

THE SYSTEMATIC WOOD ANATOMY OF THE MORACEAE (URTICALES)  
I. TRIBE CASTILLEAE<sup>1</sup>

by

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**Summary**

The wood anatomy of the tribe Castilleae sensu Berg is described. Similarities and differences are discussed in relation to his concepts of the taxonomy of the tribe. The wood anatomical variation does not enable to distinguish between *Maquira*, *Perebea* and *Pseudolmedia*. *Antiaris*, *Castilla*, *Helicostylis*, *Mesogyne* and *Naucleopsis* can be recognised on the basis of slight differences. However, no reasons are found to question the delimitation of the Castilleae sensu Berg on the basis of their wood anatomy.

**Key words:** Wood anatomy, plant systematics, Moraceae, Castilleae.

**Introduction**

The present paper is the first one of a series dealing with the systematic wood anatomy of Moraceae. It includes wood anatomical descriptions of the genera of the tribe Castilleae. This project follows in logical sequence the work of C.C. Berg, taxonomist of the family, who had experienced problems in delimiting and defining the family as a whole, as well as the individual genera and tribes. The wood and leaf anatomy of the Cecropiaceae, a segregate of the Moraceae, in relation to the taxonomy of this group has already been discussed in a paper by Bonsen and Ter Welle (1983). Their study on the systematic anatomy of the Urticaceae, closely related to the Moraceae, is in the press (1984).

Most wood anatomical literature on Moraceae is rather difficult to interpret taxonomically, due to the often dubious identifications and the frequent nomenclatural changes. Furthermore, descriptions are nearly always based on few samples and relate only to individual genera or commercially important timbers. Numerous accounts in the literature were compared with our findings. Here we only refer to literature including elaborate wood anatomical descriptions based on reliably identified material, and not mentioned elsewhere in the text: Janssonius, 1934; Koek-Noorman & ter Welle, 1976; Record & Hess, 1940; Tippo, 1938.

The main aim of the present research project is to find an answer to the following questions: What is the anatomical variability range in taxa of Moraceae as compared to closely related taxa? – To what extent can the anatomical information be used to contribute to our understanding of patterns of relationship, and aid in generic and tribal delimitation?

A thorough treatment of the wood anatomy of the tribe Olmedieae was published by Menega and Lanzing-Vinkenborg (1977). One of their conclusions was that the exclusion of *Olmedia* (Berg, 1977a) was justified. They did not discuss the relation of the Olmedieae (later renamed Castilleae) to the other Moraceae. Besides, they did not study the African genera *Antiaris* and *Mesogyne*, also placed in the Castilleae by Berg (1973). Therefore we decided to include the Castilleae in our survey of the wood anatomy of Moraceae. We intend to present a series of papers, in each of which the genera of one tribe are described and their wood anatomical similarities and differences are discussed in relation to ideas about delimitation and relationships as brought forward by, i.a., Corner (1962, and his unpublished Flora Malesiana account of 1972) and Berg (1972, 1977a, b, 1983). We will follow the most recent views of Berg on the tribal arrangement, as indicated by him in his paper on distribution and dispersal in the Urticales (1983).

We intend to publish separate papers on the tribes of the Moraceae in the following sequence:

- I. Castilleae (*Antiaris*, *Castilla*, *Helicostylis*, *Maquira*, *Mesogyne*, *Naucleopsis*, *Perebea*, *Pseudolmedia*);
- II. Dorstenieae (*Bosqueiopsis*, *Brosimum*, *Dorstenia*, *Helianthostylis*, *Trilepisium*, *Trymatococcus*; of *Scyphosyce* and *Utsetela* no material is available);
- III. Ficeae (*Ficus*);
- IV. Moreae p.p., characterised by the presence of 'urticaceous' stamens (*Broussonetia*, *Calpidochlamys*, *Cardiogyne*, *Chlorophora*, *Maclura* s.l. incl. *Plecospermum* and *Cudra*);

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*nia*, *Maillardia*, *Malaisia*, *Militia*, *Morus*, *Pachytrophe*, *Strebilus* s.l., *Trophis* s.l. incl. *Olmedia*; of *Ampalis* and *Fatouia* no material is available);

- V. Moreae p.p., characterised by the absence of 'urticaceous' stamens (*Antiaropsis*, *Artocarpus*, *Bagassa*, *Batocarpus*, *Clarisia*, *Parartocarpus*, *Poulsenia*, *Prainea*, *Sorocea*, *Spartatosyce*, *Treculia*; of *Hullettia* no material is available).

In a concluding paper we intend to discuss the taxonomic value of the various wood anatomical features on the tribal level and to compare the individual tribes.

### Material and Methods

Most wood samples studied are backed by herbarium vouchers which were identified by C.C. Berg, the taxonomist of the family. Most samples were taken from the trunk of the tree; sometimes, however, the origin was unknown. Many wood samples were provided by institutional wood collections all over the world. The Utrecht wood collection served as a first basis for this study. In the generic descriptions, only those samples are cited of which sections were made. The general features of the wood are often based upon the study of more wood samples not cited here. Sections and macerations were prepared according to standard techniques and embedded in Canada balsam and in glycerin respectively. The sections were stained with safranin and the macerations in astrablue. Besides, unstained sections were also studied.

The terminology proposed by the Committee on Nomenclature of the IAWA (1964) is followed. As for the quantitative data: vessel diameters were measured in tangential direction including the walls and averages are based on 25 measurements. Vessel frequency is based on 25 counts. In the descriptions, for both characters minimum and maximum averages found in samples of each genus are provided. The percentage of solitary vessels was calculated after examining an area with at least 100 spores. Clusters and multiples were regarded as 2, 3, 4, etc. vessels, depending on the number of vessels per group. Vessel member length and fibre length are based on at least 100 measurements per sample, and again, minimum and maximum sample averages found in the genera are provided. Additionally, the averages were used to calculate the ratio of fibre length/vessel member length, in the descriptions referred to as F/V-ratio. For the fibres, maximum wall thickness and maximum lumen diameter are given. The percentage of uniseriate rays is based on counts of at least 100 rays.

Finally, the specific gravity was established in the usual way. Measuring of the moisture content of the samples was considered unnecessary as all samples were stored in a room with central heating and an air humidity of c. 40% during at least several weeks. It is the general experience that this results in a relative moisture content of approx. 12%.

### Generic descriptions

#### *Antiaris* Lesch. (Figs. 1, 2)

From the 17 species, described since the genus was established, Corner (1962) reduced the number to four, but he already pointed out that there were no essential differences between these species. Berg (1977b) combined all species in *Antiaris toxicaria* Lesch., lowering the rank of these four species to subspecies. The genus *Antiaris* (trees, up to 40–60 m tall, or shrubs) occurs in the Palaeotropics in primary and secondary forests in wet and dry habitats, from sea level up to 1500 m altitude.

Material studied: *A. toxicaria* Lesch. Uganda: B.T. Styles 201 (Uw 19390), For. Dept. 8-1950 (Uw 18387); Zaire: C. Donis 413 (Uw 24211), J. Louis 11201 (Uw 18780); West Africa: F.P.R.L. 209 A (Uw 18386); East Africa: H.E. Desch-F.R.I.C.S. (Uw 24305); Malaysia: For. Dept. 9-1954 (Uw 18388); Indonesia, Java: Koorders 8316t/12757B (Uw 24417), 1127g/22746B (Uw 24418), 1898m/13415B (Uw 24430); Indonesia, Irian Jaya: BW 11519 (Uw 20481), BW 11916 (Uw 18169), Fokkinga 1573 (Uw 24306); Philippines: Bur. of For., Manila P.I. 21092b.f. (Uw 24431).

