634.0.17 Malvaceae: 634.0.810
582.796:581.4

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WOOD ANATOMY OF SOME SARCOLAENACEAE AND RHOPALOCARPACEAE AND THEIR SYSTEMATIC POSITION

(with a summary in Dutch)

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SUMMARY

The secondary xylem of some representatives of the to Madagascar endemic families Sarcolaenaceae (Chlaenaceae) and Rhopalocarpaceae (Sphaerosepalaceae), has been studied. A comparison was made with the secondary xylem of the families Dilleniaceae, Ochnaceae, Flacourtiaceae, Bixaceae, Cochlospermaceae, Tiliaceae, Sterculiaceae and Bombacaceae.

The two autonomous families are related to the Sterculiaceae and Tiliaceae but also, the Sarcolaenaceae maybe more than the Rhopalocarpaceae, in some extent to the Bixaceae and Cochlospermaceae. However, affinities with the Ochnaceae, especially with the subfamily Ochnoideae, exist as well.

A position of the families within the Ochnales as proposed by HUTCHINSON (1973) seems less justified, both from a wood and certainly from a bark (DEN OUTER and VOOREN, 1980) anatomical standpoint. Preference is given to TAKHTAJAN's (1969) arrangement within the Malvales.

SAMENVATTING

Een studie is gemaakt van het secundaire xyleem van een aantal vertegenwoordigers van de in Madagascar endemische families Sarcolaenaceae (Chlaenaceae) en Rhopalocarpaceae (Sphaerocepalaceae). Er is een vergelijking getrokken met het secundaire xyleem van de families Dilleniaceae, Ochnaceae, Flacourtiaceae, Bixaceae, Cochlospermaceae, Tiliaceae, Sterculiaceae en Bombacaceae.

De twee autonome families zijn verwant aan de Sterculiaceae en de Tiliaceae, maar ook – de Sarcolaenaceae wellicht meer dan de Rhopalocarpaceae – in zekere mate aan de Bixaceae en de Cochlospermaceae. Bovendien is er een verwantschap met de Ochnaceae, in het bijzonder de onderfamilie Ochnoideae.

Plaatsing van de families binnen de Ochnales, zoals HUTCHINSON (1973) dat heeft voorgesteld lijkt minder gerechtvaardigd vanuit een houtanatomische en zeker vanuit een bastanatomische (DEN OUTER en VOOREN, 1980) gezichtshoek. De voorkeur wordt gegeven aan TAKHTAJAN'S (1969) plaatsing binnen de Malvales.

INTRODUCTION

The Sarcolaenaceae, still known as Chlaenaceae in most literature and Rhopalocarpaceae also known as Sphaerosepalaceae, are small families of trees or shrubs endemic to Madagascar.

Their systematic position is still uncertain. Formerly they have been placed seperately in different orders, the Sarcolaenaceae in the Malvales and the Rhopalocarpaceae in the Parietales (Violales, Cistales). Latterly they were both arranged in the Malvales (for instance TAKHTAJAN, 1969) and recently together in the Ochnales (HUTCHINSON, 1973).

After a study of the secondary phloem (DEN OUTER and VOOREN, 1980), now a study is presented of the secondary xylem of some members of the two families. A comparison with the secondary xylem of some species from other families has been made, in order to investigate their mutual relation and systematic position.

MATERIALS AND METHODS

Wood samples were obtained from several institutional wood collections referred to according to STERN (1978). Wherever it is known that herbarium vouchers exist, this is mentioned.

The following number indications are used:
- from CTFw (Nogent-sur-Marne, France)

CTFT (Centre Technique Forestier Tropical) numbers collected by the Service Forestier in Madagascar (records are kept of the location of herbarium vouchers);
GK (Gold Coast) number collected by Kimloch (Bangor, USA) in Gold Coast;
- from Lw (Leiden, Netherlands)

BW (Boswezen) numbers collected by the former Dutch Forestry Service in West New Guinea, Indonesia, up to 1962 (herbarium vouchers present);
- from Uw (Utrecht, Netherlands)

L (Leeuwenberg) numbers collected by Leeuwenberg in Ivory Coast (1959; herbarium vouchers present);
St (Stahel) numbers collected by Stahel in Surinam (1944; herbarium vouchers present);
U (Utrecht) numbers (herbarium vouchers present);
- from WIBw (Wageningen, Netherlands)

BW (Boswezen) numbers collected by the former Dutch Forestry Service in West New Guinea, Indonesia, up to 1962 (herbarium vouchers in Lw);
de W (De Wilde) number collected by J. J. F. de Wilde in Cameroon (1975; herbarium voucher present at the Department of Plant Taxonomy and Plant Geography, Wageningen);
- from WLw (Wageningen, Netherlands)

A (Arnoldo) numbers collected by Arnoldo-Broeders and De Jong in the Netherlands Antilles (1966);
de H (De Hulster) numbers collected by Burger in Surinam (1947);
Pl (Plantkunde) numbers collected by the staff of the Department of Plant Cytology and Morphology in the botanical gardens or greenhouses of the Agricultural University, Wageningen;

St (Stahel) numbers collected by Stahel in Surinam (1944; herbarium vouchers present in Uw);
Thor (Thorenaar) numbers collected by Thorenaar in Java, Indonesia (1925; herbarium vouchers present in Lw);
V en O (Versteegh and Den Outer) numbers 1–749 collected by Versteegh and Den Outer in Ivory Coast (1969), 750–822 by Versteegh and Jansen in Liberia (1969), 850–987 by Den Outer in Surinam (1974), 988–1227 by Van Veenendaal and Den Outer in Madagascar (1978; herbarium vouchers present in Lw, Uw and Department of Plant Taxonomy and Geography, Wageningen);
Zw en R (Zwart and Rood) collected by the Forest Research Institute, Bogor, Indonesia (1925).

The species investigated are listed below, arranged alphabetically within the families; only for immature and shrub material (diameter less than 10 cm) a diameter indication is given.

Bixaceae
Bixa orellana L. (V en O 692; diam. 8 cm).

Bombacaceae
Adansonia digitata L. (V en O 301), *A. fony* H. Bn. (V en O 1091), *Bombax aquaticum* (Aubl.) K. Schum. (syn. *Pachira aquatica* Aubl.; V en O 902), B. *flaviflorum* Pulle (V en O 860), *B. glabra* (Pasq.) Robyns (V en O 401), *B. nervosum* Uitt. (St 131), *B. surinamensis* Uitt. (St 104), *Catostemma fragrans* Benth. (St 352), *Ceiba pentandra* (L.) Gaertn. (V en O 161), *Coelostegia griffithii* Benth. (Thor I 6), *Durio oxleyanus* Griff. (Thor I 7), *Gossampinus heptaphylla* Bakh. (Zw en R 73), *Ochroma lagopus* Sw. (V en O 683).

Flacourtiaceae
Banara guianensis Aubl. (V en O 899), *Caloncoba brevipes* Gilg (V en O 753), *C. echinata* (Oliv.) Gilg (V en O 670; diam. 8 cm), *Casearia arguta* H.B.K. (V en O 893; diam. 8 cm), *C. calodendron* Gilg (syn. *C. inaequalis* Hutch. et Dalz.; V en O 644), *C. grewiaefolia* Vent. (Zw en R 4), *C. javitensis* H.B.K. (St 247), *C. lucida* Hils. et Bojer ex Tul. (V en O 1185; diam. 6 cm), *C. tremula* Wright (A 3556), *Dasylepis* cf. *brevipedicellata* Chipp (V en O 225), *Erythrospermum candidum* Becc. (BW 10083), *Flacourtia flavescens* Willd. (V en O 420; diam. 4 cm), *F. ramontchi* l'Hérit. (V en O 1036; diam. 4 cm), *F. zippelii* Sloot (BW 1247), *Homalium axillaire* Baill. (V en O 1132), *H. foetidum* Benth. (BW 6975), *H. guianense* (Aubl.) Warb. (de H 218), *H. laxiflorum* Baill. (V en O 1210), *H. moniliforme* H. Perr. (V en O 1160; diam. 3 cm), *H. patoklaense* Aubr. et Pellegr. (V en O 203), *H. tomentosum* Benth. (Zw en R 101), *Itoa stapfii* Sleum. (BW 7164), *Laetia procera* (Poepp. et Endl.) Eichl. (St 124), *Lindackeria dentata* (Oliv.) Gilg (V en O 16), *Oncoba spinosa* Forsk. (V en O 499), *Osmelia philippina* Benth. (BW 10436), *Pangium edule* Reinw. (BW 7868), *Ryparosa calotricha* Mildbr. (BW

10430), *Samyda dodecandra* Jacq. (A 3535), *Scolopia spinosa* Warb. (Zw en R 131), *Trichadenia philippinensis* Merr. (BW 1207), *Trichostephanus acuminatus* Gilg (de W 8000; 6 cm).

