

Systematic wood anatomy of the tribe Guettardeae (Rubiaceae)

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TER WELLE, B. J. H., LOUREIRO, A. A., LISBOA, P. L. B. & KOEK-NOORMAN, J., 1983. Systematic wood anatomy of the tribe Guettardeae (Rubiaceae). The wood anatomy of nearly all genera of the Guettardeae (Rubiaceae, Guettardoideae) has been examined, and in this respect the tribe is heterogeneous. Suggestions are made for a delimitation of the tribe. *Guettarda*, *Bohea*, *Antirhea*, *Malanea* and *Chomelia* Jacq. are sufficiently similar in their wood anatomical characters to warrant retention in the same tribe. *Machaonia*, *Timonius* and *Dichilanthe* are anomalous. Suggestions are given for taxonomic revisions of some genera based on their wood anatomy.

KEY WORDS:—Guettardeae – Rubiaceae – taxonomy – wood anatomy.

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INTRODUCTION

Within the Rubiaceae the tribe Guettardeae is morphologically rather isolated. For a survey of the literature on the taxonomy of the family, see

Bremekamp (1966). In the two most recent accounts dealing with the classification of the family as a whole (Verdcourt, 1958; Bremekamp, 1966), the distinct character of the tribe has been expressed by its placement in the monotribal subfamily, Guettardoideae. In all floras and systematic treatments *Guettarda* and its allies are dealt with under Rubiaceae (e.g. Dwyer, 1980).

Under Guettardeae, Schumann (1891) described 10 genera: *Guettarda*, *Bobea*, *Antirhea*, *Laugeria* (currently included in *Guettarda*), *Timonius*, *Anisomeris*, *Malanea*, *Abbottia* (now *Timonius*), *Dichilanthe* and *Machaonia*. *Anisomeris* is now referred to as *Chomelia* Jacq. (Brummitt, 1978) not to be confused with *Chomelia* L. which is synonymous with *Tarennia* of the tribe Coffeae (Darwin, 1976).

The delimitation of the tribe, or subfamily according to Bremekamp (1966) and Verdcourt (1958), has also been the subject of discussion. Bremekamp's opinion is that the genus *Machaonia*, commonly placed in this tribe, definitely should be removed, and probably also *Timonius* (Bremekamp, 1966). Verdcourt (1958) does not mention *Machaonia*, but reports differences in corolla hairs between *Timonius* and the other Rubiaceae. The entirely different fruits of *Machaonia*, when compared with those of the other Guettardeae, are also noted by Schumann (1891).

When Koek-Noorman (1969a, b) presented an initial survey of the wood anatomy of this family, the Guettardeae were represented by five species of *Guettarda* and by *Chomelia tenuiflora* Bentham, the latter wrongly considered to belong to the Ixoreae (Koek-Noorman, 1969b: 388). This scanty material did not enable a discussion of the taxonomic position of the tribe. Our more comprehensive survey of the tribe, has been carried out by Loureiro and Lisboa during a research term in Utrecht.

MATERIAL AND METHODS

Guettarda, *Chomelia* Jacq., *Antirhea*, *Bobea*, *Dichilanthe*, *Machaonia*, *Malanea* and *Timonius* are represented in this study. No material was available of the monotypic genus *Neoblakea* (described by Standley (1930) and placed between *Machaonia* and *Guettarda* by Steyermark (1974).

Wood samples were sectioned (transverse, radial and tangential plane) with the aid of a microtome and stained with safranin after bleaching with a domestic bleaching agent. A set of non-bleached and non-stained sections was also prepared. All sections were mounted in canada balsam. Macerations were made using a mixture of equal parts of acetic acid and hydrogen peroxide, stained in astrablue, and mounted in glycerin.

The wood anatomical descriptions are according to the terminology proposed by the Committee on Nomenclature of the International Association of Wood Anatomists (I.A.W.A., 1964). The average elements length of individuals are based on at least 25 measurements. In the generic descriptions the smallest and greatest means recorded for individual species given. The ray height (in μm) was obtained by measuring and counting the highest rays in the tangential sections, exceptions being eliminated. Multiseriate parts were measured in the same way. The means of element lengths were also used to calculate the ratio of fibre length/vessel member length, in the descriptions referred to as F/V ratio (Fig. 1).

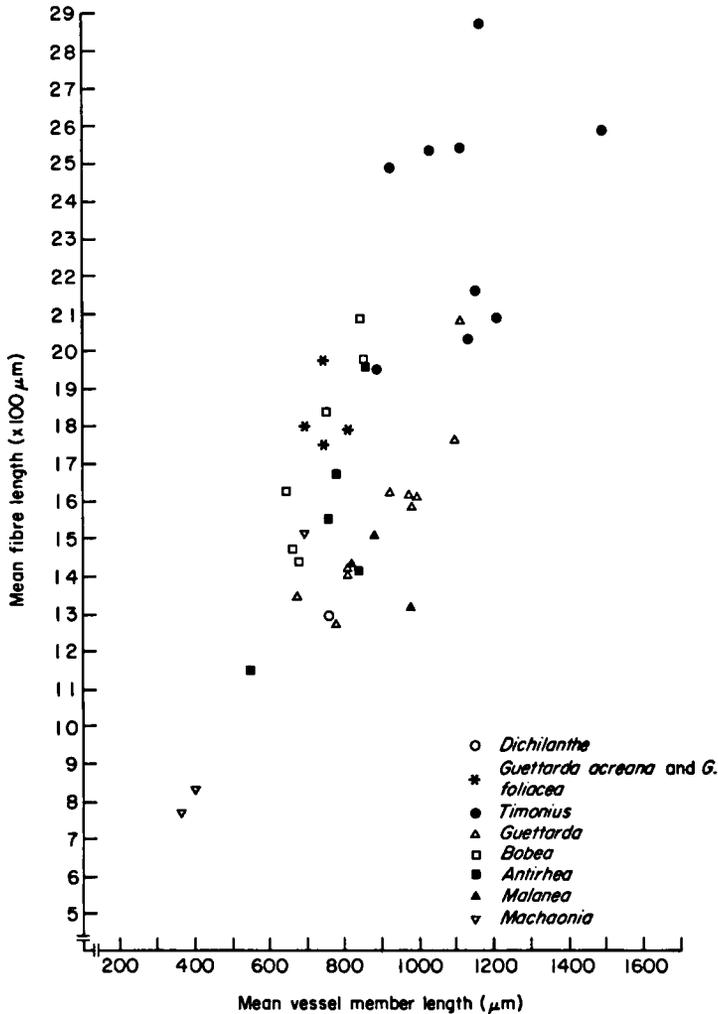


Figure 1. Mean fibre length and mean vessel member length of the tribe Guettardeae (Rubiaceae).