General features: Growth rings faint or absent; colour light brown, no difference between sapwood and heartwood. Texture coarse; grain interlocked. Specific gravity 270–530 N per cubic metre.

Microscopic features: Vessels diffuse, in some samples tending towards a diagonal arrangement; solitary (45–65%) and in short radial multiples or irregular clusters of 2–6; 3–10 per sq.mm, round to oval, diameter 145–230  $\mu$ m, vessel member length 425–575  $\mu$ m. Perforations simple, end walls transverse. Intervascular pits alternate, round, oval or polygonal, 9–13  $\mu$ m. Vessel-ray and vessel-parenchyma pits larger and irregularly shaped, half-bordered. Thin-walled tyloses occasionally present in samples from Asia. Fibres septate with small simple pits restricted to the radial walls; walls 1–3  $\mu$ m, lumina 10–30  $\mu$ m; often gelatinous; length 1030–1390  $\mu$ m; F/V-ratio 1.8–3.1. Rays uniseriate and multiseriate, 4–7 per mm. Uniseriate rays 2–15%, composed of procum-

bent and few square or upright cells, height up to 10 cells (430  $\mu\text{m}$ ). Multiseriate rays composed of procumbent cells<sup>2</sup>, uniseriate margins of 1–2 (4) rows of square and/or upright cells and occasionally few sheath cells; 4–7 cells wide and up to 1100  $\mu\text{m}$  high. Parenchyma paratracheal, vasicentric-aliform with short wings, occasionally confluent, parenchyma strands of 3–5 (8) cells. Radial latex tubes present in all samples. Rhombic crystals few, in marginal ray cells and axial parenchyma in some samples from Asia.

Note: Rhombic and elongated crystals are extremely abundant in the axial parenchyma and marginal ray cells of the sample of *Koorders 1127g/22746B*.

#### *Castilla* Sessé in Cervantes (Figs. 3, 4)

Berg (1972) monographed the genus and distinguished three species: *C. elastica* Cerv., *C. tunu* Hemsl., and *C. ulei* Warb. The genus *Castilla* occurs in Central America, the coastal region of NW. South America, and the Amazon basin. *Castilla elastica* has been introduced and naturalised in most tropical countries. *Castilla* consists of trees, about 30–40 m tall, growing in tropical rainforest up to 850 m altitude.

Material studied: *C. elastica* Cerv. Guatemala: McClay & Clara 30 (Uw 24222); Colombia, Chocó: Cuatrecasas 14218 (Uw 25161), Cuatrecasas 15217 (Uw 25289); Surinam: Lindeman 229 (Uw 23350). — *C. tunu* Hemsl. Panama: Pittier s.n. (US 715986, Uw 7048); Ecuador: Berg 424 (Uw 23615); Nicaragua: Englesing 97 (Uw 18808). — *C. ulei* Warb. Brazil, Amazonas: Prance & Berg 19852 (Uw 20943); Brazil, Mato Grosso: Krukoff 1409 (Uw 18427); Brazil, Rio Purus: Krukoff 5766 (Uw 18807); Peru: Ellenberg 2949 (Uw 8827), Williams 1802 (Uw 18433).

General features: Growth rings faint or absent; colour light yellowish brown, no demarcation between sapwood and heartwood. Texture coarse, grain straight. Specific gravity 310–480 N per cubic metre.

Microscopic features: Vessels diffuse, solitary (30–70%) and in short radial multiples or irregular clusters of 2–6; 4–8 per sq.mm, round to oval, diameter 135–215  $\mu\text{m}$ , vessel member length 350–560  $\mu\text{m}$ . Perforations simple, end walls transverse. Intervascular pits alternate, round, oval to polygonal, 8–11  $\mu\text{m}$ . Vessel-ray and vessel-parenchyma pits larger and irregularly shaped, half-bordered. Thin-walled tyloses occasionally present. Fibres all

or partly septate with small simple pits restricted to the radial walls; walls 1–3  $\mu\text{m}$ , lumina 15–25  $\mu\text{m}$ , occasionally gelatinous; length 1000–1200  $\mu\text{m}$ ; F/V-ratio 2.0–2.9. Rays uniseriate and multiseriate, 4–7 per mm. Uniseriate rays 0–25%, composed of procumbent and upright cells, height up to 6–10 cells (150–500  $\mu\text{m}$ ). Multiseriate rays composed of procumbent cells<sup>2</sup>, with uniseriate margins of 1–3 rows of square and/or upright cells and few sheath cells in some rays; 3–6 cells wide, up to 800–1300  $\mu\text{m}$  high. Parenchyma paratracheal, the pattern varying from almost restricted to vasicentric or aliform with short wings to confluent-banded, the bands up to 20 cells wide and 1–2 per mm. Parenchyma strands of 2–4 (8) cells. Radial latex tubes present in all samples. Vitreous silica present in some vessels in two samples.

Note: *Castilla ulei* (Williams 1802) deviates in the high uniseriate rays (up to 30 cells, 650  $\mu\text{m}$ ) and the narrow multiseriate rays (up to 3 cells wide) with uniseriate margins of 3–6 rows of upright cells.

#### *Helicostylis* Trécul (Fig. 13)

This Neotropical genus was monographed by Berg in 1972. He distinguished seven species, distributed mainly in the Amazon basin and the coastal regions of Venezuela and the Guianas. One species (*H. tovarensis*) occurs up to Costa Rica. Some species, originally described under *Helicostylis*, proved to belong to the genus *Brosimum*. *Helicostylis* is a genus of trees, up to 20–30 m tall, of the tropical lowland rainforest.

Material studied: *H. elegans* (Macbr.) C.C. Berg. Brazil, Mato Grosso: Prance & Berg 18613 (Uw 20924), Prance & Berg 19868 (Uw 20944); Brazil, Amazonas: Krukoff 6809 (Uw 7946), 8075 (Uw 16159), 8521 (Uw 16201). — *H. pedunculata* R. Ben. Surinam: van Donselaar 2992 (Uw 11963), Lanjouw & Lindeman 421 (Uw 1224), Lindeman 3544 (Uw 2315); French Guiana: BAFOG 165 M (Uw 5244), 267 M (Uw 5342); Brazil, Amapá: Pires 51670 (Uw 8956). — *H. scabra* (Macbr.) C.C. Berg. Brazil, Amazonas: Krukoff 6811 (Uw 7948), 7081 (Uw 8162), Prance & Berg 17967 (Uw 20953). — *H. tomentosa* (P. & E.) Rusby. Guyana: Fanshawe 148, For. Dept. 2757 (Uw 985), Maguire et al. 45735 (Uw 16775); Surinam: Lindeman 4756 (Uw 3276), 5356 (Uw 3711), 5357 (Uw 3712), 6712 (Uw 4539), LBB (Maas) 10963 (Uw 11698); Brazil, Mato Grosso: Krukoff 1557 (Uw 19400), 8859 (Uw 16256), Prance & Maas

<sup>2</sup> 'Procumbent' refers to very strongly procumbent cells with a length : height ratio of over 3; 'weakly procumbent' is used for length : height ratios of 2–3 : 1 of at least part of the procumbent ray cells.

