

WOOD ANATOMY OF TAMBOURISSA (MONIMIACEAE) FROM MADAGASCAR

R. W. DEN OUTER and W. L. H. VAN VEENENDAAL

Plantencytologie en -morfologie, Landbouwhogeschool, Arboretumlaan 4, 6703 BD Wageningen

SUMMARY

Wood structure of *Tambourissa hildebrandtii* Perk. and some other *Tambourissa* species (Monimiaceae) is described. Comparative anatomical observations are also made on several other Monimiaceae (HUTCHINSON 1964, 1973) species.

On wood anatomical grounds the investigated *Tambourissa* species fit quite well within the subfamily Monimioideae (MONEY et al. 1950; HUTCHINSON 1964; TAKHTAJAN 1980) if the genera *Amborella* and *Peumus* are excluded.

1. INTRODUCTION

The Monimiaceae s.l. is a family of usually trees and shrubs, rarely climbers, generally divided into two subfamilies viz. Monimioideae and Atherospermoideae (PAX 1894; METCALFE & CHALK 1950; HUTCHINSON 1964).

Wood anatomical descriptions of the family (STERN 1954) are of limited value because often one does not know which genera are in- or excluded and how many species were investigated (usually a rather small number).

If we adopt HUTCHINSON's (1964) concept of the family Monimiaceae, the two subfamilies to be distinguished are: Monimioideae with the tribes Hedycearyae and Monimieae, and Atherospermoideae with the tribes Laurelieae and Atherospermeae. These two subfamilies are wood anatomically usually distinguished by the rays (SOLEREDER 1899; METCALFE & CHALK 1950):

a. in the Monimioideae wide and high rays, mostly more than 7 cells wide, more than 1 and up to 15 mm high, heterogeneous with 1–4 marginal rows, composed almost entirely of square and upright cells, usually 1–4 per tangential mm, uniseriate few or absent. GARRATT (1934) and MONEY et al. (1950) add to this: scanty axial parenchyma, septate libriform fibres;

b. in the Atherospermoideae relatively narrow rays, usually up to 3–4 cells wide, less or more than 1 mm high, heterogeneous with 1–4 marginal rows, 9–14 per tangential mm; uniseriate moderately numerous. MONEY et al. (1950) add to this: a less natural subfamily, differentiated from the Monimioideae.

However, PICHON (1948) separated the Atherosperma group at familial level and established a new family Amborellaceae. MONEY et al. (1950) corroborated Pichon's Amborellaceae, treated the *Trimenia* group also as a separate related family and proposed four subfamilies of the family Monimiaceae, viz. Hortonioidae, Atherospermoideae, Monimioideae and Siparunoideae. According to

SCHODDE (1970) it seems more practical to elevate two of these subfamilies to the rank of family. The Atherospermataceae and the newly established Siparunaceae. Furthermore SCHODDE (1970) proposed a new subfamily Peumoideae (Monimiaceae). Thus within the family Monimiaceae s.s. three subfamilies can be distinguished: Monimioideae, Hortonioidae (with a single genus *Hortonia*) and Peumoideae (with a single monotypic genus *Peumus*). THORNE (1974a,b) on the other hand accepted the four subfamilies recognized by MONEY et al. (1950) and even added a fifth one, viz. the Mollinedioidae. TAKHTAJAN (1980) adopted this. Only recognition of the family Trimeniaceae appears now to be accepted (TAKHTAJAN 1969, 1980; HUTCHINSON 1964, 1973); the family Amborellaceae partly (TAKHTAJAN 1969, 1980).

The family Monimiaceae s.l. comprises about 32 genera and about 350 species (GARRATT 1934; LAWRENCE 1951; HUTCHINSON 1964). There are many monotypic genera and genera with only a few species. The larger genera include *Siparuna* Aubl. (108 spp.), *Mollinedia* Ruiz et Pav. (75 spp.), *Kibara* End. (30 spp.) and *Tambourissa* Sonn. (25 spp.). Their locations are in the tropics and subtropics, mainly of the southern hemisphere, especially South America, Malaysian archipelago, New Caledonia, East Australia, New Zealand, Madagascar and very rarely Africa; they are absent from India (but present in Sri Lanka).

The Mascarene islands harbour three (GARRATT 1934; HUTCHINSON 1964) or four (CAVACO 1959) endemic genera. Of these genera *Tambourissa* Sonn. is the largest with 25 species (HUTCHINSON 1964). CAVACO (1959) on the other hand distinguishes 26 species; one (*T. ficus* (Tul.) DC.) from Java (Indonesia), the other 25 from the Mascarene islands. Of these 25 species, 19 are endemic to Madagascar.

The family is placed in the order Laurales (TAKHTAJAN 1969, 1980; HUTCHINSON 1973) near to the Magnoliales. On wood anatomical grounds (GARRATT 1935) the greatest affinity of the family appears to be with the Myristicaceae of the Laurales (HUTCHINSON 1973), especially through the genus *Siparuna* Aubl. There is also more or less marked similarity with the Lauraceae, particularly on part of *Peumus* Mol.

