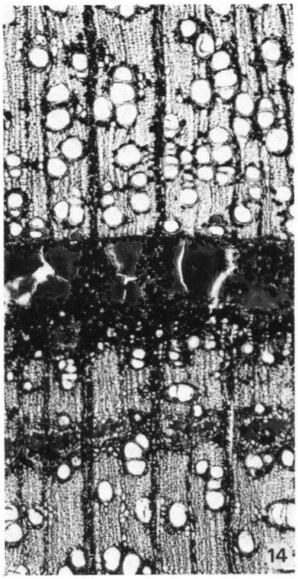

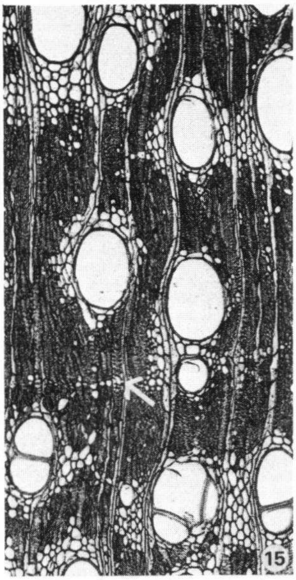

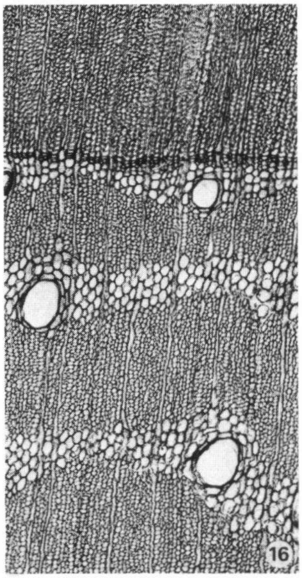

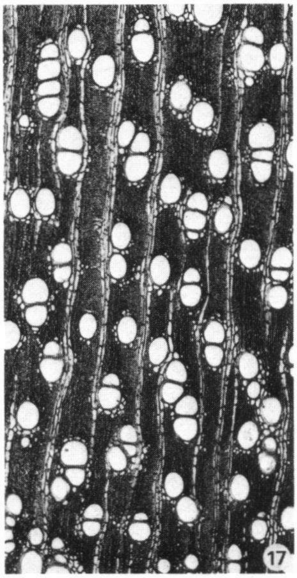

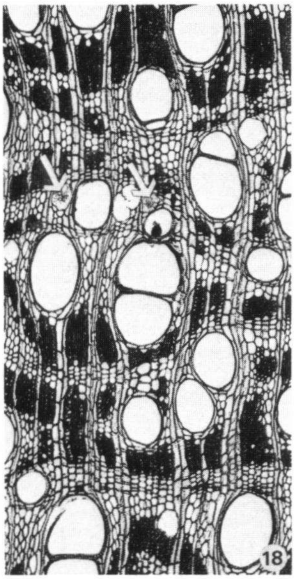

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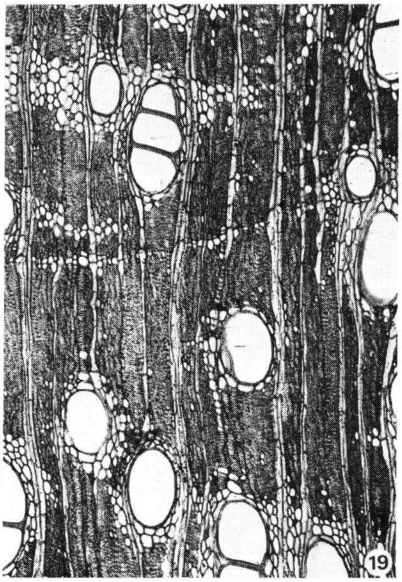
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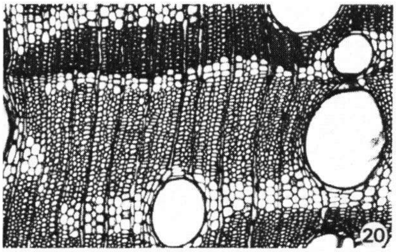
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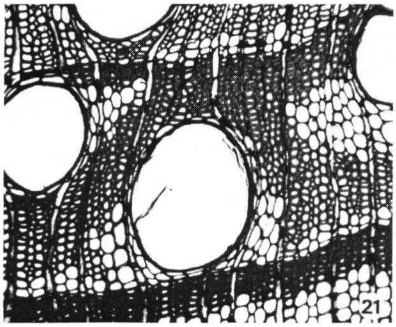
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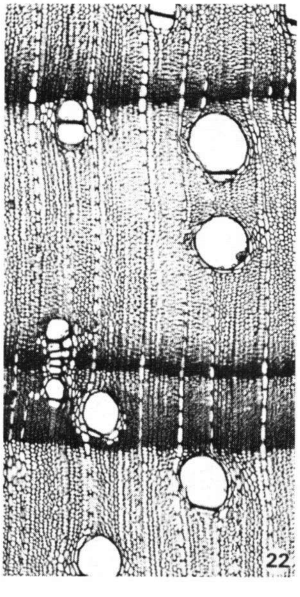