Ochnaceae
Campylospermum dybowskii v. Tieghem (V en O 64), *C. flavum* (Schum. et Thonn.) Farron (V en 0 388), *C. glaberrimum* (P. Beauv.) Farron (V en O 146; diam. 4 cm), *C. obtusifolium* (Lamk.) v. Tieghem (V en O 1148; diam. 3 cm), *Diporidium greveanum* v. Tieghem (V en O 1060; diam. 5 cm), *D. pervilleanum* (H. Bn.) v. Tieghem (V en O 1018; diam. 4 cm), *Elvasia hostmanniana* Planch. ex Gilg (St 358), *Idertia morsonii* (Hutch. et Dalz.) Farron (V en O 798), *Lophira alata* Banks var. *procera* Burtt Davy et Hoyle (CTFT ?), *Ochna rhizomatosa* (v. Tieghem) Keay (V en O 450), *Ouratea decagyna* Maguire (St 300), *O. surinamensis* (Planch.) Wehlb. (St 258), *Rhabdophyllum affine* (Hook. f.) v. Tieghem (V en O 253; diam. 6 cm), *R. calophyllum* (Hook. f.) v. Tieghem (V en O 785), *Schuurmansia henningsii* K. Schum. (?).

Rhopalocarpaceae and Sarcolaenaceae
see table 1.

Sterculiaceae
Buettneria biloba H. Bn. (V en O 1011; diam. 3 cm), *Cola buntingii* Bak. f. (V en O 777), *C. caricaefolia* (G. Don) K. Schum. (V en O 546; diam. 7 cm), *C. chlamydantha* K. Schum. (V en O 676), *C. gigantea* A. Chev. (V en O 299), *C.* cf. *gigantea* A. Chev. var. *glabrescens* Brenan et Keay (V en O 498), *C. heterophylla* Schott et Endl. (Pl 1560), *C. lateritia* K. Schum. var. *maclaudii* Brenan et Keay (V en O 697), *C. laurifolia* Mast. (V en O 362), *C. millenii* K. Schum. (V en O 331), *C. nitida* (Vent.) Schott et Endl. (V en O 20), *C. reticulata* A. Chev. (V en O 660; diam. 2 cm), *Dombeya degreana* Sond. (Pl ?), *D. mandenensis* J. Ar. (V en O 1146), *Firmiana colorata* R. Br. (Zw en R 113), *Heritiera littoralis* Dryand (BW 1261), *H. novo-guineensis* Kosterm. (BW 7525), *H. utilis* (Sprague) Sprague (V en O 781), *Kleinhovia hospita* L. (Zw en R 109), *Mansonia altissima* (A. Chev.) A. Chev. (V en O 591), *Pterocymbium beccarii* K. Schum. (BW 10077), *P. javanicum* R. Br. (Zw en R 90), *Pterospermum acerifolium* Zoll. et Mor. (Zw en R 95), *P. diversifolium* Blume (Zw en R 16), *P. javanicum* Jungh. (Zw en R 98), *Pterogota horsfieldii* Kosterm. (BW 9873), *Scaphopetalum amoenum* A. Chev. (V en O 738; diam. 6 cm), *Sterculia appendiculata* K. Schum. ex Engl. (U 15571), *S. conwentzii* K. Schum. (BW 2744), *S. foetida* L. (BW 5102), *S. javanica* R. Br. (Zw en R 84), *S. parkinsonii* F. v. M. (BW 2920), *S. prophyroclada* M. et P. (BW 1293), *S. pruriens* K. Schum. (St 64), *S. schumanniana* Mildbr. (BW 9029), *S. setigera* Del. (V en O 340), *S. shillinglawii* F. v. M. (BW 10825), *S. tragacantha* Lindley (V en O 336), *S. treubii* Hochr. (BW 4627), *Tarrietia utilis* Sprague (?), *Theobroma cacao* L. (V en O 256), *Triplochiton scleroxylon* K. Schum. (L 2877), *Waltheria indica* L. (V en O 149; diam. 5 cm).

Tiliaceae

Althoffia pleiostigma Warb. (BW 10903), *Apeiba echinata* Gaertn. (St 205), *Berrya amonilla* Roxb. (Zw en R 71), *Brownlowia argentata* Kurz. (BW 6602), *Christiana africana* DC. (V en O 214; diam. 6 cm), *Cistanthera papaverifera* A. Chev. (GK 7), *Clappertonia ficifolia* (Willd.) Decne (V en O 159; diam. 5 cm), *Colona scabra* Burr. (BW 10938), *Desplatzia chrysochlamys* (M. et B.) M. et B. (V en O 114; diam. 5 cm), *Duboscia viridifolia* (K. Schum.) Mildbr. (V en O 578), *Glyphaea brevis* (Spreng.) Monachino (V en O 12; diam. 5 cm), *Grewia carpinifolia* Juss. (V en O 289; diam. 3 cm), *G. hookerana* Exell et Mendonca (V en O 662; diam. 6 cm), *G. malacocarpa* Mast. (V en O 264; diam. 5 cm), *G. microcos* L. (Zw en R 29), *G. mollis* Juss. (V en O 298), *G. triflora* Walp. (V en O 1055), *Lueheopsis rugosa* Burr. (St. 152), *Microcos argentata* Burr. (BW 10951), *M. argentea* Bl. (BW 11176), *M. pentendra* Burr. (BW 3659), *Nesogordonia papaverifera* (A. Chev.) R. Cap. (V en O 243), *Schoutenia ovata* Korth. (syn. *Actinophora fragrans* R. Br.; Zw en R 82), *Tilia americana* L. (Pl 173), *T. cordata* Mill. (Pl 2462), *T* × *euchlora* K. Koch. (Pl 1574), *T.* × *europaea* L. (Pl 168), *T. platyphyllos* Scop. (Pl ?), *Trichospermum quadrivalve* Merr. (BW 7727).

Anatomical features were studied in transverse, radial and tangential sections varying in thickness from 10–20 µm. All sections were embedded in Kaiser's gelatin-glycerin (JOHANSEN, 1940). Means and ranges of the number of wood rays per mm in tangential direction, ray height and width, length of parenchyma-cell strands, radial vessel diameter and vessel-member length, are based on at least twenty-five measurements. Vessel-member length was measured excluding the tails, from the middle of one perforation plate to that of the next one. It is felt that, for any functional consideration, the length of the body of the element is more significant than the total vessel-member length. Vessel frequency and vessel grouping were determined over an area of at least 20 square mm in size.

Radial vessel diameter (20–)105(–280) µm (range of means 40–175 µm) in the Sarcolaenaceae for instance, means: the average radial vessel diameter of all the investigated species is 105 µm with a range from 20 µm for the smallest measured diameter to 280 µm for the largest; the lowest mean radial diameter of one of the investigated species is 40 µm, the highest 175 µm.

For our research in tropical woody species we have used the definition of tracheids and libriform fibres given by MOLL and JANSSONIUS (1906–1936), JANSSONIUS (1940) and REINDERS (1935). Wood rays were classified according to KRIBS (1935).

RESULTS

General wood anatomical descriptions of the Sarcolaenaceae and Rhopalocarpaceae. Notable differences between the investigated species can be found in table 1.

Sarcolaenaceae

Growth rings absent to hardly distinct; growth-ring boundaries if present, marked by 3–7 cells wide tangential layers of radially flattened or thicker walled tracheids in which less parenchyma and vessels. Wood diffuse-porous. Storied structure absent.

Vessels average 29/mm² (range of means 6–150/mm²), exclusively solitary except in *Leptolaena bernieri* where some multiples occur due to the large number of vessels; round to oval, radial and tangential diameters (20–)105(–280) μm (range of means 40–175 μm) and (15–)90(–245) μm (range of means 35–150 μm) respectively. Vessel-member length (140–)340(–605) μm (range of means 270–410 μm). Perforations simple in oblique to transverse end walls. Vessels usually in contact with tracheids when not in touch with rays, but also regularly with vasicentric parenchyma. Vessel-tracheid pits opposite, except in *Eremolaena*, oval or round, more or less vestured, mean horizontal diameter 3 μm (range of means 2–4 μm). Vessel-ray and vessel-parenchyma pits half-bordered to simple, 6–20 μm in diameter. Tyloses sometimes present; brown contents absent except in *Sarcolaena oblongifolia*, *S. multiflora* and more or less in *Schizolaena hystrix*.

Fibres tracheids, thick-walled (6 μm), bordered pits in radial and tangential walls less than 4 μm in diameter; also a small amount of thick-walled non-septate libriform fibres with some simple to almost simple pits confined to the radial walls occurs scattered in the tracheid ground tissue.

Parenchyma in short, irregular, uniseriate tangential bands (about 12/radial mm), but also diffuse or diffuse in aggregates and scantily paratracheal. Strands of 4 cells average (range of means 4–6 cells), mean height 515 μm (range of means 415–640 μm).

Rays mostly uniseriate, very seldom to regularly biseriate over a height of one or two cells, composed of predominantly procumbent cells with some square or erect marginal cells, sometimes exclusively composed of procumbent cells (*Leptolaena bernieri*) or almost exclusively as in *Sarcolaena grandiflora*, *Pentachlaena latifolia* and *Perrierodendron boinense*; height (25–)220(–910) μm (range of means 150–345 μm) or (2–)11(–45) cells (range of means 7–17 cells); average number per tangential mm 16 (range of means 11–21/tangential mm).

Crystals absent. Pith flecks only in *Leptolaena bernieri*, *Schizolaena microphylla* and *Eremolaena humblotiana*.