Investigations on the anatomy of the secondary xylem of the family are scarce (SOLEREDER 1899; STERN 1954; PATEL 1973), especially on older wood (GARRATT 1934; MONEY et al. 1950) of *Tambourissa* Sonn. Anatomy of the secondary phloem has never been studied as far as we know.

The present study is done to investigate if, on wood anatomical grounds, *Tambourissa* Sonn. fits within the subfamily Monimioideae of the Monimiaceae in which it is placed by MONEY et al. (1950), HUTCHINSON (1964) and TAKHTAJAN (1980).

2. MATERIALS AND METHODS

Wood samples of *Tambourissa* used in this study, were collected by the authors in Madagascar (1978) and by D. H. Lorence in Mauritius, Mascarene islands. The samples were immediately fixed in FAA. The investigated wood samples

of the other Monimiaceae species are mainly from the Department of Systematic Botany at Utrecht, The Netherlands (U-numbers).

Anatomical features were studied in transverse, radial and tangential sections and macerations. All sections were embedded in Kaiser's gelatin-glycerin. Means and ranges of the length of vessel members, parenchyma strands, radial vessel diameters, ray height and width, and the number of rays per mm in tangential direction are based on at least twenty-five individual measurements. Vessel-member length was measured including the tails.

All our investigated species belong to the subfamily Monimioideae, except for *Laurelia* and *Siparuna*, arranged in the tribe Laurelieae of the subfamily Atherospermoideae (HUTCHINSON 1964).

A list of investigated samples of species belonging to the family Monimiaceae s.l. is given below, arranged alphabetically. Indications between brackets are: sample number from Uw (Utrecht, the Netherlands, herbarium vouchers present; the numbers U en BW) and/or WLw (Wageningen, the Netherlands, herbarium vouchers present except those collected by Lorence; the numbers Pl); collector and voucher number; provenance; tree or shrub, height, and diameter at breast height if known.

Amborella trichopoda Baill.;

Anthobembix Perk. (BW 1258; Former Dutch Forestry Service; West New Guinea, Indonesia);

Hennecartia omphalandra Poisson (U 13034; Lindeman and De Haas 1326; Parana, Brazil; tree, 14 m, 20 cm and U 13143; Lindeman and De Haas 1529; Parana, Brazil; tree, 6 m, 6 cm);

Kibara Endl. (U 18378; Vink 17232; West New Guinea, Indonesia; diameter 10 cm);

Laurelia aromatica Juss. ex Poir. (U 8423; Smiths. Inst. 6612; Chili);

Laurelia serrata R. Phil. (U 2083; Heidema 55; Chili);

Levieria cf. *parvifolia* A. C. Smith (U 18324; Vink 17458; West New Guinea, Indonesia; diameter 5 cm).

Levieria Becc. (U 22964; Hoogland 9656; West New Guinea, Indonesia);

Macrotorus utriculatus (Mart.) Perk. (U 20164; Krukoff 5747; terr. Acre, Brazil; shrub, diameter 10 cm);

Mollinedia blumenaviana Perk. (U 12709; Lindeman and De Haas 717; Parana, Brazil; tree, 4.5 m, 5 cm and U 12729; Lindeman and De Haas 757; Parana, Brazil; tree 5 m, 5 cm);

Mollinedia chrysolaena Perk. (U 14129; Lindeman and De Haas 3860; Parana, Brazil; shrub, 4 m, 2.5 cm);

Mollinedia elegans Tul. (U 12580; Lindeman and De Haas 332; Parana, Brazil);

Mollinedia killipii Macbride (U 8820; Ellenberg 2919; Junin, Peru; tree, 6 m, 6 cm);

Mollinedia laurina Tul. (U 8573; Daniels and Jonker 982; Surinam; diameter 4 cm);

Mollinedia uleana Perk. (U 13532; Lindeman and De Haas 2141; Parana, Brazil; tree 6 m, 7 cm);

Peumus boldus Molina (U 14968; Meyer 9696; Chili; shrub, diameter 4.5 cm);

Siparuna crassiflora Perk. (U 19860; Krukoff 5265; terr. Acre, Brazil);

Siparuna cuspidata A. DC. (U 342 and Pl 1954; Stahel 342; Powakka, Surinam; tree);

Siparuna decipiens A. DC. (U 2387; Lindeman 3628; Surinam; diameter 7 cm and U 16218; Krukoff 8710; Brazil; tree, diameter 15 cm and Pl 1914; Stahel 299; Surinam);

Siparuna guianensis Aubl. (U 11727; Maas (Lands Bosbeheer) 11028; Nickerie, Surinam; diameter 10 cm and Pl 2643; Den Outer 982; Zanderij, Surinam; tree, 4 m, 8 cm and U 1437; Lanjouw and Lindeman 1259; Surinam; diameter 3.5 cm);

Siparuna lepidantha Perk. (U 16182; Krukoff 8349; Brazil);

Siparuna obstipa Macbride (U 8007; Krukoff 6876; Brazil);

Siparuna pachyantha A. C. Smith (U 16086; Krukoff 8667; Brazil);

