

COMPARATIVE WOOD ANATOMY OF BONNETIACEAE, THEACEAE AND GUTTIFERAE

TINE BARETTA-KUIPERS

Institute of Systematic Botany, Utrecht, The Netherlands

Summary. A description of the xylem anatomy of the genera *Archytaea*, *Ploiarium*, *Bonnetia*, *Neblinaria*, *Neotatea*, *Caraipa*, *Haploclathra*, *Mahurea*, *Marila*, *Kielmeyera*, and *Asteropeia* is given. All these genera except *Asteropeia*, were included in the family of the Bonnetiaceae by Maguire (1972). He considered the position of *Asteropeia* to be a doubtful one. Wood anatomy indicates that the genera *Archytaea*, *Ploiarium*, *Bonnetia*, *Neblinaria*, and *Neotatea* form a homogeneous group, which differs markedly from the Theaceae, as is concluded from comparisons with representatives of all groups of that family. The taxonomic position of the genera *Caraipa*, *Haploclathra*, *Mahurea*, *Marila*, and *Kielmeyera*, formerly referred to the Guttiferae, is discussed. The genera *Caraipa* and *Haploclathra* are wood anatomically similar to the other genera of the Bonnetiaceae; the genera *Mahurea* and *Marila* less so. *Kielmeyera* fits wood anatomically better in the Guttiferae than in the Bonnetiaceae. These conclusions are based on comparisons with all tribes of the Guttiferae. *Asteropeia* does not fit in with the Theaceae or Bonnetiaceae, and its wood anatomy supports the family status for this genus. *Poeciloneuron* is wood anatomically similar to the Bonnetiaceae. The taxonomic position of *Pelliciera* and of the Tetrameristaceae, in Melchior's concept (1964) belonging to the Theaceae, is also considered. A general wood anatomical description of the Bonnetiaceae excluding *Kielmeyera* and *Asteropeia* concludes this paper. Bonnetiaceae are wood anatomically intermediate between Theaceae and Guttiferae.

INTRODUCTION

Most of the genera now constituting the family Bonnetiaceae, have for a long time been incorporated as the tribe Bonnetieae in the Ternstroemiaceae. The older name Theaceae came in use again in 1895, when Szyszylowicz in the first edition of Engler's Pflanzenfamilien abandoned the name Ternstroemiaceae, in use till then. This tribe Bonnetieae was split in two parts by Engler (1888); *Bonnetia* and *Archytaea* remained in Bonnetieae of the Ternstroemiaceae, whereas *Kielmeyera*, *Caraipa*, *Mahurea*, *Marila*, and *Haploclathra* were referred to the Guttiferae, subfamily Kielmeyeroideae. As may be seen from Table 1 there was considerable confusion in the Flora Brasiliensis as to which family most genera of the Bonnetieae should be ascribed.

Poeciloneuron, which had been included for some time in the Bonnetieae, was referred later to the tribe Calophylleae of the Guttiferae.

Beauvisage (1920) established the family Bonnetiaceae, comprising only the genera *Bonnetia* and *Archytaea*. He agreed with Engler (1895) that the subfamily Kielmeyeroideae of the Guttiferae should contain *Mahurea*, *Kielmeyera* and *Marila* in the tribe Kielmeyereae and *Caraipa* and *Haploclathra* in the tribe Caraipeae. Melchior (1964) held the same view. In 1959 Hutchinson still included *Kielmeyera* and *Haploclathra* in the

WOOD ANATOMY OF BONNETIACEAE

TABLE 1. Different taxonomic treatments of the genera investigated

Benth. & Hooker (1862)	Wawra (1886) Flora Bras.	Engler (1888) Flora Bras.	Melchior (1964)	Hutchinson (1969)
Ternstroemiaceae	Ternstroemiaceae	Ternstroemiaceae	Theaceae	Bonnetiaceae
Bonnetieae	Bonnetieae	Bonnetieae	Bonneticoideae	Ploiarium
Bonnetia	Kielmeyera	Bonnetia	Bonnetia	Archytaea
Archytaea	Mahurea	Archytaea	Archytaea	Bonnetia
Kielmeyera	Marila		Ploiarium	Kielmeyera
Caraipa	Haploclathra	Guttiferae		Mahurea
Mahurea	Caraipa	Kielmeyereae	Guttiferae	Marila
Marila	Bonnetia	Kielmeyera	Kielmeyereae	Caraipa
Haploclathra	Archytaea	Mahurea	Kielmeyera	Haploclathra
Poeciloneuron		Marila	Mahurea	
		Caraipeae	Marila	
		Caraipa	Caraipeae	
		Haploclathra	Caraipa	
			Haploclathra	

Theaceae, but later (1969) his concept of the family Bonnetiaceae became wider. Maguire (1972) included in the Bonnetiaceae ten neotropical genera: *Archytaea*, *Bonnetia*, *Mahurea*, *Marila*, *Haploclathra*, *Caraipa*, *Kielmeyera*, and the new genera *Neblinaria*, *Neogleasonia*, and *Neotatea*. He also included *Ploiarium* of Malaysia, but was in doubt about the position of *Asteropeia*, an endemic of Madagascar. *Ploiarium* has been considered a synonym of *Archytaea* for a long time, but was reinstated as a genus by Melchior (1925). *Asteropeia* has always been consigned to a tribe of its own in the Theaceae.

Kobuski (1948, 1950) and Keng (1962) did not accept the family Bonnetiaceae, but kept *Bonnetia*, *Archytaea*, and *Ploiarium* as the tribe Bonnetieae in the Theaceae.

General surveys of anatomical investigations in this group of taxa were given by Solereder (1899) and Metcalfe & Chalk (1950). Previous studies devoted to Bonnetiaceae, Theaceae or Guttiferae are those by Müller (1882), Van Tieghem (1884), Beauvisage (1920), Vestal (1937), Keng (1962), Schofield (1968), and Baas (1970). The results of those studies will be referred to in the discussion.

It has already been shown by several authors that studies in the secondary xylem can often aid in solving taxonomic as well as phylogenetic problems. However, as Bailey (1957) has stressed, the role of wood anatomy is restricted in the sense, that no evidence of part of the whole plant may be used as proof affecting the whole. If, however, evidence

from all parts and organs is used, wood anatomy may give important evidence to solve problems relating to taxonomy and phylogeny.

It seemed important, therefore, to try to establish if by the structure of their wood the Bonnetiaceae can be distinguished more or less clearly from either the Theaceae or the Guttiferae. The more so as Metcalfe & Chalk (1950) already pointed out that a striking resemblance exists in the wood structure of *Bonnetia* and *Caraipa*.

In order to be able to compare the relative weight of similarities and dissimilarities, it seemed essential to include genera from all subfamilies of the Theaceae sensu Melchior (1964) in the present investigation. The same applies to the groups of the Guttiferae (including 'Clusiaceae' and 'Hypericaceae').

MATERIAL AND METHODS

The wood samples were obtained partly from the Guayana collections made by Maguire, by samples received from a number of Institutional wood collections, and from the wood collection of the Utrecht Institute of Systematic Botany. Wood samples from genera not included in the wood descriptions are listed separately. Institutional wood collections are abbreviated according to Stern (1967). As far as known, all samples are backed by herbarium vouchers.

The wood was studied from stained and unstained microtome sections. Sometimes sections had to be treated with a domestic bleaching agent to remove the dark deposits in the wood cells. Often it proved necessary to treat the wood with HF, sometimes for periods of several weeks, before sectioning was possible. *Asteropeia* in particular, was extremely difficult to section.

To study the presence of silica, radial microtome sections were prepared without previous treatment except boiling and without subsequent staining (ter Welle, 1976).

The terminology used is in accordance with that proposed by the Committee of Nomenclature of the I.A.W.A. (1964). The rays are classified according to Kribs (1935).

Length measurements of vessel members and fibres were taken of macerated material. All values listed in the present study are averages of twenty measurements. They serve only to indicate the general size of elements and are not intended to represent the exact means. Length classes are in accordance with the standard terms of the I.A.W.A. (1937).

DESCRIPTIVE PART

ARCHYTAEA Martius (Pl. 2A; Fig. 1a-b)

Colour: dark reddish brown. Heartwood and sapwood similar.

Microscopic characters: *Vessels* diffuse, exclusively solitary, 8-20 per

square mm, diameter 90–160 μm , round. Vessel members of medium length; (500–)750 (–850) μm . Perforations simple in almost transverse or slightly oblique end walls, with small tails. Thin-walled tyloses present. Vasicentric *tracheids* not seen. *Fibres* thick-walled, diameter 20–24 μm , of medium length, (650–)915(–1150) μm long, with numerous bordered pits on the tangential and radial walls. Pits *c.* 5 μm in diameter, with slightly extended apertures. *Rays* of two sizes: uniseriates of 1–7 upright cells, 100–700 μm high; multiseriates 2–3 cells wide, composed of relatively few procumbent and square cells with uniseriate extensions of 1–5 upright cells, 250–800 μm high (Kribs heterogeneous type IIA); 10–15/mm, 2–5 of which are multiseriates, 5–9 uniseriates. Pits to vessels large, mostly oval. *Parenchyma* scanty paratracheal, predominantly on the adaxial side and scantily diffuse. Strands of 2–6 cells. *Crystals* absent. *Silica grains* present in ray cells, almost always in procumbent, and only rarely in square and upright cells. Grains mostly globular and smooth; other forms occasionally present.

Material studied: *A. multiflora* Benth.: British Guyana, Maguire 46107 (Uw 17011), 45521 (Uw 16752), and 46040 (Uw 17628).

PLOIARIUM Korthals (Fig. 2a–b)

Colour: dark reddish brown. Heartwood and sapwood similar.

Microscopic characters: Vessels diffuse, exclusively solitary, 10–20 per square mm, diameter 80–150 μm , round or slightly oval. Vessel members of medium length: (600–)800(–1000) μm long. Perforations simple in almost transverse or slightly oblique end walls, with small tails. Thin-walled tyloses often abundantly present. Vasicentric *tracheids* not seen. *Fibres* thick-walled, diameter 20–24 μm , of medium length, (850–)1100(–1350) μm long, with numerous conspicuously bordered pits on the tangential and radial walls. Pits *c.* 5 μm in diameter with included or slightly extended, slitlike apertures. *Rays* of two sizes: uniseriates of 1–7 upright cells, 100–600 μm high; biseriates composed of high procumbent and square cells with uniseriate extensions of 1–4 square or upright cells, 300–900 μm high (Kribs heterogeneous type IIA); 10–15/mm, 2–5 of which are biseriates and 5–10 uniseriates. In *Ploiarium pulcherrimum* the uniseriates tend to be slightly higher. The same applies to the extensions of the multiseriates, so that these may measure up to 1100 μm . Pits to vessels large, mostly oval. *Parenchyma* partly diffuse, partly scanty paratracheal on the adaxial as well as the abaxial side of the vessels, sometimes in an incomplete vasicentric ring of 1 cell wide. Strands of 2–4, exceptionally of 6 cells. *Crystals* and *silica grains* absent.