Rhopalocarpaceae

Growth rings absent to hardly distinct; sometimes tangential zones with less vessels alternating with tangential zones with slightly more vessels per square mm than average. Wood diffuse-porous. Storied structure present, rays excluded.

Vessels average 8/mm² (range of means 4–10/mm²), exclusively solitary, sometimes in seemingly false tangential clusters induced by a vessel running locally in a more or less horizontal direction; round to slightly oval, radial and tangential diameters (30–)110(–250) μm (range of means 105–185 μm) and (25–)90(–200) μm (range of means 80–150 μm), respectively. Vessel-member length (40–)295(–600) μm (range of means 245–440 μm), sometimes with short (20–50 μm) tails. Perforations simple in oblique to transverse end walls. Vessels usually in contact with axial parenchyma on the tangential sides, with tracheids on the radial sides, but sometimes also with rays. Vessel-tracheid pits alternate, round to oval, more or less vestured, mean horizontal diameter 3 μm (range of means 2–4 μm). Vessel-ray and vessel-parenchyma pits half bordered to simple, 4–7 μm in diameter. Tyloses, brown substances and thin spiral thickenings sometimes present.

Fibres tracheids, thick-walled (6–9 μm), bordered pits in longitudinal walls less than 4 μm in diameter with vertical slit-like inner apertures, sometimes more than one small (less than 1 μm), round aperture per pit. Diameter 9–30 μm, lumen 12 μm at the most in cross section. A small amount of thick-walled, non-septate (sometimes septate) libriform fibres occurs scattered in the tracheid ground tissue.

Parenchyma in long uniseriate tangential bands, bent more or less vasicentric round the tangential vessel sides, on the average 16/radial mm (range of means 12–19/radial mm); scanty diffuse parenchyma also present. Strands of 4 cells average (range of means 2–4 cells), mean height 340 μm (range of means 260–500 μm). Cells angular to oval in cross section, except those vasicentrically arranged which are elongated and show disjunctive elements. Contents rhomboidal crystals, sometimes brown substances and starch grains.

Rays uni- and multiseriate either without tails or with at the most 3 cells high tails, often entirely composed of procumbent cells or of procumbent centre cells and square and erect marginal cells; (1–)6(–30) seriate (range of means 4–7 seriate), height (50–)610(–4375) μm (range of means 420–1050 μm), or on the average more than 20 cells high; average number per tangential mm 5 (range of means 3–6/tangential mm). Sclereids sometimes present, single or in groups in the marginal ray areas. Contents rhomboidal crystals. Rays not storied.

Crystals rhomboidal, in axial- and ray-parenchyma cells.

General wood anatomical descriptions of the other investigated families, summarized in table 2.

Bixaceae

Growth rings indistinct. Wood diffuse-porous. Storied structure weakly present, not as pronounced as in the secondary phloem, multiseriate rays excluded.

Vessels average 17/mm^2, solitary and in radial multiples, occasionally in radial multiples of more than 4 and in clusters; oval; radial diameter (30–)75(–130) μm; perforations simple, in oblique end walls; inter-vessel pits bordered, alternate, average horizontal diameter 6 μm; vessel-ray and vessel-parenchyma pits half-bordered, average diameter 6 μm; vessel-member length (70–)200(–300) μm; tyloses and deposits absent.

Fibres tracheids or transitional tracheids to non-septate libriform; thick-walled; bordered pits in radial, less in tangential walls, average horizontal diameter 5 μm.

Parenchyma rather scanty, diffuse, occasionally diffuse in aggregates, in uniseriate short tangential bands and more or less vasicentric; strands (2–)4(–6) cells long, averaging 500 μm.

Rays heterogeneous II, predominantly composed of procumbent cells, (1–)2(–6) seriate, average height 300 μm, averaging 13/tangential mm.

Crystals absent.

Bombacaceae

Growth rings regularly absent, not in *Bombax aquaticum*, *B. flaviflorum*, *B. surinamensis* and *Ochroma lagopus*. Wood diffuse-porous. Storied structure present except in *Bombax aquaticum*, *B. flaviflorum* and *Ochroma lagopus*, rays excluded.

Vessels average 4/mm^2 (range of means 1–8/mm^2), solitary and in radial multiples, occasionally (5 out of 13 examined specimens) of more than 4, usually (10 out of 13) also in clusters, in *Durio oxleyanus* also in oblique chains; round to oval, (40–)230(–600) μm in radial diameter (range of means 140–370 μm); vessel-member length (200–)510(–960) μm (range of means 320–700 μm); perforations simple in transverse to weakly oblique, rarely oblique end walls; intervessel pits bordered, vestured in *Ochroma lagopus*, averaging 9 μm in horizontal diameter (range of means 3–13 μm), alternate; vessel-parenchyma pits half-bordered, 3–60 μm in diameter; tyloses abundant in *Bombax glabra*, more or less so in *Ochroma lagopus*; deposits more or less present in *Gossampinus heptaphylla* and *Ochroma lagopus*.

Fibres libriform, generally non-septate, partly non-septate in *Adansonia fony* and *Ochroma lagopus*, septate in *Adansonia digitata* and *Catostemma fragrans*; occasionally thick-walled; pits simple or more or less bordered, only distinctly bordered in *Coelostegia griffithii*, *Durio oxleyanus* and *Gossampinus heptaphylla*; tracheids more or less present in *Bombax aquaticum* only.

Parenchyma abundant, in *Adansonia* and more or less in *Bombax glabra* occurring in two kinds, namely in large, thin-walled cells and smaller apparently more lignified cells; vasicentric parenchyma always present; diffuse or diffuse in aggregates except in *Adansonia fony*, *Catostemma fragrans*, *Gossampinus heptaphylla* and *Ochroma lagopus*; generally also in uniseriate tangential bands, in *Adansonia digitata*, *Bombax glabra* and *Ceiba pentandra* in multiseriate bands as well and in *Adansonia fony*, *Catostemma fragrans* and *Ochroma lagopus* exclusively in multiseriate tangential bands; tangential bands short (9 out of 13 examined specimens) or long, average number per radial mm 8 (range of means 1–17/radial mm).

Rays heterogeneous II, predominantly composed of procumbent cells, (1–)5(–12) seriate (range of means 2–8 seriate), average height 980 μm (range of means 460–2000 μm), average number 5/tangential mm (range of means 1–10/tangential mm); tile cells present in *Coelostegia griffithii* and *Durio oxleyanus*, sheath cells present in *Ochroma lagopus*.

Crystals usually present (not in *Bombax aquaticum*, *B. nervosum* and *B. surinamensis*), simple or druse, in ray cells.

Flacourtiaceae

Growth rings usually present, not always distinct. Wood diffuse-porous, storied structure absent, pith flecks occasionally present.

Vessels average 48/mm^2 (range of means 6–140/mm^2), solitary and in radial multiples, often of more than 4 and usually also in clusters; round to oval, rarely angular; (10–)85(–260) μm (range of means 30–180 μm) in radial diameter; vessel-member length (120–)740(–1900) μm (range of means 430–1400 μm); perforations simple, or more or less scalariform as well as in *Caloncoba*, *Homalium axillaire*, *H. laxiflorum*, *Oncoba spinosa* and *Trichostephanus acuminatus*, or exclusively scalariform as in *Dasylepis* cf. *brevipedicellata* and *Erythrospermum candidum*, usually in oblique end walls; inter-vessel pits bordered, generally in tangential walls, horizontally oval, average horizontal diameter 5 μm (range of means 3–10 μm), alternate (*Erythrospermum candidum* also opposite); vessel-ray and vessel-parenchyma pits half bordered, average horizontal diameter 10 μm (range of means 3–50 μm), generally in radial walls; deposits only in *Casearia javitensis* and *Flacourtia zippelii*.

Fibres septate libriform, septate to non-septate in *Caloncoba echinata*, *Casearia arguta*, *C. lucida*, *Itoa stapfii*, *Oncoba spinosa*, *Pangium edule*, *Scolopia spinosa* and *Trichadenia philippinensis*; some tracheids present in *Homalium axillaire;* moderately thick-walled, pits simple to distinctly bordered, tending to be confined to radial walls, when bordered then only in radial walls.

Parenchyma absent or rare; when present then vasicentric as in *Homalium patoklaense*, *Itoa stapfii* and *Pangium edule*.

Rays generally heterogeneous I and II, less often either heterogeneous I or heterogeneous II; in *Samyda dodecandra* and *Trichostephanus acuminatus* homogeneous I and II; composed of predominantly procumbent cells or of square and upright cells as in *Caloncoba brevipes*, *Flacourtia flavescens*, *Samyda dodecandra* and *Trichostephanus acuminatus*; (1–)3(–12) seriate (range of means 1–5 seriate), mean height 1300 μm (range of means 440–3400 μm), average number per tangential mm 14 (range of means 6–20/tangential mm); generally composed of more than 3 storeys; simple or scalariform perforated ray cells regularly present.

Crystals generally (30 out of 32 examined specimens) present (not in *Banara guianensis* and *Laetia procera*), always in ray cells, in *Casearia calodendron*, *Flacourtia zippelii*, *Homalium foetidum*, *H. guianense*, *Itoa stapfii*, *Oncoba spinosa* and *Pangium edule* also in axial parenchyma; simple (in *Casearia calodendron* also druses).