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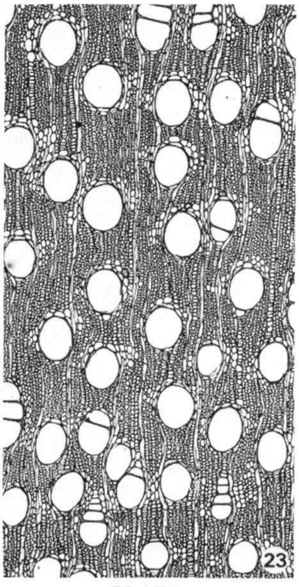
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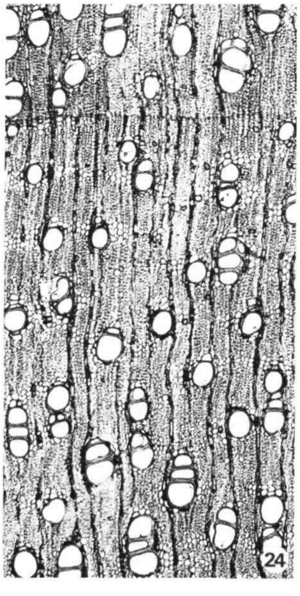
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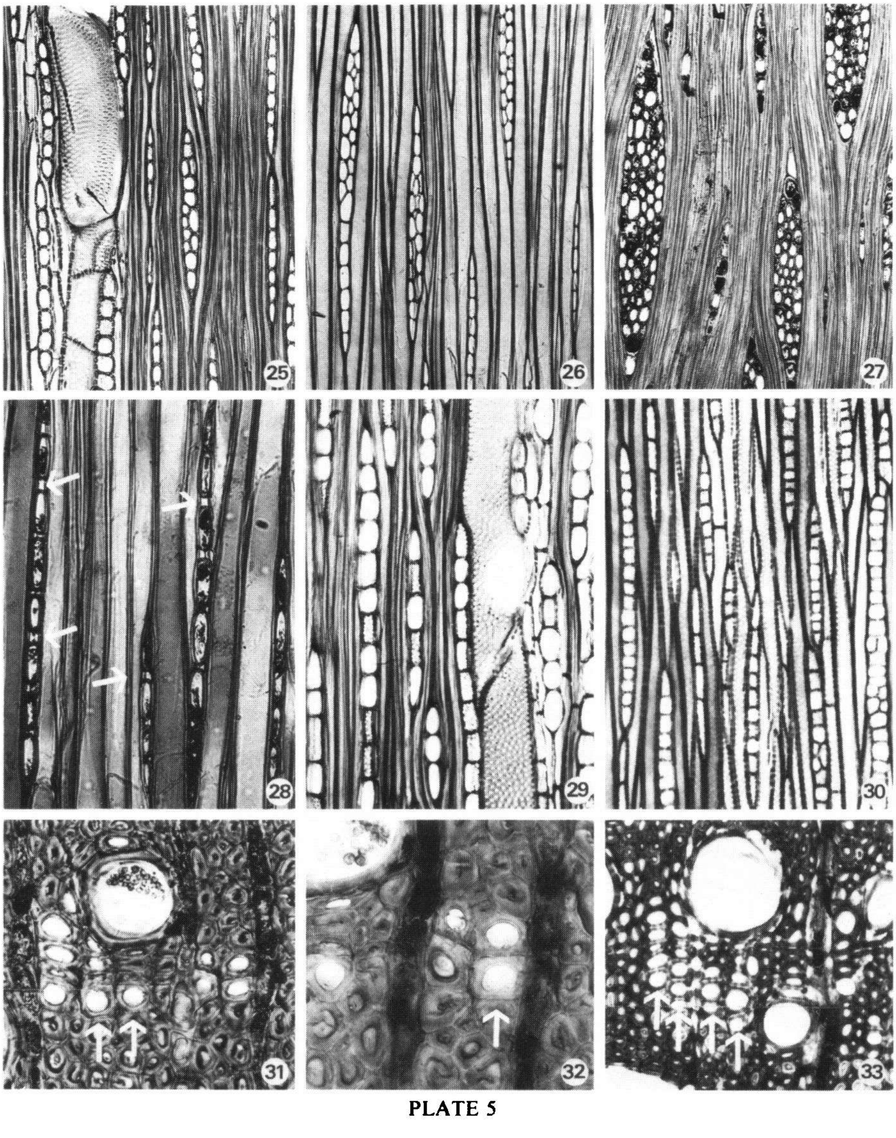

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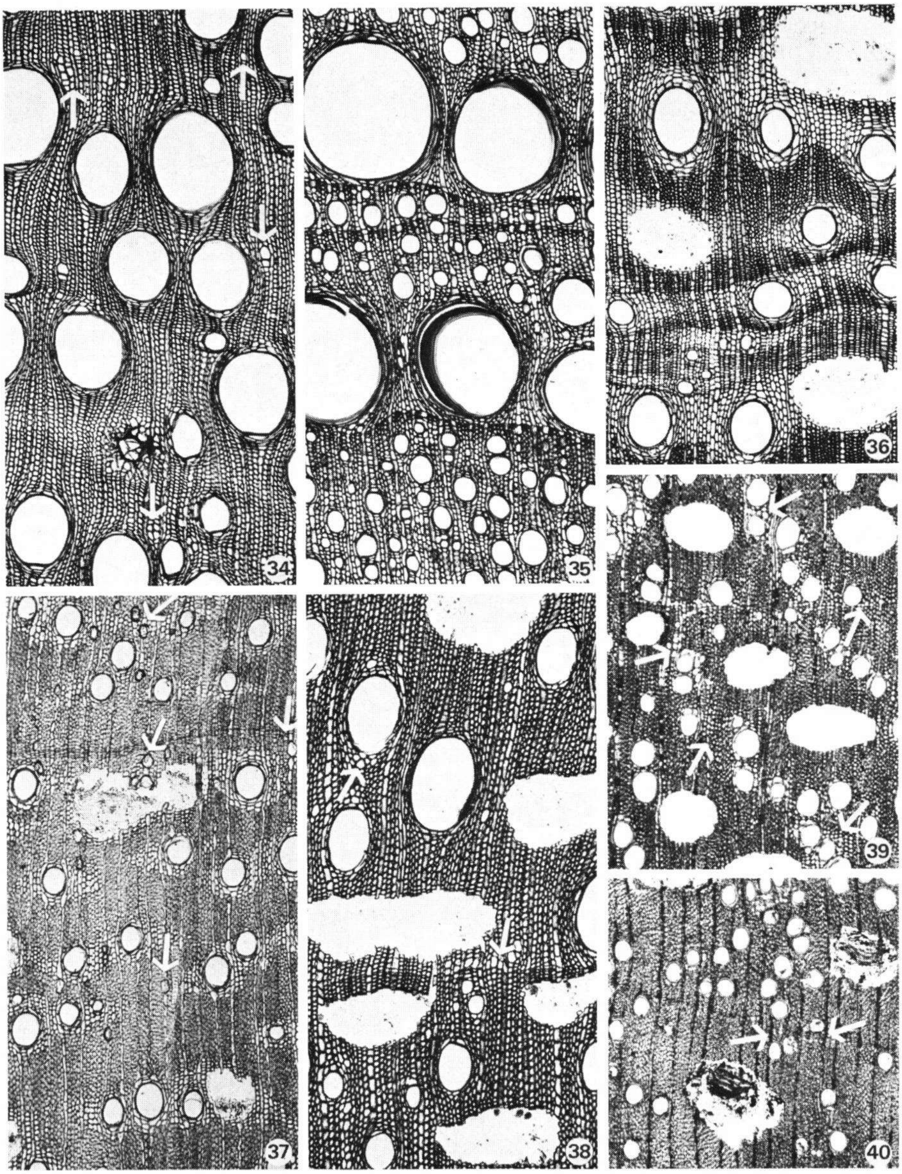

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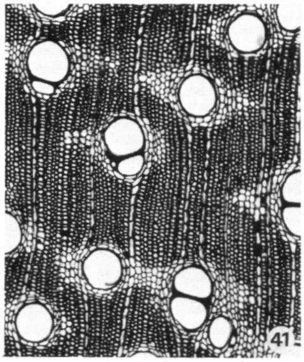
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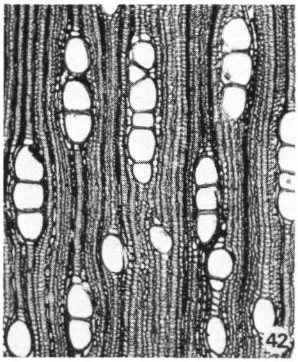
