

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

by

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**Summary**

The wood anatomy of the tribe Dorstenieae sensu Berg is described. Similarities and differences are discussed in relation to his concepts of the taxonomy of the tribe. Wood anatomically the tribe Dorstenieae is fairly homogeneous, *Dorstenia* deviating most in the juvenilistic composition of its rays, and the small diameter and high frequency of its vessels. *Bosqueiopsis* differs from the other genera in the presence of fibre pits in the radial and tangential walls. *Helianthostylis* and *Trymatococcus* are highly similar. *Brosimum* shows a variation range exceeding that of the entire tribe. Nevertheless, individual species of *Brosimum* can often not be distinguished.

The genera *Brostmum*, *Helianthostylis*, *Trymatococcus*, and *Trilepisium* are closely related. The tribe Dorstenieae can be separated from the tribe Castilleae on wood anatomical characters such as: presence or absence of septate fibres; distribution pattern of the vessels; paratracheal parenchyma unilateral or not, and ray composition.

**Key words:** Systematic wood anatomy, *Bosqueiopsis*, *Brosimum*, *Dorstenia*, *Helianthostylis*, *Trilepisium*, *Trymatococcus*.

**Introduction**

This paper is part of a series, in which the wood anatomy of the Moraceae is described in detail and discussed in relation to the taxonomy of the family. For an outline of the project as well as for the chapter Material and Methods, we refer to our first contribution, the treatment of the tribe Castilleae (Koek-Noorman et al., 1984). In the tribe Dorstenieae, Berg (1973, 1977) included the tribe Brosimeae and the genus *Dorstenia* (considered to be the sole genus of the tribe Dorstenieae by Corner, 1962), because of an intermediate position of one species of *Dorstenia*. The Dorstenieae, 'clearly delimited against the Castilleae ...' show, at least

in some genera and in some features, connections with the 'dump-like' tribe Moreae (Berg, 1977). The tribe consists of eight genera. In our study the Neotropical genera *Brosimum*, *Helianthostylis* and *Trymatococcus* and the African genera *Bosqueiopsis* and *Trilepisium* are represented as well as some African species of the, partly Neotropical, genus *Dorstenia*. Of *Scyphosyce* and *Utsetela*, no samples were available.

**Generic descriptions**

*Bosqueiopsis* De Wild. & Th. Dur. (Figs. 1, 2).

This African genus, monographed by Berg (1977), is monotypic since the four species described before, are united in his revision. The genus occurs in Zaïre and southern Congo, as trees up to 35 m tall in primary and old secondary forest up to 500 m altitude. In eastern Tanzania and Moçambique as tall shrubs and treelets up to 6 m, in thickets, open forests or young secondary forest, often on sandy soils, from sea level to 500 m altitude (Berg, 1977).

**Material studied:** *B. gillettii* De Wild. & Th. Dur. East Africa: Schlieben 423 (Uw 15590).

**General features:** Growth rings faint; colour light brown; texture fine, grain straight. Specific gravity 800 N per cubic metre.

**Microscopical features:** Vessels diffuse, solitary (30%) and in short radial multiples and irregular clusters of 2–6, 60 per sq. mm, round to oval, diameter 45 µm, vessel member length 325 µm. Perforations simple, end walls almost transverse. Intervascular pits alternate, round and oval, size 6–9 µm. Vessel-ray and vessel-parenchyma pits larger and irregularly shaped, half-bordered. Thin-walled tyloses abundant. Fibres non-septate with small simple pits in radial walls and less frequent in tangential walls; walls 2–4 µm, gelatinous fibres marking the

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Table 1. Some wood anatomical features of species of *Brosimum*.

	Vessels				Parenchyma						
	frequency (per sq. mm)	diameter (in $\mu\text{m}$ )	pit size (in $\mu\text{m}$ )	tyloses	confluent-wavy	regular bands	unilateral arrangement	arc-shaped wings	radial latex tubes	rhombic crystals	specific gravity
<i>B. acutifolium</i>	4-9	130-185	7-13	-	-	-	-	-	+	r (a)	520-700
<i>B. alicastrum</i>	9-16 (30)	70-120	5-7	(t, T)	+	+	+	-	+	rr (a)	750-1020
<i>B. costaricanum</i>	11	120	5-6	-	-	-	-	-	+	rr, a	830
<i>B. gaudichaudii</i>	17	110	9	t	+	+	-	-	+	-	800
<i>B. glaziovii</i>	8-14	70-80	7-9	(t)	+	(+)	+	-	-	r	570-800
<i>B. guianense</i>	6-10	90-130	4-6	T	(+)	-	+	-	-	rr (a)	880-1320
<i>B. lactescens</i>	7-16	100-135	3-4	t	(+)	-	-	-	+	(r)	690-760
<i>B. parinarioides</i>	3-6	140-170	9-11	-	-	(+)	+	+	+	-	700-800
<i>B. potabile</i>	3	155	9-11	(t)	(+)	+	+	+	+	r, a	670-790
<i>B. rubescens</i>	4-5	125-185	5-9	T	-	(+)	+	+	+	(r, a)	1040-1200
<i>B. utile</i>	3-7	130-185	8-13	(t)	(+)	(+)	-	-	+	-	440-650

T: thick-walled; t: thin-walled; r: in marginal ray cells; rr: abundant in marginal ray cells; a: in axial parenchyma; +: present; -: absent; between brackets: occasionally present.

growth rings, lumina 4–8  $\mu\text{m}$ ; length 830  $\mu\text{m}$ ; F/V-ratio 2.6. Rays uniseriate and multiseriate, 9 per mm. Uniseriate rays 13%, composed of procumbent, square and upright cells, up to 4–5 (1–9) cells and 190 (320)  $\mu\text{m}$ . Multiseriate rays composed of procumbent cells except for the uniseriate margins of 1 (3) rows of square and upright cells, and few sheath cells; 2–4 cells wide, up to 560  $\mu\text{m}$  high. Parenchyma paratracheal, vasicentric aliform to confluent, often forming wavy bands; strands of 4 (2–6) cells.