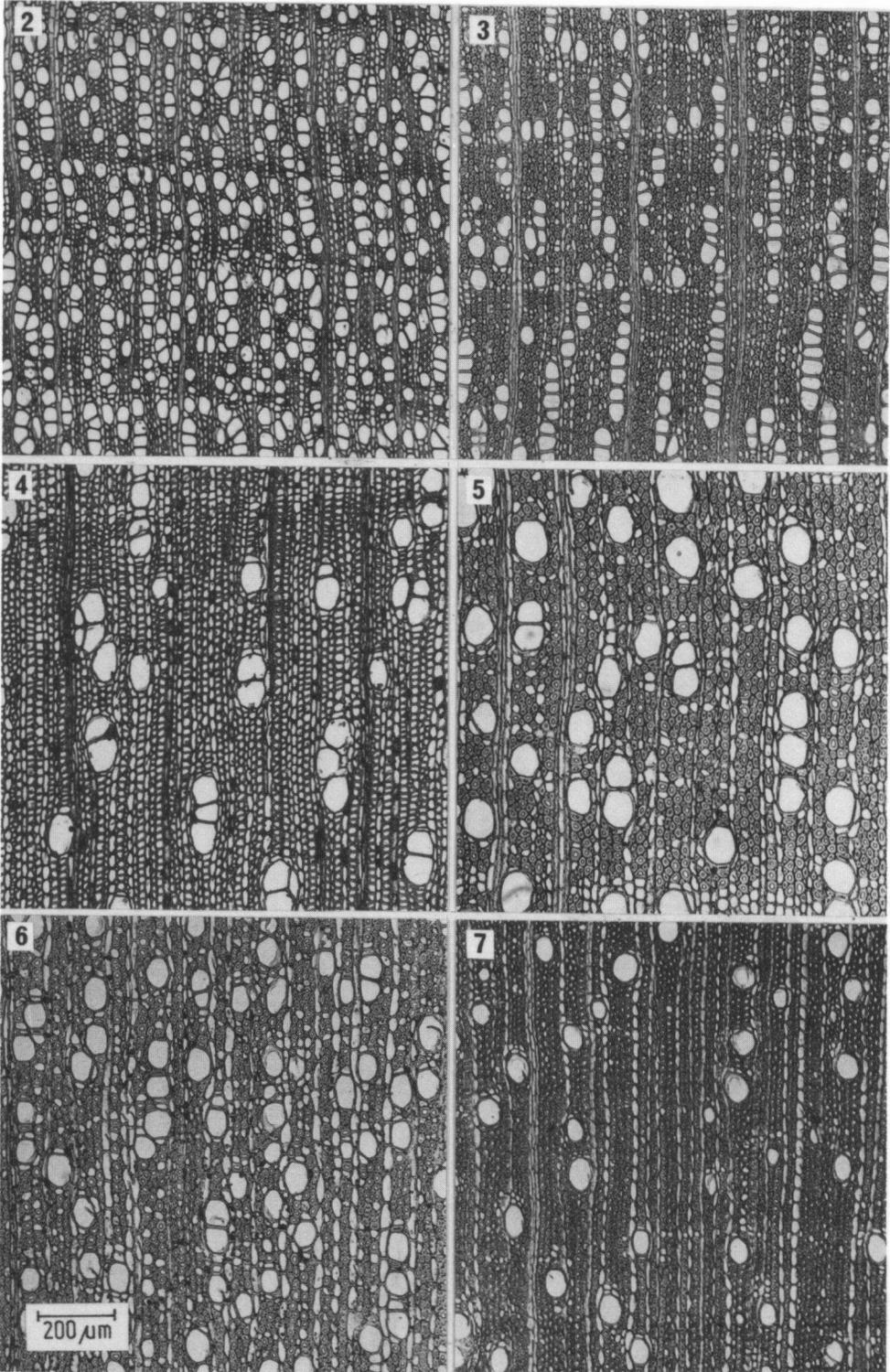
GENERIC DESCRIPTIONS

Antirhea Commerson ex Juss.

Trees and shrubs, occurring in East Asia, Mascarene Islands, Madagascar, Central America and the Antilles.

Material studied: *A. chinensis* (Champ.) Benth. & Hook. fil.: Hongkong, *C. Ford s.n.* (Uw 17716, ex K-Jw) (Fig. 3); *A. frangulacea* DC.: Mexico, *Balfour s.n.* (Uw 17717, ex K-Jw); *A. jamaicensis* urban: Jamaica, Uw 17744 (ex PRFw); Costa Rica, Uw 20503 (AJA 10) (Fig. 4); *A. lucida* Benth. & Hook. fil.: Jamaica, Uw 17718 (ex USw 5861).

GROWTH RINGS sometimes present, formed by bands of apotracheal parenchyma. **VESSELS** diffuse, solitary (15–100%), and in short radial chains and/or irregular



Figures 2–7. Fig. 2. *Chomelia recordii* Uw 17743. Fig. 3. *Antirhea chinensis* Uw 17716. Fig. 4. *Antirhea jamaicensis* Uw 17744. Fig. 5. *Bobea eliator* var. *molokaiensis* Uw 17779. Fig. 6. *Bobea sandwicensis* Uw 17778. Fig. 7. *Dichilanthe zeylanica* Lw.

clusters of 2–5, 21–135 per mm², round to oval (but angular in *A. jamaicensis*), diameter 34–80 µm, vessel member length 555–855 µm. Perforations simple, intervacular pits alternate, vested, round, *c.* 3 µm. Vessel-ray and vessel-parenchyma pits similar to the intervacular pits. FIBRES non-septate (but septate in one specimen of *A. jamaicensis*, Uw 20503), lumen diameter 4–24 µm, walls 4–8 µm. Pits indistinctly bordered, more frequent on the radial than on the tangential walls. Length 1155–1975 µm, F/V ratio 1.96–2.12. RAYS heterogeneous and heterocellular, uniseriate and 2–3 seriate, composed of procumbent cells, cells square in section and upright cells. The multiseriate parts composed of procumbent cells, with long uniseriate tails composed of variable amounts of cells square in section and upright cells. Height very variable, from 500 µm in *A. frangulacea* up to 1600 µm in *A. jamaicensis*, the multiseriate parts up to 150–400 µm. Vertically fused rays common. Number per mm: 14–19. PARENCHYMA always diffuse and scanty paratracheal, sometimes in short apotracheal bands and occasionally as tangential bands (see growth rings). Crystal sand present in all ray cells of *A. lucida*.