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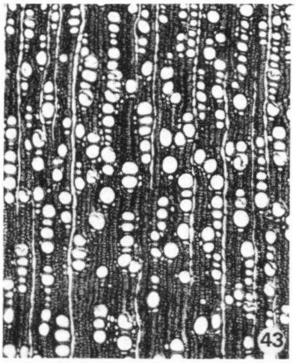
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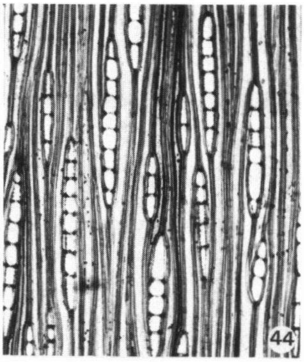
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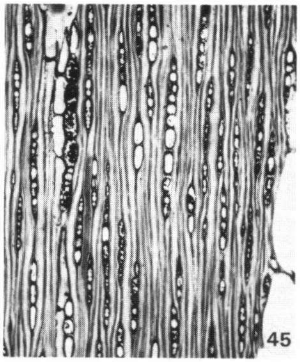
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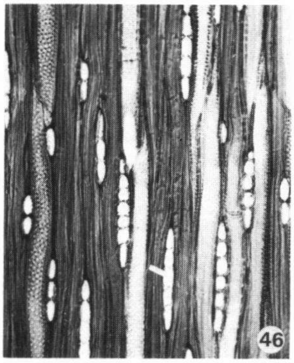
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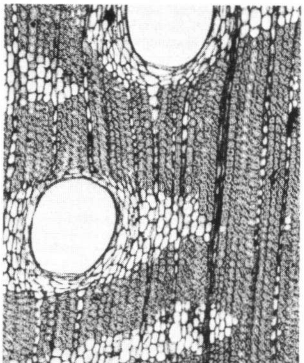
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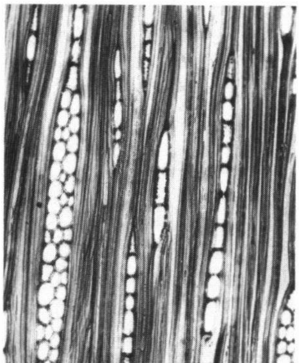