*Brosimum* Schwartz (Figs. 3–12)

Berg (1972) recognised *Brosimum sensu lato* (including *Brosimopsis* Moore, *Piratinera* Aublet and *Ferolla* Aublet) and distinguished between two subgenera on the basis of some morphological features. *Brosimum* is a genus of trees, often of considerable height, with most species in evergreen, mainly tropical rainforests. *Brosimum gaudichaudii* is a common species of the campos cerrados region of central South America. The genus is distributed from Mexico and the Greater Antilles, Cuba and Jamaica to southern Brazil, with the highest concentration of species in the Amazon Basin. Some species, mainly *B. guianense* and *B. rubescens*, produce valuable timbers (letterwood, satiné rubané).

Material studied: *B. acutifolium* Huber ssp. *acutifolium*. Surinam: Lanjouw & Lindeman 2945 (Uw 1978). – *B. acutifolium* Huber ssp. *obovatum* (Ducke) C.C. Berg. Guyana: A.C. Smith 2617 (Uw 21528); Brazil, Amazonas: Krukoff 5378 (Uw 19921), 6355 (Uw 7659). – *B. alicastrum* Sw. ssp. *alicastrum*. Jamaica: U.S. Nat. Herb. 5914 (Uw 8318); Guatemala: Peten 23112 (Uw 18018). – *B. alicastrum* Sw. ssp. *bolivariense* C.C. Berg. Guyana: A.C. Smith 3464 (Uw 21660); Venezuela: Breteler 3972 (Uw 12193); Peru: Uw 18000 (via MADw). – *B. costaricanum* Liebm. Costa Rica: Ilica CCO-24 (Uw 20677). – *B. gaudichaudii* Tréc. Brazil: Maguire et al. 56136 (Uw 16368). – *B. glaziovii* Taub. Brazil, Paraná: Lindeman & de Haas 2060 (Uw 13491), 2201 (Uw 13588). – *B. guianense* (Aubl.) Huber. Surinam: BBS 55 (Uw 652), Stahel 3a (Uw 3a), 219 (Uw 219); Guyana: For. Dept. 3366 (Uw 986), 3424 (Uw 987); Brazil, Amazonas: Krukoff 5477 (Uw 19984). – *B. lactescens* (S. Moore) C.C. Berg. Guyana: A.C. Smith 2876 (Uw 21589); Venezuela: Breteler 3934 (Uw 12179), 3965 (Uw 12190), 3970 (Uw 12192); Brazil, Amazonas: Krukoff 5377 (Uw 19920), 8420 (Uw 16193). – *B. parinarioides* Ducke ssp. *parinarioides*. Guyana: A.C. Smith 2901 (Uw 21593); Surinam: Lindeman 4461 (Uw 3120), Palle 316 (Uw 13846). – *B. potable* Ducke. Brazil, Amazonas: J. Chagas X1200 (Uw 10536), Krukoff 6685 (Uw 7873). – *B.*

*rubescens* Taub. Surinam: BBS 62 (Uw 659), Stahel 170a (Uw 170a); French Guiana: BAFOG 349M (Uw 5423); Colombia, Chocó: Cuatrecasas 14030 (Uw 25316); Panama: USW 4489 (Uw 11076). – *B. utile* (H.B.K.) Pitt. ssp. *occidentale* C.C. Berg. Colombia, Chocó: Cuatrecasas 14291 (Uw 25174), 15595 (Uw 25345), 16084 (Uw 25208). – *B. utile* (H.B.K.) Pitt. ssp. *ovatifolium* (Ducke) C.C. Berg. Brazil, Amazonas: Krukoff 6656 (Uw 7852). – *B. utile* (H.B.K.) Pitt. ssp. *utile*. Colombia, Chocó: van Rooden, Topper & ter Welle 526 (Uw 25607).

General features: The woods of the species of *Brosimum* are very variable in appearance (Table 1). Highly remarkable are the differences in colour and specific gravity. The heaviest, dark reddish brown woods are found in *B. guianense* and *B. rubescens* commercially known as 'letterwood' and 'satiné rubané'. Most other species are of considerably lower weight (see Table 1) and light brown. Growth rings absent. Texture fine to medium. Grain straight or interlocked.

Microscopical features. Vessels diffuse, solitary (20–70%) and in short radial multiples and irregular clusters of 2–4, 3–16 (30) per sq. mm, round to oval, diameter 70–185  $\mu\text{m}$ . Vessel member length 400–600  $\mu\text{m}$ . Perforations simple, end walls almost transverse. Intervascular pits alternate, round, oval or polygonal, 3–13  $\mu\text{m}$ . Vessel-ray and vessel-parenchyma pits variable, irregular in size and shape, half-bordered. Thin-walled tyloses often present; sometimes thick-walled tyloses occur. Fibres non-septate with small simple pits restricted to the radial walls; walls 2–3 (4)  $\mu\text{m}$ , lumina 3–16 (19)  $\mu\text{m}$ , rarely gelatinous; length 980–1600  $\mu\text{m}$ , F/V-ratio 2.0–3.4. Rays uniseriate and multiseriate, 5–9 per mm. Uniseriate rays 0–20%, composed of upright cells only or intermingled with some rows of procumbent cells, 3–6 cells (120–300  $\mu\text{m}$ ) high. Multiseriate rays composed of procumbent cells with uniseriate margins of 1–2 (7) rows of square and upright cells; 2–4 (7) cells wide, up to 370–610  $\mu\text{m}$  high. Parenchyma paratracheal, vasicentric aliform with narrow long wings, which are sometimes arc-shaped, occasionally confluent, sometimes banded; mostly unilateral; strands of 2–5 (1–8) cells. Rhombic crystals varying from absent to extremely abundant; in marginal ray cells, rarely in axial parenchyma. Radial latex tubes common, although in variable amounts and with different diameters.

Note: Silica was found in *B. lactescens* (A.C. Smith 2876). Latex tubes are lacking in part of the samples of *B. glaziovii* and *B. guianense*.