15027 (Uw 19122); Brazil, Amapá: Pires 51834 (Uw 9077). — *H. tovarensis* (Klotzsch & Karsten) C.C. Berg. Colombia, Chocó: Cuatrecasas 14424 (Uw 24955). — *H. turbinata* C.C. Berg. Brazil, Amazonas: Krukoff 8832 (Uw 16258), type.

**General features:** Growth rings absent; sapwood golden yellowish brown, heartwood light to dark brown, sometimes with dark brown streaks on the tangential surfaces. The demarcation between sapwood and heartwood generally irregular. Texture moderately fine, grain straight. Specific gravity 590–1070 N per cubic metre.

**Microscopic features:** Vessels diffuse but with a tendency towards a diagonal arrangement; mostly solitary (70–90%) and in short radial multiples of 2–4; 5–12 per sq.mm, round to oval, diameter 90–200  $\mu\text{m}$ , vessel member length 400–550  $\mu\text{m}$ . Perforations simple, end walls almost transverse; intervacular pits alternate, round, oval or polygonal, 8–10  $\mu\text{m}$ . Vessel-ray and vessel-parenchyma pits larger and irregularly shaped, half-bordered. Thin-walled tyloses often present. Fibres all or partly septate, in some specimens non-septate; with small simple pits restricted to the radial walls; walls 2–5  $\mu\text{m}$ , lumina 7–14  $\mu\text{m}$ ; in some samples partly gelatinous; length 1140–1585  $\mu\text{m}$ ; F/V-ratio 2.4–2.9. Rays uniseriate and multiseriate, 4–7 per mm. Uniseriate rays 0–20%, generally composed of few rows of procumbent cells and few to many rows of upright cells, height up to 8 cells (150–350  $\mu\text{m}$ ). Multiseriate rays entirely composed of (weakly) procumbent cells<sup>2</sup> except for the uniseriate margins of 1–2 (5) rows of square and/or upright cells and few sheath cells in some of the rays; 2–5 (6) cells wide, up to 310–900  $\mu\text{m}$  high. Parenchyma paratracheal, vasicentric aliform with narrow to broad wings; sometimes tending towards unilateral arrangement abaxially, sometimes confluent; sometimes terminal parenchyma present. Parenchyma strands of 4 (2–8) cells. Rhombic crystals in variable amounts in rays and axial parenchyma. Vitreous silica present occasionally in the fibres, rarely also in the axial parenchyma. Radial latex tubes always present, albeit sometimes sporadically. Sclerotic cells occasionally noticed in the rays and/or axial parenchyma.

**Note:** *H. turbinata* deviates in its F/V-ratio (3.9), due to the relatively long fibres (1585  $\mu\text{m}$ ) and short vessel members (400  $\mu\text{m}$ ). The parenchyma is often confluent and locally forms long parenchyma bands, up to 7–8 cells wide. Furthermore, the multiseriate rays are frequently up to 7 cells wide and no diagonal vessel arrangement was found.

### *Maquira* Aublet (Fig. 7)

This Neotropical genus was revised by Berg in 1972. Species of this genus were formerly assigned to i.a. *Olmedia* and *Perebea*. Berg distinguishes five species, all being medium-sized or small trees of the tropical rainforest, up to 20–50 m tall, distributed in northern South America with one species up to Nicaragua.

**Material studied:** *M. calophylla* (P. & E.) C.C. Berg. Brazil, Amazonas: Krukoff 6347 (Uw 7655), 6655 (Uw 7851), 8580 (Uw 16208), 8642 (Uw 16210). — *M. coriacea* (Karst.) C.C. Berg. Brazil, Amazonas: INPA-Manaus X-3885 (Uw 18851), Krukoff 6615 (Uw 7817), 6705 (Uw 7886); Brazil, Amapá: Pires 51743 (Uw 9012); Venezuela: Breteler 3726 (Uw 11746). — *M. costaricana* (Standl.) C.C. Berg. Colombia, Chocó: Cuatrecasas 14135 (Uw 25382). — *M. guianensis* Aublet. Surinam: Lanjouw & Lindeman 2187 (Uw 1644), 2811 (Uw 1936), LBB (Maas) 10795 (Uw 11210); Schulz 8980 (Uw 8855); Stahel 222 (Uw 222); Brazil, Amazonas: Pires 51803 (Uw 9634), France & Berg 18609 (Uw 20921); Brazil, Amapá: Pires, Rodrigues & Irwin 51612 (Uw 8949). — *M. sclerophylla* (Ducke) C.C. Berg. Surinam: Lindeman 5040 (Uw 3424); Brazil, Pará: Krukoff 1133 (Uw 19224).

**General features:** Growth rings faint or absent; colour (light) brown, no demarcations between heartwood and sapwood. Texture medium, grain slightly interlocked. Specific gravity 610–1000 N per cubic metre.

**Microscopic features:** Vessels diffuse with a slight tendency towards a diagonal arrangement, solitary (40–90%) and in short radial multiples of 2–4, 5–20 per sq.mm, round to oval, diameter 90–160  $\mu\text{m}$ , vessel member length 400–640  $\mu\text{m}$ . Perforations simple, end walls almost transverse. Intervacular pits alternate, round, oval to polygonal, 7–9  $\mu\text{m}$ . Vessel-ray and vessel-parenchyma pits larger and irregularly shaped, half-bordered. Thin-walled tyloses often present. Fibres all or partly septate with small simple pits restricted to the radial walls; walls 3–5  $\mu\text{m}$ , lumina 5–9  $\mu\text{m}$ , occasionally gelatinous; length 1015–1600  $\mu\text{m}$ ; F/V-ratio 2–3. Rays uniseriate and multiseriate, 6–8 per mm. Uniseriate rays 0–10%, composed of upright and few procumbent cells, height up to 3–6 cells (150–300  $\mu\text{m}$ ). Multiseriate rays composed of procumbent cells<sup>2</sup> except for the uniseriate margins of 1–3 rows and square and/or upright cells and few sheath cells; 3–5 cells wide, up to 300–1200  $\mu\text{m}$  high. Parenchyma paratracheal, variable: wide to narrow vasicentric, aliform with short wings to confluent

(text continued on page 191)