Material studied: *P. alternifolium* (Vahl) Melchior: Malaysia, Sarawak, Anderson 661, PRFw 21336 (Uw 21475); Malaya, Johore, KEPw 2580 (Uw 21392); Desch 2580, PRFw 11608 (Uw 21476). *P. pulcherrimum* (Becc.) Melchior: Malaya, KEPw 7879 (Uw 21404).

BONNETIA Mart. & Zucc. (Pl. 2B–C; Fig. 3a–b)

Colour: in *B. tristyla* and *B. kathleenae* light reddish grey for heartwood and sapwood, in *B. martianum* and *B. stricta* the sapwood light reddish brown and the heartwood dark reddish brown, in *B. neblinae* the wood is dark reddish brown all over.

Microscopic characters: *Vessels* diffuse, with occasionally a slight tendency towards a diagonal arrangement, exclusively solitary, round; 10–25 per square mm, diameter 50–100 μm for most species; in *B. crassa* and *B. stricta* 5–10 per square mm, diameter 100–200 μm . Vessel members of medium length or rather long: in *B. kathleenae* (650–)750(–1000) μm , in *B. martianum* (500–)640(–800) μm , in *B. neblinae* (500–)800(–900) μm , in *B. stricta* (500–)735(–950) μm , in *B. tristyla* (500–)850(–1150) μm . Perforations simple in almost transverse or slightly oblique end walls; tails usually small, sometimes rather long. Thin-walled tyloses often abundantly present. Vascentric *tracheids* present. *Fibres* mostly thick-walled, walls of medium thickness in *B. kathleenae* and *B. stricta* (in one sample of *B. tristyla* a distinct zonation caused by differences in fibre wall thickness was found; the two other samples of this species showed no great variation), diameter 16–20 μm , rather short or of medium length: in *B. kathleenae* (700–)850(–1100) μm ; in *B. martianum* (500–)800(–1000) μm ; in *B. neblinae* (700–)900(–1000) μm ; in *B. stricta* (900–)1150(–1600) μm ; in *B. tristyla* (750–)1050(–1300) μm long. Pits with conspicuous borders, 5–6 μm in diameter, numerous on tangential and radial walls, with included or slightly extended lenticular or slit-like apertures. *Rays* of two sizes: uniseriates of 1–11 upright cells, 100–1000 μm high; multiseriates 2–4 cells wide, composed of square and short upright cells, procumbent cells absent, with uniseriate extensions of 1–4 upright cells (Kribs heterogeneous type IIA). The variation in height (300–1000 μm) is primarily due to the number of upright cells; the height of the multiseriate portion of the ray is rather uniform; 10–15/mm, 1–3 of which are multiseriates, 6–10 uniseriates. Pits to vessels large, oval. *Parenchyma* unilateral paratracheal on the adaxial side of the vessels, never more than 2 cells wide; often only a few cells present. The parenchyma may be either fusiform, septate or consist of strands of 2–4 cells. Rhombic *crystals* sometimes present in the axial parenchyma. *Silica grains* absent.

Material studied: *B. crassa* Gleason: Venezuela, Mt. Duida, Tate 539, Yw 16186.—*B. kathleenae* Lasser: Venezuela, Cerro Sipapo, Maguire 27928 (Uw 20410).—*B. martianum* Maguire: Venezuela, Sabana El Venado, Maguire 41801 (Uw 20415).—*B. neblinae* Maguire: Venezuela, Cerro de la Neblinae, Maguire 37059 (Uw 20411).—*B. stricta* (Nees) Nees & Mart.: Brazil, Bahia near Oliveira, Kubitzki 74–56 HBG (Uw 20972).—*B. tristyla* Gleason: Venezuela, Cerro Duida, Tate 536, Yw 16185; Canon Grande, Maguire 42179 (Uw 20422), and 42460 (Uw 20427).

NEBLINARIA Maguire (Plate 1A–B; Fig. 4a–c)

Colour: sapwood light reddish grey, sharply delimited from the dark reddish brown heartwood.

Microscopic characters: *Vessels* diffuse, exclusively solitary, 30–40 per square mm, diameter 50–100 μm , often slightly angular or radially flattened. Vessel members of 80

medium length: (320–)400(–550) μm . Perforations predominantly simple, sometimes scalariform with few bars in almost transverse or slightly oblique end walls, with very small tails as well as very broad ones (Fig. 4a). Thin-walled tyloses present. Vasicentric *tracheids* not seen. *Fibres* very thick-walled (walls 12–14 μm) as well as rather thin-walled (walls 4–6 μm), diameter 30–36 μm , very short, (400–)550(–700) μm long, with numerous conspicuously bordered pits on the tangential and radial walls. Pits *c.* 5 μm in diameter, with slit-like slightly extended apertures. Fibres with forked endings, with ‘shoulders’ or even completely blunt (Fig. 4b). *Rays* of two sizes: uniseriates of 2–15 upright or square cells, 100–1000 μm high, sometimes for a small part biseriate; multiseriates 2–3 cells wide, composed of square cells with uniseriate extensions of 1–2 square cells, 400–650 μm high. Procumbent cells absent (Kribs heterogeneous type II A); 10–15/mm, 1–2 of which are multiseriates, 10–15 uniseriates. Pits to vessels large, mostly elongated. *Parenchyma* scanty paratracheal, predominantly adaxial. Cells fusiform, septate or in 2-celled strands. *Crystals* and *silica grains* absent.

Material studied: *N. celiae* Maguire: Venezuela, Cerro de la Neblina, Maguire 42139 (Uw 20421), holotype.

NEOTATEA Maguire (Plate 1C–D; Fig. 5a–b)

Colour: reddish beige.

Microscopic characters: *Vessels* diffuse, exclusively solitary in *Uw 20416*, with a few radial multiples in *Uw 20412*, *c.* 65 per square mm in *Uw 20416*, *c.* 130 in *Uw 20412*, diameter 40–70 μm , slightly angular in outline. Vessel members long to very long: (800–)1200(–1450) μm . Perforations in very oblique end walls, predominantly simple, but a few scalariform perforations present as well, with few or numerous bars. Tails mostly long. Thin-walled tyloses abundant. Vasicentric *tracheids* not seen. *Fibres* very thick-walled, walls 12–14 μm , diameter 25–30 μm , of medium length, (1120–)1440(–1680) μm long. A small amount of thin-walled fibres present, which are shorter than the thick-walled ones. Lenticular simple pits restricted to the radial walls, *Rays* exclusively uniseriate of 2–18 cells, 80–800 μm high, composed of square and short upright cells (Kribs heterogeneous type III); 6–10/mm. Pits to vessels scalariform. *Parenchyma* very scanty, some strands diffuse, but mostly paratracheal on the adaxial side of the vessels. Cells fusiform, septate or in 2–4 celled strands. *Crystals* and *silica grains* absent.

Material studied: *N. neblinae* Maguire: Venezuela, Cerro de la Neblina, Maguire 37290 (Uw 20412), holotype; Maguire 42178 (Uw 20416).

CARAIPA Aublet (Plate 2D; Fig. 6a–b)

Colour: reddish beige. Heartwood and sapwood similar.

Microscopic characters: *Vessels* typically in a diagonal pattern, exclusively

T. BARETTA-KUIPERS

solitary, 5–15 per square mm for most species, 20–30 per square mm in *C. llanorum* and *C. parvifolia*, diameter 100–200 μm in most species, round. Vessel members rather long: in *C. ampla* (800–)1150(–1500) μm , in *C. densifolia* (560–)850(–1250) μm , in *C. llanorum* (700–)925(–1300) μm , in *C. longipedicellata* (700–)1125(–1450) μm , in *C. parvifolia* (750–)1150(–1450) μm , in *C. punctulata* (900–)1100(–1250) μm , in *C. richardiana* (900–)1065(–1500) μm , in *C. valioi* (800–)965(–1300) μm . Perforations simple, mostly in almost transverse end walls, tails very small or heavy. Tyloses not seen. Vasicentric *tracheids* always present. *Fibres* thick-walled in most species, walls 6–8 μm , diameter 20–24 μm ; in *C. densifolia* and *C. punctulata* part of the fibres is medium thick-walled; of medium length: in *C. ampla* (1200–)1550(–1990) μm , in *C. densifolia* (1000–)1400(–1700) μm , in *C. llanorum* (1200–)1450(–1750) μm , in *C. longipedicellata* (100–)1485(–1750) μm , in *C. parvifolia* (1300–)1600(–1900) μm , in *C. punctulata* (1300–)1500(–1800) μm , in *C. richardiana* (1100–)1600(–1900) μm , in *C. valioi* (1000–)1350(–1700) μm . Pits with conspicuous borders (5–6 μm) numerous on tangential as well as radial walls, with lenticular, included apertures. *Rays* predominantly uniseriate, 2–16 cells, 150–650 μm , occasionally up to 900 μm high, composed mainly of square and short upright cells, almost without procumbent cells (Kribs heterogeneous type III); 10–15/mm. Pits to vessels large, oval or elongate. *Parenchyma* unilateral paratracheal (cap-like) on the abaxial side of the vessels, mostly one or two cells wide. *Parenchyma* strands of 2–8 cells. Rhombic *crystals* often seen in the *parenchyma* strands. *Silica grains* absent.

Material studied: *C. ampla* Ducke: French Guiana, Cayenne, BAFOG 1226 (Uw 5715), BAFOG 1285 (Uw 5773).—*C. densifolia* Mart.: Surinam, Stahel 126 (Uw 126); Nickerie, Maas 11062 (Uw 11739); Brazil, Krukoff 6229 (Uw 7573), 6252 (Uw 7595), 7220 (Uw 8251), and 8874 (Uw 16092).—*C. llanorum* Cuatrec. ssp. *llanorum*: Venezuela, Maguire 41679 (Uw 20414).—*C. longipedicellata* Steyerl.: Venezuela, Maguire 42225 (Uw 20424).—*C. parvifolia* Aubl.: French Guiana, BAFOG 42 N (Uw 5541).—*C. punctulata* Ducke.: Surinam, Lanjouw & Lindeman 2769 (Uw 1914), Lindeman 7019 (Uw 4734); Venezuela, Maguire 41694 (Uw 20413).—*C. richardiana* Camb.: Surinam, Lindeman 6311 (Uw 4322); Brazil, Belem 51876 (Uw 9101).—*C. valioi* Paula: Brazil, Krukoff 8991 (Uw 16098).

HAPLOCLATHRA Bentham (Plate 2E; Fig. 7a–b)

Colour: sapwood golden brown, heartwood reddish brown.