(text continued on page 325)

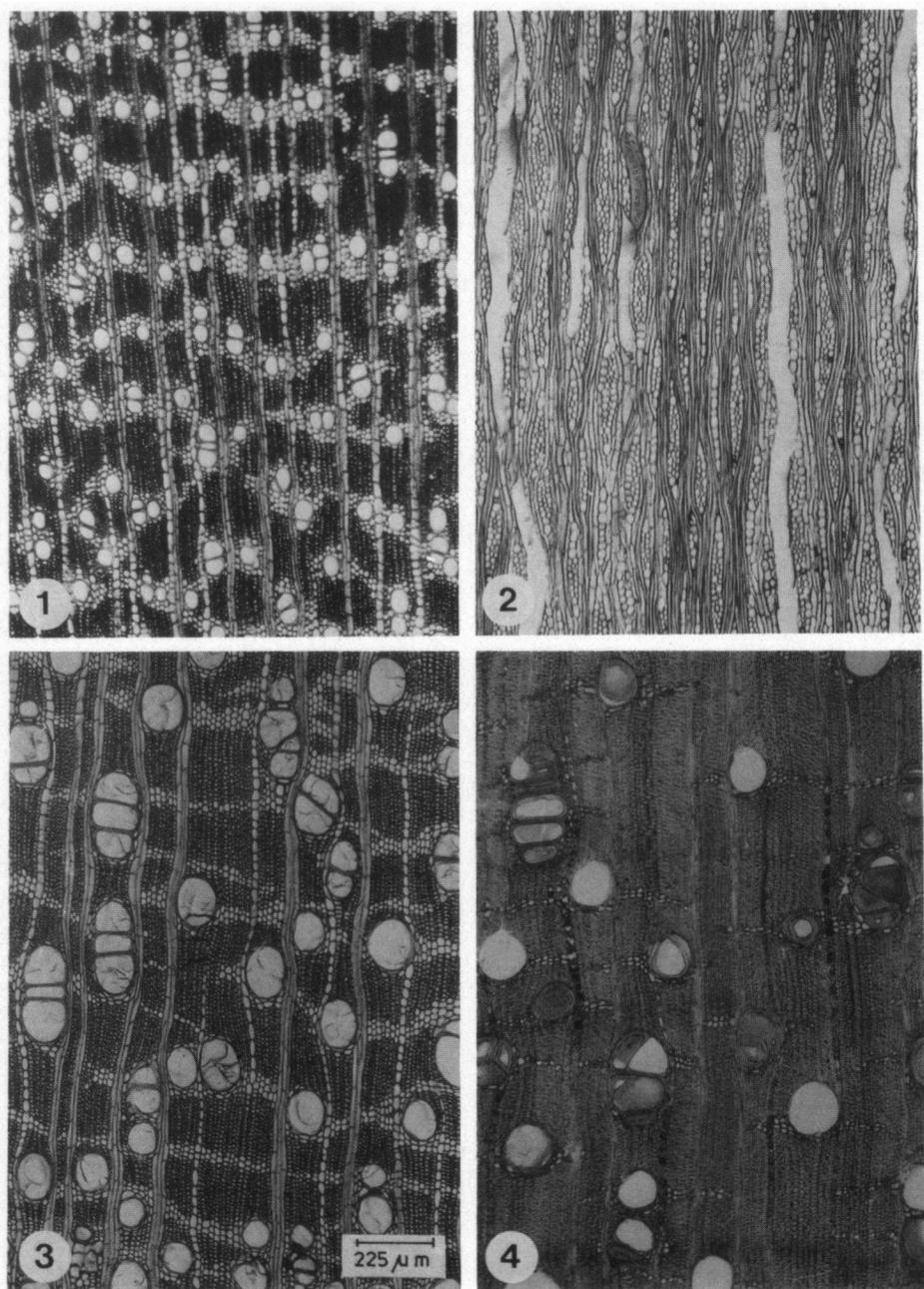


Fig. 1. *Bosqueiopsis gilletii*, Uw 15590. — Fig. 2. Ibid. — Fig. 3. *Brosimum gaudichaudii*, Uw 16368. — Fig. 4. *B. guianense*, Uw 652.