Siparuna sarmentosa Perk. (U 19751; Krukoff 5091; State of Amazonas, Brazil);

Siparuna sprucei A. DC. (U 2574; Maguire 24807; Tafelberg, Surinam; diameter 3 cm);
Tambourissa amplifolia (Bak. ex Tul.) A. DC. (Pl 3187; Lorence 2259; Mauritius, Mascarene islands; diameter 1.5 cm);
Tambourissa hildebrandtii Perk. (Pl 2866; Van Veenendaal and Den Outer 994; 10 km south-east of Ambalavao, Madagascar, in a vestigial forest about 800 m above sea-level; tree, 4 m, 40 cm);
Tambourissa tetragona (Tul.) A. DC. (Pl 3188; Lorence 2286; Mauritius, Mascarene islands; diameter 1.5 cm);
Tambourissa trichophylla Bak. (Pl 3189; Lorence 1879; Mascarene islands; diameter 1 cm and Pl 2653 of which the provenance is unknown);
Tambourissa Sonn. (Pl 3009; Van Veenendaal and Den Outer 1136; 10 km north of Fort Dauphin, Madagascar, in a rainforest about 100 m above sea-level; tree, 4 m, 6 cm).

3. RESULTS

The secondary xylem of the investigated *Tambourissa* species shows the following characters (see also table 1 and figures 1–4).

Growth rings absent. Wood diffuse-porous.

Vessels on average 55 per mm² (range of means 13–75 per mm²), solitary in radial multiples of 2(–6) and in clusters; round to slightly oval or flattened where in contact with each other; radial diameter (20–)70(–160) µm (range of means 45–110 µm). Vessel-member length (470–)970(–1740) µm (range of means 660–1180 µm) including tails. Perforations scalariform in very oblique end walls with 25 bars (range of means 15–30 bars); inter-vessel pits opposite to scalariform, bordered, with a horizontal diameter of 30 µm (range of means 8–50 µm), vested in *Tambourissa hildebrandtii*; vessel-ray and vessel-parenchyma pits half-bordered to almost simple, average horizontal diameter 40 µm (range of means 30–50 µm). Vessels usually in contact with libriform fibres and rays. Thin-walled tylosis present in *Tambourissa trichophylla*; vessel contents absent.

Fibres libriform, septate, thin-walled (6–8 µm), with small bordered pits only in the radial walls, sometimes in two vertical rows.

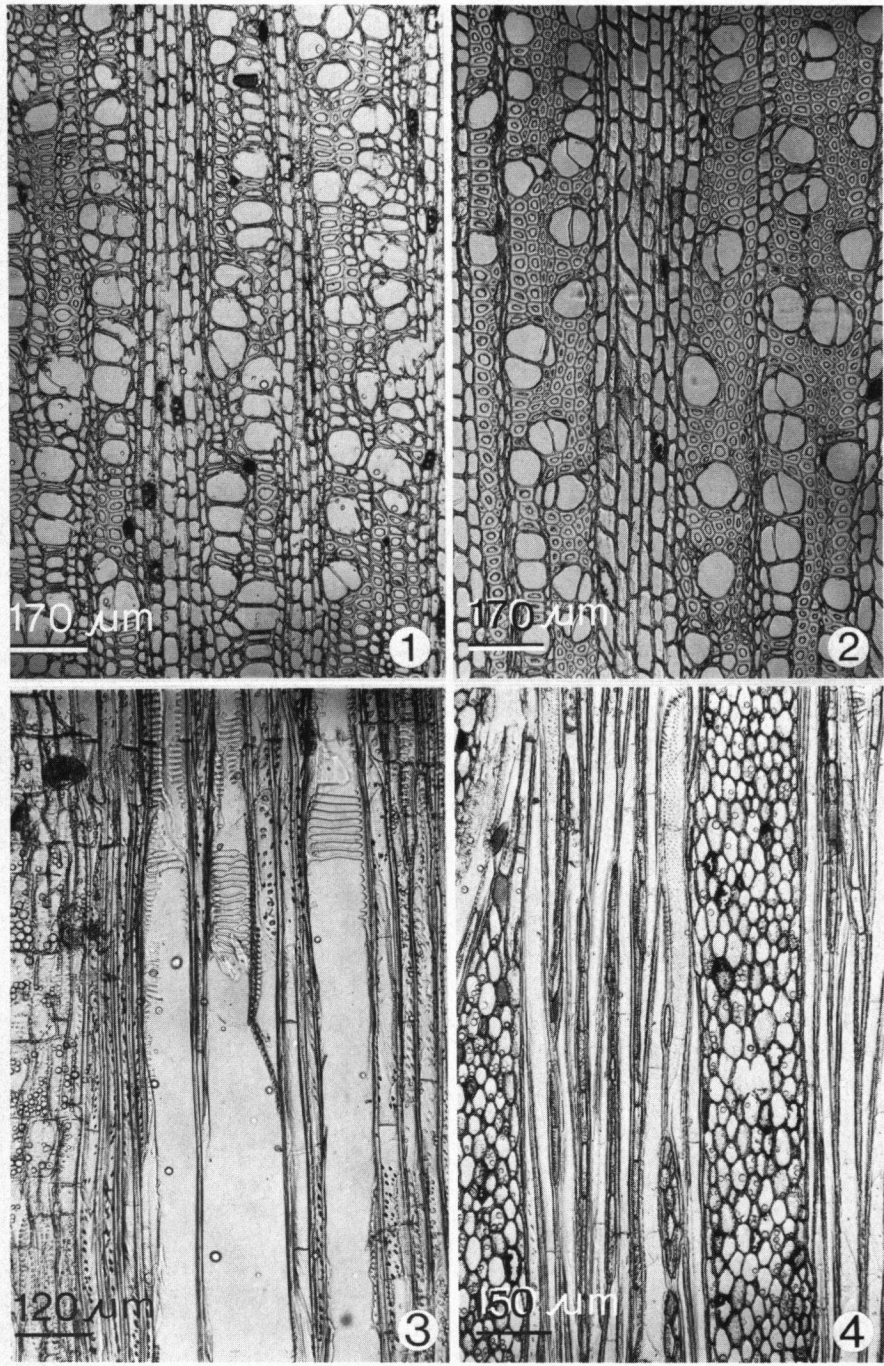
Parenchyma scanty, diffuse and vasicentric. Strands of 5 cells (range of means 3–7 cells), 840 µm long (range of means 360–1000 µm long).