Microscopic characters: Vessels diffuse, sometimes in conspicuous diagonal rows, mostly solitary, in *H. leiantha* and *H. paniculata* also with a small part in radial multiples, 5–10 per square mm, diameter 100–200 μm , in *H. paniculata* locally 50–100 μm , round or slightly flattened radially. Vessel members rather long: in *H. leiantha* (650–)825(–1000) μm ; in *H. paniculata* (650–)925(–1000) μm ; in *H. verticillata* (600–)850(–1000) μm . Perforations always simple, most often in almost transverse end walls; tails generally small. Thin-walled tyloses often abundantly present. Vasicentric *tracheids* present. *Fibres* very thick-walled in all species, walls 8–10 μm , diameter mostly 20–24 μm , of medium length: in *H. leiantha* (1450–)1575(–1900) μm ; in *H. paniculata*

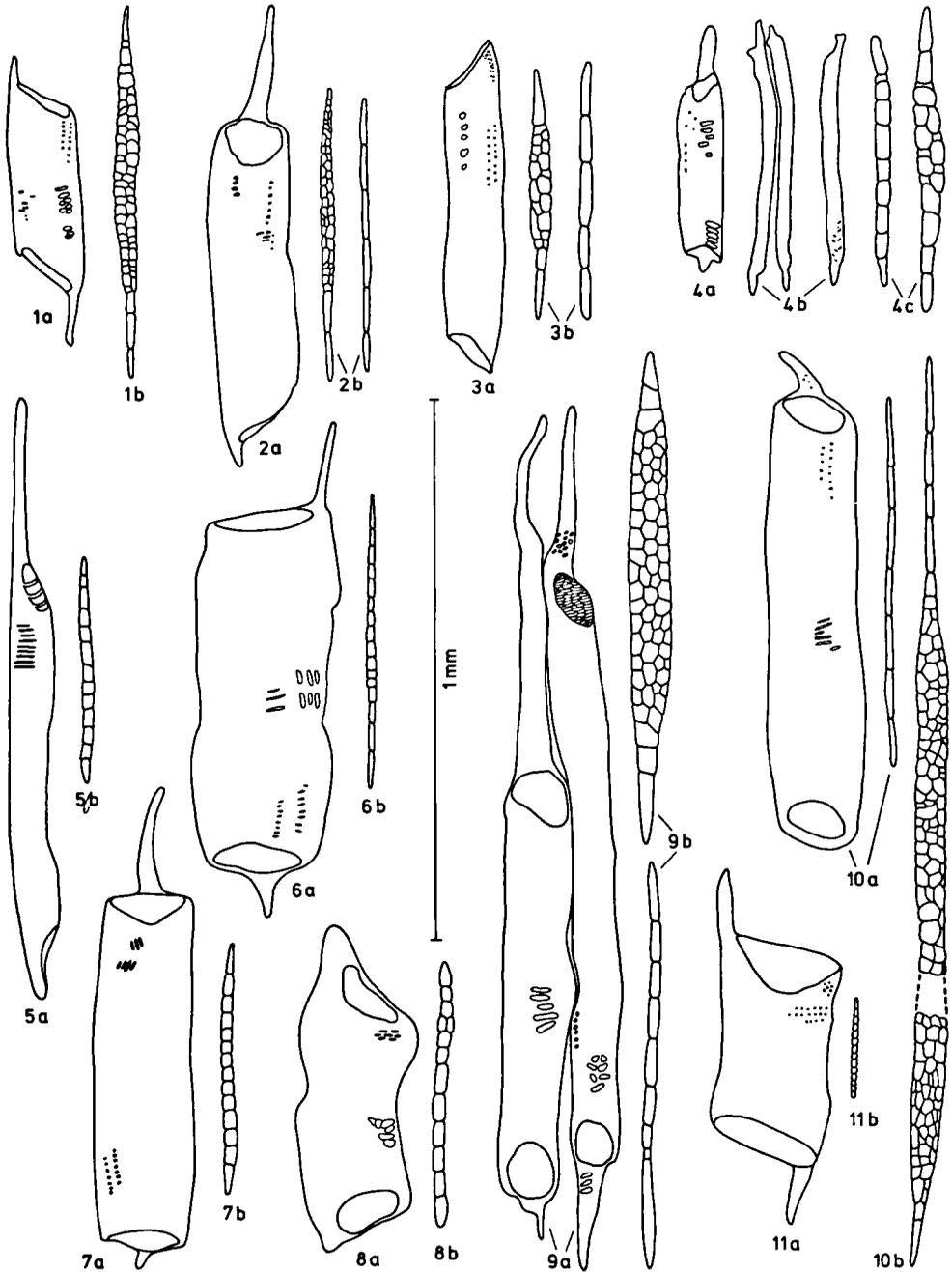


Fig. 1-11. Camera lucida drawings of vessel members, fibres, and rays.—1. *Archytaea multiflora* (Uw 17011).—2. *Ploiarium alternifolium* (Uw 21393).—3. *Bonnetia neblinae* (Uw 20411).—4. *Neblinaria celiae* (Uw 20421).—5. *Neotatea neblinae* (Uw 20416).—6. *Caraipa valioi* (Uw 16098).—7. *Haploclathra leiantha* (Uw 20752).—8. *Kielmeyera* spec. (Uw 16586).—9. *Mahurea palustris* (Uw 5709).—10. *Marila laxiflora* (Uw 15743).—11. *Asteropeia multiflora* (Uw 20853).

T. BARETTA-KUIPERS

(1200–)1475(–1600) μm , in *H. verticillata* (1100–)1475(–1600) μm long. Small, round, simple pits confined to radial walls. *Rays* exclusively uniseriate, 2–25 cells, 100–800 μm , mostly ca. 500 μm high, composed almost entirely of square and short upright cells (Kribs heterogeneous type III); 10–15/mm. Pits to vessels large, oval. *Parenchyma* unilateral paratracheal (cap-like) on the abaxial side, mostly 2–3 sometimes more cells wide. Strands of 4–10, mostly of 6–8 cells. *Crystals* absent. *Silica* grains present in the ray cells, mostly globular and rather smooth, 3–13 μm in diameter.

Material studied: *H. leiantha* Benth.: Brazil, Rio Negro, *Ducke* 158 (*Uw* 20752).—*H. paniculata* (Mart.) Benth.: Brazil, Manaus, *Ducke* 306 (*Uw* 20751).—*H. verticillata* *Ducke*.: Brazil, Rio Negro, *Ducke* 257 (*Uw* 20819).

MAHUREA Aublet (Fig. 9a–b)

Colour: Sapwood light reddish brown, heartwood purplish red.

Microscopic characters: Vessels diffuse, solitary (25–40%), as well as in short radial multiples, 30–40 per square mm, diameter 50–100 μm , round. Vessel members mostly very long, in *M. exstipulata* (750–)1150(–1600) μm , in *M. palustris* (950–)1535(–2000) μm . Perforations mostly simple in slightly oblique end walls; occasional perforation plates with numerous interconnected bars present in all samples (Fig. 9a); tails sometimes small, mostly long and rather broad. Intervascular pits crowded, alternate, large (8–10 μm). Vascentric *tracheids* not seen. *Fibres* septate, of medium wall thickness. walls 6–8 μm . diameter 30–36 μm . of medium length: *M. exstipulata* (1000–)1300(–1550) μm , rather long: *M. palustris* (1400–)1750(–2250) μm . Small, elongated or slit-like simple pits, mainly on the radial walls. *Rays* of two kinds: uniseriates of 2–15 upright cells, 400–850 μm high; multiseriates 2–3 cells wide, composed of procumbent, square and upright cells, often with very long uniseriate extensions, 800–2000 μm high (Kribs heterogeneous type I); 10–15/mm, 2–5 of which are multiseriates, 6–9 uniseriates. Pits to vessels very large, oval or elongated. *Parenchyma* absent in *M. palustris*, extremely scarce and diffuse in *M. exstipulata*. Rhombic *crystals* in non-chambered fibres. *Silica* grains not seen.

Material studied. *M. exstipulata* Benth.: British Guyana, *Maguire* 45520 (*Uw* 16751).—*M. palustris* Aubl.: French Guiana, Cayenne, *BAFOG* 1034 (*Uw* 5577), *BAFOG* 1220 (*Uw* 5709).

MARILA Swartz (Fig. 10a–b)

Colour: sapwood light reddish brown, heartwood slightly darker.

Microscopic characters: *Vessels* diffuse, exclusively solitary in *M. laxiflora* and *M. macrophylla*, in *M. grandiflora* small radial multiples occasionally present, 20–45

per square mm, diameter 50–100 μm , round. Vessel members rather long to very long: in *M. grandiflora* (640–)900(–1200) μm ; in *M. laxiflora* (800–)1100(–1700) μm ; in *M. macrophylla* (850–)950(–1200) μm long. Perforations simple as well as scalariform, often in the same vessel member, with 1–20 bars; most often 2–5 exceptionally broad bars are present. Perforations in slightly oblique end walls. Tails absent, very small, or very long and/or broad. Vasicentric *tracheids* not seen. *Fibres* septate and non-septate; the septate ones with thin walls, 4–5 μm , the non-septate ones with thick walls, 8–10 μm , diameter of both kinds 20–26 μm ; the non-septate fibres of medium length and rather long: in *M. grandiflora* (1150–)1600(–1900) μm , in *M. laxiflora* (1100–)1700(–1900) μm , in *M. macrophylla* (1200–)1400(–1600) μm ; the septate fibres c. 1000 μm long. Septate fibres with simple pits mainly on the radial walls; non-septate fibres with large bordered pits (4–6 μm) on tangential and radial walls. In *M. grandiflora* the septate fibres are abundant and more or less distributed in bands. *Rays* of two kinds: uniseriatae of 2–20 upright cells, 200–1500 μm high and very high multiseriatae, 3–6 cells wide of high procumbent, square and upright cells with long uniseriate extensions of upright cells (Kribs heterogeneous type I); the multiseriatae are often over 2000 μm in *M. laxiflora* and *M. macrophylla*, in *M. grandiflora* somewhat lower; 10–15/mm, 2–4 of which are multiseriatae, 8–14 uniseriatae. Pits to vessels large, oval or elongated. *Parenchyma* very scarce, diffuse or diffuse in aggregates. Strands of 5–8 cells. Large rhombic *crystals* (20–30 μm) present in all species in the square ray cells. *Silica grains* not seen.

Material studied. *M. grandiflora* Griseb.: Trinidad, PRFw 5029 (Uw 21474).—*M. laxiflora* Rusby.: Colombia, Fuchs 22002 (Uw 15743).—*M. macrophylla* Benth.: Colombia, Fuchs 21779 (Uw 15722); Panama, USw 16319 (Uw 11070).

KIELMEYERA Martius (Plate 3D, Fig. 8a, b)

Colour: sapwood light sandy brown, heartwood slightly darker.

Microscopic characters: *Vessels* diffuse, solitary as well as in short radial multiples of up to 4 and in small clusters. Never more than 50% of the vessels solitary; mostly less, in Uw 16586 only c. 20%; 5–10 vessels per square mm (clusters and multiples counted as one), diameter 100–200 μm , round or slightly flattened radially. Vessel members of medium length and rather long: in Uw 20981 (450–)600(–750) μm ; in Uw 20980 (550–)685(–950) μm ; in Uw 16586 (850–)960(–1400) μm . Perforations simple in almost transverse or slightly oblique end walls; without tails, or with very small or very broad ones. Vessel to vessel pits crowded, alternate, large (c. 15 μm). Thin-walled tyloses present. Vasicentric *tracheids* present. *Fibres* thin-walled (walls 4–5 μm) in Uw 20980, moderately thick-walled (walls 6–8 μm) in Uw 20981 and in Uw 16586, diameter 20–28 μm , of medium length and rather long: in Uw 20981 (950–)1050(–1200) μm , in Uw 20980 (1400–)1600(–2000) μm , in Uw 16586 (1400–)1600(–2200) μm long. Large, slit-like pits with small borders mainly confined to the radial walls. *Rays* predominantly uniseriate,

T. BARETTA-KUIPERS

sometimes partly biseriate in *Uw 16586*; 2–23 cells, 100–800 μm high, composed mainly of square and short upright cells with very few procumbent cells (Kribs heterogeneous type III); 10–15/mm. Pits to vessels very large, oval or elongated, *Parenchyma* in irregular bands, mostly 1–2 cells wide, locally wider, 3 or more bands per mm; in *Uw 20981* the bands are more regular, more widely spaced and mostly 1 cell wide. Locally some more or less aliform parenchyma is present as well as some diffuse parenchyma strands. Strands of 4–8 cells. In *Uw 16586* numerous rhombic *crystals* present in the parenchyma strands. In *Uw 20981* numerous *silica grains* are present in the ray cells, globular and smooth up till 8 μm as well as more like lumps of silica sand of different shapes.