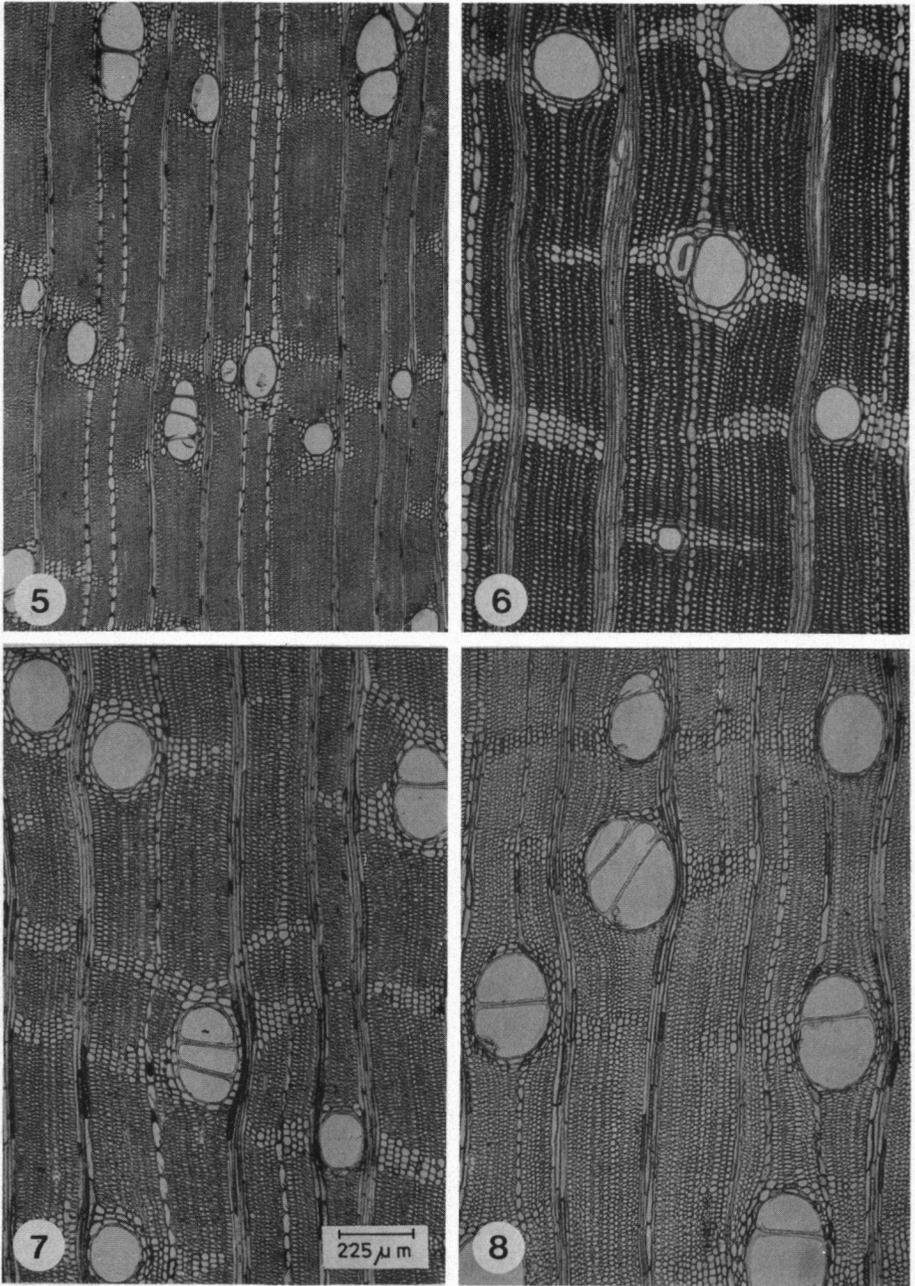


Fig. 5. *Brosimum lactescens*, Uw 19920. — Fig. 6. *B. parinarioides*, Uw 3120. — Fig. 7. *B. potable*, Uw 10536. — Fig. 8. *B. utile*, Uw 7852.

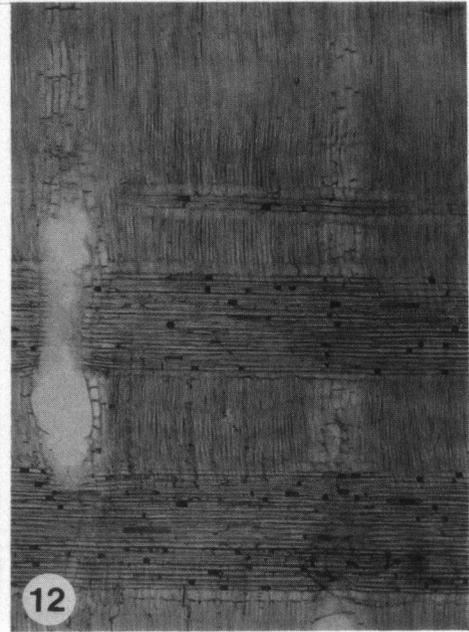
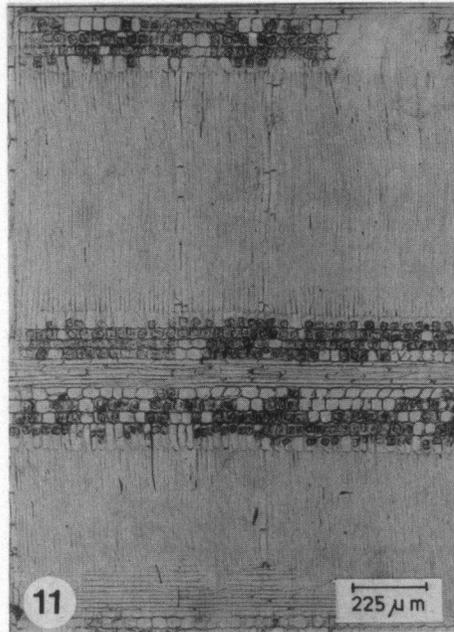
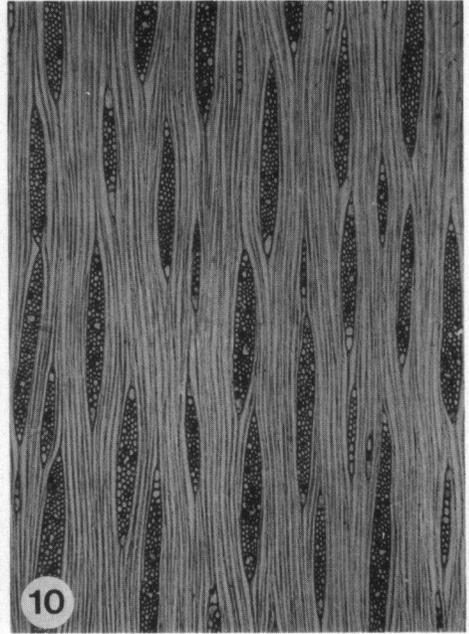
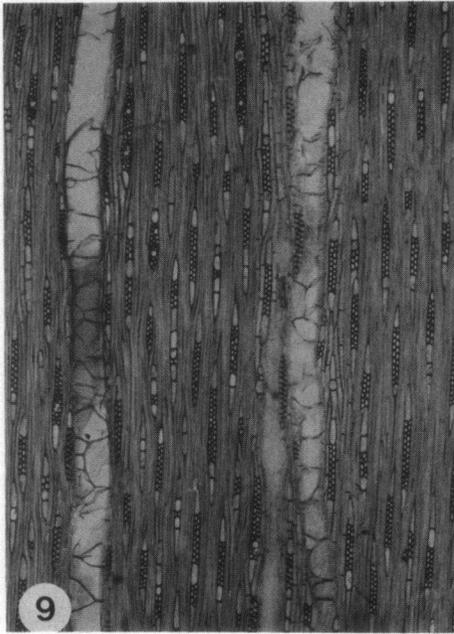


Fig. 9. *Brosimum guianense*, Uw 19984. — Fig. 10. *B. utile*, Uw 7852. — Fig. 11. *B. alicastrum*, Uw 12193. — Fig. 12. *B. utile*, Uw 25607.