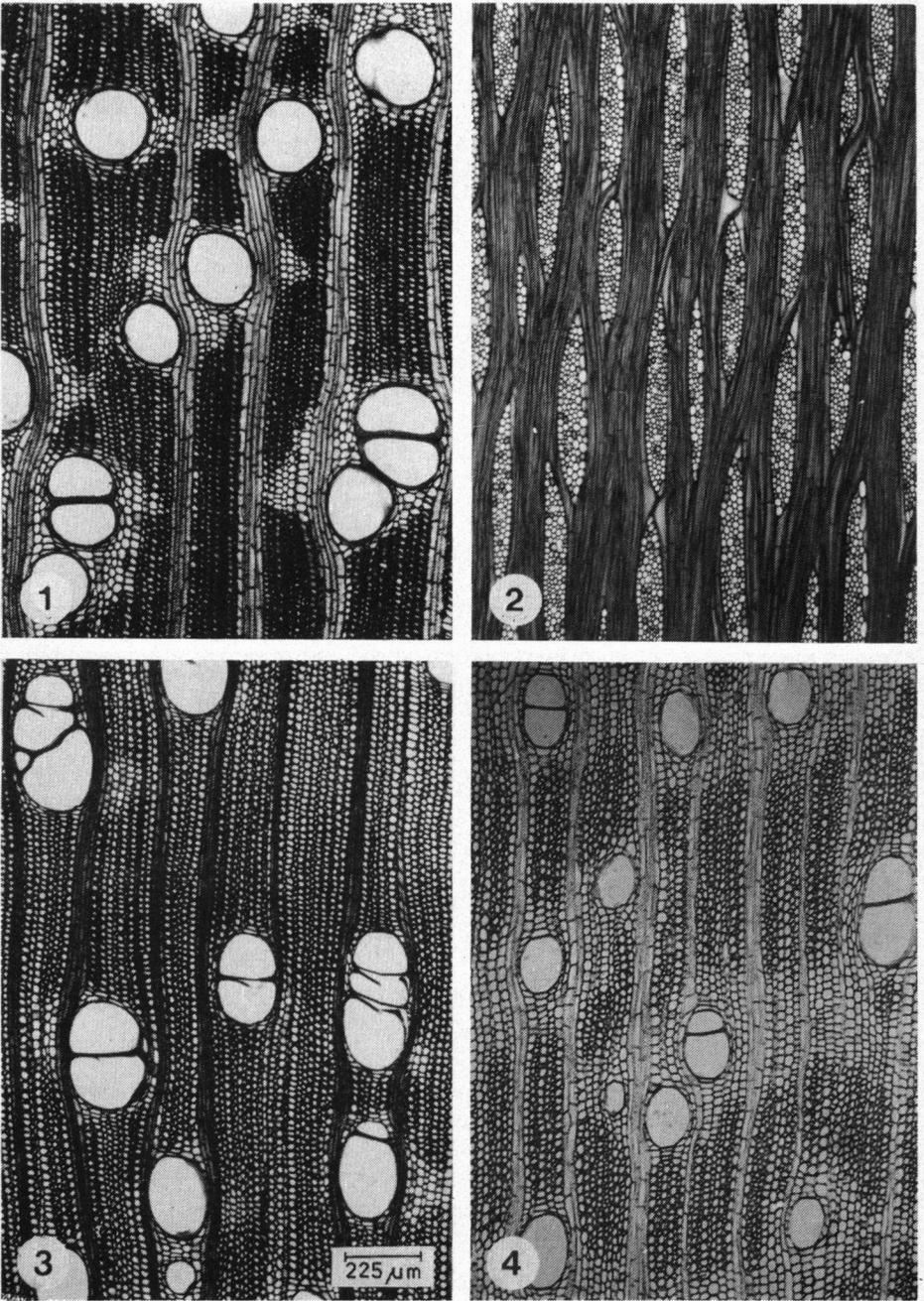


Fig. 1. *Antiaris toxicaria*, Uw 24430. — Fig. 2. *Ibid.*, Uw 18780. — Fig. 3. *Castilla elastica*, Uw 25289. — Fig. 4. *C. ulei*, Uw 20943. — All x 360.

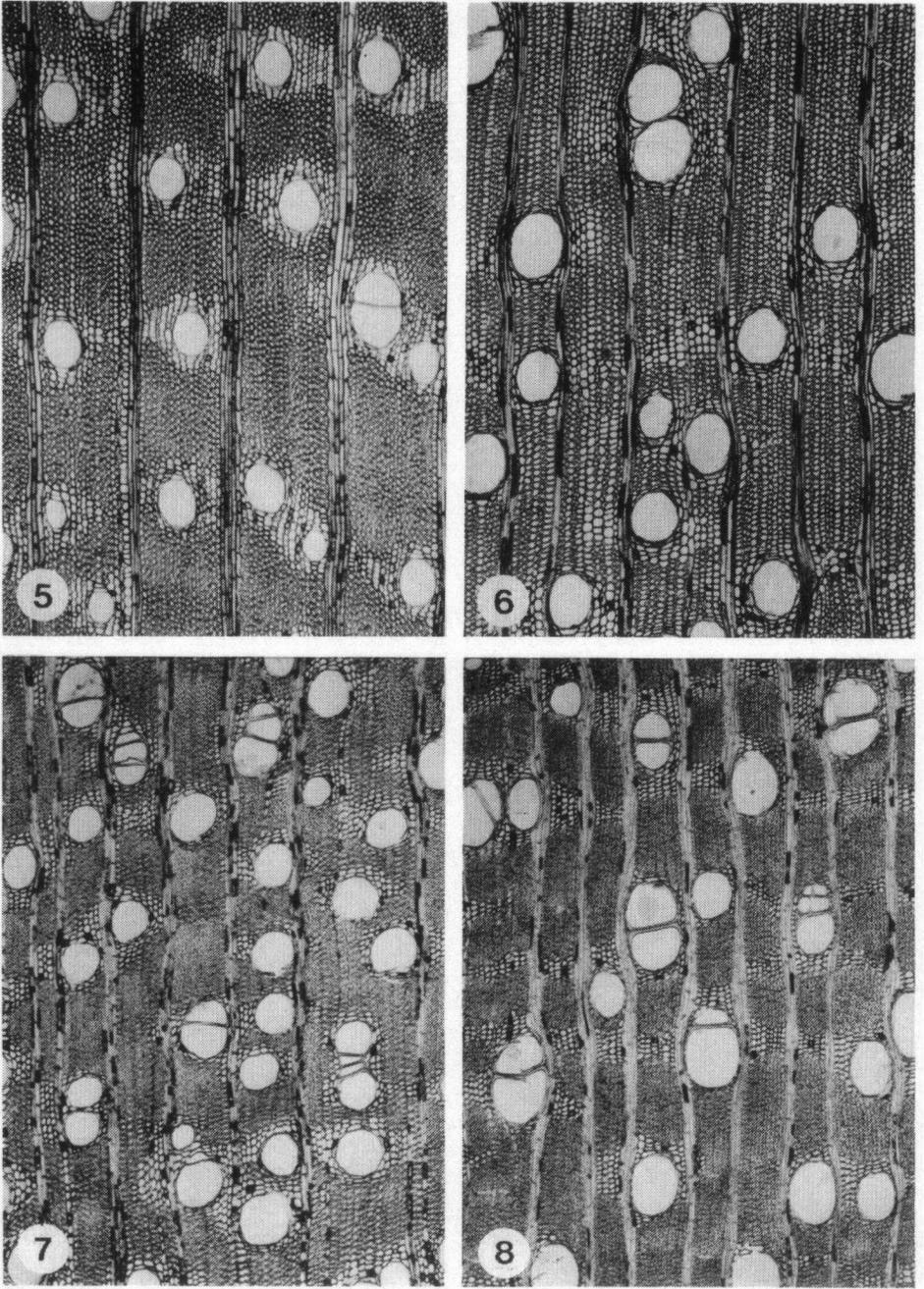


Fig. 5. *Perebea xanthochyma*, Uw 18431. — Fig. 6. *P. guianensis*, Uw 16183. — Fig. 7. *Maquira coriacea*, Uw 9012. — Fig. 8. *Pseudolmedia laevis*, Uw 11817. — All x 360.