Material studied. K. spec.: Brazil, Kuhlmann 32 (*Uw 20980*); Murça Pires 9182 (*Uw 20981*); Maguire 57032 (*Uw 16586*).

ASTEROPEIA Thouars (Plate 3A–B; Fig. 11a–b)

Colour: sapwood golden brown, sharply delimited from the reddish brown heartwood.

Microscopic characters: *Vessels* diffuse, exclusively solitary, 10–15 per square mm in most species, 1–6 in *A. rhopaloides*, diameter 50–100 μm , round or slightly flattened radially. Vessel members of medium length: in *A. micraster* (430–)535(–650) μm ; in *A. multiflora* (300–)500(–650) μm ; in *A. rhopaloides* (500–)575(–700) μm long. Perforations simple in almost transverse or slightly oblique end walls, mostly with rather long tails. Thin-walled tyloses present. Vasicentric *tracheids* not seen. *Fibres* very thick-walled, walls 6–8 μm , diameter 16–20 μm , rather short: in *A. micraster* (600–)735(–900) μm , in *A. multiflora* (500–)650(–800) μm , in *A. rhopaloides* (700–) 875(–1150) μm , in *A. spec.* (700–)790(–900) μm long. Small bordered pits (2–4 μm) on tangential and radial walls. *Rays* uniseriate only, 2–12 cells, up till 200 μm high, of procumbent cells only (Kribs homogeneous type III), 5–10/mm. Pits to vessels crowded, alternate, very small. *Parenchyma* unilateral paratracheal (cap-like), with extensions on either side, on the abaxial side of the vessels, 1–2 cells wide, often with a few fibres between the vessels and parenchyma cells. In *A. rhopaloides* the ‘caps’ are often 3 cells wide and aliform and diffuse parenchyma are present as well. The parenchyma cells in all samples have bulging shapes; strands of 4–6 cells. *Crystals* and *silica grains* absent.

Material studied. *A. micraster* Hallier: Madagascar, Thouvenot 149 (*Uw 20852*).—*A. multiflora* Thouars: Madagascar, Lamarque 272 R 16 (*Uw 20853*).—*A. rhopaloides* Bak.: Madagascar, Thouvenot 46 (*Uw 20854*).—*A. spec.*: Madagascar, C.T.F.T. R 933–34 (*Uw 20454*).

MATERIAL STUDIED FOR COMPARISON

GUTTIFERAE

- Allanblackia floribunda* Oliv.: Zaïre, *Corbier-Baland* 117 (Uw 20336).—*A. spec.*: Uganda, *PRFw* 16301 (Uw 21478).
- Calophyllum brasiliense* Camb.: Surinam, *Yale* 17525 (Uw 416).—*C. costatum* Baill.: New Guinea, *B. W.* 2271 (Uw 20476).—*C. curtisii* King: Malaysia, *KEPw* 5236 (Uw 21427).—*C. inophylloides* King: Malaysia, *KEPw* 6537 (Uw 21430).—*C. rubiginosum* Hind. & Wyatt Smith: Malaysia, *KEPw* 459 (Uw 21382).—*C. wallichianum* Planch.: Malaysia, *KEPw* 6538 (Uw 21432).
- Chrysochlamys clusiaefolia* Maguire: Venezuela, *Uw* 15689.—*C. floribunda* Cuatr.: Colombia, *Fuchs* 22276 (Uw 15760).
- Clusia palmicida* L. C. Rich.: Surinam, *Yale School of For.* 35636 (Uw 418).—*C. pana-panari* (Aubl.) Choisy: Surinam, *Yale School of For.* 35634 (Uw 417).—*C. nemorosa* G. F. W. Mey: Guyana, *A. C. Smith* 2265 (Uw 21568).
- Cratogeomys arborescens* Bl.: Malaysia, *KEPw* 3800 (Uw 21436).—*C. cochinchinense* (Lour.) Bl.: Malaysia, *KEPw* 2614.—*C. formosum* (Jack) Dyer: Malaysia, *KEPw* 4201 (Uw 21439).
- Eliaea articulata* Cambess.: Madagascar, *Tananarive Herb.* 14577 SF.
- Garcinia cereoflava* Engl.: Zaïre, *de Briey* 85 (Uw 20326).—*G. corymbosa* Wall.: New Caledonia, *USw* 4614 (Uw 7408).—*G. nutans* Robr.: Brazil, *Krukoff* 7995 (Uw 16153).—*G. stolzii* Engl.: East Africa, *Schlieben* 1504 (Uw 15487).
- Harungana madagascariensis* Lam.: Kenya, *PRFw* 10203 (Uw 21481).
- Havetia laurifolia* H.B.K.: Venezuela, *PRFw* 22663 (Uw 21482).
- Hypericum balearicum* L.: Mallorca, *Baretta* 345 (Uw 20974).—*H. galioides* Lam.: Florida, *USw* 14006 (Uw 8528).—*H. lanceolatum* Lam.: East Africa, *Schlieben* 288 (Uw 15925).
- Lebrunia bushiae* Staner: Zaïre, Kivu, *Ghesquière s. n.* (Uw 20431).
- Mammea africana* G. Don: Zaïre, *Corbier-Baland* 833 (Uw 20341).—*M. americana* L.: Jamaica, *USw* 6023 (Uw 8359).
- Mesua grandis* (King) Kosterm.: Malaysia, *KEPw* 832 (Uw 21386).—*M. lepidota* var. *parviflora* (Ridley) Whitmore: Malaysia, *KEPw* 2471 (Uw 21384)—*M. racemosa* (Pl.) Kosterm.: Malaysia, *KEPw* 456 (Uw 21381).
- Moronobea coccinea* Aubl.: Brazil, *Krukoff* 6404 (Uw 7697).
- Oedematopus* spec. Guyana, *Maguire* 45903 (Uw 16811).
- Pentadesma butyracea* Sabine: Zaïre, *de Briey* 158 (Uw 20327).
- Pentapthalangium pachycarpum* A. C. Smith: New Guinea, *B.W.* 6003 (Uw 20477).
- Platonia insignis* Mart.: French Guiana, *BAFOG* 234 M (Uw 5309).
- Poeciloneuron indicum* Bedd., India, Mysore, *PRFw* 28370 (Uw 21479).
- Psorospermum* spec.: Nigeria, *PRFw* 23095 (Uw 21477).
- Rheedia kappleri* Eyma: Surinam, *Stahel* 204 (Uw 204); *Yale School of For.* 35528 (Uw 419).—*R. macrophylla* (Mart.) Pl. & Tr.: Surinam, *Yale School of For.* 35856 (Uw 420).—*R. martinii* Maguire: Surinam, *Maguire* 24427 (Uw 2505).
- Symphonia globulifera* L.f.: French Guiana, *BAFOG* 66 M (Uw 5151); *BAFOG* 1288 (Uw 5776); Zaïre, *Corbier-Baland s.n.* (Uw 20354).
- Thysanostemon pakaraimae* Maguire: Guyana, *Maguire* 46026 (Uw 17002).
- Tovomita secunda* Poepp.: Surinam, *Lindeman* 3716 (Uw 2706).
- Tovomitopsis grandifolia* Standl. & L. Wms.: Costa Rica, Allen, *Usw* 30166 (Uw 10382).
- Vismia angusta* Miq.: Surinam, *Yale School of For.* 35478 (Uw 421).—*V. cayennensis* (Jacq.) Pers.: Surinam, *Stahel* 276 (Uw 276).—*V. confertiflora* Spruce: Columbia, via Kew Bot. Gardens Mus. (Uw 2122).—*V. guianensis* (Aubl.) Choisy: Surinam, *Yale School of For.* 35474 (Uw 422).—*V. latifolia* (Aubl.) Choisy: Surinam, *Stahel* 217 (Uw 217).

THEACEAE

- Adinandra schliebenii* Melch.: East Africa, *Schlieben 1618 (Uw 15549)*.
Anneslea crassipes Hk.f.: Malaya, *KEPw 1390 (Uw 21390)*.
Camellia lanceolata Seem.: Philippines, *Jacobs 7516 (Uw 20528)*.—C. spec.: Philippines, *Jacobs 7099 (Uw 20527)*.
Cleyera theoides Choisy: Costa Rica, Ica, *CCO-16 (Uw 20691)*.
Eurya acuminata D.C.: Indonesia, *Koorders 15296 (Uw 20536)*.—*E. obovata* Korth.: Indonesia, *Koorders & Val. 8161 (Uw 20535)*.—*E. tigang* K. Schum. & Lauterb.: New Guinea, *van Royen 3699 (Uw 20534)*.
Freziera undulata Willd.: Lesser Antilles, Saba, *Stoffers 3472 (Uw 5431)*.
Gordonia lasianthus Ellis: USA, *USw 3428 (Uw 7319)*.—*G. papuana* Kob.: New Guinea, *B.W. 11798 (Uw 18135)*; *B.W. 4897 (Uw 20469)*; *B.W. 7970 (Uw 20749)*.
Laplacea amboinensis Miq.: New Guinea, *B.W. 9725 (Uw 20470)*.—*L. fruticosa* (Schrader) Kobuski: *Lindeman 4939 (Uw 3368)*.
Pentaphylax arborea Ridley: Malaya, *KEPw 1376 (Uw 21403)*.
Pyrenaria acuminata Planch.: Malaya, *KEPw 7819 (Uw 21394)*.—P. spec.: Indonesia, Sumatra, *Krukoff 4228 (Uw 21484)*.
Schima noronhae Reinw.: Malaya, *KEPw 1399 (Uw 21396)*.
Ternstroemia dentata (Aubl.) Sw.: Surinam, *Stahel 240 (Uw 240)*.—*T. punctata* (Aubl.) Sw.: Surinam, *Maguire 23271 (Uw 20409)*.—*T. schomburgkiana* Benth.: Guyana, *Maguire 23239 (Uw 20408)*.—T. spec.: Venezuela, *Maguire 42131 (Uw 20420)*, *42196 (Uw 20423)*, *42356 (Uw 20425)*, *42522 (Uw 20429)*.
Visnea mocanera L.: Canary Isl., *Madrid W 2433 (Uw 15470)*.