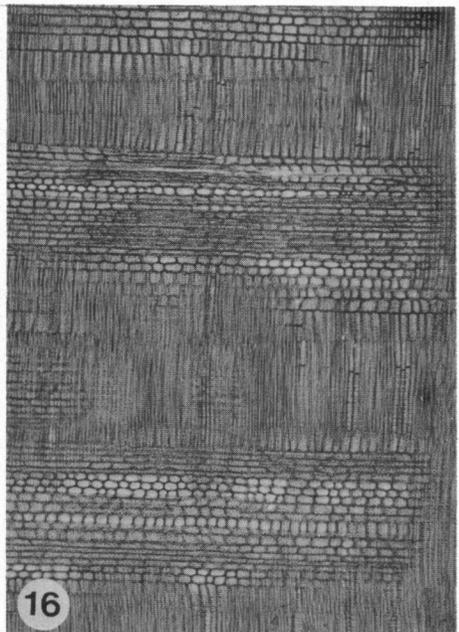
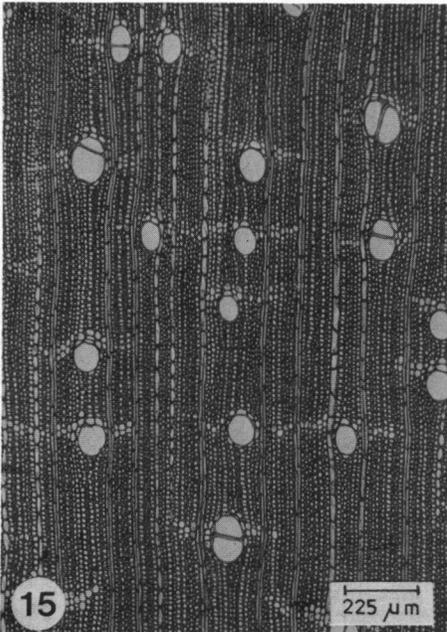
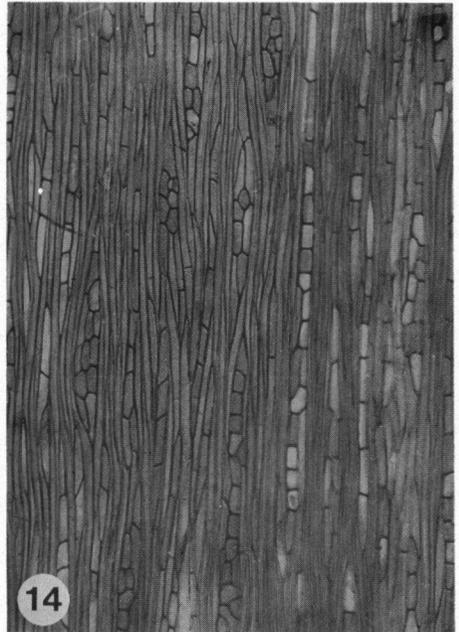
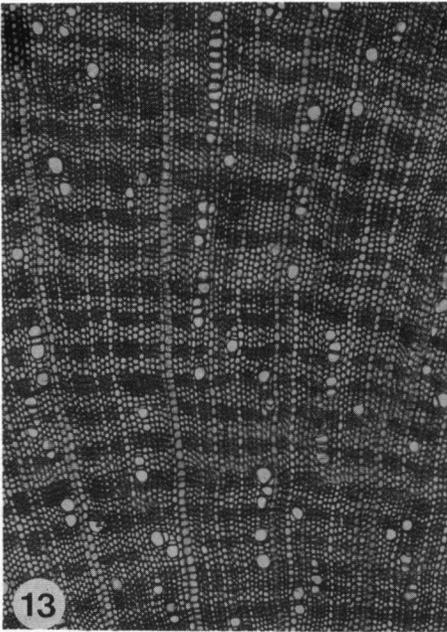


Fig. 13. *Dorstenia africana*, Uw 25827. — Fig. 14. *D. involuta*, Uw 25826. — Fig. 15. *Helianthostylis sprucei*, Uw 23663. — Fig. 16. *Ibid.*, Uw 24625.

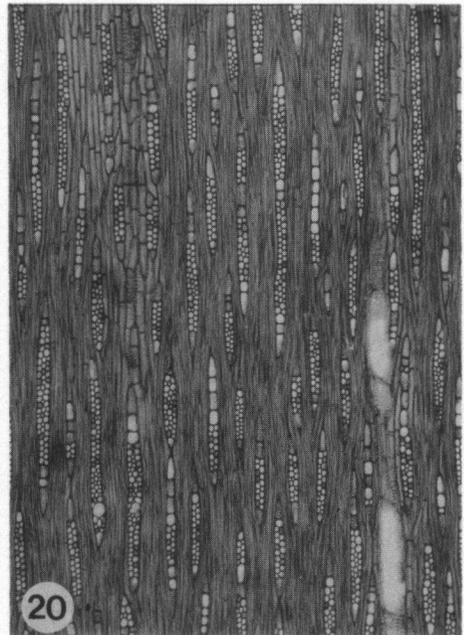
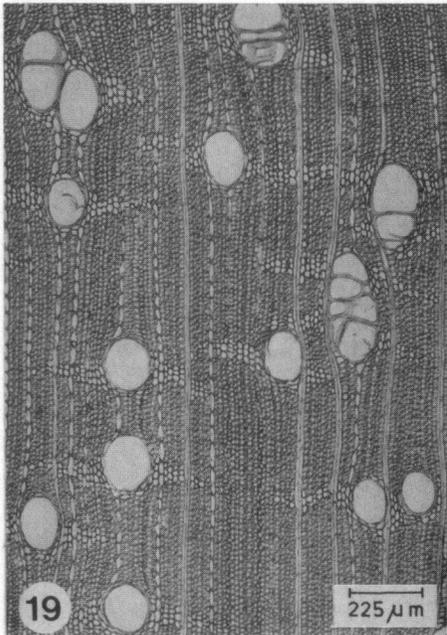
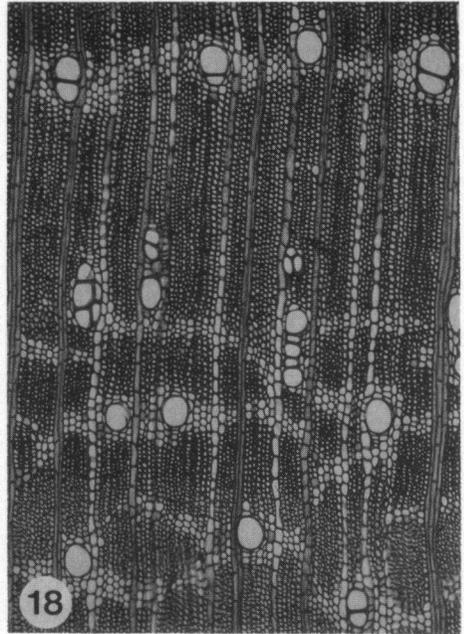
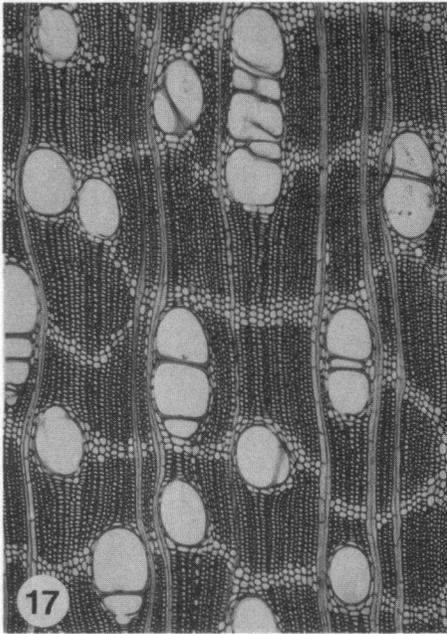


Fig. 17. *Trilepisium madagascariense*, Uw 18391. — Fig. 18. *Ibid.* — Fig. 19. *Trymatococcus amazonicus*, Uw 2671. — Fig. 20. *T. oligandrus*, Uw 21199.