The wood anatomy of this genus is not uniform in all characters. Ray height, percentage of solitary vessels, and parenchyma distribution vary. *Antirhea jamaicensis* has thin-walled fibres, while the fibres of the other species have to be considered as thick-walled. However, there is insufficient evidence to remove one or more taxa from this genus.

Bobeia Gaudid.

Trees from the Sandwich Islands

Material studied: *B. aff. brevipes* A. Gray: Hawaii, *Stern & Herbst 505* (Uw 18588); *B. elatior* Gaudich. var. *molokaiensis* Rock: Hawaii, *Korte s.n.* (Uw 17779, ex MAD-SJRw 49334) (Fig. 5); *B. hookeri* Hillebrand: Hawaii, *Korte s.n.* (Uw 4809, ex MAD-SJRw 49354); *B. mannii* Hillebrand: Hawaii, *Stern s.n.* (Uw 10435, ex MAD-SJRw 26001); Hawaii, Uw 17719 (ex USw 1305); Hawaii, *Carls s.n.* (Uw 17780, ex FHOw 11227); *B. sandwicensis* Hillebrand: Hawaii, *Korte s.n.* (Uw 17778, ex FHOw 18691) (Fig. 6).

GROWTH RINGS absent. VESSELS diffuse, solitary (11–46%) and in radial multiples or radial chains of 4–8, 16–22 per mm² (and in *B. sandwicensis* up to 40), angular to oval and/or round, diameter 60–94 µm, vessel member length 645–855 µm. Perforations simple, intervacular pits alternate, vested, round to oval, 4–6 µm. Vessel-ray and vessel-parenchyma pits similar to the intervacular pits. Spiral thickenings common in *B. sandwicensis*. FIBRES non-septate, lumen diameter 9–20 µm, walls (4)–7–11 µm. Pits indistinctly bordered, confined to the radial walls. In *B. sandwicensis* the borders of the pits are more distinct and they also occur on the tangential walls. Length 1440–2185 µm, F/V ratio 2.22–2.59. RAYS heterogeneous and heterocellular, uniseriate and multiseriate, up to 3 cells wide, composed of procumbent cells, cells square in section and some upright cells. The multiseriate parts mainly composed of procumbent cells, the long uniseriate tails mainly composed of cells square in section and upright cells. Height up to 800–1200 µm, the multiseriate parts up to 300–600 µm. Vertically fused rays very common in this genus. Number per mm: 8–12. PARENCHYMA diffuse and in short apotracheal bands, scanty paratracheal and

occasionally a continuous tangential band of 2–3 cells wide. Crystals, variable in size and number in some parenchyma cells of *B. sandwicensis*.

The genus has a uniform wood anatomy. Only *B. sandwicensis* differs in some characters from the other species. The suggestion made by Rock (1974), that *B. hookeri* and *B. sandwicensis* may be varieties of one species is not supported by the wood anatomy of these species.

Chomelia Jacq.

Small trees and shrubs occurring in Central America and South America with 50 species.

Material studied: *C. aff. anisomeris* Muell. Arg.: Brazil, Parana, Lindeman & Horreus de Haas 1497, 3421, 4836 (Uw 13112, Uw 14052, Uw 14182); *C. barbellata* Standley: Brazil, Amazonas, Krukoff 8326 (Uw 16176); *C. recordii* (Standley) Standley: Nicaragua, Uw 17743 (ex PRFw) (Fig. 2); *C. tenuiflora* Benth.: Suriname, Stahel 378 (Uw 378); Lindeman & Heyde (Uw 23154); *C. vauthieri* Muell. Arg.: Brazil, Parana, Lindeman & Horreus de Haas 169 (Uw 12454).

In the literature considerable confusion exists about the nomenclature of *Chomelia* Jacq. and *Anisomeris* K. B. Presl. They are congeneric, and according to Brummitt (1978), the name *Chomelia* Jacq. has to be used.

The wood anatomy of the samples investigated is extremely variable, to the extent that it is hardly believable that it could occur within one genus. Some samples have fibre-tracheids while others show libriform fibres, the fibres may be septate or non-septate, up to 80% of the vessels are solitary or up to 80% again may be found in long radial chains, the fibre length varies from 1280 to 2170 μm , parenchyma may be absent or present as diffuse, scanty paratracheal, and long and short bands.

Except for two herbarium specimens, the material is sterile. The enormous variation within the wood anatomy, and the fact that the identifications have been made on sterile material, led us to the conclusion that for the time being the wood anatomy of this genus cannot be described properly and has to wait until the genus *Chomelia* Jacq. has been revised.

Based on the wood anatomy three groups can be recognized:

'Chomelia I:' *C. recordii* (Standley) Standley.

'Chomelia II:' *C. aff. anisomeris* Muell. Arg.

'Chomelia III:' *C. barbellata* Standley; *C. tenuiflora* Benth.; *C. vauthieri* Muell. Arg.

Dichilanthe Thwaites

Trees from Sri Lanka and East Asia.

Material studied: *D. zeylanica* Thwaites: Sri Lanka, Tirvengadam & Hostermans 646 (ex Lw) (Fig. 7).