Ochnaceae

Growth rings usually, sometimes more or less, present; not in *Campylospermum glaberrimum*, *Lophira alata* and *Schuurmansia henningsii*. Wood diffuse-porous. Storied structure absent.

Vessels (0–)50(–165)/mm^2 (range of means 2–145/mm^2), exclusively solitary (in *Ochna rhizomatosa* almost so), except in *Lophira alata* and *Schuurmansia henningsii* where vessels are in radial multiples and in clusters; round to oval, (12–)78(–415) μm in radial diameter (range of means 33–220 μm); perforations simple (in *Schuurmansia henningsii* rarely scalariform) in transverse to oblique, rarely nearly vertical end walls; vessel-tracheid pits bordered, averaging 4 μm in horizontal diameter (range of means 2–7 μm), not crowded, in *Ouratea* pits to tracheids and rays vestured; vessel-ray and vessel-parenchyma pits similar but half bordered. Deposits in *Campylospermum dybowskii, C. glaberrimum, Idertia morsonii*, more or less in *Lophira alata* and *Ouratea surinamensis*.

Fibres tracheids (in *Lophira alata* and *Schuurmansia henningsii* non-septate and septate libriform respectively), thick-walled except in *Campylospermum flavum* and *Schuurmansia henningsii*, pits distinctly bordered except in *Lophira alata* and *Schuurmansia henningsii*.

Parenchyma neither scanty nor abundant, vasicentric, diffuse or diffuse in aggregates (not in *Lophira alata* and *Schuurmansia henningsii*), occasionally (6 out of 15 examined specimens) in uniserate short tangential bands, in *Lophira alata* 4 cells wide long tangential bands (2/radial mm); brown contents sometimes present.

Rays heterogeneous II, sometimes heterogeneous I, in *Campylospermum dybowskii* and *Lophira alata* homogeneous II; usually predominantly composed of upright cells with or without square cells, or of procumbent, upright and square cells equally; in *Lophira alata* and *Schuurmansia henningsii* predominantly composed of procumbent cells; (1–)2(–8) seriate (range of means 2–4 seriate), height (100–)950(–8000) μm (range of means 430–2000 μm), averaging 13/tangential mm (range of means 9–20/tangential mm).

Crystals usually present except in *Campylospermum dybowskii, Idertia morsonii* and *Schuurmansia henningsii*; simple, in ray-parenchyma cells, except *Lophira alata*; in *Elvasia hostmanniana, Lophira alata* and *Ochna rhizomatosa* in axial parenchyma as well; large often thick-walled crystal cells in *Campylospermum flavum, C. glaberrimum, Diporidium* and *Elvasia hostmanniana*.

Sterculiaceae

Growth rings absent to indistinct. Wood diffuse-porous, in *Buettneria biloba* more or less ring-porous. Storied structure more or less present, except in *Scaphopetalum amoenum* and *Waltheria indica*, rays generally (31 out of 43 investigated specimens) excluded.

Vessels (1–)6(–50)/mm^2 if *Dombeya* and *Waltheria indica* are not included (range of means 1–37, if *Buettneria biloba* is also excluded 1–16/mm^2), (1–)11(–140)/mm^2 (range of means 1–91/mm^2) otherwise; solitary and in radial multiples, regularly of more than 4 (32 out of 43 examined specimens), often also in clusters (37 out of 43); round to oval, (10–)135(–420) μm (range of means 38–270 μm) in radial diameter; vessel-member length (110–)350(–690) μm (range of means 165–550 μm); perforations simple in more or less oblique end walls; inter-vessel pits bordered, mean horizontal diameter 6 μm (range of means 3–10 μm), usually alternate (35 out of 43); vessel-ray and vessel-parenchyma pits similar but half-bordered; spiral thickenings only more or less present in *Tarrietia utilis*; tyloses and deposits generally absent.

Fibres libriform, with simple to occasionally distinctly bordered pits, non-septate except in *Sterculia setigera* and partly septate in *Sterculia foetida*; occasionally thick-walled.

Parenchyma abundant, always vasicentric and occasionally (10 out of 43) also aliform, often diffuse or diffuse in aggregates and/or in uni-(short) or multiseriate (long) tangential bands of 1 to more than 20/radial mm. Strands of 4 cells average (range of means 2–6 cells), mean height 380 µm (range of means 250–590 µm).

Rays heterogeneous II, (1–)6(–20) seriate (range of means 1–12 seriate), regularly (25 out of 43) more than 100 µm wide with a maximum of 320 µm, predominantly composed of procumbent cells with square and upright marginal cells, regularly (25 out of 43) with sheath cells, rarely with tile cells (*Kleinhovia hospita*, *Scaphopetalum amoenum* and *Triplochiton scleroxylon*); mean height 1140 µm (range of means 220–2700 µm); average number per tangential mm 5 (range of means 2–14/tangential mm).

Crystals generally present, simple, rarely druses as well, in ray cells and usually also in axial parenchyma, rarely exclusively in axial parenchyma.

Tiliaceae

Growth rings usually absent to distinct. Wood diffuse-porous. Storied structure more or less present, rays often excluded.

Vessels (0–)36(–200)/mm^2 (range of means 1–165/mm^2), solitary and in radial multiples, regularly of more than 4 and usually also in clusters (*Althoffia pleiostigma* often exclusively solitary), round to oval, (10–)107(–380) µm (range of means 37–230 µm) in radial diameter; vessel-member length (175–)385(–745) µm (range of means 230–655 µm); perforations simple in oblique to transverse end walls; inter-vessel pits bordered, oval, average horizontal diameter 6 µm (range of means 2–11 µm), generally alternate; vessel-ray and vessel-parenchyma pits half-bordered, average horizontal diameter 6 µm (range of means 2–16 µm). Spiral thickenings only present in *Tilia*; tyloses and deposits usually absent.

Fibres libriform (only in the genus *Tilia* also tracheids present), with simple to minutely bordered pits, non-septate, rarely thick-walled.

Parenchyma neither rare to absent nor abundant, vasicentric, apotracheally diffuse or diffuse in aggregates, and in short uniseriate tangential bands or less often in long multiseriate tangential bands.

Rays heterogeneous I, regularly tails with less than 4 marginal rows; in *Clappertonia ficifolia*, *Nesogordonia papaverifera* and *Tilia* homogeneous II or almost so; predominantly composed of procumbent cells, tile cells regularly present; (1–)3(–12) seriate (range of means 1–4 seriate), mean height 675 µm (range of means 250–1500 µm), average number per tangential mm 10 (range of means 4–17/tangential mm).

Crystals if present (19 out of 29 investigated specimens) simple, in ray cells and usually also in axial parenchyma.

DISCUSSION

The Sarcolaenaceae is represented by 8 genera with 33 species (CAVACO, 1952), or by 10 genera with 34 of 28 species (CAPURON, 1970). CAPURON divides the genus *Leptolaena* into 3 genera, viz. *Xerochlamys*, *Mediusella* and *Leptolaena*; furthermore it is questionable if one has to distinguish 7 *Sarcolaena* species (CAVACO, 1952) instead of one.

The Rhopalocarpaceae is represented by 2 genera, viz. *Rhopalocarpus* with 13 species and *Dialyceras* with one species (CAPURON, 1962).

TAKHTAJAN (1969) placed both the Sarcolaenaceae and Rhopalocarpaceae in the Malvales. This was based on morphological as well as anatomical characteristics. In his classification the order Malvales is the end of an evolutionary line starting with the order Magnoliales. He considers the Dilleniales a connecting link between the Magnoliales on one hand and the Theales and Violales on the other. In the Theales the most primitive family nearest to the Dilleniaceae, is the Ochnaceae. The Lophiraceae occopies in many respects an intermediate position between the Ochnaceae and the Dipterocarpaceae. In the Violales, a taxon closely related to the Theales, the family Flacourtiaceae (see also MILLER, 1975) is the nearest to the Dilleniaceae, followed amongst others by the Bixaceae, related to the Flacourtiaceae, and the Cochlospermaceae, very near to the Bixaceae. Evidently derived from the Violales is the Malvales which exhibits many features in common with the Flacourtiaceae.

The order is composed of the families Elaeocarpaceae, Tiliaceae, Scytopetalaceae, Sarcolaenaceae, Rhopalocarpaceae, Sterculiaceae, Bombacaceae and Malvaceae.

HUTCHINSON (1973) on the other hand, working with morphological characteristics and with anatomical characteristics as well, placed both the families Sarcolaenaceae and Rhopalocarpaceae in the Ochnales. In his classification the Dilleniales is a basal group rather remotely related to the Magnoliales and perhaps showing a connecting link between that group and the Bixales and Theales. Derived from the Theales is the order Ochnales composed amongst others of the Ochnaceae, Sarcolaenaceae, Rhopalocarpaceae and Dipterocarpaceae. The Lophiraceae is included in the Ochnaceae. The Bixales with for instance the families Bixaceae, Flacourtiaceae and Cochlospermaceae forms a step towards the fairly advanced group of the Tiliales with the important families Tiliaceae, Sterculiaceae and Bombacaceae and further on towards the Malvales with only one, very natural family the Malvaceae. The last mentioned family is clearly a climax in this line of evolution.