MISCELLANEOUS GENERA

- Pelliciera rhizophorae* Tr. & Pl.: Colombia, *Fuchs 21841 (Uw 15731)*. *Tetramerista glabra* Miq.: Indonesia, via SFCw, *Austr. R 575-141 (Uw 20452)*; SFCw *R 139-6 (Uw 20453)*; *Hildebrand 23352 (Uw 20471)*; Malaya, *Tervuren 11601 (Uw 20438)*.

DISCUSSION

The wood anatomical data presented above together with data on putatively related groups will be discussed in this section. This is aimed at contributing to our understanding of the natural affinities of the genera described and of members of the Guttiferae s.l. and of the Theaceae s.l. For reasons of convenience the subfamilies recognized by Melchior (1964) in his broad concept of the Theaceae will be discussed first. Subsequently the genera treated by some authors as members of the Guttiferae, but now thought to form part of the family of the Bonnetiaceae will be dealt with. Finally a comparison will be made between Bonnetiaceae in Maguire's family concept and Theaceae s.s. (Keng, 1962) and the suprageneric taxa of the Guttiferae.

Melchior (1964) recognized six subfamilies in his system for the Theaceae: (1) Theoideae with the tribes Theae and Gordoniae; (2) Ternstroemioideae with the tribes Ternstroemieae, Sladenieae and Adinandreae; (3) Bonnetoideae (*Bonnetia*, *Archytaea*, and *Ploiarium*); (4) Asteropeioideae (*Asteropeia*); (5) Tetrameristoideae (*Tetramerista*, and the genus *Pentamerista* described by Maguire in Maguire *et al.*, 1972); (6) Pelliceroideae (*Pelliciera*).

Keng (1962) comprehensively treated anatomy and morphology of the Theoideae

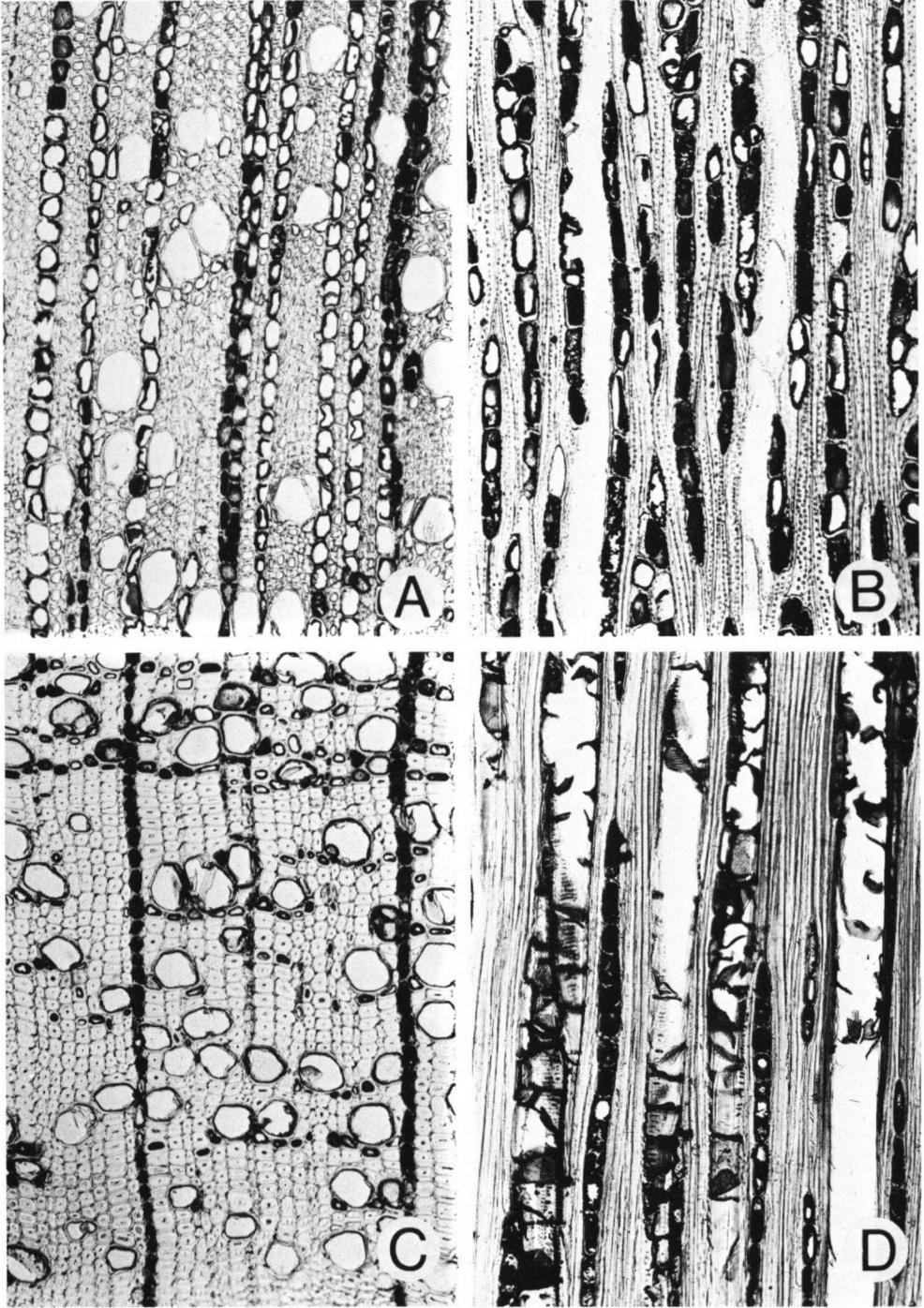


Plate 1. Transverse and tangential sections ($\times 90$).—A, B. *Neblinaria celiae* (Uw 20421).—C, D. *Neotatea neblinae* (Uw 20416).

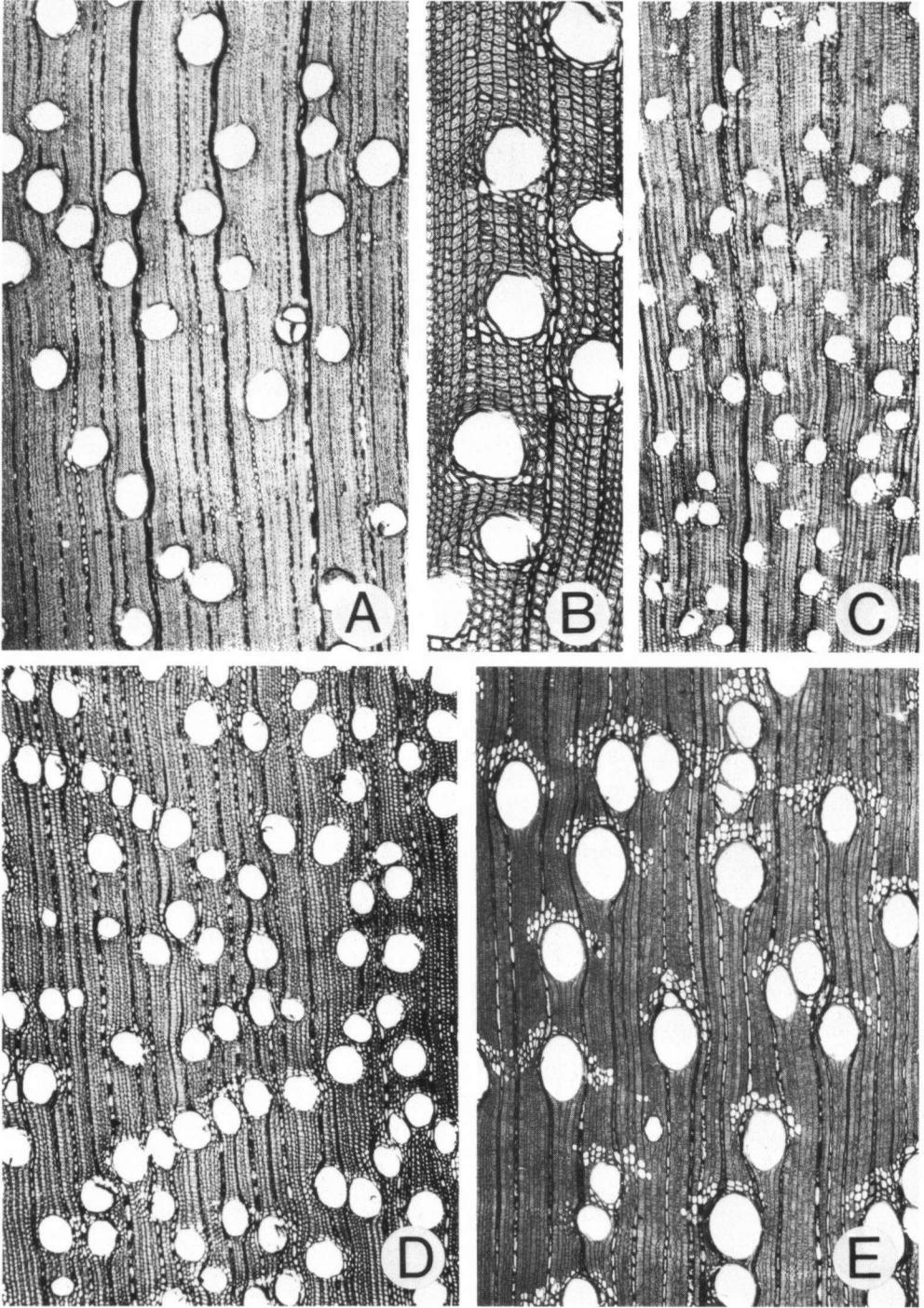


Plate 2. Transverse sections (B \times 90; others \times 37).—A. *Archytaea multiflora* (Uw 17628).—B, C. *Bonnetia tristyla* (Uw 20422).—D. *Caraipa densifolia* (Uw 11739).—E. *Haploclathra verticillata* (Uw 20919).