*Dorstenia* L. (Figs. 13, 14)

This is the second large genus of the Moraceae, with representatives in tropical America and West Africa, up to Zaïre and Angola. Berg (1977) united the genus *Craterogyne* Lanjouw (the African species formerly assigned to *Trymatococcus*) and *Dorstenia* L. In this delimitation, two African sections of the genus are woody. The other African *Dorstenia* species are partly herbaceous plants with tuberous subterranean parts and succulent stems found in the drier regions outside the rainforest; partly they are herbaceous to suffrutescent plants and shrubs found in the rainforests. The American species are all herbaceous.

**Material studied:** *D. africana* (Baillon) C. C. Berg. Cameroon: Hijman & Weerdenburg 303 (Uw 25827), 328 (Uw 25831); Leeuwenberg 9780 (Uw 25777). — *D. involuta* Hijman & Berg. Cameroon: Hijman & Weerdenburg 302 (Uw 25826). — *D. kameruniana* Engl. Zaïre: Louis 3078 (Uw 24224). — *D. turbinata* Engl. Cameroon: Hijman & Weerdenburg 320 (Uw 25829).

**General features:** Growth rings absent; colour light brown to cream-coloured, without heartwood (all diameters 1–2 cm). Texture fine, grain straight. Specific gravity 900–1200 N per cubic metre.

**Microscopical features:** Vessels diffuse, solitary (30–70%) and in short multiples of 2–4; 20–40 per sq. mm, angular, sometimes round, diameter 30–45  $\mu\text{m}$ , vessel member length 450–600  $\mu\text{m}$ . Perforations simple, end walls almost transverse. Intervascular pits alternate, round, oval to polygonal, 4–6  $\mu\text{m}$ . Vessel-ray and vessel-parenchyma pits larger, tending towards a scalariform arrangement, half-bordered. Thin-walled tyloses occasionally present. Fibres non-septate with small pits restricted to the radial walls; walls 3–4  $\mu\text{m}$ , often gelatinous; lumina 9–11  $\mu\text{m}$ ; length 960–1350  $\mu\text{m}$ ; F/V-ratio 2.1–2.8. Rays uniseriate and multiseriate, 12–16 per mm. Uniseriate rays 50–80%, composed of 4–8 (–20) rows of upright and occasionally square cells, up to 420–645 (–1550)  $\mu\text{m}$  high. Multiseriate rays composed of upright and occasionally square cells with uniseriate margins of 4–13 rows of upright cells; 2–3 cells wide; height of the multiseriate parts strongly varying within one sample from 2–50 cells (100–1500  $\mu\text{m}$ ). Parenchyma arrangement varying from regular concentric bands (2–6 cells wide, 5–8 per mm) to irregular, narrow vasicentric to aliform patches of parenchyma tissue, occasionally apotracheal; strands of 2–4 (1–7) cells. Rhombic crystals scanty in marginal ray cells. Radial latex tubes narrow, present in part of the samples.

**Note:** In the wood structure, a number of differences between the samples of the two sections can be found: in *D. africana* and *D. kameruniana* (sect. *Nothodorstenia*) the parenchyma is arranged in regular concentric bands; radial latex tubes and tyloses are present. In *D. involuta* and *D. turbinata* (sect. *Eudorstenia*) the narrow and irregular vasicentric to aliform pattern is found; latex tubes and tyloses are absent.

*Helianthostylis* Baillon (Figs. 15, 16)

This Neotropical genus was considered as a monotypical genus by Berg (1972). It consists of shrubs or trees up to 15 m tall in the tropical rainforest and secondary growths in the Amazon Basin of Brazil, from the Rio Tapajoz (Pará) to Colombia. Of the species *H. steyermarkii*, described by Berg afterwards, no wood samples are available.

**Material studied:** *H. sprucei* Baillon. Brazil, Amazonas: Ducke 180 (Uw 18422), Prance & Berg 18780 (Uw 20927), Rodrigues & Coelho 7336 (Uw 23663); Brazil, Pará: Prance et al. 25509 (Uw 24081); Colombia: Rio Calima: Cuatrecasas 16303 (SJRw 43019A, Uw 24625).

**General features:** Growth rings absent; colour yellowish white, heartwood absent or indistinguishable from the sapwood. Texture medium, grain straight. Specific gravity 750–850 N per cubic metre.

**Microscopical features:** Vessels diffuse, solitary (30–60%) and in short radial multiples of 2–4, 15–25 per sq. mm, round to oval, diameter 60–90 (130)  $\mu\text{m}$ , vessel member length 340–350  $\mu\text{m}$ . Perforations simple, end walls almost transverse. Intervascular pits alternate, round, oval or polygonal, 7–9  $\mu\text{m}$ . Pits between vessels and procumbent ray cells comparable with the intervacular pits in size; vessel-parenchyma pits and pits between vessels and upright ray cells larger and irregularly shaped, occasionally tending to scalariform arrangement, half-bordered. Thin-walled tyloses occasionally present. Fibres non-septate with small pits restricted to the radial walls; walls 2–3  $\mu\text{m}$ , occasionally gelatinous; lumina 5–10  $\mu\text{m}$ ; length 800–900  $\mu\text{m}$ ; F/V-ratio 2.3–2.6. Rays uniseriate and multiseriate, 7–11 per mm. Uniseriate rays 10–25%, composed of few rows of strongly and weakly procumbent cells and many rows of upright cells, 3–6 (10) cells (165–280  $\mu\text{m}$ ) high. Multiseriate rays entirely composed of strongly and weakly procumbent cells with uniseriate margins of 1–2 (8) rows of square and/or upright cells; 2–3 (4) cells wide, up to 230–550  $\mu\text{m}$  high. Parenchyma paratracheal, often unilateral, aliform with long narrow wings, occasionally confluent to banded;

strands of 2–3 (1–4) cells. Radial latex tubes present but few and narrow.