A discussion about the systematic position of the Sarcolaenaceae and Rhopalocarpaceae based on the anatomy of the secondary phloem only, is given by DEN OUTER and VOOREN (1980). Now a similar comparison is given between some of the families mentioned above and the Sarcolaenaceae and Rhopalocarpaceae, this time based on characteristics of the secondary xylem.

Trends of evolution, based mainly on anatomical investigations of woods of temperate regions as well as economically important tropical trees, were established by, among others, KRIBS (1935), TIPPO (1946), BAILEY (1953), CARLQUIST (1966, 1975). Some of these specialization trends are:

a) short vessel elements with broad diameter, circular in cross section are derived from long, narrow vessel elements, angular in cross section;
b) vessel elements with simple perforation plates or multiple perforation plates with a few bars and alternate inter-vascular pits are derived from multiple perforation plates with numerous bars and opposite inter-vascular pits;
c) various aggregate groupings of vessel arrangements are derived from a solitary arrangement;
d) septate fibres and fibres with few and small, rarely bordered pits are derived from fibre-tracheids with large, distinctly bordered pits (this means that evolution has proceeded from fibre-tracheids to tracheids to wood fibres (libriform));
e) various aggregate arrangements and paratracheal parenchyma types are derived from diffuse parenchyma;
f) homogeneous, narrow, low wood rays composed of procumbent cells are derived from heterogeneous, broad, high ones composed of upright cells.

The features of the secondary xylem of the Sarcolaenaceae and Rhopalocarpaceae are quite uniform. The differences between the genera within a family (see table 1) are no more important than those between species within a genus or even between individuals of a species. This is in support of CAPURON's (1970) suggestion for instance, that the genus *Sarcolaena* might consist of one instead of 7 species.

The wood anatomical results of the investigated families are summarized in table 2. Herewith the family Ochnaceae is divided into two subfamilies, viz. Ochnoideae and Sauvagesioideae. The monogeneric african tribe Lophirae is placed within this last mentioned subfamily (KANIS, 1968; DEN OUTER, 1977). The data of the also in two subfamilies divided Dilleniaceae, are from DICKISON (1967), whereas those of the Cochlospermaceae are derived from KEATING (1968). Of the two genera *Cochlospermum* and *Amoreuxia* of the family Cochlospermaceae, only data of *Cochlospermum* were used in this present study. *Amoreuxia* was not used in these comparisons because it is a perennial herb, it does not have imperforate tracheary elements and it produces only a small amount of secondary xylem.

An arrangement of the different families according to degree of specialization could be done as shown in table 2. The wood of the Dilleniaceae reveals a rather low level of specialization whereas that of the Bombacaceae is the most advanced. The sequence in which the taxa in table 2 (apart from the Sarcolaenaceae and Rhopalocarpaceae) have been placed is a modified representation of TAKHTAJAN's views (1969). Pending the discussion in this paper the Sarcolaenaceae and the Rhopalocarpaceae have not been placed in this system. The position of the Sauvagesioideae and the Flacourtiaceae could be as in table 2 if only vessel arrangement, vessel perforations, inter-vascular pits and storied structure are taken into consideration. If the ground tissue of these two groups is included in the considerations a position below the Bombacaceae seems preferable. This position, indicating a high stage of development within the studied families, is justified by the septate libriform fibres of the Sauvagesioideae and the Flacourtiaceae. The obvious position then for the Sarcolaenaceae and the Rhopalocarpaceae is in the first case within the Ochnaceae, viz. between the two subfamilies; in the second case between the Ochnoideae and the Bixaceae, even if one includes the arrangement of the axial parenchyma in the consideration. The vessel diameters however of the Sarcolaenaceae and the Rhopalocarpaceae correspond with those of the Tiliaceae, as does the number of vessels per square mm of the Sarcolaenaceae, whereas the Rhopalocarpaceae show a more probable relationship in this respect with the Sterculiaceae and the Cochlospermaceae.

Vessel-member length of the Sarcolaenaceae and the Rhopalocarpaceae puts them between the Sterculiaceae and the Bixaceae. Average and maximal ray width of the Sarcolaenaceae and the Rhopalocarpaceae put these families close to respectively the Bixaceae and the Sterculiaceae. Average ray height and ray type finally indicate a position for the Sarcolaenaceae very near to the Bixaceae and for the Rhopalocarpaceae between the Tiliaceae and the Sauvagesioideae.

From the above mentioned facts a probable relationship of the Sarcolaenaceae and the Rhopalocarpaceae with the Ochnaceae, and especially with the subfamily Ochnoideae may seem the logical one. However, the generally advanced wood of the Sarcolaenaceae and the Rhopalocarpaceae – within the studied families – renders an arrangement closer to the Tiliaceae and the Sterculiaceae more justified. At the same time the woods of these families, especially of the Sarcolaenaceae, show clearly affinities with the woods of the Bixaceae and the Cochlospermaceae. Arrangement of the Sarcolaenaceae and the Rhopalocarpaceae between the orders Violales and Malvales of TAKHTAJAN (1969) seems already closer to the truth.

KEATING's opinion (1968) that the wood of the Cochlospermaceae appears most similar to that of the Malvaceae, Sterculiaceae, Tiliaceae and Bixaceae is quite conflicting with what we have found. Especially the difference in the characteristics of the ground tissue is an argument against this similarity. An arrangement is preferred of the Rhopalocarpaceae and especially of the Sarcolaenaceae within the Malvales (TAKHTAJAN, 1969) but close to the Bixaceae and the Cochlospermaceae of the Violales (TAKHTAJAN, 1969). This is in agreement with CAPURON (1962).

It seems quite feasible to consider the Dilleniaceae a common origin for both the Violales and the Theales as stated by TAKHTAJAN (1969; see also DICKISON, 1967). Consequently there is a relationship between the Tiliaceae and the Sterculiaceae on one hand, via the Bixaceae and the Cochlospermaceae with the Ochnaceae on the other hand. The same can be said for the relationship of the Sarcolaenaceae and the Rhopalocarpaceae with the Ochnaceae.

Conflicting with this view, as far as the Rhopalocarpaceae is concerned, is KEATING'S (1973) opinion based on pollen morphology. He states that on the basis of pollen grains the Violales (TAKHTAJAN, 1969) seems to be a related group of families with the Flacourtiaceae as the oldest living family of this group. The Ochnaceae, according to TAKHTAJAN (1969) a basal group in his Theales, have pollen grains which bear strong resemblance to those of the Flacourtiaceae. The pollen grains of the Rhopalocarpaceae do not point to a probable relationship with the Flacourtiaceae (KEATING, 1973) and therefore not with the Ochnaceae either. HUARD (1965a and b) on the other hand placed the Rhopalocarpaceae from a wood-anatomical point of view close to the Sterculiaceae (and the Tiliaceae) although he also sees affinities with HUTCHINSON's (1973) Ochnales and above all with the Bixaceae.

The Sarcolaenaceae might also be related to the Dipterocarpaceae via *Pakaraimaea* of the subfamily Monotoideae of the Dipterocarpaceae. DE ZEEUW's (1977) observation that the Sarcolaenaceae is remarkably close to *Pakaraimaea* points this way; yet he also found enough differences arguing against a grouping with *Pakaraimaea.*

In this paper distinctions have been made between possible relationships and phylogeny. A high degree of relationship is found when two or more taxa have a number of important characteristics in common. But phylogenetically they may have reached this similar level of development through parallel pathways or through blocked development of one or more taxa. One could argue e.g. that the Flacourtiaceae may have the level of development as indicated by TAKHTAJAN (1969) but that they could never have arosen from the Dilleniales since they are lacking axial parenchyma, which is generally considered a primitive trait. Thus they should have reached this level of development from a different ancestor, which may be extinct and which may also be a common ancestor of TAKHTAJAN's (1969) Dilleniales. Equally it would be difficult to imagine the Sarcolaenaceae and the Rhopalocarpaceae as descendants from TAKHTAJAN's (1969) Violales since both possess exclusively solitary vessels, which is also generally considered a more primitive trait than radial groups and clusters of vessels. Ignoring the possibility of a development whereby a seemingly primitive trait is derived from a more advanced one, the Sarcolaenaceae and the Rhopalocarpaceae cannot have reached their level of development by way of the Violales. It would however seem logical that they have reached this stage by evolving directly, or indirectly through extinct groups, from TAKHTAJAN's (1969) Theales. However, theorizing like this can be done on safer, less speculative grounds, when not only wood anatomical characteristics are taken into consideration but all other characteristics of the plant as well, as for instance BAILEY (1957) and DE ZEEUW (1977) have also, and quite rightly, pointed out.

Bearing in mind all these arguments a position within HUTCHINSON's (1973) Ochnales seems doubtful. Not only from a bark anatomical point of view (DEN OUTER and VOOREN, 1980), but also when the secondary xylem is taken into consideration, preference is given to TAKHTAJAN's (1969) arrangement within the Malvales.

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TABLE 1. Notable differences of the secondary xylem between the investigated Sarcolaenaceae and Rhopalocarpaceae species.