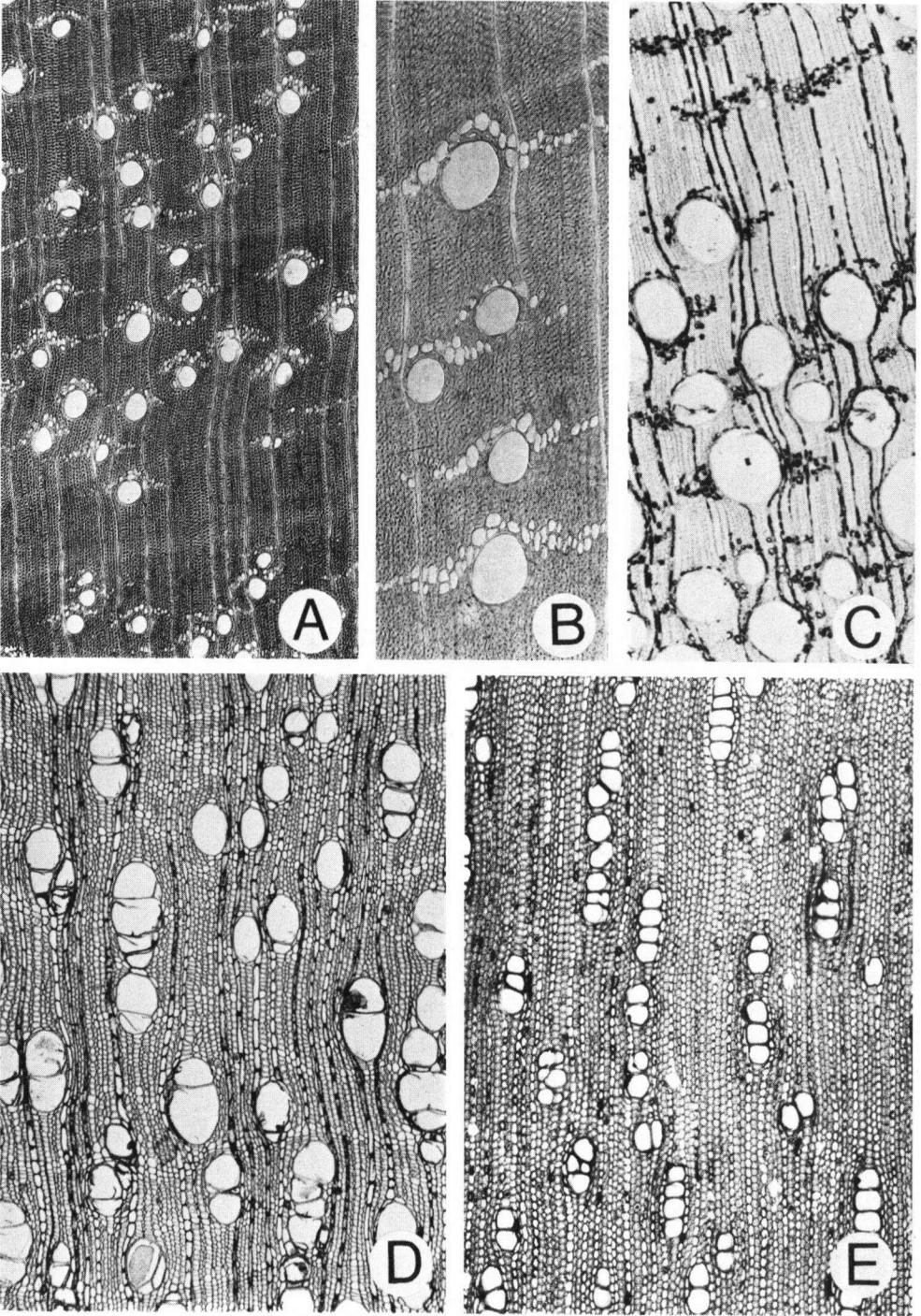


Plate 3. Transverse sections (B \times 90; others \times 37).—A, B. *Asteropeia multiflora* (Uw 21479).—C. *Poeciloneuron indicum* Bedd. (Uw 21479).—D. *Kielmeyera* spec. (Uw 16586).—E. *Pelliciera rhizophorae* (Uw 15731).

and Ternstroemioidae. Wood anatomically they are quite homogeneous (see also Table 2).

Tetramerista had already been raised to family rank by Hutchinson (1959), and further taxonomic and anatomical studies on this genus and its close relative *Pentamerista* (Maguire *et al.*, 1972) support this. Their wood is highly distinct from that of Theaceae s.s. (comprising the Theoideae and Ternstroemioidae sensu Melchior only), in having pore multiples, simple perforations and raphide-bearing ray cells.

Pelliciera is the only genus belonging to the subfamily Pellicieroideae in Melchior's concept. Beauvisage (1920) already gave *Pelliciera* family status, mainly based on anatomical evidence. In his opinion it should be placed between Ternstroemiaceae (= Theaceae) and Marcgraviaceae. Other authors who discussed the affinities of *Pelliciera* are Baillon (1873), Hallier (1923), Metcalfe & Chalk (1950), Kobuski (1951), and de Roon (1975). According to Kobuski (1951), it is a matter of preference whether *Pelliciera* should be treated as a family of its own near Theaceae, or as a distinct tribe or subfamily within the Theaceae. Its wood anatomy is like that of *Tetramerista*, with pore multiples, raphides, and simple perforations. This supports the exclusion from Theaceae. Hallier (1923) in fact included *Tetramerista* and *Pelliciera* in the Marcgraviaceae, a family also containing raphides in its wood. De Roon (1975), however, considered that there are no convincing arguments to claim that the affinities of both genera should be greater with the Marcgraviaceae than with the Theaceae.

Asteropeia, the only genus of Melchior's subfamily Asteropeioideae, and endemic in Madagascar, has been assigned to several families e.g.: Samydaceae (Bentham & Hooker, 1862), Ternstroemiaceae (Szyszlowicz, 1895), and Flacourtiaceae (Beauvisage, 1920). From the description and Plate 3A–B its wood appears to be distinct from that of Theaceae, Bonnetiaceae, and Guttiferae because of its very low, homocellular, uniseriate rays composed of procumbent cells (Kribs 1935, homogeneous type III). This type of ray may be considered an advanced character. It is for instance found in most genera of the Leguminosae. The fibre-tracheids of *Asteropeia* constitute, however, a primitive character. The parenchyma distribution in *Asteropeia* recalls that of most genera of the Bonnetiaceae, especially that of *Caraipa* and *Haploclathra* (Plate 2D–E). The abaxial paratracheal parenchyma caps, mostly with tangential extensions could also be described as abaxially aliform. Very often there are a few fibres between the parenchyma and the vessels, and in this respect *Asteropeia* also differs from the Bonnetiaceae. In *Asteropeia rhopaloides* the parenchyma is more abundant than in the other two species studied; here it is often aliform as encountered in many Leguminosae, although I would certainly not suggest a real relationship between *Asteropeia* and that family. Erdtman's (1966) conclusion based on pollen morphology, that *Asteropeia* is distinct from Theaceae as well as Flacourtiaceae is confirmed by wood anatomy. In his recent wood anatomical survey of the Flacourtiaceae, Miller (1975) also excluded *Asteropeia* from that family. In my opinion there are neither affinities with the Theaceae, nor with the Tetrameristaceae. A family status for *Asteropeia* as proposed by Takhtajan (1969) is supported by wood anatomy. There may be relationships with

Bonnetiaceae, but the wood structure of *Asteropeia* seems more advanced than that of the Bonnetiaceae.

The genera which will be discussed now are those constituting the family Bonnetiaceae in Maguire's concept, and which were distributed over the subfamilies Bonnetioideae (Theaceae) and Kielmeyeroideae (Guttiferae) by e.g. Melchior (1964). The Bonnetioideae comprise the genera *Bonnetia*, *Archytaea*, and *Ploiarium*. These three genera have always been kept together by all authors, irrespective of whether their results were based on external morphology or on anatomy. Because *Ploiarium* has been considered a synonym of *Archytaea* until 1925, when Melchior reinstated the genus, it is not mentioned in the older literature. Solereder (1899) already noted that *Bonnetia* and *Archytaea* have rubiaceous (= paracytic) stomata, whilst the other Theaceae have other stomatal types. *Kielmeyera*, *Caraipa*, *Mahurea*, *Marila*, and *Haploclathra* of the Kielmeyeroideae also have rubiaceous stomata. However, as already pointed out by Müller (1882) and Van Tieghem (1884), *Bonnetia* and *Archytaea* lack secretory cavities in pith and phloem, which are typical for Kielmeyeroideae and other Guttiferae. This in fact induced Engler (1888) to split the tribe Bonnetieae into a Theaceous and Guttiferous part (see introduction). When Beauvisage (1920) established the small family Bonnetiaceae comprising *Archytaea* and *Bonnetia*, he placed it between the Theaceae (then Ternstroemiaceae) and Guttiferae. He considered the genus *Kielmeyera* to provide a link between his Bonnetiaceae and Guttiferae. Vestal (1937) agreed with Engler (1895) that *Bonnetia* and *Archytaea* could be regarded as a link between Theaceae and Guttiferae, but he did not object to their inclusion in the Theaceae. Metcalfe & Chalk (1950) referred *Bonnetia* to the Bonnetiaceae and mentioned the close resemblance between its species and some members of the Kielmeyeroideae. *Archytaea*, although treated under Theaceae by these authors was said to deviate from the other Theaceae in several characters, and *Ploiarium* was mentioned amongst the genera, the exclusion of which from the Theaceae would make that family much more uniform in anatomy.

From the wood anatomical descriptions it is clear that the genera *Bonnetia*, *Archytaea*, and *Ploiarium* are very much alike. This particularly applies to *Archytaea* and *Ploiarium*, which only differ in some aspects of parenchyma distribution (scanty paratracheal and predominantly adaxial in *Archytaea*; also occurring sometimes on the abaxial side of the vessels in *Ploiarium*) and in the presence (*Archytaea*) or absence (*Ploiarium*) of silica grains in the rays. *Bonnetia* is quite similar to these two genera in wood anatomy, but has slightly more abundant parenchyma with a more pronounced cap-like appearance (Plate 2B–C), always situated on the adaxial side of the vessels.

The new genera *Neblinaria* and *Neotatea* incorporated in the Bonnetiaceae by Maguire (1972) resemble these three Bonnetiaceous genera to a certain extent. *Neblinaria* is quite similar, but has the shortest vessel members (Fig. 4 and 12). *Neotatea*, however, differs in more respects: it has very long vessel members, angular in transverse section; scalariform vessel-ray pits, and libriform fibres instead of fibre-tracheids. Both *Neblinaria* and *Neotatea* have a few scalariform perforation plates in addition to simple ones, which also distinguishes them from the Bonnetiaceae discussed before.

According to Maguire (1972), *Neotatea* is the most primitive member of the Bonnetiaceae. For vessel characters (length of the elements, perforations and vessel-ray pitting) this is supported by wood anatomy. Its fibres belong, however, to the more advanced type.

Within the Kielmeyeroideae of the Guttiferae sensu Melchior two tribes are recognized: The Caraipae and the Kielmeyereae. The taxonomic history of the genera constituting this subfamily has already been reviewed in the introduction and above. Kubitzki (1976, in press) states: 'the Kielmeyeroideae sensu Engler (= sensu Melchior) cannot be defined by one or several universally applicable characters, but there exist overlapping features which knit this group of genera together and which leave no doubt that they constitute a homogeneous assemblage'. In Kubitzki's opinion there is an unmistakable relationship of this alliance with the Guttiferae rather than with the Theaceae. Wood anatomy gives some support for this view for the genera *Caraipa* and *Haploclathra* of the Caraipae. These genera have many wood anatomical characters in common, but are different in the type of ground tissue: *Caraipa* has fibre-tracheids; *Haploclathra* has libriform fibres. They both stand out, however, through their unilateral paratracheal, cap-like, parenchyma which is situated on the abaxial side of the vessels. In *Archytaea*, *Ploiarium*, and *Bonnetia* the unilateral paratracheal parenchyma is always adaxial and less abundant. Unilateral paratracheal parenchyma is extremely unusual in the taxa surveyed in this study and in the other families of the Theales as delimited by Takhtajan (1969). It is interesting to note that the genus *Poeciloneuron* also has abaxial parenchyma caps, sometimes extended to bands (Pl. 2E). This genus was included in Bentham & Hooker's tribe Bonnetieae of the Ternstroemiaceae (1862; and followed by Baillon in 1873), but later referred to the tribe Calophylleae of the Guttiferae. *Poeciloneuron* has, moreover, fibre-tracheids, which make it stand out in the Guttiferae where *Mammea* and *Eliaea* (Baas, 1970) are the only other genera with conspicuously bordered pits on the fibre walls. Perhaps this character is, however, not of great taxonomic importance in this group of genera because transitions between libriform fibres and fibre-tracheids occur in the tribe Calophylleae.