Note. One sample (Prance et al. 25509) is slightly deviating in the presence of abundant vitreous silica in the fibres, its ray height (up to 1000  $\mu\text{m}$ ) and the ray margins (not over 1 cell row high). According to Berg (1972), collections from the same area (Pará) are slightly deviating in some morphological features as well.

*Trilepisium* Thouars (Figs. 17, 18)

Although this genus is highly variable (Berg, 1977) the lack of clear morphological distinguishing characters forced Berg to unite all formerly described species in one species: *T. madagascariense* DC. It occurs in tropical Africa, Madagascar and the Seychelles in primary and secondary forest from sea level up to 2000 m altitude.

Material studied: *T. madagascariense* DC. Nigeria: F.H.I. 7174 (Uw 18391); South Africa: Visser s.n. (Uw 25778); Tanzania: F.P.R.L. 20039 (Uw 18382); Uganda: F.P.R.L. 23233 (Uw 18384), 23235 (Uw 18392); Zaïre: Vermoesen 1660 (Uw 18768), Dechamps 136 (Uw 24223); Zimbabwe: Swynnerton 16-1910 (Uw 18393).

General features: Growth rings absent or faint; colour light brown, no demarcation between sapwood and heartwood; texture fine to medium, grain slightly interlocked. Specific gravity 500–720 N per cubic metre.

Microscopical features. Vessels diffuse, solitary (25–30%) and in radial multiples and irregular clusters of 2–5, 8–13 per sq.mm, round to oval, diameter 80–150  $\mu\text{m}$ , vessel member length 390–450  $\mu\text{m}$ . Perforations simple, end walls almost transverse. Intervascular pits alternate, round, oval to polygonal, 6–7 (9)  $\mu\text{m}$ . Vessel-ray and vessel-parenchyma pits larger and slightly irregular, the pits between vessels and procumbent ray cells comparable in size with the intervascular pits, half-bordered. Thin-walled tyloses occasionally present. Fibres non-septate with small simple pits restricted to the radial walls; walls 2–3  $\mu\text{m}$ , lumina 7–14  $\mu\text{m}$ ; length 900–1180  $\mu\text{m}$ ; F/V-ratio 2.0–2.9. Rays uniseriate and multiseriata, 6–8 per mm. Uniseriate rays 5–25%, composed of upright and square cells, up to 160–275  $\mu\text{m}$  (5–6 cells) high. Multiseriate rays composed of (weakly) procumbent cells, with uniseriate margins of 1–3 rows of square/upright cells; 2–4 cells wide, up to 290–540  $\mu\text{m}$  high. Parenchyma paratracheal, in continuous but often wavy bands, 2–4 cells wide, partly or completely including the vessels; strands of 2–4 cells. Rhombic crystals abundant in the marginal ray cells, occasionally also in procumbent

ray cells and axial parenchyma. Vitreous silica scarce, observed in vessels, fibres, and axial parenchyma. Radial latex tubes present or absent, see also the note below.

Note. Although the material studied is very homogeneous, some differences correlated with the geographical distribution occur. In samples from Zimbabwe, Tanzania and South Africa the vessel diameter is 80–100  $\mu\text{m}$ , and latex tubes are absent. In the other samples, from Nigeria, Uganda, and Zaïre, latex tubes are always present; the vessel diameter varies from 135–150  $\mu\text{m}$ .

*Trymatococcus* P. & E. (Figs. 19, 20)

In the most recent revision (Berg, 1972), in *Trymatococcus* three species are distinguished. The genus consists of shrubs and trees (up to 30 m tall) and occurs from the upper Amazon Basin to the Guyanas.

Material studied: *T. amazonicus* P. & E. Surinam: Lindeman 3773 (Uw 2759), 4735 (Uw 3258), 4928 (Uw 3358), 5042 (Uw 3425), 6442 (Uw 4422), Maas (LBB) 10832 (Uw 11241); Peru: Williams 3767 (SJRw 18304); Brazil, Amazonas: Ducke 174 (Uw 2671), Krukoff 6092 (Uw 7474), Prance & Maas 13725 (Uw 18990), 14012 (Uw 19050), Prance & Berg 17972 (Uw 20880). – *T. oligandrus* (R. Ben.) Lanjouw. Surinam: Stahel 366 (Uw 366), Lanjouw & Lindeman 2177 (Uw 1640); Guyana: Fanshawe 116 (Uw 989); French Guiana: Maas et al. 2195 (Uw 21199). – *T. paraensis* Ducke. Surinam: Lanjouw & Lindeman 2297 (Uw 1697).

General features: Growth rings absent, rarely faint; colour light brown, heartwood probably present in one sample, dark brown. Texture fine to medium, grain straight or slightly interlocked. Specific gravity 600–850 N per cubic metre.

Microscopical features: Vessels diffuse, solitary (50–70%) and in short radial multiples and irregular clusters of 2–4; 7–9 per sq.mm, round to oval, diameter 95–110  $\mu\text{m}$ , vessel member length 370–465  $\mu\text{m}$ . Perforations simple, end walls almost transverse. Intervascular pits alternate, round to oval, 7–11  $\mu\text{m}$ . Pits between vessels and procumbent ray cells comparable with the intervascular pits in size; pits between vessels and upright cells and vessel-parenchyma pits irregular, round to elongate, tending towards a scalariform pattern, half-bordered. Thin-walled tyloses often present. Fibres non-septate with small simple pits restricted to the radial walls; walls 2–3  $\mu\text{m}$ , occasionally partly gelatinous; lumina 5–13  $\mu\text{m}$ , length 1000–1200  $\mu\text{m}$ ; F/V-ratio 2.6–2.8. Rays uniseriate and multiseriata, 8–10 per mm. Uniseriate rays 10–30%, composed of square and upright cells,

Table 2. Some diagnostic features in Dorstenieae (Moraceae).