Rays (1–)7(–15)-seriate (range of means 4–10-seriate), heterogeneous with short uniseriate tails, composed of predominantly procumbent and square cells; height 4870(–10,000) µm (range of means 1,000–5,000 µm) average width 160 µm, 4 per tangential mm (range of means 2–5 per tangential mm).

Crystals sand or small rhomboidal, sometimes present in ray-parenchyma cells.

Fig. 1–4. Secondary xylem of *Tambourissa hildebrandtii* Perk. (1, 3 and 4) and *Tambourissa* spec. (2).

1. Transverse section. Growth rings absent; axial parenchyma scanty, diffuse and vasicentric; rays also more than 3–4-seriate; some parenchyma cells with red-brown contents.
2. Transverse section. Like *T. hildebrandtii*, but slightly more libriform fibres with somewhat thicker walls and less axial parenchyma.
3. Radial section. Vessels with scalariform perforation plates; libriform fibres septated (right hand side).
4. Tangential section. Rays uniseriate and multiseriate with short tails; libriform fibres septated without pits in the tangential walls.



The following differences were found in the other investigated species when compared with *Tambourissa* (see table 1).

Growth rings distinct to vague (in *Amborella trichopoda* not observed). Wood slightly ring-porous in *Peumus boldus*.

Vessels absent in *Amborella trichopoda*, on the average 50 per mm² (range of means 6–150 per mm² for *Siparuna pachyantha* and *Laurelia serrata* respectively); radial multiples of more than 4 usually present in *Siparuna*; radial diameter (12–)80(–240) µm (range of means 45–180 µm for *Siparuna guianensis* and *S. pachyantha*, respectively). Vessel-member length (270–)1035(–2520) µm (range of means 560–1690 µm for *Siparuna crassiflora* and *Levieria*, respectively). Perforations usually simple in *Peumus boldus*, also reticulate and often simple in *Siparuna*, 19 bars (range of means about 3 bars for *Peumus boldus* and *Siparuna* to 55 bars for *Levieria* cf. *parvifolia*); inter-vessel pits alternate in *Siparuna*, horizontal diameter 22 µm (range of means about 5 µm for *Peumus boldus* and *Siparuna* to 70 µm for *Levieria* cf. *parvifolia*). Spiral thickenings present in *Peumus boldus* and *Siparuna pachyantha*.

Fibres libriform (in *Amborella trichopoda* tracheids, in *Laurelia* tracheids and some septate libriform), non-septate and thick-walled in *Peumus boldus*, *Siparuna* and probably in *Macrotorus utriculatus*; mainly non-septate in *Kibara* although JANSSONIUS (1934) found the opposite for *Kibara coriacea* Tub. and *K. macrophylla* Perk.; pits not bordered in *Peumus boldus* and *Siparuna*.

Parenchyma rare to absent in *Amborella trichopoda*, *Hennecartia omphalandra*, *Laurelia*, *Levieria*, many species of *Mollinedia* and *Peumus boldus*, or present in short, uniseriate apotracheal bands like in *Siparuna* (on the average 11 per radial mm) and *Macrotorus utriculatus* (7 per radial mm). Strands 1125 µm long (range of means 600 µm for *Siparuna decipiens* to 1550 µm for *Kibara*).

Rays (1–)4 (–16)-seriate (range of means about 2–3-seriate for *Amborella trichopoda*, *Laurelia* and *Siparuna* to 9-seriate for *Mollinedia uleana*), homogeneous with long uniseriate tails composed of square and upright cells in *Amborella trichopoda*; height 1570(–10,000) µm (range of means 340 µm for *Laurelia serrata* to 3,000 µm for *Levieria* cf. *parvifolia*), 8 per tangential mm (range of means 1–2 for *Kibara* to 15 per tangential mm for *Amborella trichopoda*).