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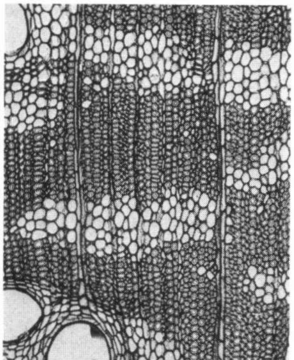
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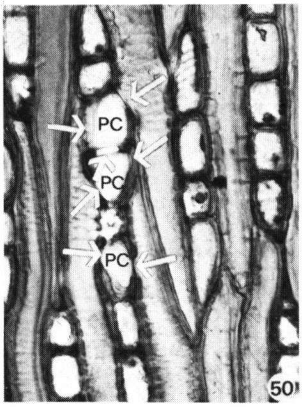
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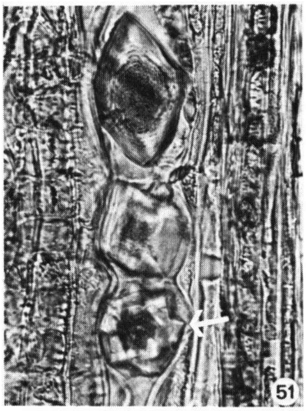
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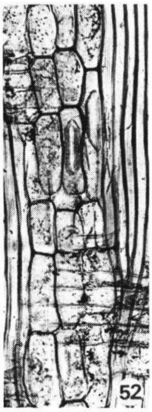
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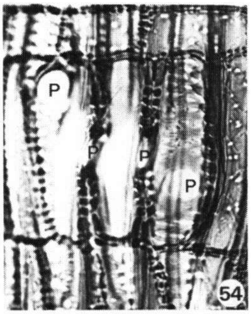
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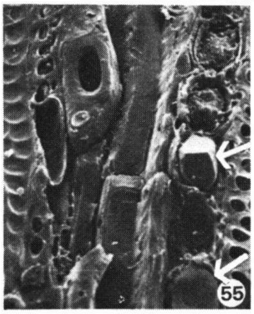