	Vessels			Fibres	Rays					Parenchyma					
	frequency (per sq. mm)	diameter (in $\mu\text{m}$ )	pit size (in $\mu\text{m}$ )		percentage uniseriate rays	rows of marginal cells	weakly procumbent cells present	width (number of cells)	frequency (per mm)	confluent	way/diagonal	bands	unilateral	radial latex tubes	rhombic crystals
<i>Bosquetopsis</i>	60	45	6-9	13	1 (3)	-	2-4	9	+	+	+	-	-	-	800
<i>Brosimum</i>	3-16 (30)	70-185	3-13	0-20	1-2 (7)	-	2-4 (7)	5-9	(+) (+) (+)	(+) (+) (+)	(+)	+	+	+/-	440-1320
<i>Dorstenia</i>	20-40	30-45	4-6	50-80	4-13	-	2-3	12-16	-	-	-	-	(+)	(n)	900-1200
<i>Helianthostylis</i>	15-25	60-90	7-9	10-25	1-2 (8)	±	3-6	7-11	(+) (-) (+)	(+) (-) (+)	(+)	+	+	-	750-850
<i>Trilepisium</i>	8-13	80-150	6-7	5-20	1-3	±	2-4	6-8	-	+	+	(+)	(+)	+	500-720
<i>Trymatococcus</i>	7-9	95-110	7-11	10-30	1-4 (6)	-	2-4	8-10	(+) (-) (+)	(+) (-) (+)	(+)	+	+	(n)	600-850

+: present; -: absent; u: in upright and/or square ray cells; between brackets: occasionally present.

up to 6–9 cells (210–265  $\mu\text{m}$ ) high. Multiseriate rays composed of procumbent cells with uniseriate margins of 1–4 (6) rows of square and upright cells; 2–4 cells wide, up to 300–900  $\mu\text{m}$  high. Parenchyma paratracheal, often unilateral, narrowly aliform with long wings, occasionally confluent-banded; in some samples terminal parenchyma present; strands of 2–4 cells. Rhombic crystals occasionally present in marginal ray cells. Radial latex tubes present in all samples.

### Discussion

The representatives of this tribe, seen in the perspective of the whole family of the Moraceae, constitute a wood anatomically fairly homogeneous group, although there are some diagnostic differences between individual genera.

The Dorstenieae are characterised by a regular arrangement of (small to) moderately sized vessels; non-septate libriform fibres; rays of Kribs (1968) type heterogeneous II, rarely I, i.e. uniseriate rays composed of upright and square cells; multiseriate rays with 2–6-seriate parts composed of procumbent cells, accompanied by short (to longer) uniseriate margins of upright and square cells; parenchyma aliform-confluent to banded and at least partly in unilateral arrangement. Crystals, when present, are found nearly exclusively in the marginal ray cells.

The samples of *Dorstenia*, a mainly herbaceous genus, are most deviating (see Table 2). The vessels are narrower and more frequent than in the other genera. The rays are composed of square and upright cells only, and the percentage of uniseriate rays is high. It may be questioned whether these features indicate an isolated position of *Dorstenia*, or if these features are due to the small diameter of the samples: all woody species of *Dorstenia* are (sub-)shrubs. The ray type suggests a paedomorphic structure (Carlquist, 1974: 394–399 and the references given there). As already indicated in the generic description, some differences are found between the two represented sections of the genus. Remarkable are the parenchyma patterns: regular concentric bands in the samples of section *Nothodorstenia*, and narrowly aliform, often irregular patches in section *Eudorstenia*. Both patterns deviate from the arrangement found in the other genera of Dorstenieae, in particular the regular bands of section *Nothodorstenia*. The species of this section belonged formerly to the genus *Craterogyne*, established by Lanjouw (1935) to accommodate the African species of *Trymatococcus*. Although the bands found in *Nothodorstenia* could be thought to be related, for instance, the aliform-

confluent to banded parenchyma found in the remaining Neotropical species of *Trymatococcus*, the relatively low number and the small diameter of the samples of *Dorstenia* do not justify a suggestion to return to the former inclusion of *Nothodorstenia* in *Trymatococcus*.

Of the other genera studied, the Neotropical genera *Helianthostylis* and *Trymatococcus* are highly similar, the main difference being found in the vessel frequency (Table 2).

*Trilepisium* (Africa) deviates from *Helianthostylis* and *Trymatococcus* in the parenchyma which is arranged in continuous, but often wavy bands and the abundant occurrence of the rhombic crystals in the ray margins.

Already at first view, *Bosqueiopsis* differs from the other genera of the Brosimeae, because of the pattern formed by the small and numerous vessels, all included in confluent to wavy parenchyma (Table 2; Fig. 1). Another remarkable difference is found in the presence of fibre pits on radial and tangential walls, whereas in all other Brosimeae they are restricted to the radial fibre walls.

In the samples of *Brosimum*, we found for some features a range of variation that exceeds the variation found in the other Dorstenieae (size of the intervascular pits, parenchyma pattern, specific gravity, the abundance of crystals, etc., see Table 1). Nevertheless, several species are difficult to separate. In itself, this is not surprising, if we consider the frequent taxonomic changes in the generic delimitation and subdivision within *Brosimum* (for a historical survey, see Berg, 1972). No features, fully correlated with the subdivision proposed by Berg are found. Neither were wood anatomical features found, justifying the proposal of another grouping of species.

In conclusion we may say that within the tribe Dorstenieae, the wood anatomy suggests an eccentric position of *Dorstenia*. *Bosqueiopsis*, too, differs in some noteworthy aspects from the other representatives studied. The close relationships of the other genera is confirmed.

Berg (1977) stated that the Castilleae and Dorstenieae in his circumscription are clearly distinguished. If we compare both tribes (see Koek-Noorman et al., 1984), we too find some features and tendencies which separate the two tribes.

### Castilleae:

- fibres septate, at least partly,
- vessels often in more or less diagonal arrangement,
- parenchyma mostly surrounding the vessels,
- uniseriate rays partly composed of procumbent cells (Kribs heterogeneous III, rarely II).

Dorstenieae:

- fibres not septate,
- vessels regularly distributed,
- parenchyma mostly tending towards unilateral arrangement,
- uniseriate rays composed of upright and square cells (Kribs heterogeneous II, rarely I).

Three species formerly assigned to *Brosimum*, were transferred to genera placed in the Castilleae: *Naucleopsis mello-barettoi*, *Pseudolmedia oxyphyllaria* and *Pseudolmedia spuria*. In *Naucleopsis mello-barettoi* we found a unilateral parenchyma arrangement, but in all other respects the wood anatomical structure of the three species support their transfer to the Castilleae.

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