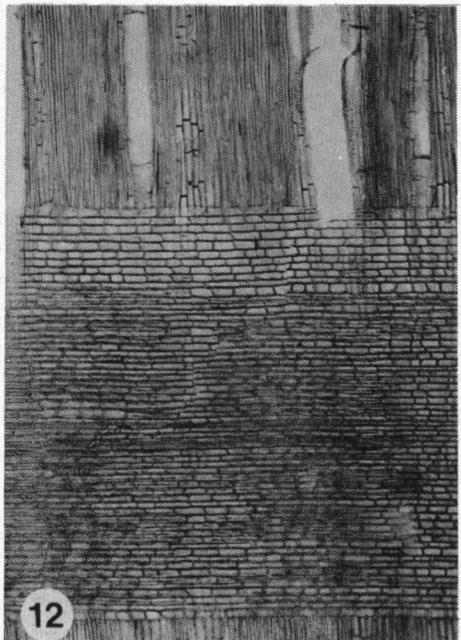
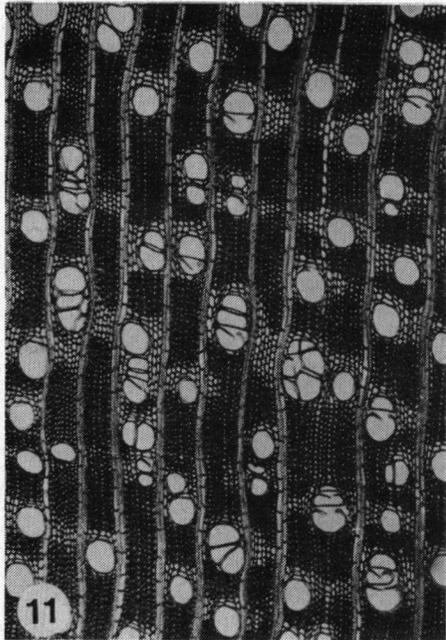
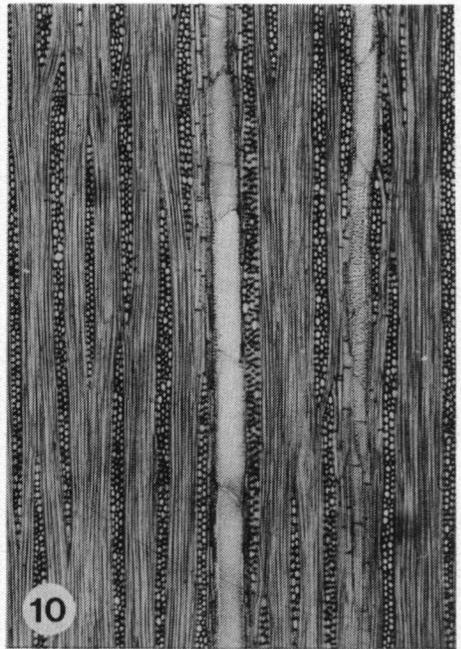
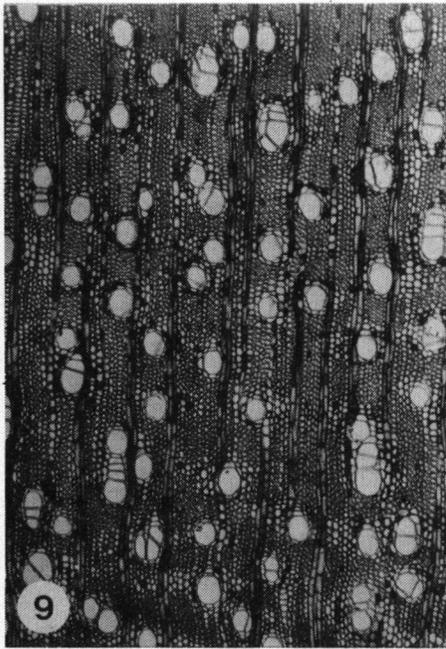


Fig. 9. *Naucleopsis ulei*, Uw 18428. — Fig. 10–12. *N. imitans*, Uw 19991. — All x 360.

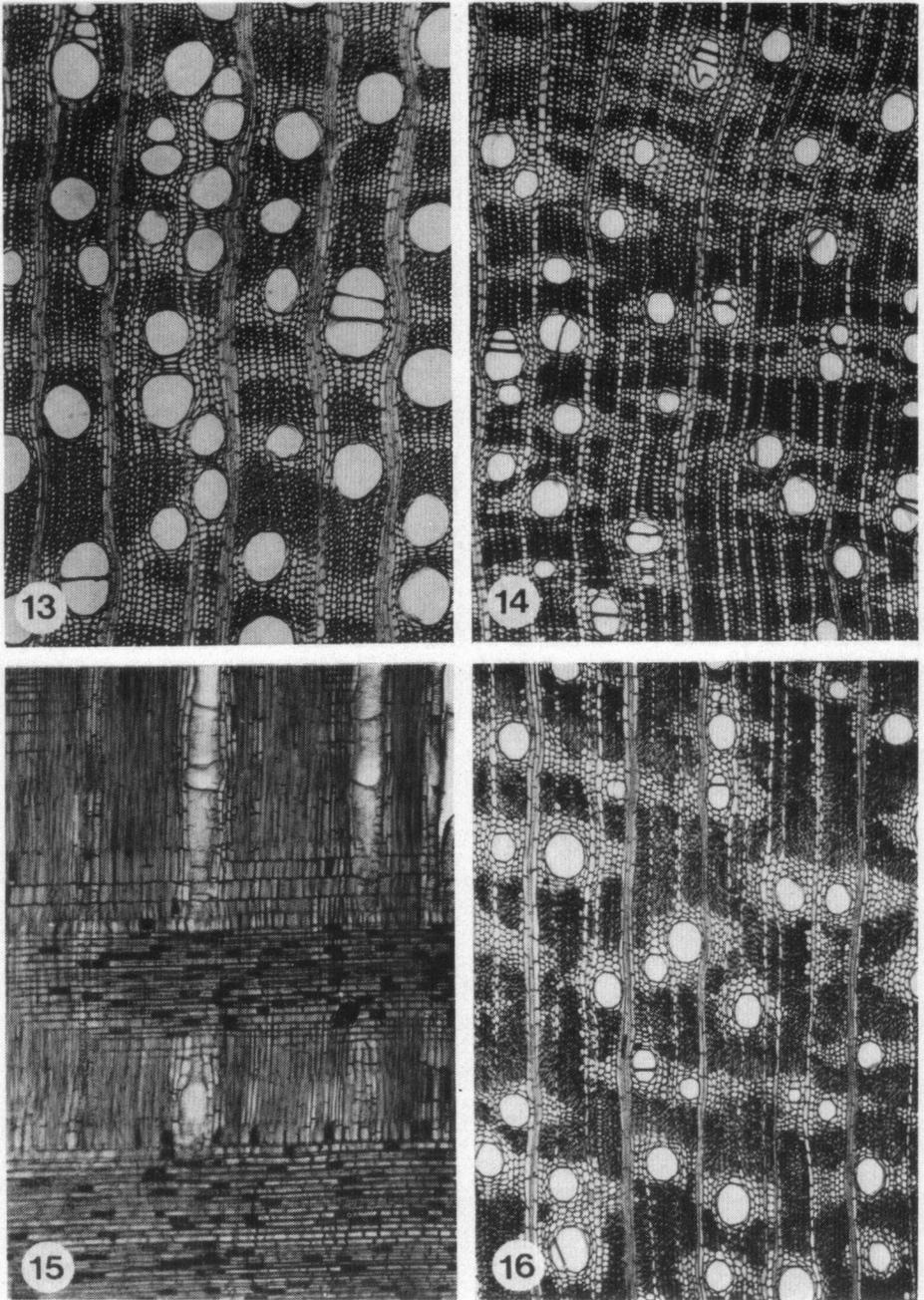


Fig. 13. *Helicostylis turbinata*, Uw 16258. — Fig. 14–15. *Mesogyne insignis*, Uw 25797. — Fig. 16. *Ibid.*, Uw 25686. — All x 360.

and in narrow bands, sometimes wavy; strands of 3–4 (2–8) cells. Radial latex tubes generally present, though sometimes very infrequent. Rhombic crystals occasionally present in the rays and rarely in the axial parenchyma. Vitreous silica sometimes present in the axial parenchyma, rarely also in the vessels and fibres.