Crystals rhomboidal, present in ray-parenchyma cells of *Anthobembix*, *Hennecartia omphalandra*, *Kibara*, *Levieria* cf. *parvifolia*, *Macrotorus utriculatus* and *Mollinedia*.

4. DISCUSSION

Only few and incomplete wood characteristics of *Tambourissa* are available from literature (METCALFE & CHALK 1950; GARRATT 1934). Data not in agreement with ours are; vessels moderately numerous (10–20 per mm²; GARRATT 1934); vessels of *Tambourissa* rather larger than moderately small (50–100 µm mean tangential diameter); axial parenchyma scarce, predominantly paratracheal; libriform fibre walls thick (METCALFE & CHALK 1950).

From our results it is evident that the following genera are exceptional: *Amborella* placed by MONEY et al. (1950) and TAKHTAJAN (1980) in the family Amborellaceae, by HUTCHINSON (1964) in the subfamily Monimioideae of the Monimiaceae (no vessels, tracheids, narrow homogeneous rays with long tails, large number of rays per tangential mm, crystals absent); *Peumus* placed in the subfamily Monimioideae by all three authors mentioned (slightly ringporous, radial multiples of more than 4 vessels regularly present, spiral thickenings in vessels, alternate inter-vessel pits, non-septate libriform fibres, narrow rays); *Siparuna* placed by MONEY et al. (1950) and TAKHTAJAN (1980) in the subfamily Siparunioideae, by HUTCHINSON (1964) in the subfamily Atherospermoideae of the Monimiaceae (radial pore multiples of more than 4 vessels usually present, often reticulate vessel perforation plates, alternate inter-vessel pits, non-septate thick-walled libriform fibres without distinctly bordered pits confined to the radial walls, often heterogeneous rays with long uniseriate tails, axial parenchyma not rare or absent but in many short uniseriate tangential bands, crystals absent). It is clear that *Amborella* does not fit in any tribe of the family Monimiaceae, but the bare fact of its vesselless structure is not enough to remove it from the Monimiaceae (MONEY et al. 1950). Also *Peumus* could be treated separately or possibly together with *Siparuna*. However, we do not agree with SCHODDE (1970) who proposed a subfamily Peumoideae (of the Monimiaceae), amongst other things because *Peumus* should have exclusively vessels with simple perforations; we regularly found scalariform perforations with 3 bars on the average. *Laurelia* and *Siparuna* are both arranged within the tribe Laurelieae of the subfamily Atherospermoideae (HUTCHINSON 1964). The wood anatomy of especially *Siparuna* is different from the other investigated species (see above); also according to GARRATT (1934) whose observations agree with ours and according to MONEY et al. (1950) who based their arguments mainly on morphological grounds.

PATEL (1973) investigated the wood anatomy of *Hedycarya arborea* J.R. et G. Forst (tribe Hedycaryeae) and *Laurelia novae-zelandiae* A. Cunn. (tribe Laurelieae). The main anatomical features which separate the New Zealand species of these genera are that *H. arborea* has fewer vessels, more numerous sheath cells, and fewer and larger rays, which contain small crystals. He therefore concluded that this anatomical evidence supports the inclusion of *H. arborea* in the Monimioideae (his Monimiaceae) and *L. novae-zelandiae* in the Atherospermoideae (his Atherospermataceae). In our opinion only wider rays are of importance.

Also according to GARRATT (1934) the only essential difference in the structure of the wood of the Monimiaceae if we exclude *Peumus*, *Siparuna* and *Bracteanthus* (he did not investigate *Amborella*), lies in the size of the rays and this is not always absolutely clear cut.

So, if we exclude *Amborella* from the subfamily Monimioideae and place it in a separate family, which has been done by MONEY et al. (1950) and TAKHTAJAN (1980), but not by HUTCHINSON (1964) and also exclude *Peumus*, which has not been done by the above mentioned authors, *Tambourissa* fits quite well within

Table 1. Secondary xylem characters of the investigated Monimiaceae species.

