THE SYSTEMATIC WOOD ANATOMY OF THE MORACEAE (URTICALES)
I. TRIBE CASTILLEAE

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 Pseudomedia. 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 woody 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 Mennega 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 Urticaleae (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, Pseudomedia);
II. Dorstenieae (Bosqueiopsis, Brosimun, Dorstenia, Helianthostylis, Trilepisium, Trymatococcus; of Scyphosyce and Utsetela no material is available);
III. Ficace (Ficus);
IV. Moraeae p.p., characterised by the presence of 'urticaceous' stamens (Broussonetia, Calpidochlamys, Cardiogyne, Chlorophora, Machura s.l. incl. Plecospermum and Cudra-

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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 8316 t/127S7B (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 µm, vessel member length 425–575 µm. Perforations simple, end walls transverse. Intervascular pits alternate, round, oval or polygonal, 9–13 µm. 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 µm, lumina 10–30 µm; often gelatinous; length 1030–1390 µm; F/V-ratio 1.8–3.1. Rays uniseriate and multisierate, 4–7 per mm. Uniseriate rays 2–15%, composed of procum-
bent and few square or upright cells, height up to 10 cells (430 μm). Multiseriate rays composed of procumbent cells, 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 μm 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: Engelsing 97 (Uw 18808). *C. ulei* Warb. Brazil, Amazonas: France & 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 μm, vessel member length 350–560 μm. Perforations simple, end walls transverse. Intervascular pits alternate, round, oval to polygonal, 8–11 μm. Vessel-ray and vessel-parenchyma pits larger and irregularly shaped, half-bordered. Thin-walled tyloses occasionally present. Fibres all or partly separte with small simple pits restricted to the radial walls; walls 1–3 μm, lumina 15–25 μm, occasionally gelatinous; length 1000–1200 μm; 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 μm). Multiseriate rays composed of procumbent cells, 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 μm 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 μm) and the narrow multiseriate rays (up to 3 cells wide) with uniseriate margins of 3–6 rows of upright cells.

**Helicostylis Trécui** (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. touarenensis*) 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: France & Berg 18613 (Uw 20924), France & Berg 18686 (Uw 20944), Brazil, Amazonas: Krukoff 6809 (Uw 7946), 8075 (Uw 16159), 8521 (Uw 16201). *H. pedunculata* K. 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), France & 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), France & Maas
15027 (Uw 19122); Brazil, Amapá: Pires 51834 (Uw 9077). — *H. tovarenensis* (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 μm, vessel member length 400–550 μm. Perforations simple, end walls almost transverse; intervessel pits alternate, round, oval or polygonal, 8–10 μm. 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 μm, lumina 7–14 μm; in some samples partly gelatinous; length 1140–1585 μm; 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 μm). Multiserate rays entirely composed of (weakly) procumbent cells except for the uniseriate margins of 1–2 (5) rows of square and/or upright cells and few shear cells in some of the rays; 2–5 (6) cells wide, up to 310–900 μm 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 μm) and short vessel members (400 μm). 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: Breterel 3726 (Uw 11746). — *M. costaricana* (Standl.) C.C. Berg. Colombia, Chocó: Cuatrecasas 14135 (Uw 25382). — *M. guianensis* Aublet. Surinam: Lannouj & Lindeman 2187 (Uw 1644), 2811 (Uw 1936), LBB (Maas) 10795 (Uw 11210); Schulz 8980 (Uw 8855); Stahl 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 μm, vessel member length 400–640 μm. Perforations simple, end walls almost transverse. Intervessel pits alternate, round, oval to polygonal, 7–9 μm. 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 μm, lumina 5–9 μm, occasionally gelatinous; length 1015–1600 μm; 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 μm). Multiseriate rays composed of procumbent cells except for the uniseriate margins of 1–3 rows and square and/or upright cells and few shear cells; 3–5 cells wide, up to 300–1200 μm high. Parenchyma paratracheal, variable: wide to narrow vasicentric, aliform with short wings to confluent.

(text continued on page 191)
Fig. 1. *Antiart* 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. *Naucleopsisulei*, Uw 18428. — Fig. 10—12. *N. imitans*, Uw 19991. — All x 360.
Fig. 13. *Helicoxylon 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 *Helcoestylis*, *Perebea*, and *Pseudomolbmedia*.