Specimens studied	number	storied structure (rays excl.)	vessels					
			rd. diam. µm	av. number per sq. mm	pitting	tyloses	member length µm	height µm
Sarcolaenaceae								
Sarcolaena grandiflora Dup.-Thou.	CTFT 13614	–	(40–)115(–165)	12	o	–	(225–)330(–465)	(40–) 160(–
Sarcolaena oblongifolia Gér.	VenO 1171	–	(25–) 60(–100)	30	o	–	(170–)310(–520)	(30–) 220(–
Sarcolaena multiflora Dup.-Thou.	VenO 1167	–	(25–) 65(–120)	30	o	±	(160–)300(–510)	(30–) 210(–
Sarcolaena codonochlamys Bak.	CTFT 9121	–	(40–)105(–165)	29	o	–	(250–)310(–415)	(50–) 150(–
Sarcolaena codonochlamys Bak.	CTFT 13610	–	(25–) 90(–140)	20	o	–	(200–)300(–380)	(65–) 150(–
Leptolaena bojeriana (H. Bn.) Cavaco	VenO 1012	–	(20–) 60(– 80)	120	o	–	(140–)270(–380)	(30–) 180(–
Leptolaena bernieri H. Bn.	CTFT 9170	–	(20–) 45(– 75)	150	o	–	(260–)340(–420)	(30–) 240(–
Leptolaena multiflora Dup.-Thou.	CTFT 447	–	(30–)160(–240)	11	o	–	(200–)330(–510)	(40–) 200(–
Leptolaena multiflora Dup.-Thou.	CTFT 13624	–	(40–) 90(–190)	8	o	±	(280–)350(–520)	(40–) 200(–
Schizolaena hystrix R. Cap.	CTFT 13612	–	(40–)155(–280)	7	o	±	(290–)410(–605)	(40–) 260(–
Schizolaena hystrix R. Cap.	CTFT 13625	–	(40–)175(–240)	6	o	–	(265–)380(–465)	(50–) 240(–
Schizolaena hystrix R. Cap.	VenO 1173	–	(25–) 95(–140)	21	o	±	(225–)320(–440)	(65–) 180(–
Schizolaena microphylla H. Perr.	CTFT 13622	–	(40–) 70(–115)	19	o	–	(200–)280(–365)	(50–) 235(–
Schizolaena cf. pectinata R. Cap.	CTFT 9139	–	(50–)150(–215)	9	o	–	(250–)360(–465)	(40–) 250(–
Schizolaena cf. pectinata R. Cap.	CTFT 9755	–	(50–)140(–240)	12	o	±	(325–)410(–505)	(25–) 260(–
Rhodolaena bakeriana H. Bn.	CTFT 13609	–	(50–)130(–215)	12	o	±	(290–)365(–415)	(100–) 345(–
Rhodolaena bakeriana H. Bn.	CTFT 16590	–	(25–)120(–165)	21	o	–	(190–)280(–380)	(65–) 270(–
Rhodolaena humblotii H. Bn.	CTFT 9086	–	(25–) 90(–140)	17	o	–	(250–)370(–440)	(75–) 220(–
Pentachlaena latifolia H. Perr. ssp. orientalis R. Cap.	CTFT 9014	–	(30–)125(–190)	10	o	+	(250–)330(–430)	(25–) 160(–
Eremolaena humblotiana H. Bn.	CTFT 9141	–	(40–)130(–250)	12	a±o	±	(240–)360(–550)	(30–) 300(–
Eremolaena rotundifolia (Gér.) P. Danguy	CTFT 9101	–	(30–) 80(–130)	18	a	–	(200–)380(–510)	(25–) 240(–
Perrierodendron boinense (H. Perr.) Cavaco	CTFT 13621	–	(20–) 40(– 90)	63	o	–	(315–)365(–465)	(30–) 155(–
Rhopalocarpaceae								
Dialyceras parvifolium R. Cap. var. coriaceum R. Cap. forma discolore R. Cap.	CTFT 12077	+	(30–)110(–165)	10	a	±	(40–)260(–375)	(85–) 525(–1
Dialyceras parvifolium R. Cap. var. coriaceum R. Cap. forma discolore R. Cap.	CTFT 12089	+	(30–)110(–165)	10	a	±	(40–)260(–375)	(85–) 525(–1
Rhopalocarpus binervius R. Cap.	CTFT 12078	+	(65–)185(–250)	4	a	–	(75–)440(–600)	(75–)1050(–4
Rhopalocarpus coriaceus (Scott-Elliot) R. Cap.	VenO 1168	+	(35–) 75(–112)	10	a	±	(50–)250(–350)	(110–) 630(–1
Rhopalocarpus coriaceus (Scott-Elliot) R. Cap.	VenO 1205	+	(55–)110(–135)	7	a	–	(190–)305(–375)	(160–) 420(–1
Rhopalocarpus louvelii (P. Danguy) R. Cap.	CTFT 12082	+	(50–)115(–175)	4	a	–	(100–)300(–450)	(165–) 800(–2
Rhopalocarpus louvelii (P. Danguy) R. Cap.	CTFT 12086	+	(50–)115(–175)	4	a	–	(100–)300(–450)	(165–) 800(–2
Rhopalocarpus lucidus Bojer	CTFT 12079	+	(50–)105(–165)	9	a	+	(90–)310(–400)	(90–) 455(–2
Rhopalocarpus lucidus Bojer	CTFT 12081	+	(50–)105(–170)	10	a	+	(50–)300(–365)	(115–) 455(–2
Rhopalocarpus lucidus Bojer	VenO 1090	+	(55–)105(–135)	10	a	–	(175–)245(–290)	(125–) 560(–1
Rhopalocarpus triplinervius H. Baill.	CTFT 12048	+	(35–)105(–165)	5	a	+	(60–)250(–315)	(50–) 515(–1

rays						parenchyma			crystals	further information
. ight lls	av. width cells	max. width cells	type (pred. p. cells)	number per tg.mm	sclereids	diff. or diff. in aggr.	av. number long uniseriate tg. bands per rd. mm	av. height par.-cell strand in μm (cells)	in pc and wr	
	1	2 (seldom)	He(Ho)III	14	–	+	–	530(4)	–	wr and pc regularly with br. cont.
	1	2 (seldom)	HeIII	11	–	+	–	515(4)	–	
	1	2 (very seldom)	HeIII	14	–	+	–	540(6)	–	irr. arr. of vessels and pc
	1	2 (regularly)	HeIII	14	–	+	–	450(4)	–	wr and pc with br. cont.; feeble gr. layers
	1	2 (sometimes)	HeIII	14	–	+	–	450(4)	–	wr and pc with br. cont.; some gr. layers
	1	2 (seldom)	HeIII	16	–	+	–	440(4)	–	
	1	2 (seldom)	HoIII	17	–	+	–	450(4–6)	–	pith flecks; feeble gr. layers
	1	2 (seldom)	HeIII	14	–	+	–	500(4)	–	irr. arr. of vessels and pc
	1	2 (sometimes)	HeIII	15	–	+	–	420(4)	–	irr. arr. of vessels and pc
	1	2 (sometimes)	HeIII	18	–	+	–	620(4)	–	wr and pc with light br. cont.; feeble gr. layers
	1	2 (sometimes)	HeIII	16	–	+	–	620(4)	–	wr and pc with light br. cont.; feeble gr. layers
	1	2 (sometimes)	HeIII	20	–	+	–	415(4)	–	
	1	2 (sometimes)	HeIII	16	–	+	–	415(4)	–	pith flecks; feeble gr. layers
	1	2 (very seldom)	HeIII	18	–	+	–	515(5–6)	–	feeble gr. layers
	1	2 (sometimes)	HeIII	21	–	+	–	500(4–5)	–	wr and regularly pc with br. cont.; feeble gr. layers
	1	2 (regularly)	HeIII	19	–	+	–	585(4)	–	
	1	2 (seldom)	HeIII	16	–	+	–	630(4)	–	
	1	2 (sometimes)	HeIII	14	–	+	–	600(4)	–	feeble gr. layers
	1	2 (seldom)	He(Ho)III	13	–	+	–	570(4)	–	wr and pc with br. cont.; feeble gr. layers
	1	2 (seldom)	HeIII	13	–	+	–	630(4)	–	pith flecks; irr. arr. of vessels and pc
	1	2 (regularly)	HeIII	14	–	+	–	450(4)	–	irr. arr. of vessels and pc
	1	2 (seldom)	He(Ho)III	17	–	+	–	450(4)	–	wr and sometimes pc with br. cont.; feeble gr. layers
20	6	20	Ho(He)II	3	±	±	17	350(4)	+	
20	6	20	Ho(He)II	3	±	±	17	290(2–4)	+	
20	6	25	Ho(He)II	4	±	±	12	500(4)	+	gum ducts
20	4	15	HoII	6	–	±	19	280(4)	+	
20	4	11	HoII	3	–	±	19	320(4)	+	
20	6	25	Ho(He)II	6	±	±	13	450(3–4)	+	
20	6	30	Ho(He)II	6	±	±	13	340(2–4)	+	
20	5	15	Ho(He)II	5	±	±	13	330(4)	+	feeble gr. layers
20	5	15	Ho(He)II	5	±	±	17	330(4)	+	growth layers
20	7	22	HoII	3	–	±	17	260(4)	+	
20	7	20	HoII	6	–	±	17	265(4)	+	