GROWTH RINGS absent. VESSELS solitary (100%), 21 per mm^2 , round and slightly oval, diameter 65 μm , vessel member length 760 μm . Perforations simple, intervascular pits alternate, vestured, round, 4–5 μm . Vessel-ray and vessel-parenchyma pits similar to the intervascular pits. FIBRES non-septate, lumen diameter 14 μm , walls 4–6 μm . Pits bordered, on the radial and on the

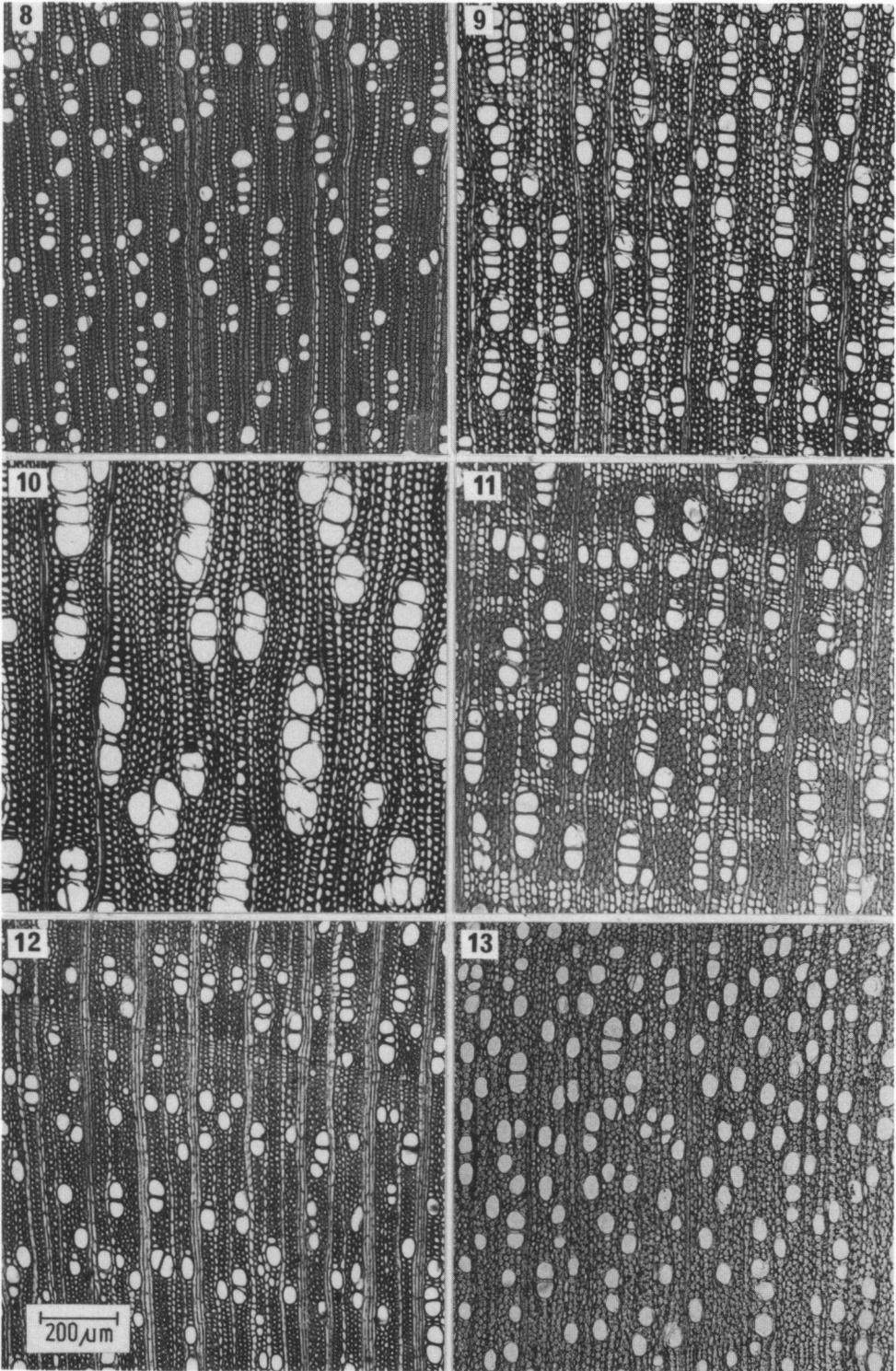
tangential walls, 4–5 μm . Length 1295 μm , F/V ratio 1.70. RAYS heterogeneous and heterocellular, uni- and biseriate, composed of weakly procumbent cells, cells square in section and some upright cells. The multiseriate parts composed of weakly procumbent cells, and with long uniseriate tails of square and upright cells. Height up to 720 μm , the multiseriate parts up to 140 μm . Vertically fused rays scarce. Number per mm: 14. PARENCHYMA diffuse, reticulate and unilaterally paratracheal, occasionally unilaterally aliform.

Guettarda L. *sensu stricto*

Shrubs and trees, occurring in the neotropics. One species, *G. speciosa*, is pantropic.

Material studied: *G. argentea* Lam: Jamaica, Uw 17761 (ex PRFw 11352); *G. combsii* Urban: Mexico, Uw 17826 (ex FHOW 18787); Belize, *Conservator of Forests* 262 (Uw 20211, ex RBHw 10859); *G. crispiflora* Vahl: Dominica, *Wasshausen & Ayensu* 333 (Uw 14746); *Chambers* 2737 (Uw 15426) (Figs 10 & 16); *G. divaricata* Standley: Venezuela, *Breteler* 3993 (Uw 11832) (Fig. 9); *G. elliptica* Sw.: U.S.A., Florida Keys, *Stern & Brizicky* 223 (Uw 6095, ex Yw 51068); *Stern & Brizicky* 530 (Uw 6305, ex Yw 51311); *Stern et al.* 3051 (Uw 20274, ex MARYw); *G. pungens* Urban: Dominica, Uw 7279 (ex USw 1989) (Fig. 8); *G. sabiceoides* Standley: Colombia, Chocó, *Cuatrecasas* 17240 (Uw 25152); *G. scabra* (L.) Lam.: U.S.A., Florida Keys, *Stern & Brizicky* 320 (Uw 6172, ex Yw 51145); Dominica, *Wasshausen & Ayensu* 383 (Uw 14765a); *G. seleriana* Standley: Mexico, *I.N.I.F.* X 163 (Uw 20654); *G. speciosa* L.: Marshall Is., *Kukachka* 15718 (Uw 17762, ex PRFw 20767); *G. cf. spruceana* Muell. Arg.: Suriname, *Lindeman* 6214 (Uw 4256); *G. steyermarkii* Standley: Venezuela, Uw 20213 (ex RBHw 10984); Uw 17763 (ex PRFw 22684); *G. viburnioides* Cham. & Schldl.: Brazil, *Brown* 1909 (Uw 17764, ex PRFw 7173); *Krukoff* 1906 (Uw 19483).