**Note:** Wood anatomically, the individual species show only part of the variation indicated above. As a genus, however, *Maquira* is very heterogeneous in, at least, the parenchyma pattern, the ray structure, the presence and frequency of crystals and silica, and the diameter and density of the vessels. The wood structure shows an overlap with that found in *Helicostylis*, *Perebea*, and *Pseudolmedia*.

#### *Mesogyne* Engler (Figs. 14–16)

An African genus, monotypic according to Berg (1977b). It consists of shrubs or trees, up to 15 (occasionally 40) m tall, of the lower stories of the tropical rainforest, between 500 and 1300 m altitude, occurring in eastern Tanzania and Sao Tomé.

**Material studied:** *M. insignis* Engler. Tanzania: Holst 2290 (Uw 25797), Scheffer 22 (Uw 25795), Schlieben 158 (Uw 25686).

**General features:** Growth rings absent; colour light brown, no demarcation between heartwood and sapwood. Texture fine, grain interlocked. Specific gravity 700–750 N per cubic metre.

**Microscopic features:** Vessels diffuse, solitary (60–80%) and in short radial multiples of 2–4, 13–20 per sq. mm, weakly angular (to round), diameter 85–105  $\mu\text{m}$ , vessel member length 375–505  $\mu\text{m}$ . Perforations simple, end walls almost transverse. Intervascular pits alternate, round or polygonal, 7–10  $\mu\text{m}$ . Vessel-ray and vessel-parenchyma pits larger and irregularly shaped, half-bordered, apertures sometimes coalescent. Thin-walled tyloses present. Fibres septate with simple pits restricted to the radial walls; walls 2–4  $\mu\text{m}$ , lumina 9–12  $\mu\text{m}$ ; occasionally gelatinous; length 1125–1280  $\mu\text{m}$ ; F/V-ratio 2.4–3.4. Rays uniseriate and multiseriate, 8–11 per mm. Uniseriate rays 15–45%, composed of few rows of weakly procumbent cells<sup>2</sup> and many rows of upright cells, height up to 11 cells (500  $\mu\text{m}$ ). Multiseriate rays composed of (weakly) procumbent cells except for the uniseriate margins of 1–6 rows of square and upright cells and few sheath cells in some rays; 2–4 cells wide, up to 700  $\mu\text{m}$  high. Parenchyma abundant; paratracheal long aliform-confluent to banded, and apotracheal in some diffuse strands. Parenchyma strands of 4 (1–9) cells. Vitreous silica scarce, in fibres and axial parenchyma.

#### *Naucleopsis* Miquel (Figs. 9–12)

In this Neotropical genus Berg (1972) combined two *Perebea* species with the species formerly assigned to *Acanthosphaera*, *Ogcodeia* and *Palmolmedia*. The genus consists of small to medium-sized trees of the tropical lowland and is distributed from Honduras to Rio de Janeiro (Brazil).

**Material studied:** *N. amara* Ducke. Brazil, Mato Grosso: Krukoff 1406 (Uw 19340). — *N. concinna* (Standl.) C.C. Berg. Brazil, Amazonas: Krukoff 6620 (Uw 7822), 6687 (Uw 7875). — *N. glabra* Spruce ex Baillon. Brazil, Acre: Krukoff 5323 (Uw 19899); Brazil, Amazonas: Berg et al. 754 (Uw 24080), Krukoff 1300 (Uw 19277), 1392 (Uw 19331), 6198 (Uw 7549), 8271 (Uw 16170), Prance & Berg 18241 (Uw 20901), 19805 (Uw 20938); Brazil, Mato Grosso: Krukoff 1347 (Uw 19304). — *N. guianensis* (Mildbr.) C.C. Berg. Surinam: van Donselaar 3791 (Uw 12167), Lindeman 3790 (Uw 2776). — *N. imitans* (Ducke) C.C. Berg. Brazil, Acre: Krukoff 5485 (Uw 19991). — *N. inaequalis* (Ducke) C.C. Berg. Brazil, Mato Grosso: Krukoff 1458 (Uw 19364). — *N. krukovii* (Standl.) C.C. Berg. Brazil, Amazonas: Krukoff 4544 (Uw 19524). — *N. macrophylla* Miq. Brazil, Amazonas: Ducke 232 (Uw 2667), Maguire et al. 56684 (Uw 16478), Prance & Berg 18543 (Uw 20920). — *N. mello-barettoi* (Standl.) C.C. Berg. Brazil, Amazonas: Krukoff 6839 (Uw 7974). — *N. stipularis* Ducke. Brazil, Amazonas: Ducke 370 (Uw 18423). — *N. ternstroemiflora* (Mildbr.) C.C. Berg. Brazil, Amazonas: Krukoff 1306 (Uw 19281). — *N. ulei* (Warb.) Ducke. Brazil, Amazonas: Krukoff 1301 (Uw 19278); Peru: Williams 5194 (Uw 18428).

**General features:** Growth rings faint or absent; colour light brown, no demarcation between heartwood and sapwood. Texture fine to medium; grain straight. Specific gravity between 570 and 990 N per cubic metre.

**Microscopic features:** Vessels diffuse with a tendency towards a diagonal arrangement, solitary (20–80%) and in short radial multiples of 2–4; 20–45 per sq. mm, angular, round or oval, diameter 60–110  $\mu\text{m}$ , vessel member length 355–535  $\mu\text{m}$ . Perforations simple, end walls almost transverse. Intervascular pits alternate, round, oval to polygonal, 6–9  $\mu\text{m}$ . Vessel-ray and vessel-parenchyma pits larger and irregularly shaped, half-bordered. Thin-walled tyloses occasionally present. Fibres septate with small simple pits restricted to the radial walls; walls 2–4  $\mu\text{m}$ , lumina 5–10  $\mu\text{m}$ ; occasionally gelatinous; length 1000–1250  $\mu\text{m}$ ; F/V-ratio 2.1–2.9. Rays uniseriate and multiseriate, 6–8 per mm. Uniseriate rays 0–15%, composed of procumbent<sup>2</sup> and/or square to

upright cells, height up to 4–7 cells (200–350  $\mu\text{m}$ ). Multiseriate rays composed of (weakly) procumbent cells except for the uniseriate margins of 1–6 rows of square and/or upright cells and few sheath cells; 2–4 (5) cells wide, and up to 600–1500  $\mu\text{m}$  high, sometimes vertically fused. Parenchyma paratracheal, vascentric aliform, occasionally locally confluent, the vascentric ring often incomplete and lacking on the adaxial side; strands of 2–4 (1–8) cells. Latex tubes present, generally with a small diameter in comparison to the surrounding ray cells. Rhombic crystals present in the ray cells of about 50% of the samples, rarely also in the parenchyma tissue. Vitreous silica occasionally present in the fibres and parenchyma.