specimens studied	number	growth rings	vessels						fibres		
			rd. mult. > 4	rd. diam. in μm	numbr per mm^2	perf. (number of bars)	inter- vessel pits in μm	member length in μm	fibres	thick- walled	pits dist. bordered
Tambourissa ampliifolia	Pl 3187	+	-	(25-) 50(- 75)	75	sc (25)	30	(360-) 1000(-1200)	ls	-	+ (rd)
Tambourissa hildebrandtii	Pl 2866	-	+	(30-) 70(-110)	55	sc (15)	8 (40)	(470-) 690(- 950)	ls	-	+ (rd)
Tambourissa tetragona	Pl 3188	-	-	(25-) 60(-100)	65	sc (25)	30	(500-) 660(-1000)	ls	-	+ (rd)
Tambourissa trichophylla	Pl 3189	-	-	(20-) 45(- 65)	75	sc (30)	30	(600-) 950(-1100)	ls	-	+ (rd)
Tambourissa trichophylla	Pl 2653	-	-	(25-) 110(-160)	13	sc (20)	50	(930-) 1325(-1740)	ls	-	+ (rd)
Tambourissa spec.	Pl 3009	-	-	(25-) 70(-120)	44	sc (30)	40	(810-) 1180(-1740)	ls	-	+ (rd)
Average of Tambourissa			±	(20-) 70(-160)	55	sc (25)	30	(470-) 970(-1740)	ls	-	+ (rd)
Amborella trichopoda		?	-	no vessels	-	-	-	-	t	-	+
Anthembix spec.	BW 1258	±	-	(40-) 90(-160)	30	sc (32)	8	(760-) 960(-1200)	ls	-	+ (rd)
Hennecartia omphalandra	U 13034	+	-	(25-) 70(-100)	62	sc (13)	12	(755-) 985(-1310)	ls	+	+ (rd)
Hennecartia omphalandra	U 13143	+	-	(20-) 55(- 80)	75	sc (16)	10	(750-) 1020(-1330)	ls	-	+ (rd)
Kibara spec.	U 18378	+	-	(55-) 85(-115)	17	sc (46), ret	10	(1000-) 1250(-1400)	ln, ± ls	±	±-
Laurelia aromatica	U 8423	+	-	(25-) 60(-110)	85	sc (23)	50	(520-) 850(-1150)	t, ± ls	-	+
Laurelia serrata	U 2083	+	-	(25-) 60(-100)	150	sc (50)	60	(710-) 965(-1380)	±, ± ls	-	+
Levieria cf. parvifolia	U 18324	-	-	(30-) 70(-125)	18	sc (55)	70	(1230-) 1660(-2140)	ls, ± ln	-	+ (rd)
Levieria spec.	U 22964	-	+	(50-) 100(-165)	50	sc (40)	60	(1000-) 1690(-2520)	ln, ± ls	-	+
Macrotorus utriculatus	U 20164	±	-	(25-) 90(-125)	28	sc (13)	10	(700-) 1120(-1420)	ln?	+	+
Mollinedia blumenaviana	U 12709	+	-	(30-) 60(- 95)	65	sc (18)	40	(630-) 890(-1085)	ls	-	±
Mollinedia blumenaviana	U 12729	+	-	(30-) 70(-110)	56	sc (22)	50	(600-) 880(-1130)	ls	-	+ (rd)
Mollinedia chrysolaena	U 14129	±	-	(25-) 55(- 90)	62	sc (25)	45	(980-) 1230(-1500)	ls	-	+ (rd)
Mollinedia elegans	U 12580	±	-	(25-) 50(- 95)	84	sc (26)	40	(510-) 885(-1310)	ls	-	+ (rd)
Mollinedia hillipii	U 8820	±	-	(25-) 50(- 80)	54	sc (40)	40	(1040-) 1360(-1740)	ls	-	+ (rd)
Mollinedia laurina	U 8573	±	-	(30-) 55(- 85)	74	sc (35)	40	(470-) 910(-1220)	ls	-	+ (rd)
Mollinedia uleana	U 13532	±	-	(30-) 80(-130)	30	sc (35)	50	(1040-) 1630(-2030)	ls	-	+ (rd)
Peumus boldus	U 14968	+	+	(20-) 60(- 95)	83	s, ± sc (3)	6	(270-) 590(- 750)	ln, ± ls	-	-
Siparuna crassiflora	U 19860	+	±	(30-) 80(-120)	58	s, sc (6), ret	5	(275-) 560(- 910)	ln?	+	-
Siparuna cuspidata	U 342	+	±	(25-) 75(-110)	47	± s, sc (5), ret	5	(355-) 660(- 870)	ln?	+	-
Siparuna cuspidata	Pl 1954	+	+	(30-) 70(-120)	40	sc (7), ret	4-6	(360-) 700(- 990)	ln?	+	-
Siparuna decipiens	U 2387	±	+	(30-) 90(-150)	16	sc (8), ret	6	(430-) 1000(-1540)	ln?	+	-
Siparuna decipiens	U 16218	±	+	(30-) 105(-175)	14	sc (5), ± ret	8	(590-) 840(- 995)	ln?	+	-
Siparuna decipiens	Pl 1914	±	+	(40-) 120(-160)	18	± s, sc (7), ret	6	(660-) 1000(-1450)	ln?	+	-
Siparuna guianensis	U 11727	±	+	(25-) 70(-100)	44	sc (4), ret	4-5	(670-) 1070(-1580)	ln?	+	-
Siparuna guianensis	Pl 2643	+	+	(25-) 70(-110)	70	sc (4), ret	4-5	(720-) 1070(-1600)	ln?	+	-
Siparuna guianensis	U 1437	±	+	(12-) 44(- 70)	54	sc	5	(855-) 1160(-1500)	ln?	+	-
Siparuna lepidantha	U 16182	±	+	(30-) 80(-140)	42	sc (5), ret	6	(810-) 1130(-1650)	ln?	+	-
Siparuna obstipa	U 8007	±	-	(30-) 110(-165)	28	± s, sc (3), ret	6	(460-) 900(-1100)	ln?	+	-
Siparuna pachyantha	U 16086	±	-	(15-) 180(-240)	6	s	10	(580-) 1170(-1425)	ln?	+	-
Siparuna sarmentosa	U 19751	+	-	(30-) 90(-125)	25	sc (8), ret	5	(580-) 930(-1275)	ln?	+	-
Siparuna sprucei	U 2574	±	-	(30-) 60(- 95)	31	sc (3)	5	(555-) 1005(-1310)	ln?	+	-