GROWTH RINGS faint, occasionally absent, formed by a decrease of the lumen diameter of the fibres. VESSELS diffuse, solitary (9–64%) and often in short to long radial chains and sometimes irregular clusters of 2–7, 14–90 per mm^2 , round to slightly oval, sometimes slightly angular, diameter 40–120 μm , in general 60–90 μm , vessel member length 675–1115 μm . Perforations simple, intervascular pits alternate, vestured, round, 4–7 μm . Vessel-ray and vessel-parenchyma pits similar to the intervascular pits. FIBRES septate, lumen diameter 12–30 μm , walls 4–9 μm . Pits indistinctly bordered, on the radial walls and absent or scarce on the tangential walls. Length (850) 1275–1750 (2080) μm , F/V ratio (1.25)–1.61–1.99. RAYS heterogeneous and heterocellular, uniseriate and 2–3(5) seriate, composed of procumbent cells, cells square in section and upright cells. The multiseriate parts composed of procumbent cells, with long uniseriate tails mainly composed of upright cells. (The proportion of upright cells in this genus greater than in one of the other genera studied here.) Height up to 800–1200 μm , the multiseriate parts up to 140–500 μm . Vertically fused rays commonly present. Number per mm: 10–17. PARENCHYMA absent, rarely scanty paratracheal. Rhombic crystals, sometimes in combination with crystal sand, and restricted to the cells square in section and upright ray cells in *G. argentea*, *G. combsii* and *G. scabra*. Crystal sand in the same kind of ray cells in *G. crispifolia*.



Figures 8–13. Fig. 8. *Guettarda pungens* Uw 7279. Fig. 9. *Guettarda divaricata* Uw 11832. Fig. 10. *Guettarda crispiflora* Uw 15426. Fig. 11. *Guettarda foliacea* Uw 24701. Fig. 12. *Machaonia spinosa* Uw 17728. Fig. 13. *Machaonia brasiliensis* Uw 20202.

In some species of *Guettarda*, particularly *G. sabiceoides*, two kinds of fibres occur. One kind is characterized by the presence of intercellular spaces. Bands of fibres with and without these intercellular spaces can be observed on the transverse plane as more or less concentric tangential bands suggesting rather vague 'parenchyma'. This phenomenon has also been described by Janssonius (1926) for *G. speciosa*. The wood anatomical characters of these *Guettarda* species are uniform. The lack of parenchyma and the presence of septate fibres clearly defines the genus.

Guettarda acreana and *G. foliacea*

Material studied: *G. acreana* Krause: Suriname, *B.B.S. 123* (Uw 716); *Helstone 237* (Uw 4786); Guyana, *F.D. 2317* (Uw 1081); *G. foliacea* Standley: Panama, *Cooper & Slater 227* (Uw 24701, ex FHOw 3492) (Fig. 11).

GROWTH RINGS absent. VESSELS diffuse, solitary (13–40%) and in short radial chains of 2–5, 45–85 per mm², round to slightly oval, diameter 48–60 μm, vessel member length 745–975 μm. Perforations simple, intervacular pits alternate, vestured, round, 2–3 μm. Vessel-ray and vessel-parenchyma pits similar to the intervacular pits. FIBRES non-septate, lumen diameter 12–15 μm, walls 6–8 μm. Pits simple or indistinctly bordered, scarce and restricted to the radial walls. Length 1615–1975 μm, F/V ratio 1.66–2.66. RAYS heterogeneous, uniseriate and 2–3(4) seriate, composed of procumbent cells, cells square in section and upright cells. The multiseriate part composed of procumbent cells, with long uniseriate tails composed of cells square in section and upright cells. Height up to 800–1300 μm, the multiseriate parts up to 360–420 μm. Vertically fused rays present. Number per mm: 13–16. PARENCHYMA abundant, diffuse, in short and long tangential bands and sometimes scanty paratracheal. Small, more or less rhombic crystals in every ray cell and every parenchyma cell. This kind of crystal and pattern of distribution not observed in any of the other specimens investigated.

The differences in wood anatomy between the two groups of *Guettarda sensu stricto* and these two species are substantial. Parenchyma distribution, septation of the fibres, vessel member length and fibre length (see also Fig. 1) and the presence of a typical crystal shape clearly characterize these two species. On wood anatomy there is sufficient evidence to remove this group from the genus *Guettarda*.

Machaonia Humb. & Bonpl.

Trees and shrubs from Central America, the Antilles and South America.

Material studied: *M. brasiliensis* (Hoffm. ex Humb.) Cham. & Schldl.: Argentina, Uw 20202 (ex RHBw-RAKF 4122) (Fig. 13); *M. spinosa* Cham. & Schldl.: Argentina, Uw 17728 (I.F.I. 233, ex K-Jw) (Fig. 12); *Molfino s.n.* (Uw 17797, ex FHOw 9879).

GROWTH RINGS faint or absent, formed by tangential zones of more vessels per mm². VESSELS diffuse, solitary (20–82%) and in irregular clusters or short radial chains of 2–4(7), 64–80 per mm², round to oval, diameter 42–56 μm, vessel member length 365–400 μm in *M. spinosa*, 695 μm in *M. brasiliensis*. Perforations

simple, intervacular pits alternate, vested, round, 4 μm . Vessel-ray and vessel-parenchyma pits similar to the intravascular pits. FIBRES septate in *M. spinosa* and non-septate in *M. brasiliensis*, lumen diameter 12–15 μm , walls about 3 μm in *M. spinosa* and 4–8 μm in *M. brasiliensis*. Pits indistinctly bordered and confined to the radial walls in *M. spinosa*; distinctly bordered and equally frequent on the radial and tangential walls in *M. brasiliensis*. Length 770–830 μm in *M. spinosa*, and 1515 μm in *M. brasiliensis*, F/V ratio 2.10–2.18. RAYS heterogeneous and heterocellular, uniseriate and 3–6 seriate, composed of procumbent cells, cells square in section and upright cells. The multiseriate parts mainly composed of procumbent cells, with long uniseriate tails composed of square and upright cells. Height up to 720–800 μm , the multiseriate parts up to 300–600 μm . Vertically fused rays frequent. Number per mm: 12 in *M. spinosa*, and 18 in *M. brasiliensis*. PARENCHYMA diffuse and scanty paratracheal. Crystal sand observed in some procumbent cells, cells square in section and upright ray cells.