The tribe Kielmeyereae with the genera *Kielmeyera*, *Mahurea*, and *Marila* is a very heterogeneous one. The occurrence of xanthonenes in *Kielmeyera* as well as in *Caraipa*, demonstrated by Gottlieb *et al.* (1971) is according to Kubitzki (in the press) an unmistakable indication of affinities with Guttiferae rather than with Theaceae. Xanthonenes have been found in *Bonnetia* as well (Kubitzki, personal communication). Schofield (1968) was of the opinion that *Kielmeyera* belongs to the Guttiferae on the basis of petiole anatomy. The wood anatomy of the Kielmeyereae is highly diverse. *Mahurea* as well as *Marila* show a rather low level of specialization. In one species of *Mahurea* axial parenchyma is totally absent, in the other species and in *Marila* it is extremely scanty and diffuse. In both genera the rays are of Kribs' most primitive type heterogeneous I and the vessel members are long. In *Marila* many scalariform perfora-

tions occur, greatly varying in number of bars. In *Mahurea* only few scalariform perforations are present, but with many bars (Fig. 9). *Mahurea* has libriform fibres. *Marilia* is outstanding in having septate libriform fibres and non-septate fibre-tracheids with large bordered pits. The genus *Kielmeyera* is very different from these two genera because of its banded parenchyma: a common feature of the Calophylleae, Garcineae and Moronoboideae of the Guttiferae. Its frequent vessel multiples also recall Guttiferae. The heterogeneous uniseriate rays are like those of *Neotatea*, *Caraiipa*, and *Haploclathra*, and some Guttiferae. A position in the Guttiferae rather than in the Bonnetiaceae seems therefore indicated.

Comparison of the Theaceae s.s. and Guttiferae with the Bonnetiaceae.

Figure 12 shows a diagram of the fibre/vessel member length ratio of all Bonnetiaceous genera, one genus of the Theaceae, and one genus of each tribe of the Guttiferae. This ratio may be used as an indication for the degree of specialization: the nearer the ratio approaches one, the less specialized the wood. In the diagram the average length of the vessel elements in μm is on the left of each column, the average length of the fibres on the right. The length of the elements of *Ternstroemia* stands out. The Bonnetiaceous genera *Archytaea*, *Ploiarium*, *Neotatea*, *Mahurea*, *Bonnetia*, and *Neblinaria* are rather

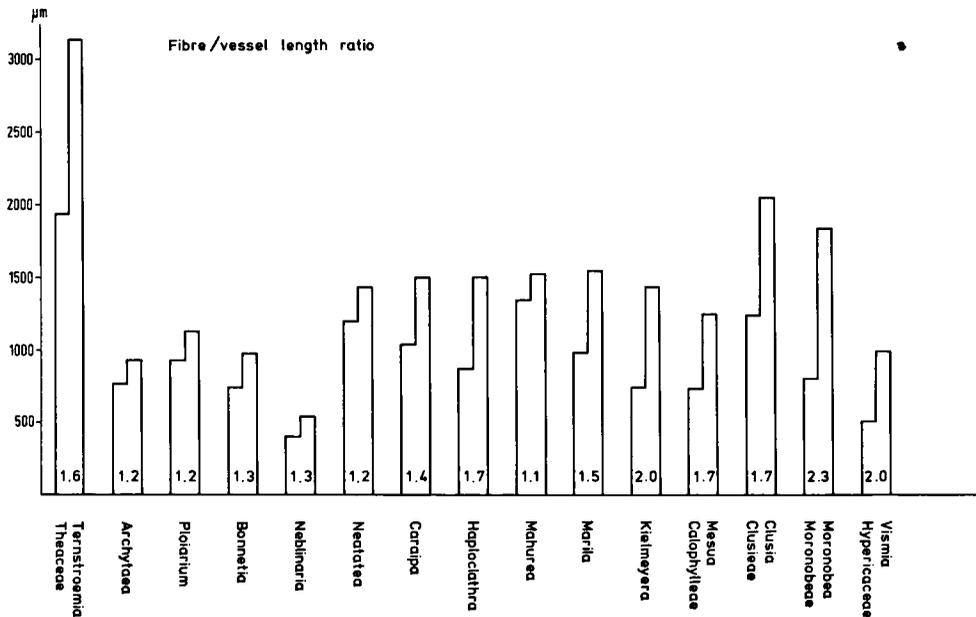


Fig. 12. Vessel member length, fibre length and fibre/vessel ratio in selected Theaceae and Guttiferae and in the genera of the Bonnetiaceae.

similar in fibre/vessel member length ratio. *Caraipa*, *Haploclathra*, and *Marila* have a somewhat higher ratio, and *Kielmeyera* is again aberrant with a ratio of 2.0, only equalled or surpassed in some Guttiferae. Moronobeae with a value of 2.3 are in other wood anatomical features as well the most specialized of the Guttiferae. It is obvious that the data of Fig. 12 are only of restricted significance, because the values for Theaceae and Guttiferae are based on such limited material. They only serve to show a possible trend, and it is interesting to note that there is a rather good agreement between the deductions from these data and the trend apparent from other characters summarized in Table 2.

To facilitate the comparison between the Theaceae, Guttiferae, and Bonnetiaceae, some characters reflecting different degrees of xylem specialization are compiled in Table 2. Frost (1930), Kribs (1935, 1937), Tippe (1938), Metcalfe & Chalk (1950), and Carlquist (1961) discussed major trends of xylem specialization. The trends which will be considered here are:

(1) Scalariform perforation plates with many bars in very oblique end walls are the most primitive; simple perforations in slightly oblique or almost transverse walls are more advanced.

(2) Very long vessel members are more primitive than short ones.

(3) Solitary vessels (pores) are more primitive than vessels in multiples.

(4) Kribs (1935) heterogeneous type I rays are the most primitive; his heterogeneous type IIA is somewhat more specialized; the uniseriate heterogeneous type III is presumably phylogenetically derived from these former types.

(5) Diffuse parenchyma is more primitive than paratracheal and banded parenchyma.

(6) Fibre-tracheids are more primitive than libriform fibres.

In Table 2 the characters listed in the different columns become more specialized from left to right. It appears that the Bonnetiaceae have a quite different and higher specialization level than the Theaceae, and that they tend to be more primitive than the Guttiferae in their wood structure.

The genera of the Theaceae s.s. are all rather similar in their wood anatomy, and have characters of the lowest specialization level. Only the rays of the Camellioideae show some degree of specialization.

The Bonnetiaceae genera *Archytaea*, *Ploiarium*, *Bonnetia*, *Neblinaria*, *Caraipa*, and *Haploclathra* are also homogeneous wood anatomically. They have simple perforations, vessel members which are long or of medium length, rays of Kribs' heterogeneous IIA or III types, and unilateral paratracheal parenchyma which may be scanty or cap-like. All genera except *Haploclathra* have fibre-tracheids. The genus *Neblinaria* is the only one with sporadic scalariform perforation plates.

Neotatea differs somewhat from this group in having occasional scalariform perforations, very long vessel members, heterogeneous type III rays, and libriform fibres. *Mahurea* and *Marila* resemble this genus somewhat but are more primitive in structure or frequency of scalariform perforation plates, in their heterogeneous I rays, and in having diffuse parenchyma.

TABLE 2

	perforation	vessel member length	pore distr.	rays	parenchyma distr.	fibres
	scalariform scal. + simple simple/oblique simple/transverse	very long long medium + short	solitary multiples	Kribs heter. I " heter. IIA " heter. III otherwise	diffuse scanty paratr. banded	fibre-trach. libriform
Theaceae						
Ternstroemiodeae						
Ternstroemia	++	++	++	++	++	++
Anneslea	+++	+++	+++	+++	+++	+++
Adinandra	+++	+++	+++	+++	+++	+++
Visnea	+++	+++	+++	+	+++	+++
Eurya	+++	+++	+++	+++	+++	+++
Cleyera	+++	+++	+++	+++	+++	+++
Freziera	+++	+++	+++	+++	+++	+++
Theoideae						
Gordonia	+	+	+	+	+	+
Laplacea	+++	+++	+++	+++	+++	+++
Schima	+++	+++	+++	+++	+++	+++
Camellia	+++	+++	+++	+++	+++	+++
Pyrenaria	+	+	+	+	+	+
Bonnetiaceae						
Archytaea		+	+	+		+
Ploiarium			+	+		+
Bonnetia			+	+		+
Neblinaria	+		+	+		+
Neotatea	+	+	+	+	+	+
Caraipa		+	+	+	+	+
Haploclathra		+	+	+	+	+
Mahurea	+	+	+	+	+	+
Marila	+	+	+	+	+	+
Kielmeyera			+	+		+
Asteropeiaceae						
		+	+		+	+
Guttiferae						
Calophylleae						
Mammea		+	+	+	+	+
Poeciloneuron		+	+	+	+	+
Calophyllum		+	+	+	+	+
Mesua		+	+	+	+	+
Clusiaceae						
Clusia	+	+	+	+	+	+
Tovomita		+	+	+	+	+
Tovomitopsis	+	+	+	+	+	+
Oedematopus	+	+	+	+	+	+
Chrysochlamys	+	+	+	+	+	+
Havetia	+	+	+	+	+	+
Garcinieae						
Allanblackia	+	+	+	+	+	+
Rheedia	+	+	+	+	+	+
Garcinia	+	+	+	+	+	+
Pentapalangium	+	+	+	+	+	+
Moronobeae						
Pentadesma	+	+	+	+	+	+
Platonia	+	+	+	+	+	+
Moronobeia	+	+	+	+	+	+
Symphonia	+	+	+	+	+	+
Hypericeae						
Hypericum	+	+	+	+		+
Cratoxyleae						
Cratoxylon	+	+	+	+		+
Eliaea	+	+	+	+		+
Vismieae						
Vismia	+	+	+	+		+
Psorospermum	+	+	+	+		+
Harungana	+	+	+	+		+

Kielmeyera stands out from all these genera in having banded parenchyma. This specialized feature is accompanied by two others, viz. numerous pore multiples and thin-walled libriform fibres.

In comparing the Bonnetiaceae with the different groups of the Guttiferae it appears that *Mahurea* and *Marila* have several links with the Clusiaceae. Some genera of this wood anatomically least specialized tribe of the Guttiferae, share the mixed simple and scalariform perforations. In other Clusiaceae the perforations are simple but in very oblique end walls. Vessel member length, ray type and the occurrence of septate fibres are other characters in common. The presence of scalariform inter-vessel pits in all Clusiaceae remains, however, a character which distinguishes them from *Mahurea* as well as from *Marila*.

The tribes Garcineae and Moronobeae are wood anatomically very homogeneous and mutually similar. They differ markedly from the Bonnetiaceae. Their rays, classified in Table 2 as 'otherwise' comprise Kribs' (1935) type heterogeneous II B, in which the uniseriate are almost absent, or if present, are very low as well as Kribs' homogeneous type I.