Note: The samples of *N. stipularis*, *N. amara* and *N. ulei* (Williams 5194) do not completely fit the generic description. *N. amara* deviates in the diameter (150  $\mu\text{m}$ ) and number (15 per sq.mm) of the vessels and in its fibre length (1450  $\mu\text{m}$ ). *N. stipularis* shows abundant parenchyma in wavy paratracheal bands and ray margins of up to 8 cells high. Both samples of *N. ulei* differ from each other in the vessel diameter and ray height: the values are among the lowest (Williams 5194) and highest (Krukoff 1301) values found in the genus.

#### *Perebea* Aublet (Figs. 5, 6)

Ever since this Neotropical genus was established, the generic delimitation has been the subject of discussion. In his monograph, Berg (1972) distinguished eight species in two sections. The genus consists of small to medium sized trees or shrubs. Representatives are found in tropical lowland forest in tropical South America and Panama.

Material studied: *P. guianensis* Aublet ssp. *guianensis*. Brazil: Irwin 48718 (Uw 16989), Krukoff 8350 (Uw 16183); Brazil, Amazonas: Krukoff 7041 (Uw 8128), Krukoff 7209 (Uw 8241). – *P. mollis* (P. & E.) Huber ssp. *mollis*. Brazil: Ducke 175 (Uw 2668); Brazil, Amazonas: Krukoff 1289 (Uw 19268), 6985 (Uw 8080). – *P. mollis* ssp. *rubra* (Trécul) C.C. Berg. Surinam: Stahel 211 (Uw 211). – *P. xanthochyma* Karsten. Peru: Williams 3412 (Uw 18431).

General features: Growth rings faint or absent; colour (light) brown, no demarcation between heartwood and sapwood. Texture medium; grain straight. Specific gravity 530–830 N per cubic metre.

Microscopic features: Vessels diffuse with a tendency towards a diagonal arrangement, solitary (40–80%) and in short radial multiples of 2–4; 5–15 per sq.mm, round to oval, diameter 95–160  $\mu\text{m}$ , vessel member

length 420–550  $\mu\text{m}$ . Perforations simple, end walls almost transverse. Intervascular pits alternate, round, oval or polygonal, 7–9  $\mu\text{m}$ . Vessel-ray and vessel-parenchyma pits larger and irregularly shaped, half-bordered. Thin-walled tyloses occasionally present. Fibres septate with small simple pits restricted to the radial walls; walls 2–4  $\mu\text{m}$ , lumina 7–18  $\mu\text{m}$ ; occasionally gelatinous; length 1050–1600  $\mu\text{m}$ ; F/V-ratio 1.9–3.4  $\mu\text{m}$ . Rays uniseriate and multiseriate, 5–7 per mm. Uniseriate rays 0–17%, composed of procumbent<sup>2</sup> and upright cells, height up to 5–7 cells (150–340  $\mu\text{m}$ ). Multiseriate rays composed of procumbent cells except for the uniseriate margins of 1(–3) rows of square (upright) cells and few sheath cells; 3–6 cells wide and up to 500–1000  $\mu\text{m}$  high. Parenchyma paratracheal in generally complete, narrow, aliform vascentric rings, often confluent in tangential or diagonal direction over a short distance, the sheaths usually widest on the abaxial side of the vessels; strands of 4 (2–8) cells. Radial latex tubes often present, some axial latex tubes present in one sample (cf. Topper & Koek-Noorman, 1980). Rhombic crystals absent or scarce in ray cells; in one sample abundant in rays and axial parenchyma. Vitreous silica scarce in one sample, in both vessels and fibres.

Note: One sample of *P. guianensis* (Krukoff 7209) deviates in its narrow-aliform parenchyma, without confluent bands. The two sections of *Perebea*, as defined by Berg, cannot be distinguished by their wood anatomy in the available samples.

#### *Pseudolmedia* Trécul (Fig. 8)

Berg revised the genus and reduced the number of species to nine. Some species were transferred to other genera (Berg, 1972). *Pseudolmedia* occurs in the northern part of South America, Central America and the Greater Antilles, as small or medium-sized to large trees of various habitats.

Material studied: *P. laevigata* Trécul. Guyana: A.C. Smith 3633 (Uw 21706); Brazil, Rio Solimoes: Ducke 359 (SJRw 40090, Uw 2669); Brazil, Amazonas: Krukoff 6697 (Uw 7880), 8383 (Uw 16186), Prance & Berg 18611 (Uw 20923); Colombia: J. de Bruijn 1543 (Uw 14493). – *P. laevis* (R. & P.) Macbr. Guyana: Fanshawe 5378 (Uw 988); Brazil, Amazonas: Krukoff 5188 (Uw 19815); Brazil, Acre: Krukoff 5217 (Uw 19823), 5312 (Uw 19889); Venezuela: Breteler 3929 (Uw 11817). – *P. macrophylla* Trécul. Brazil, Amazonas: Prance & Berg 18376 (Uw 20906); Bolivia: Krukoff 10738 (SJRw 39639, Uw 2670). – *P. oxyphylaria* Donn. Smith. Mexico: I.N.I.F. X152 (Uw 20653); Belize: Stevenson 119 (SJRw 14901).

– *P. rigida* (Klotzsch & Karsten) Cuatrecasas. Ecuador: Maas, Berg & ter Welle 2918 (Uw 23575). – *P. spuria* (Swartz) Griseb. Guatemala: McClay & Clara 31 (Uw 18027); Belize: Brown 35 (SJRw 15351).

**General features:** Growth rings absent; colour (light) brown, no demarcation between heartwood and sapwood. Texture fine to medium; grain straight or slightly interlocked. Specific gravity 710–940 N per cubic metre.

**Microscopic features:** Vessels diffuse, solitary (30–80%) and in short radial multiples of 2–4; 8–25 per sq.mm, round to oval, diameter 70–165  $\mu\text{m}$ , vessel member length 350–540  $\mu\text{m}$ . Perforations simple, end walls almost transverse; intervacular pits alternate, round, oval to polygonal, 7–10  $\mu\text{m}$ . Vessel-ray and vessel-parenchyma pits larger and irregularly shaped, half-bordered. Thin-walled tyloses often present, sclerotic in some samples of *P. laevigata*. Fibres all or partly septate, with small simple pits restricted to the radial walls; walls 3–4  $\mu\text{m}$ , lumina 4–9  $\mu\text{m}$ ; sometimes gelatinous; length 1000–1600  $\mu\text{m}$ ; F/V-ratio 2.4–3.4. Rays uniseriate and multiseriate, 5–8 per mm. Uniseriate rays 0–15%, composed of procumbent and square, rarely upright cells, height up to 3–7 cells (150–600  $\mu\text{m}$ ). Multiseriate rays composed of procumbent cells<sup>2</sup>, with or without 1–2 rows of square (rarely upright) marginal cells; 3–5 cells wide and up to 370–1000  $\mu\text{m}$  high. Parenchyma paratracheal, confluent to wavy banded, occasionally aliform with short to long wings; strands of 3–6 (11) cells. Radial latex tubes are present, but infrequent and inconspicuous. Axial latex tubes present in one sample of *P. spuria*. Rhombic crystals present in marginal ray cells and in axial parenchyma cells. Vitreous silica in most samples in vessels, fibres or axial parenchyma.