The differences in wood anatomical characters of the two species are considerable.

Malanea Aublet

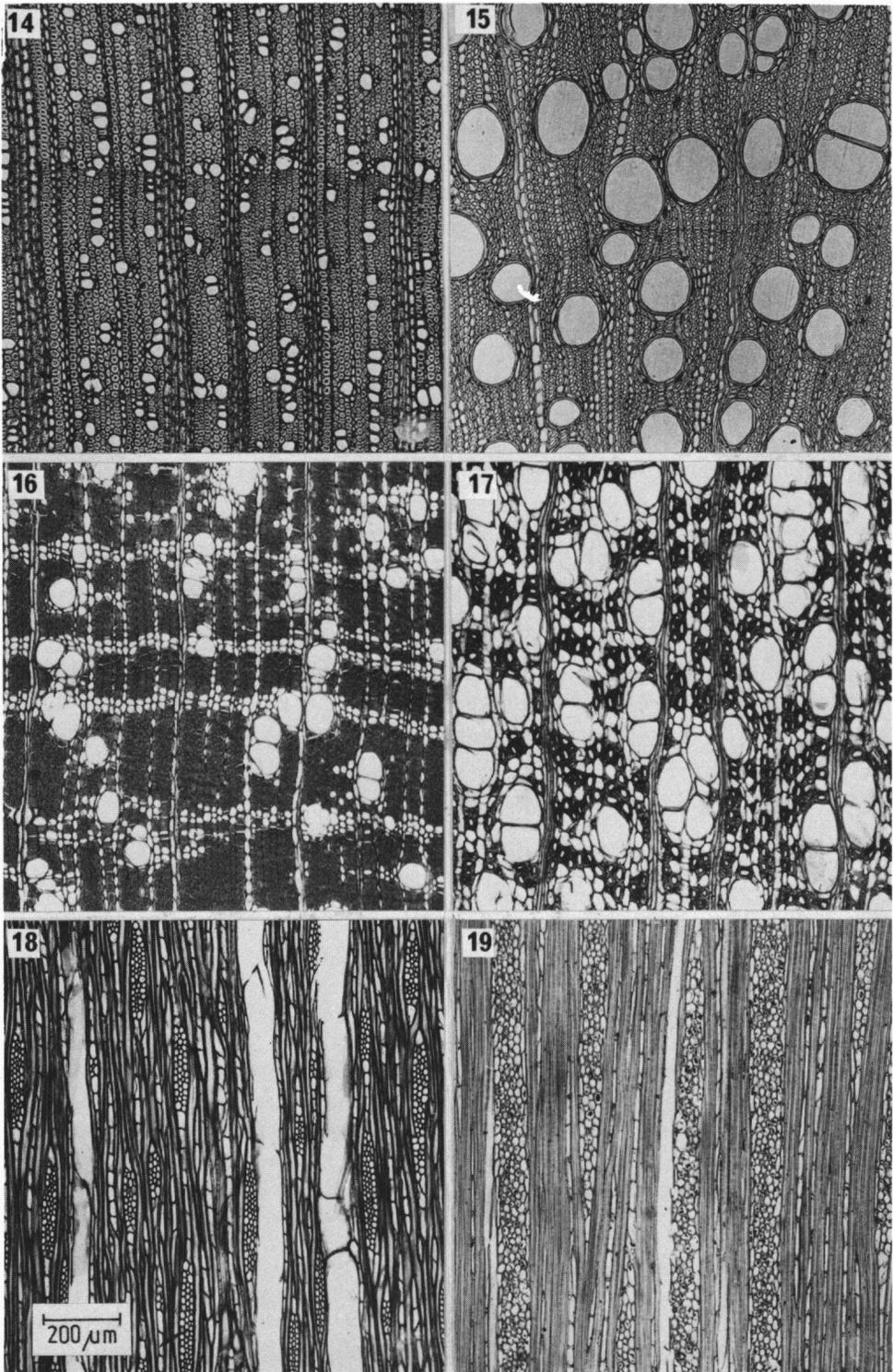
Scandent shrubs, rarely small trees, from South America and the Antilles.

Material studied: *M. gabrielensis* Muell. Arg.: Venezuela, Williams 16009 (Uw 12434) (Figs 14 & 17); *M. macrophylla* Bartling: Suriname, Lindeman 6623 (Uw 4485) (Fig. 15); Lindeman & Heyde 549 (Uw 23195); *M. sarmentosa* Aublet: Trinidad, R.A.K.F. 6576.

The differences in wood anatomical characters are substantial, owing to the fact that three samples (those of *M. macrophylla* and *M. sarmentosa*) are from lianas, contrary to the sample of *M. gabrielensis*, which is from a small tree or shrub. Wood anatomical data between brackets apply to *M. gabrielensis*.

GROWTH RINGS present or absent. VESSELS solitary (70–80%) and in small irregular clusters of 2–3 (in *M. gabrielensis* in general in radial chains of 2–10 and solitary for only 17%), 13–15(85) per mm^2 , round and oval (angular), diameter 140–170(39) μm , vessel member length 885–980(820) μm . Perforations simple, intervacular pits alternate, vested, round, 4–5 (2–3) μm . Vessel-ray and vessel-parenchyma pits similar to the intervacular pits. FIBRES non-septate, lumen diameter 18–24(9) μm , walls (4)6–8 μm . Pits bordered, on radial and tangential walls, 4–6 μm (indistinctly bordered, on the radial walls only, 2–3 μm). Length 1320–1510 μm , F/V ratio 1.35–1.74. RAYS heterogeneous and heterocellular, uni- and multiseriate, composed of procumbent cells, cells square in section and upright cells. The multiseriate parts 2–3 cells wide and composed of procumbent cells (the multiseriate parts up to 6 cells wide and composed of procumbent cells, cells square in section and upright cells) with long uniseriate tails composed of cells square in section and upright cells. Height up to 1250 (6000!) μm , the multiseriate parts up to 360–480 (5000!) μm . Vertically fused rays common. Number per mm: 12–13 (8). PARENCHYMA scarce, diffuse and scanty paratracheal. Crystal sand observed in some procumbent cells, cells square in section and upright ray cells of *M. macrophylla* and *M. sarmentosa*.

The differences in wood anatomical characters due to the difference in habit will be dealt with in the discussion.