The tribe Calophylleae is wood anatomically heterogeneous, the more so through the inclusion of *Poeciloneuron*. As mentioned before, *Poeciloneuron* which Bentham & Hooker (1862) included in the tribe Bonnetieae of the Ternstroemiaceae shares the typical cap-like parenchyma distribution of most Bonnetiaceous genera. As in *Caraipa* and *Haploclathra* it is abaxial. Moreover, *Poeciloneuron* has fibre-tracheids as most Bonnetiaceae. This genus could therefore be incorporated in the Bonnetiaceae on wood anatomical grounds. *Mammea* is also aberrant in this tribe, having fibre-tracheids which in the Guttiferae only occur in *Eliaea*, and diffuse parenchyma which otherwise only occurs in some Clusiaceae. Leaving *Mammea* and *Poeciloneuron* out of consideration, it appears that the Calophylleae are wood anatomically very similar to *Kielmeyera*. *Caraipa* and *Haploclathra* have also some characters in common with this tribe, for instance the vasicentric tracheids. As such they constitute a link with the Guttiferae. On the whole, however, the Calophylleae are clearly distinct from the Bonnetiaceae by their wood anatomy, mainly by the type of parenchyma distribution.

The Hypericeae, Cratoxyleae, and Vismieae are all quite different from the Bonnetiaceae (Table 2), and will not be further discussed here.

CONCLUSIONS

The Bonnetiaceae are a family distinctly separate from the Theaceae in its restricted sense. The anatomy of the wood of this family, as well as anatomical evidence derived from various other parts of the plants according to investigations by others, all point in the same direction.

From the evidence derived from the wood structure, it is also clear that there are

several links connecting the family with the Theaceae, viz. through *Neotatea* and to a lesser degree through *Mahurea* and *Marila*. Even more connections exist with the tribes Clusiaceae and Calophylleae of the Guttiferae. The genera *Caraipa* and *Haploclathra*, by Melchior (1964) still included in his tribe Caraipeae of the Guttiferae, fit in well with the Bonnetiaceae, but at the same time they have salient characters in common with the Calophylleae, viz. the vasicentric tracheids, which are found in *Bonnetia* as well. *Kielmeyera* on the contrary, could better be excluded from the Bonnetiaceae and returned to the Guttiferae. *Mahurea* as well as *Marila* have several characters in common with the Clusiaceae; nevertheless they do not fit in with this tribe because of their different type of intervacular pitting.

It cannot be denied that the wood structure of the family Bonnetiaceae is not exactly homogeneous. Leaving out *Kielmeyera* would make the family much more an entity. The genera *Archytaea*, *Ploiarium*, *Bonnetia*, *Neblinaria*, *Caraipa*, and *Haploclathra* are wood anatomically quite similar. All genera together form a kind of gradual transition in the structure of their wood from Theaceae to Guttiferae.

Poeciloneuron could from evidence of the structure of the wood, be incorporated in the Bonnetiaceae as it was before.

Asteropeia, although similar to the Bonnetiaceae in its rather remarkable parenchyma distribution, seems in general more advanced in wood structure. A rather close relationship with the Bonnetiaceae may be present, but an incorporation in the family as Maguire (1972) suggested, seems in my opinion not appropriate. A family status near the Bonnetiaceae seems the best taxonomic solution.

Pelliciera shows in several unusual features of its wood structure a striking resemblance with Tetrameristaceae. They seem to be very closely related to each other and, probably, to the Marcgraviaceae.

General description of the wood of the family Bonnetiaceae (Kielmeyera and Asteropeia excluded)

Vessels diffuse, solitary, partly in multiples in *Mahurea*. Vessel members mostly long or of medium length, very long in *Neotatea*, *Mahurea*, and *Marila*. Perforations typically simple, slightly oblique to almost transverse; a few scalariform perforations present in *Neblinaria*, *Neotatea*, and *Mahurea*, about as many scalariform as simple perforations in *Marila*. *Vasicentric tracheids* present in *Bonnetia*, *Caraipa*, and *Haploclathra* only. *Fibres* thick-walled, of medium length, except in *Neblinaria* where they are very short; partly septate in *Marila* and then thin-walled, septate in *Mahurea*, of the fibre-tracheid type except in *Neotatea*, *Haploclathra*, *Mahurea* pro parte and *Marila*. *Rays* Kribs' heterogeneous type I in *Mahurea* and *Marila*, heterogeneous type II A in *Archytaea*, *Ploiarium*, *Bonnetia*, *Neblinaria*, heterogeneous type III in *Neotatea*, *Caraipa*, and *Haploclathra*. *Parenchyma* scanty to somewhat more abundant unilateral, paratracheal, adaxial or abaxial, except in *Mahurea* and *Marila* where it is diffuse. Parenchyma strands usually of 2–6 cells, sometimes of more cells in *Caraipa*, *Haploclathra*, and *Marila*.

ACKNOWLEDGEMENTS

Sincere thanks are due to Dr. A. M. W. Mennega for her continuing help and stimulation in this investigation; to Dr. K. Kubitzki for providing me with his manuscript on *Caraipa* and providing wood samples, to Ben ter Welle for preparing the excellent slides, to Messrs T. Schipper and A. Kuiper for the drawings and photographs. I am grateful to the many botanical institutes all over the world for providing me with the material for this investigation, especially the Smithsonian Institution, Washington.

REFERENCES

- BAAS, P. 1970. Floral and vegetative anatomy of *Eliaea* from Madagascar and *Cratoxylum* from Indo-Malesia (Guttiferae). *Blumea* 18: 369–391.
- BAILEY, I. W. 1957. Potentialities and limitations of wood anatomy in the study of the phylogeny and classification of angiosperms. *J. Arnold Arbor.* 38: 243–254.
- BAILLON, H. E. 1873. *Histoire des Plantes* 4.
- BEAUVISAGE, L. 1920. Contribution à l'étude anatomique de la famille des Ternstroemiaceées. Thésis Paris.
- BENTHAM, G. & J. D. HOOKER. 1862. *Genera Plantarum* 1.
- CARLQUIST, S. 1961. Comparative plant anatomy.
- ENGLER, A. 1888. Guttiferae. *In Flora Brasiliensis* 12, 1: 382–486. 1895. Guttiferae, *In Engler & Prantl, Natürl. PflFam.* (Ed. 1) 3(6): 194–242.
- ERDTMANN, G. 1966. Pollen morphology and plant taxonomy.
- FROST, F. H. 1930. Specialization in secondary xylem of Dicotyledons I & II, *Bot. Gaz.* 89: 67–94; 90: 198–212.
- GOTTLIEB, O. R., A. A. LINS MESQUITA, & T. J. NAGEM. 1971. Guttiferae. Xanthones from *Kielmeyera rubriflora*. *Phytochem.* 10: 2253–2255.
- HALLIER, H. 1923. Beiträge zur Kenntnis der Linaceae (DC. 1819) Dumort. *Beih. bot. Zbl.* 39, 2: 1–178.
- HUTCHINSON, J. 1959. The families of flowering plants 1.
- HUTCHINSON, J. 1969. Evolution and phylogeny of flowering plants.
- I.A.W.A. 1937. Standard terms of length of vessel members and wood fibres. *Trop. Woods* 51: 21.
- I.A.W.A. 1964. Multilingual glossary of terms used in wood anatomy.
- KENG, H. 1962. Comparative morphological studies in Theaceae. *Univ. Calif. Publ. Bot.* 33: 269–370.
- KOBUSKI, C. E. 1948. Studies in the Theaceae 17: Review of the genus *Bonnetia*. *J. Arnold Arbor.* 29: 393–413.
- KOBUSKI, C. E. 1950. Studies in the Theaceae 19: The genera *Archytaea* and *Ploiarium*. *J. Arnold Arbor.* 31: 196–207.
- KOBUSKI, C. E. 1951. Studies in the Theaceae 23: The genus *Pelliciera*. *J. Arnold Arbor.* 32: 256–262.
- KRIBS, D. A. 1935. Salient lines of structural specialization in the wood rays of Dicotyledons. *Bot. Gaz.* 96: 547–557.
- KRIBS, D. A. 1937. Salient lines of structural specialization in the wood parenchyma of Dicotyledons. *Bull. Torrey bot. Cl.* 64: 177–183.
- KUBITZKI, K. (in the press) A monograph of the genus *Caraipa* (Bonnetiaceae). *Mem. N.Y. bot. Gdn.*
- MAGUIRE, B. 1972. Bonnetiaceae. *In The Botany of the Guayana Highland* 9. *Mem. N.Y. bot. Gdn* 23: 131–165.
- MAGUIRE, B., C. DE ZEEUW, YUNG-CHAN HUANG, & C. C. CLARE. 1972. Tetrameristaceae, *in The Botany of the Guayana Highland* 9. *Mem. N.Y. bot. Gdn* 23: 165–192.
- MELCHIOR, H. 1925. Theaceae, *In Engler & Prantl, Natürl. PflFam.* (Ed. 2) 21: 109–154.
- MELCHIOR, H. 1964. Guttiferales. *In Engler, Syllabus PflFam.* 2.
- METCALFE, C. R. & L. CHALK. 1950. Anatomy of the Dicotyledons.
- MILLER, REGIS B. 1975. Systematic anatomy of the xylem and comments on the relationships of Flacourtiaceae, *J. Arnold Arbor.* 56: 20–102.

WOOD ANATOMY OF BONNETIACEAE

- MÜLLER, K. 1882. Vergleichende Untersuchung der anatomischen Verhältnisse der Clusiaceen, Hypericaceen, Dipterocarpaceen und Ternstroemiaceen. *Bot. Jb.* 2: 430–464.
- ROON, A. C. DE. 1975. Contributions towards a monograph of the Marcgraviaceae. Thesis, Utrecht.
- SCHOFIELD, E. K. 1968. Petiole anatomy of the Guttiferae and related families. *Mem. N.Y. bot. Gdn* 18: 1–55.
- SOLEREDER, H. 1899. Systematische Anatomie der Dicotyledonen.
- STERN, W. L. 1967. Index Xylariorum. *Regnum Vegetabile* 49.
- SZYSZYLOWICZ, I. VON. 1895. Theaceae. *In* Engler & Prantl, *Natürl. PflFam* 3(6): 175–192.
- TAKHTAJAN, A. 1969. Flowering plants. Origin and dispersal.
- TIEGHEM, M. P. VAN. 1884. Sur la disposition des canaux sécréteurs dans les Clusiacées, les Hypéricacées, les Ternstroemiacées et les Diptérocarpées. *Bull. Soc. bot. Fr.* 6: 141–151.
- TIPPO, O. 1938. Comparative anatomy of the Moraceae and their presumed allies. *Bot. Gaz.* 100: 1–99.
- VESTAL, P. A. 1937. The significance of comparative anatomy in establishing the relationship of the Hypericaceae to the Guttiferae and their allies. *Philipp. J. Sci.* 64: 199–256.
- WAWRA, H. 1886. Ternstroemiaceae. *In* *Flora Brasiliensis* 12(1): 262–334.
- WELLE, B. J. TER. 1976. Silica grains in the woody plants of the Neotropics, especially Surinam. *Leiden bot. Ser.* (this issue).