Symbols and abbreviations used in Table 1:

+ = present
 - = absent
 ± = scarcely present
 aggr. = aggregates
 av. = average
 diam. = diameter
 diff. = diffuse
 dist. = distinctly
 ln = non-septate libriform

ls = septate libriform
 mult. = multiple
 perf. = perforations
 rd. = radial
 (rd) = in radial walls only
 ret = reticulate perforation
 s = simple perforation
 sc = scalariform perforation
 tg. = tangential

Wood-ray type:

He = heterogeneous; procumbant and upright cells are present
 Ho = homogeneous; only procumbant or only upright cells are present
 I = uniseriate rays and multiseriate rays with long uniseriate tails
 II = uniseriate rays and multiseriate rays with short uniseriate tails

rays						axial parenchyma				crystals (if present in rays)	
av. height in μ m	seriate	av. width > 100 μ m	type	number per tg.mm	pits to vessels in μ m (up to)	rare or absent	diff. or diff. in aggr.	uniseriate tg. bands (number per rd.mm)	vasicentric	av. length of strands in (number of cells)	
3600(- 6000)	(1-) 4 (- 6)	110	He II	4	30	-	$\pm$	-	$\pm$	720(5)	+
5000(-10000)	(1-)10 (-15)	200	He II	2-3	50	-	$\pm$	-	$\pm$	1000(7)	+
4000(- 7000)	(1-) 4 (- 8)	-	He II	4	35	-	$\pm$	-	$\pm$	400(3-4)	-
10000(-20000)	(1-) 5 (- 7)	-	He II	5	30	-	$\pm$	-	$\pm$	360(2-4)	+
2600(- 5700)	(1-) 6 (-11)	140	He II	2-3	30	-	$\pm$	-	$\pm$	560(6-7)	-
4000(- 8000)	(1-)10 (-15)	200	He II	4	50	-	$\pm$	-	$\pm$	990(5)	-
4870	(1-) 7 (-15)	-	He II	4	40	-	$\pm$	-	$\pm$	840(5)	-
2700(- 9600)	(1-) 2 (- 5)	-	Ho I	15	-	+	-	-	-	-	-
1100(- 3400)	(1-) 8 (-15)	150	He II	5	30	-	$\pm$	-	$\pm$	730(4)	+
1750(- 6000)	(1-) 5 (- 9)	110	He II	7	35	+	-	-	-	-	+
1900(- 5700)	(1-)3,4(- 7)	-	He II	10	30	+	-	-	-	-	+
2600(-10000)	(3-) 6 (- 9)	280	He II	1-2	45	-	$\pm$	-	$\pm$	1550(8)	+
420(- 1100)	(1-) 2 (- 4)	-	He II	8	40	+	-	-	-	-	-
340(- 720)	(1-)2,3(- 4)	-	He II	10	50	+	-	-	-	-	-
3000(- 8000)	(1-) 8 (-16)	200	He II	4-5	75	+	-	-	-	-	+
780(- 1600)	(1-) 3 (- 6)	-	He II	4	50	+	-	-	-	-	-
1200(- 2900)	(1-) 4 (- 6)	-	$\pm$ He/He II	8	40	-	$\pm$	+ (7)	$\pm$	1280(7)	+
1900(- 5000)	(1-) 5 (-10)	125	He II	5	35	-	$\pm$	-	$\pm$	1085(6)	+
1100(- 2370)	(1-) 5 (-10)	120	He II	4	35	-	$\pm$	-	$\pm$	920(5)	+
1730(- 7000)	(1-) 4 (- 8)	100	He II	8	40	+	-	-	-	-	+
1440(- 2450)	(1-) 4 (- 9)	100	He II	8	40	+	-	-	-	-	+
2300(- 6000)	(1-) 5 (- 8)	120	He II	7	40	-	$\pm$	-	$\pm$	1350(6)	+
2000(- 4500)	(1-)3,4(- 6)	-	He II	10	40	+	-	-	-	-	+
2300(- 4870)	(1-) 9 (-15)	280	He II	4	50	+	-	-	-	-	+
1400(- 4600)	(1-)3,4(- 7)	-	He II	5	30	+	-	-	-	-	-
730(- 2100)	(1-)2,3(- 4)	-	He II	13	25	-	+	+ (14)	$\pm$	760(4-5)	-
1000(- 2700)	(1-)2,3(- 4)	-	He II	9	25	-	+	+ (13)	$\pm$	940(6)	-
1080(- 2900)	(1-) 3 (- 5)	-	He II	9	25	-	+	+ (15)	$\pm$	820(6)	-
1350(- 3000)	(1-)2,3(- 4)	-	He II	6	40	-	+	+ (11)	$\pm$	1170(5)	-
1510(- 4500)	(1-) 3 (- 5)	-	He II	5	40	-	+	+ (10)	$\pm$	1160(4)	-
1880(- 5000)	(1-) 3 (- 6)	-	He II	9	30	-	+	+ (6)	$\pm$	600(4)	-
1690(- 3800)	(1-) 3 (- 5)	-	$\pm$ He I/He II	9	30	-	+	+ (8)	$\pm$	1240(6)	-
1740(- 3000)	(1-) 3 (- 5)	-	He I/II	10	25	-	+	+ (12)	$\pm$	1300(6)	-
1390(- 6000)	(1-) 2 (- 4)	-	He I/II	10	25	-	+	+ (12)	$\pm$	1375(6)	-
1100(- 4500)	(1-) 2 (- 4)	-	He I/II	8	25	-	+	+ (12)	$\pm$	1410(6)	-
1330(- 3360)	(1-)2,3(- 4)	-	He I/II	10	40	-	+	+ (8)	$\pm$	970(5)	-
2000(- 4000)	(1-) 2 (- 4)	-	He II	4	50	-	+	+ (10)	+	1360(4)	-
2280(- 5500)	(1-) 3 (- 4)	-	$\pm$ He I/He II	9	30	-	+	+ (10)	$\pm$	1160(6)	-
1130(- 4000)	(1-) 2 (- 5)	-	He I/II	5	20	-	+	+ (14)	$\pm$	1290(6)	-