Figures 14–19. Fig. 14. *Malanea gabrielensis* Uw 12434. Fig. 15. *Malanea macrophylla* Uw 4485. Fig. 16. *Timonins wrayi* Uw 17736. Fig. 17. *Timonius* sp. Uw 27024. Fig. 18. *Guettarda crispiflora* Uw 15426. Fig. 19. *Malanea gabrielensis* Uw 12434.

Timonius DC.

Trees and shrubs of tropical Asia and Australia.

Material studied: *T. borneensis* Valetton: Sarawak, *G. H. Pickles 3948* (Uw 17812, ex FHOw 19947); *T. rumphii* DC.: Singapore, *Ridley s.n.* (Uw 17735, ex K-Jw); *T. wallichianus* Valetton: Sarawak, *G.H. Pickles 3714* (Uw 17811, ex FHOw 20016); *T. wrayi* King & Gamble: Malaya, Uw 17736 (ex K-Jw); *T. sp.*: New Guinea, BW 4390 (ex Lw); BW 10834 (ex Lw), BW 11925 (ex Lw); BW 12465 (ex Lw); Borneo, *Jacobs 5404* (ex Lw).

GROWTH RINGS absent. VESSELS diffuse, solitary (18–44%), and in short radial chains and sometimes irregular clusters of 2–5, 8–23 per mm², angular and round or oval, diameter 85–106 µm, vessel member length 890–1495 µm. Perforations simple, intervascular pits alternate, vested, round or polygonal, 4–6 µm. Vessel-ray and vessel-parenchyma pits similar to the intervascular pits. FIBRES non-septate, lumen diameter 6–21 µm, in general 9–15 µm, walls 7–16 µm. Pits rather few, simple or indistinctly bordered, restricted to the radial walls. Length 1950–2875 µm, F/V ratio 1.73–2.69. RAYS heterogeneous, uniseriate and 2–4 seriate, composed of procumbent cells, cells square in section and upright cells. The multiseriate parts composed of procumbent cells only, with long uniseriate tails composed of cells square in section and upright cells. Height 1050–1800 µm, the multiseriate parts 420–1300 µm. Vertically fused rays common. Number per mm: 9–13. PARENCHYMA always rather abundant. In general diffuse, short and/or long apotracheal bands and scanty paratracheal. Occasionally the parenchyma bands also more or less aliform-confluent. Crystals observed in some ray cells of *T. wallichianus*, crystal sand and rhombic crystals observed in some ray cells and some parenchyma cells.

The wood anatomy of *Timonius* is rather uniform.

DISCUSSION

The wood anatomy of most woody rubiaceous tribes has been described in detail by Koek-Noorman (1969a, 1969b, 1970, 1972, 1974). A very important differentiating character at the level of tribes and genera in the family is the kind of fibre, namely libriform fibres as opposed to fibre tracheids. Considerable variations are found, not only in this character, but also in others. Therefore a generalized description for the family is difficult to provide, although heterogeneous multiseriate rays with uniseriate margins of over 3 cells, together with small vested intervascular pits, may be considered as typical for rubiaceous woods.

It is clear that the differences in wood anatomical characters between, and in part within, the genera of the Guettardeae are also substantial. For a discussion on the classification of the tribe, the genus *Guettarda* is considered to occupy a more or less central position.

Wood anatomy of Guettarda: Most of the species investigated show a rather homogeneous wood structure (see also Table 1). They are characterized by vessels in more or less long and short radial chains, fibres septate, with simple pits on the radial walls only, parenchyma only scanty paratracheal, and a mean fibre length of 1200–1800 µm.

Within the genus *Guettarda*, *G. seleriana* from Mexico has the greatest values for the

Table 1. Some differentiating wood anatomical characters of genera of the tribe Guettardeae *sensu* Schumann (1891)

Taxa	Parenchyma distribution												
	Solitary vessels (%)	Rad. chains	Number vessels/mm ²	Vessel member length (µm)	Septate fibres	Bordered pits	Occurrence of pits	Fibre length (µm)	Diffuse	Reticulate	Short bands	Long bands	Scanty paratracheal
<i>Guettarda</i>	9-64	±	14-90	675-1115	+	-	r	1275-1750	-	-	-	-	+
'Chomelia I'	30	+	160	805	+	-	r(t)	1490	-	-	-	-	+
<i>Bobea</i>	11-46	±	16-40	645-855	+	-	r	1440-2185	-	-	-	-	+
<i>Antirhea</i>	15-100	-	21-135	555-855	-	±	r(t)	1155-1975	+	-	+	-	+
<i>Malanea</i> (lianas)	70-80	+	13-15	885-980	-	+	r,t	1320-1510	+	-	+	-	+
<i>Malanea</i> (shrub)	17	+	85	820	-	+	r	1430	+	-	-	-	+
'Chomelia II'	38	±	160	805	+	+	r,t	1235	+	-	-	-	+
'Chomelia III'	20-33	±	35-100	830-1170	+	±	r(t)	1580-2530	+	+	+	+	+
<i>Machaonia spinosa</i>	20-32	-	64-68	365-400	+	-	r	770-830	+	-	-	-	+
<i>Machaonia brasiliensis</i>	82	-	80	695	-	+	r,t	1515	+	-	-	-	+
<i>Guettarda acreana</i>													
and <i>G. foliacea</i>	13-40	±	45-85	745-975	-	-	r	1615-1975	±	-	+	+	+
<i>Timonius</i>	18-44	±	8-23	890-1495	-	-	r	1950-2875	±	-	+	+	+
<i>Dichilanthe</i>	100	-	69	760	-	+	r,t	1295	+	+	+	+	*+

+ = present; - = absent; ± = sometimes present or not well-developed.

* = unilaterally paratracheal.

mean fibre and mean vessel member length. In this species we also observed the so far unknown phenomenon in which some true septate fibres show septa that are identical to the walls between two cells of parenchyma strands. Nevertheless, there is no reason to doubt that this species belongs in *Guettarda*.