TABLE 2. Some wood anatomical characteristics of the studied families.

	growth rings	storied structure (rays excl.)	vessels: excl. solitary (or almost so)	rd. multiples and solitary	> 4 per rd. multiple	cluster	av. rd. diam. µm	av. number per sq. mm	perforations	hor. diam. bordered pits µm	pitting	av. member length µm	libriform
Sarcolaenaceae	±	–	+	–	–	–	105	29	s	3	o	340	±(n–s)
Rhopalocarpaceae	±	+	+	–	–	–	110	8	s	3	a	295	±(n–s)
Dilleniaceae													
Dillenioideae	–	–	+	–	–	–	145	23	sc	7–40	sc-o	1530	–
Tetraceroideae	–	–	+	–	–	–	275	6	sc+s	7–40	o	765	–
Ochnaceae													
Ochnoideae	±	–	+	–	–	–	62	56	s	3	scarce	445	–
Sauvagesioideae	–	–	–	+	±	±	180	6	s	6	a	560	+(n-s, s)
Flacourtiaceae	+	–	–	+	±	±	85	48	s, ±sc	5	a	740	+(s, ±n-
Bixaceae	±	±	–	+	±	±	75	17	s	6	a	200	±
Cochlospermaceae	?	±	–	+	±	±	155	6	s	6	a	410	–
Tiliaceae	±	±	–	+	±	±	107	36	s	6	a	385	+(n-s)
Sterculiaceae	–	+	–	+	±	±	135	11	s	6	a	350	+(n-s)
Bombacaceae	–	+	–	+	±	±	229	4	s	9	a	507	+(n-s, ±

Symbols and abbreviations used in tables 1 and 2.

+	=	present
–	=	absent
±	=	scarcely present
a	=	alternate pitting
aggr.	=	aggregates
arr.	=	arrangement
av.	=	average
br. cont.	=	brown contents
diam.	=	diameter
diff.	=	diffuse
dr.	=	druse crystal
excl.	=	exclusive
gr. layer	=	growth layer
hor.	=	horizontal
irr.	=	irregular
l	=	long uniseriate tg. bands
o	=	opposite pitting
n-s	=	non-septate libriform
p	=	procumbent wood-ray cell
pred.	=	predominant
pc	=	axial wood parenchyma
raph.	=	raphide crystal
rd.	=	radial
s	=	simple perforation or septate libriform
sc	=	scalariform perforation or scalariform pitting
sh	=	sheath wood-ray cell
sim.	=	simple crystal
sq.	=	square

fibres		rays							parenchyma					crystals	
thick-walled	pits dist. bordered	av. height µm	pred. cell type	excl. uni-seriate	seriate	type	number per tg. mm	pits to vessels µm	rare to absent	diff.- or diff.- in aggr.	short uniseriate tg. bands	long multiseriate tg. bands	vasicentric	type	in wr and/or pc
+	+	220	p	+	(1–) 1(– 2)	HeIII	16	6–20	–	+	+	–	±	–	–
+	+	610	p	–	(1–) 6(–30)	HoII	5	4–7	–	±	+(1)	–	±	sim.	wr, pc
±	+	1300?	?	–	(1–) 9(–18)	HeI	?	7–40	–	+	–	–	–	raph.	?
±	+	3050?	?	–	(1–)22(–41)	HeI/II	?	7–40	–	+	–	–	±	raph.	?
+	+	1015	u, ±p	–	(1–) 3(– 8)	HeII	14	4	–	+	±	–	+	sim.	wr
±	–	530	p	–	(1–) 2(– 8)	Ho/HeII	10	6	–	–	–	±	+	sim.	pc
±	–	1300	p	–	(1–) 3(–12)	HeI/II	14	10	+	–	–	–	±	sim.	wr
–	+	300	p	–	(1–) 2(– 6)	HeII	13	6	–	+	+	–	±	–	–
–	–	1300	p, u	–	(1–) 4(–12)	HeII	6	6–25	–	±	–	+	+	± dr	?
–	–	675	p, t	–	(1–) 3(–12)	HeI/II	10	6	–	+	+	±	+	sim.	wr, pc
±	±	1140	p, (sh)	–	(1–) 6(–20)	HeII	5	6	–	+	+	+	+	sim.	wr, pc
±	±	985	p	–	(1–) 5(–12)	HeII	5	3–60	–	±	+	±	+	sim; dr	wr

t = tile wood-ray cell
tg. = tangential
u = upright wood-ray cell
wr = wood-ray parenchyma

Wood-ray type classified according to Kribs (1935):
He = heterogeneous wood rays; procumbant and upright cells are present
Ho = homogeneous wood rays; only procumbent or only upright cells are present
I = uniseriate rays and multiseriate rays with long uniseriate tails
II = uniseriate rays and multiseriate rays with short uniseriate tails
III = only uniseriate rays are present.

LEGENDS TO THE PLATES

Plate I. Sarcolaenaceae. Transverse sections of the secondary xylem. 1. *Sarcolaena grandiflora* Dup.-Thou.; 2. *Schizolaena hystrix* R. Cap.; 3. *Rhodolaena bakeriana* H.Bn.; 4. *Leptolaena multiflora* Dup.-Thou. Growth rings absent to hardly distinct; vessels exclusively solitary; parenchyma in short, irregular, uniseriate tangential bands, but also diffuse or diffuse in aggregates and scanty paratracheal; rays uniseriate.

Plate II. Sarcolaenaceae. 5. *Eremolaena humblotiana* H.Bn., transverse section of the secondary xylem; 6, 7, and 8. *Pentachlaena latifolia* H.Perr. ssp. *orientalis* R.Cap., transverse, radial and tangential sections respectively of the secondary xylem. Note the vessels with tyloses and low uniseriate rays.

Plate III. Rhopalocarpaceae. Growth rings absent to hardly distinct; vessels exclusively solitary; parenchyma in long uniseriate tangential bands, scanty diffuse parenchyma also present; rays uni- and multiseriate; storied structure, rays excluded. 9. *Rhopalocarpus binervius* R.Cap., transverse section of the secondary xylem showing a tangential layer of traumatic gum ducts surrounded by parenchyma; 10, 11 and 12. *Dialyceras parvifolium* R. Cap. var. *coriaceum* R. Cap. forma *discolore* R. Cap., transverse, radial and tangential sections of the secondary xylem. Note in 11 and 12 the storied structure of axial parenchyma and less visible that of libriform fibres and vessel-members.