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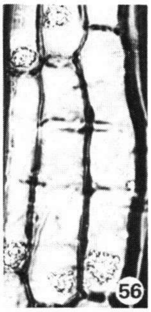
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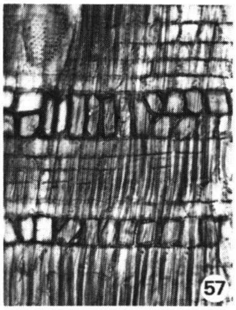
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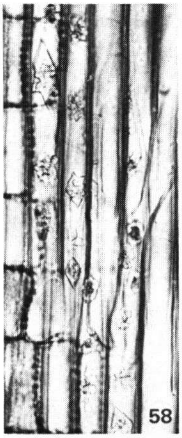
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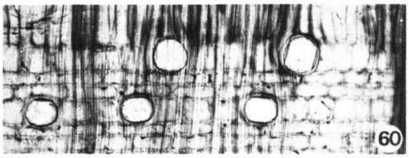
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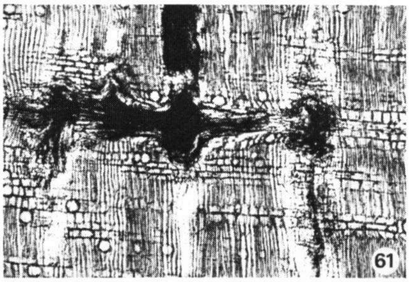
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PLATE 8