The wood anatomy of *Guettarda acreana* and *Guettarda foliacea* differs from the general description for *Guettarda* in the presence of small, more or less rhombic crystals in ray and parenchyma cells, short to long parenchyma bands, non-septate fibres and small (2–3 μm) intervacular pits. *Guettarda acreana* is a species that occurs in Venezuela, and the State of Acre in Brazil. In our study only material from Guyana and Surinam has been investigated. One of the specimens (*Helstone 237*) is the type specimen of *Antirhea surinamensis* (described by Bremekamp (1959). Some years before he had already described another species of this genus, *Antirhea guianensis* (1952) from Guyana. However, *Antirhea* is a genus not represented in South America according to Dwyer (1980). Koek-Noorman (1969b) who studied the type specimen of Bremekamp, concluded that *Antirhea surinamensis* should be considered as synonymous with *Guettarda acreana*. Steyermark re-identified determined as *Guettarda acreana* specimens identified by Bremekamp as *A. surinamensis*. In his original description of *Antirhea surinamensis*, Bremekamp (1959) considered *Antirhea panamensis* to be its nearest ally. Dwyer (1980) transferred this species to *Chomelia* and renamed it *C. panamensis* (Standl.) Dwyer.

Dwyer (1980) studied the herbarium material of *Guettarda foliacea* of which we studied the wood specimen (*Cooper & Slater 227*). No taxonomic problems exist for this species.

If the wood anatomical data from this study are compared with the taxonomy the following conclusions may be drawn:

Guettarda acreana from Suriname and Guyana should not be considered as a species of *Guettarda*. The classification by Bremekamp (1959) could be preferred or, re-investigation of the material may result in a placement in another genus. Although no proposals have previously been made to remove *Guettarda foliacea* from this genus, similarity between the wood anatomy of *G. foliacea* and *G. acreana*, suggest that *G. foliacea* should be reassigned also. These two species may be more appropriately placed outside the tribe *Guettardeae*.

Wood anatomy of Bobea, malanea, 'Chomelia P and Antirhea: in terms of the wood anatomy the phenetically nearest relatives of *Guettarda* are found in *Bobea*, *Malanea*, 'Chomelia I, and *Antirhea*. *Bobea* and *Guettarda* have many characters in common, especially those of the vessels. However, in *Bobea* septate fibres occur and the F/V ratio is slightly greater. Finally, the amount of parenchyma is greater, being diffuse and reticulate instead of scanty paratracheal distribution.

Our conclusions only apply to the shrubby species of *Malanea*. Important deviating characters in the wood of the lianes are: few vessels per mm^2 , vessel diameter over 130 μm , and the occurrence of fibre tracheids. These character states have often been described for taxa with a liana-habit and can hardly be interpreted in terms of affinity (Mennega, 1980). Therefore, only the wood anatomy of the non-climbing species is compared. The main difference between *Guettarda* and the shrubby species of *Malanea* is found in the rays. They are much higher and wider in *Malanea*.

As already indicated, the genus *Chromelia* Jacq. has to be revised before the wood anatomy can be used for classification purposes. Nevertheless, it is possible

to indicate that 'Chomelia I' from Nicaragua fits very well within the wood anatomical blueprint of *Guettarda*. The only deviating features are the number of vessels per mm² and the fact that, contrary to those of *Guettarda*, the fibres have some pits on the tangential walls. 'Chomelia II' is more or less similar to 'Chomelia I', but deviates in the fibre pits, which are bordered, and are relatively frequent on radial and tangential walls. 'Chomelia III' deviates in fibre-type and parenchyma distribution.

Antirhea is phenetically related to *Guettarda* also, but perhaps may be less so than the genera discussed previously. Long radial chains of vessels are lacking, the fibres are non-septate and have slightly bordered pits on the radial walls and less frequent on the tangential walls. Finally, the parenchyma distribution is in tangential bands, although these bands are scarce.

Wood anatomy of Machaonia, Timonius, and Dichilanthe: Machaonia brasiliensis and *M. spinosa* differ from each other in many features (see also Table 1), and both deviate from *Guettarda*. In *M. spinosa* only the vessel member lengths are far beyond the ranges shown by *Guettarda*. *Machaonia brasiliensis* deviates from *Guettarda* in the absence of radial pore chains, in the bordered pits on both radial and tangential walls and in the lower ray height. Again, a close affinity with *Guettarda* has to be excluded.

Long tangential bands of parenchyma combined with non-septate libriform fibres as observed in *Timonius* are rare in the *Rubiaceae*. As with the mean vessel member length and mean fibre length (see Fig. 1), these values are not in agreement with the blueprint of *Guettarda*. As a result, the wood anatomy does not support a classification of *Timonius* within the Guettardeae. If we accept the deviating features in *Timonius* as important differentiating characters, then we have to assume that of *Guettarda acreana* from the Guyanas and *G. foliacea* from Panama, do not belong in this tribe either, and should be placed elsewhere in the *Rubiaceae*. Although we cannot suggest a better position in the family, there is no doubt that these taxa are definitely rubiaceous.

Finally, *Dichilanthe* is also quite different in wood anatomical characters from *Guettarda*. The non-septate fibre tracheids with bordered pits on the radial and tangential walls, the exclusively solitary vessels and the diffuse, reticulate and unilaterally paratracheal parenchyma distribution are characteristic for this genus. These characters have not been observed in *Guettarda*, *Bobea* and *Antirhea*, consequently there is no wood anatomical reason to place *Dichilanthe* in the

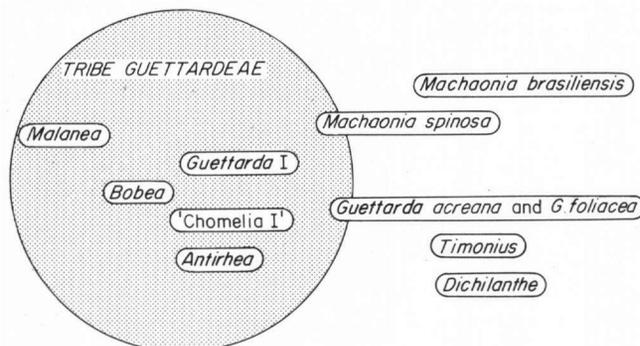


Figure 20. Phenetic affinities between the genera of the tribe Guettardeae *sensu* Schumann (1891) based on wood anatomical characters.

Guettardeae. This genus, on grounds of wood anatomy, resembles more closely some representatives of the Coffeae (= Ixoreae), and Gardenieae.

A classification of the Guettardeae based on wood anatomical characters is not simple; our present knowledge is best represented in Fig. 20.

These results are in remarkable agreement with the views of recent authors (Verdcourt, 1958; Bremekamp; 1966).

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