**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 µm, vessel member length 375–505 µm. Perforations simple, end walls almost transverse. Intervascular pits alternate, round or polygonal, 7–10 µm. 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 µm, lumina 9–12 µm; occasionally gelatinous; length 1125–1280 µm; 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 and many rows of upright cells, height up to 11 cells (500 µm). 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 µm 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*, *Ogodeia* and *Palmolimedia*. 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. 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), France & 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. Amazonas: Krukoff 4544 (Uw 19524).— *N. macrophylla* Miqu. Brazil, Amazonas: Krukoff 232 (Uw 2667), Maquiere et al. 56684 (Uw 16478), France & Berg 18543 (Uw 20920).— *N. mello-barettii* (Standl.) C.C. Berg. Brazil, Amazonas: Krukoff 6839 (Uw 7974).— *N. stipularis* Ducke. Brazil, Amazonas: Krukoff 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 µm, vessel member length 355–535 µm. Perforations simple, end walls almost transverse. Intervascular pits alternate, round, oval to polygonal, 6–9 µm. 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 µm, lumina 5–10 µm; occasionally gelatinous; length 1000–1250 µm; F/V-ratio 2.1–2.9. Rays uniseriate and multiseriate, 6–8 per mm. Uniseriate rays 0–15 %, composed of procumbent and/or square to
upright cells, height up to 4–7 cells (200–350 μm). 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 μm high, sometimes vertically fused. Parenchyma paratracheal, vasicentric aliform, occasionally locally confluent, the vasicentric 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. ama-*
ra* and *N. ullei* (Williams 5194) do not completely fit the generic description. *N. amara* deviates in the diameter (150 μm) and number (15 per sq.mm) of the vessels and in its fibre length (1450 μm). *N. stipularis* shows abundant parenchyma in wavy paratracheal bands and ray margins of up to 8 cells high. Both samples of *N. ullei* 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. xantho- chyma* 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 μm, vessel member length 420–550 μm. Perforations simple, end walls almost transverse. Intervascular pits alternate, round, oval or polygonal, 7–9 μm. 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 μm, lumina 7–18 μm; occasionally gelatinous; length 1050–1600 μm; F/V-ratio 1.9–3.4 μm. Rays uniseriate and multiseriate, 5–7 per mm. Uniseriate rays 0–17%, composed of procumbent* and upright cells, height up to 5–7 cells (150–340 μm). Multiseriate rays composed of procumbent cells except for the uniseriate margins of 1–3 rows of square (upright) cells and few sheath cells; 3–5 cells wide and up to 500–1000 μm high. Parenchyma paratracheal in generally complete, narrow, aliform vasicentric 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: Kru- koff 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. oxyphyl- laria* Donn. Smith. Mexico: I.N.I.F. X152 (Uw 20653); Belize: Stevenson 119 (SJRW 14901).

**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 μm, vessel member length 350–540 μm. Perforations simple, end walls almost transverse; intervacular pits alternate, round, oval to polygonal, 7–10 μm. 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 μm, lumina 4–9 μm; sometimes gelatinous; length 1000–1600 μm; 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 μm). Multiseriate rays composed of procumbent cells, with or without 1–2 rows of square (rarely upright) marginal cells; 3–5 cells wide and up to 370–1000 μm 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, 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 conspecific (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, partially 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. *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. si-
### Table 1. Some wood anatomical features of the Castilleae.

| Feature                                                                 | Antennaria | Castilla | Helleborus | Heraclea | Ilex aquifolium | Ilex crenata | Ilex aquifolium | Ilex crenata | Ilex crenata | Ilex crenata | Ilex crenata | Ilex crenata | Ilex crenata | Ilex crenata | Ilex crenata | Ilex crenata | Ilex crenata | Ilex crenata | Ilex crenata | Ilex crenata | Ilex crenata | Ilex crenata | Ilex crenata |
|------------------------------------------------------------------------|------------|----------|------------|----------|-----------------|--------------|-----------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| Tracheids                                                             | (u, a)     | (u, a)   | (u, a)     | (u, a)   | (u, a)          | (u, a)       | (u, a)          | (u, a)       | (u, a)       | (u, a)       | (u, a)       | (u, a)       | (u, a)       | (u, a)       | (u, a)       | (u, a)       | (u, a)       | (u, a)       | (u, a)       | (u, a)       | (u, a)       | (u, a)       |
| Lax lunes                                                             | (r)        | (r)      | (r)        | (r)      | (r)             | (r)          | (r)             | (r)          | (r)          | (r)          | (r)          | (r)          | (r)          | (r)          | (r)          | (r)          | (r)          | (r)          | (r)          | (r)          | (r)          |
| Parenchyma                                                           |            |          |            |          |                 |              |                 |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| Unilateral arrangement of wood rays                                   | +          | -        | +          | -        | +               | -            | +               | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            |
| Bands                                                                 | +          | -        | +          | -        | +               | -            | +               | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            |
| Way of diagonal arrangements                                         | +          | -        | +          | -        | +               | -            | +               | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            |
| Contiguous                                                           | +          | -        | +          | -        | +               | -            | +               | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            |
| Vessels                                                               |            |          |            |          |                 |              |                 |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| Lysis                                                                 | +          | +        | +          | +        | +               | +            | +               | +            | +            | +            | +            | +            | +            | +            | +            | +            | +            | +            | +            | +            | +            | +            |
| Rays                                                                  |            |          |            |          |                 |              |                 |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| Rows of marginal cells                                                | +          | -        | +          | -        | +               | -            | +               | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            |
| Weekly procumbent cells                                               | 1–2 (4)    | 1–2 (4)  | 1–2 (4)    | 1–2 (4)  | 1–2 (4)         | 1–2 (4)      | 1–2 (4)         | 1–2 (4)      | 1–2 (4)      | 1–2 (4)      | 1–2 (4)      | 1–2 (4)      | 1–2 (4)      | 1–2 (4)      | 1–2 (4)      | 1–2 (4)      | 1–2 (4)      | 1–2 (4)      | 1–2 (4)      | 1–2 (4)      | 1–2 (4)      |
| % Uniseriate rays                                                     |            |          |            |          |                 |              |                 |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| Fibres                                                                |            |          |            |          |                 |              |                 |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| Dendroscopic arrangement                                              | +          | -        | +          | -        | +               | -            | +               | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            | -            | +            |
| Pit size (in μm)                                                      |            |          |            |          |                 |              |                 |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| Vessels                                                               |            |          |            |          |                 |              |                 |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |              |
| Footnote 185. a: 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 shortaliform parenchyma, occasionally tending towards a unilateral arrangement, and the presence of weakly procumbent ray cells.

As already indicated by Mennega and Lanzing-Vinkenborg (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.

References