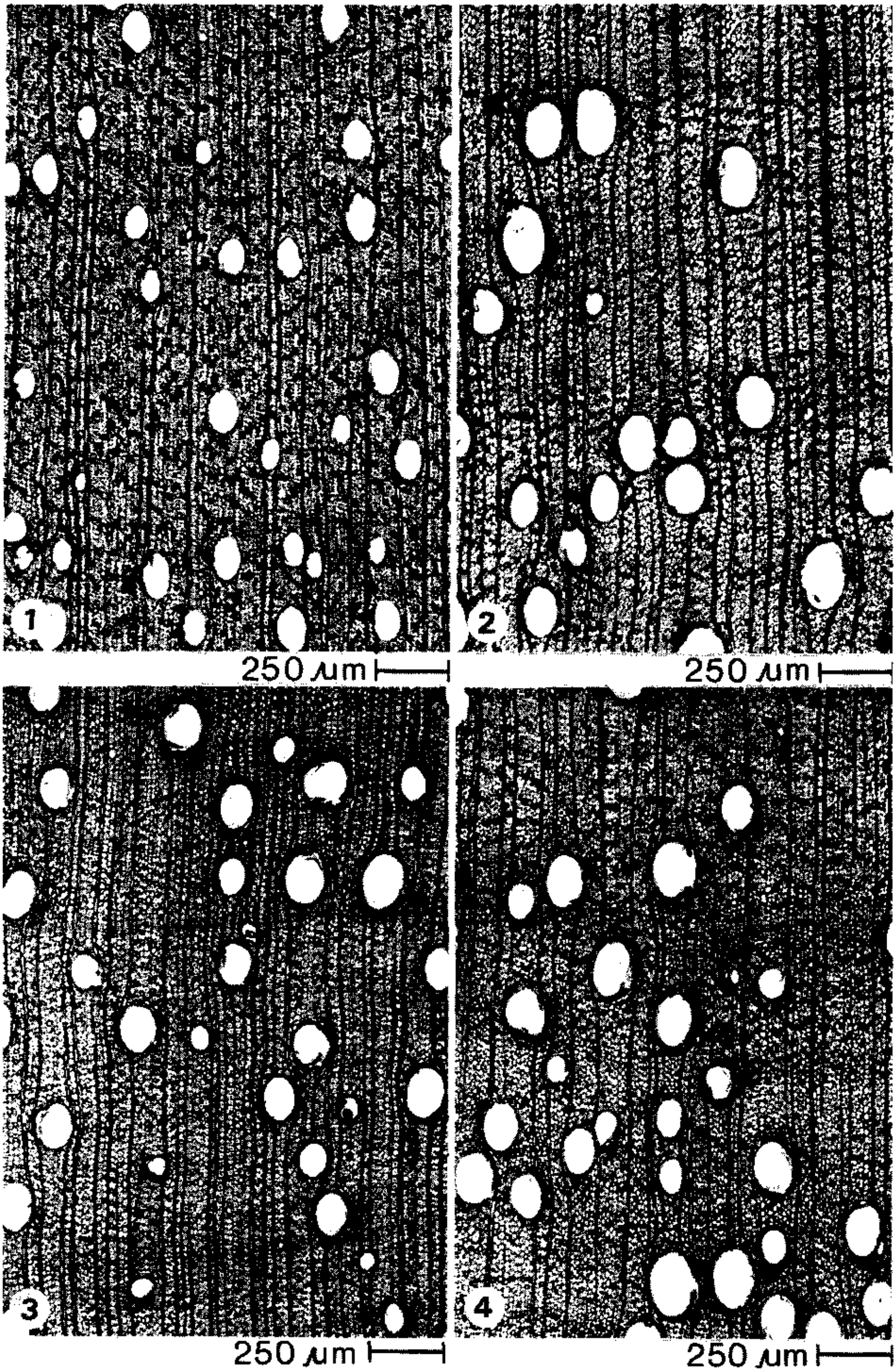

Plate I

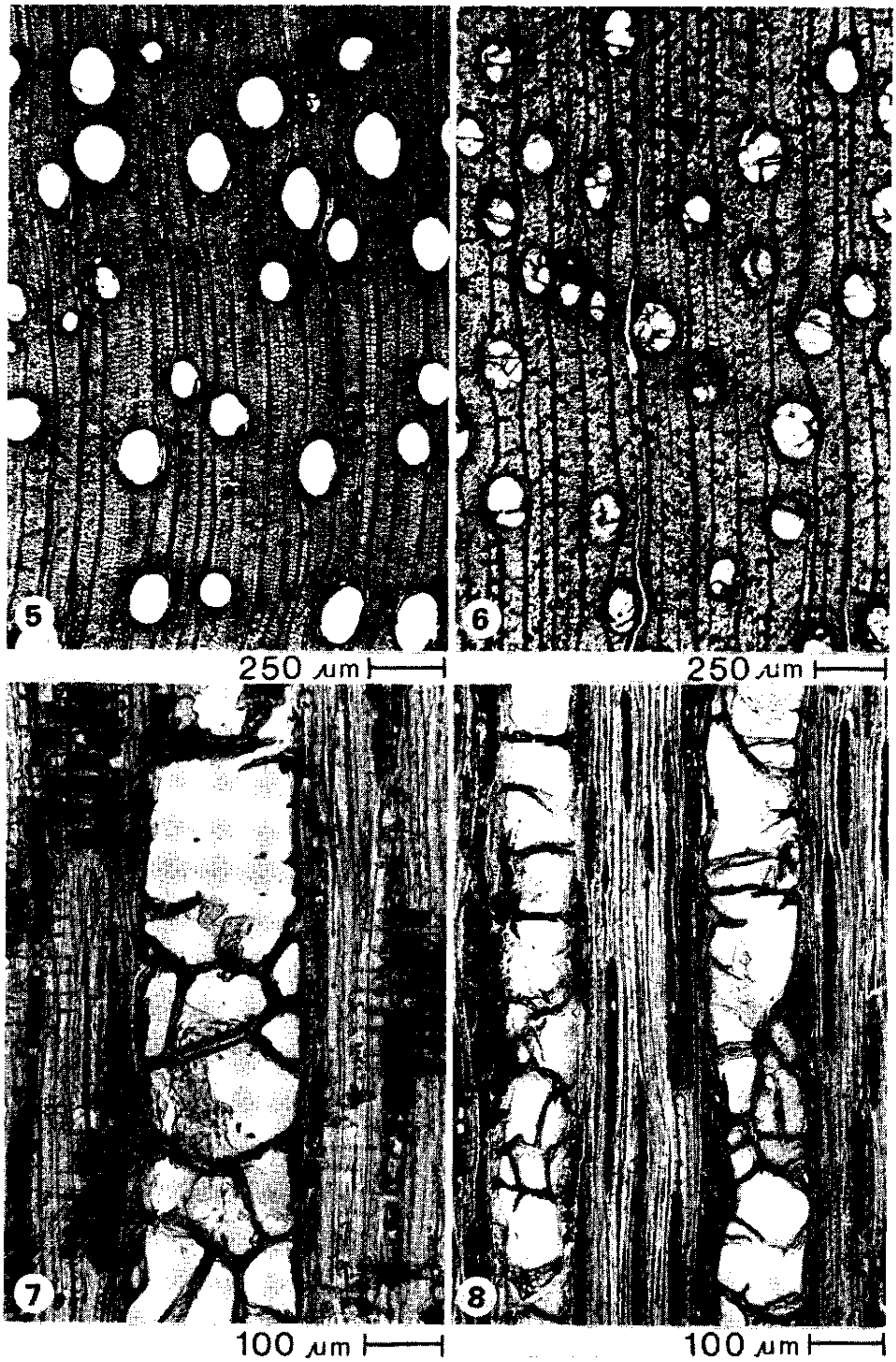

Plate II

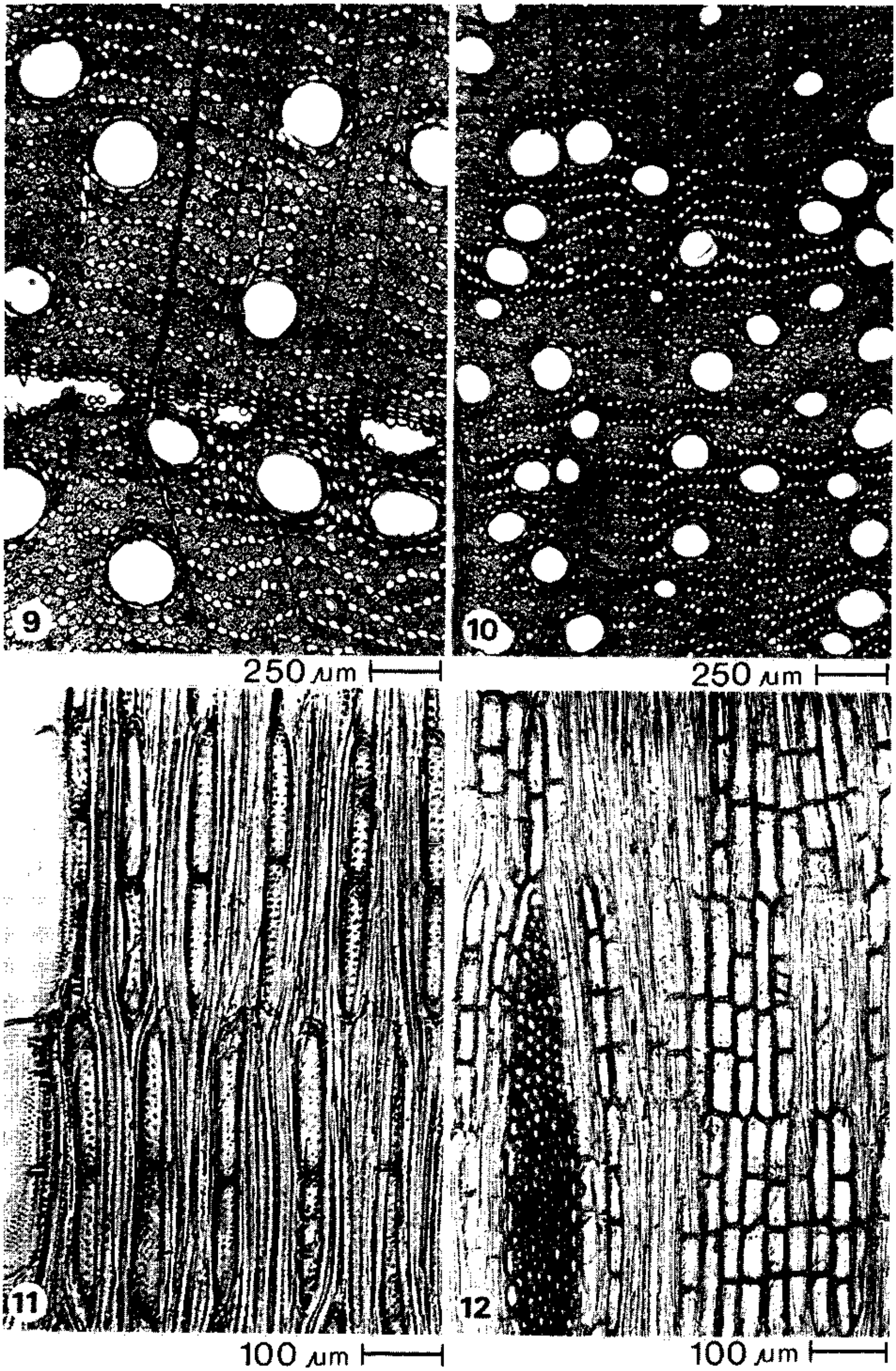

Plate III