this taxon. One has to bear in mind that we did not investigate specimens of all genera of this taxon, especially not of *Monimia*. On wood anatomical grounds alone it is difficult to distinguish the genera.

ACKNOWLEDGEMENTS

Our sincere thanks for Mrs. M. H. van den Bergh, who prepared the slides used for this study. We also wish to express our appreciation to the Institute of Systematic Botany of the University of Utrecht, The Netherlands, for providing most valuable wood samples.

REFERENCES

- CAVACO, A. (1959): Monimiaceées. In H. HUMBERT: *Flore de Madagascar et des Comores* 80: 1–44. Paris.
- GARRATT, G. A. (1934): Systematic anatomy of the woods of the Monimiaceae. *Trop. Woods* 39: 18–44.
- HUTCHINSON, J. (1964): *The genera of flowering plants*. I. Clarendon Press, Oxford: 110–123.
- (1973): *The families of flowering plants*. Third edition. Clarendon Press, Oxford, 968 p.
- JANSSONIUS, H. H. (1934): *Mikrographie des Holzes der auf Java vorkommenden Baumarten*. Brill, Leiden, V: 64–72.
- LAWRENCE, G. H. M. (1951): *Taxonomy of vascular plants*. McMillan Company, New York: 510–512.
- LORENCE, D. H. (1980): *A systematic and eco-evolutionary study of the Monimiaceae in the Malagasy region*. Ph. D. Washington University, 527 p. (not seen).
- METCALFE, C. R. & L. CHALK (1950): *Anatomy of the dicotyledons*. II. Clarendon Press, Oxford: 1138–1145.
- MONEY, L. L., I. W. BAILEY & B. G. L. SWAMY (1950): The morphology and relationships of the Monimiaceae. *J. Arnold Arb.* 31: 372–404.
- PATEL, RAJNI N. (1973): Wood anatomy of the dicotyledons indigenous to New Zealand. 3. Monimiaceae and Atherospermataceae. *New Zealand J. Bot.* 11: 587–598.
- PAX, F. (1894): Monimiaceae. In A. ENGLER & K. PRANTL: *Die natürlichen Pflanzenfamilien*. W. Engelmann, Leipzig. III, 2: 94–105.
- PICHON, M. (1948): Les Monimiaceées, famille hétérogène. *Bull. Mus. Hist. Nat. Par. sér. 2*, 20: 383–384.
- SCHODDE, R. (1970): Two new suprageneric taxa in the Monimiaceae alliance (Laurales). *Taxon* 19: 324–328.
- SOLEREDER, H. (1899): *Systematische Anatomie der Dicotyledonen*. Verlag Ferdinand Enke, Stuttgart: 788–791.
- STERN, W. L. (1954): Comparative anatomy of xylem and phylogeny of Lauraceae. *Trop. Woods* 100: 1–73.
- TAKHTAJAN, A. (1969): *Flowering plants, origin and dispersal*. Oliver and Boyd, Edinburgh, 310 p.
- (1980): Outline of the classification of flowering plants (Magnoliophyta). *Bot. Rev.* 46 (3): 225–359.
- THORNE, R. F. (1974a): A phylogenetic classification of the Annoniflorae. *Aliso* 8 (2): 147–209.
- (1974b): The “Amentiferae” or Hamamelidae as an artificial group. A summary statement. *Brittonia* 25: 395–405.