**Note:** *P. spuria* shows rhombic crystals in procumbent as well as square and upright ray cells.

## Discussion

In his monograph of the tribe Olmedieae, Berg (1972) presented a detailed survey of the taxonomic history of the tribe. In a subsequent paper, Berg excluded *Olmedia* from the tribe and renamed it Castilleae (1977a). As already indicated in the Introduction, Mennega and Lanzing-Vinkenborg (1977) thoroughly studied the six Neotropical genera now assigned to the tribe Castilleae. For a detailed discussion of the wood anatomy of these taxa we refer to their paper. Berg (1977a) also included two African genera, *Antiaris* and *Mesogyne*, in the Castilleae. The Palaeotropical genera *Antiaropsis* and *Spa-*

*rattosyce*, formerly included in the tribe Olmedieae (Corner, 1962) were excluded by Berg and transferred to the Moreae.

The eight genera of the tribe Castilleae are similar in many features and show considerable overlap, the differences being in quantitative features only. As far as we can judge now, characters like vessel member and fibre length, pit size and arrangement, ray structure, and occurrence of crystals are of no or very little diagnostic or taxonomic value in this group. In Table 1 the characters with at least some diagnostic value are listed: frequency and diameter of the pores, the (tendency towards a) diagonal vessel arrangement, the presence of either weakly or strongly procumbent ray cells<sup>2</sup>, the parenchyma distribution, the presence or absence of radial latex tubes, and the specific gravity. For these characters, in particular for diagonal vessel arrangement and presence of latex tubes, a careful examination of large areas is required. Notwithstanding the high degree of similarity and overlap, some genera can be recognised by a combination of features.

The samples of *Antiaris* studied are all very similar. Only one sample is remarkable in the abundance of crystals. There are no wood anatomical features which contradict the combination of all species into one species, as Berg (1977b) proposed. The genus can be recognised by its very low specific gravity, a low number of relatively large pores per sq.mm, and parenchyma only in aliform (confluent) arrangement. These features are also found in other Castilleae, but not in this combination. The wood anatomical features thus do not contradict inclusion of *Antiaris* in this tribe. Corner's suggestion (1962) that *Pseudolmedia* might be one of the nearest allies of *Antiaris*, is not confirmed, neither is his idea, that *Mesogyne* and *Antiaris* might be congeneric (see below).

*Castilla* shares the low specific gravity (already mentioned by Mennega and Lanzing-Vinkenborg, 1977) and the low number of relatively large vessels with *Antiaris*, but differs in its more abundant parenchyma, partly arranged in bands, comparable with those found in *Mesogyne* and *Maquira* p.p. Like in *Mesogyne* and *Pseudolmedia*, no trace of diagonal vessel arrangement was found.

*Mesogyne* and *Naucleopsis* both show relatively narrow vessels. At least part of the procumbent ray cells are weakly procumbent<sup>2</sup>. *Mesogyne* is characterised by abundant parenchyma and the highest number of rays per mm; latex tubes are lacking. A remarkable feature in most specimens of *Naucleopsis* studied is the unilateral arrangement of the paratracheal parenchyma. This feature was not found in *N. sti-*

Table 1. Some wood anatomical features of the Castilleae.

|                     | Vessels                |                       |                       |                      | Fibres | Rays              |                        |                                      |                                   | Parenchyma         |           |                 | latex tubes | rhombic crystals | specific gravity (N/m <sup>3</sup> ) |          |
|---------------------|------------------------|-----------------------|-----------------------|----------------------|--------|-------------------|------------------------|--------------------------------------|-----------------------------------|--------------------|-----------|-----------------|-------------|------------------|--------------------------------------|----------|
|                     | frequency (per sq. mm) | diameter (in $\mu$ m) | pit size (in $\mu$ m) | diagonal arrangement |        | % uniseriate rays | rows of marginal cells | weakly procumbent cells <sup>2</sup> | multiseriate ray width (in cells) | frequency (per mm) | confluent | way or diagonal |             |                  |                                      | bands    |
| <i>Anitaria</i>     | 3-10                   | 145-230               | 9-13                  | (+)                  | < 15   | 1-2 (4)           | -                      | 4-7                                  | 4-7                               | (+)                | -         | -               | -           | r                | (u, a)                               | 270-530  |
| <i>Castilla</i>     | 4-8                    | 135-215               | 8-10                  | -                    | < 25   | 1-3               | -                      | 3-6                                  | 4-7                               | +                  | -         | (+)             | -           | r                | -                                    | 310-480  |
| <i>Helicostylis</i> | 5-12                   | 90-200                | 8-10                  | (+)                  | < 20   | 1-2 (5)           | +                      | 2-5                                  | 4-7                               | (+)                | -         | -               | (+)         | r                | (p, u, a)                            | 590-1070 |
| <i>Maquira</i>      | 5-20                   | 90-160                | 7-9                   | +                    | < 10   | 1-3               | -                      | 3-5                                  | 6-8                               | (+)                | (+)       | (+)             | (+)         | r                | (p, u, a)                            | 610-1000 |
| <i>Mesogyne</i>     | 13-20                  | 85-105                | 7-10                  | -                    | 15-45  | 1-6               | +                      | 2-4                                  | 8-11                              | +                  | (+)       | -               | -           | -                | -                                    | 700-750  |
| <i>Nauclieopsis</i> | 20-45                  | 60-110                | 6-9                   | +                    | < 15   | 1-6               | +                      | 2-4                                  | 6-8                               | (+)                | -         | -               | +           | r                | (p, u, a)                            | 570-990  |
| <i>Perebea</i>      | 5-15                   | 95-160                | 7-9                   | +                    | < 17   | 1(-3)             | -                      | 3-6                                  | 5-7                               | +                  | +         | -               | -           | r (ax)           | (p, u, a)                            | 530-830  |
| <i>Pseudolmedia</i> | 8-25                   | 70-165                | 7-10                  | -                    | < 15   | 1-2               | -                      | 3-5                                  | 5-8                               | +                  | +         | -               | -           | r (ax)           | u, a                                 | 710-940  |

+: present; -: absent; r: in radial direction; ax: in axial direction; u: in upright and/or square ray cells; p: in procumbent ray cells; a: in axial parenchyma cells; between brackets: occasionally present.

<sup>2</sup>: see footnote on page 185.

For quantitative features the range of sample averages is given.

*pularis* where the parenchyma is arranged in wavy irregular bands, including the vessels.

*Helicostylis*, with the exception of the sample of *H. turbinata*, is characterised by its short-aliform parenchyma, occasionally tending towards a unilateral arrangement, and the presence of weakly procumbent ray cells.

As already indicated by Mennega and Lanzing-Vinkenburg (1977), and as may appear after a glance at Table 1, the remaining genera *Maquira*, *Perebea* and *Pseudolmedia* are extremely difficult to separate on their wood structure. The absence of diagonal vessel arrangement in the samples of *Pseudolmedia* alone can hardly be considered as a sufficiently reliable diagnostic and distinguishing feature. Berg (1972) distinguished sections in each *Maquira*, *Perebea* and *Pseudolmedia*. In the wood anatomy these sections cannot be recognised. As will be evident from the above, we are not able to suggest any other arrangement, in genera or subgenera, than the one already proposed by Berg.

In conclusion, in the material described in this paper, we find no reason to question the delimitation of the tribe Castilleae sensu Berg. The genera *Antiaris*, *Castilla*, *Helicostylis*, *Mesogyne*, and *Naucleopsis* can be recognised. *Mesogyne* is the most deviating genus. However, there are no features that are restricted to this genus only. All are shared by at least one other genus.

*Maquira*, *Perebea* and *Pseudolmedia* are hardly separable and they are highly similar to *Helicostylis*.

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