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BARK ANATOMY OF SOME SARCOLAENACEAE AND RHOPALOCARPACEAE AND THEIR SYSTEMATIC POSITION

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Summary

The secondary phloem of some representatives of the families *Sarcolaenaceae (Chlaenaceae)* and *Rhopalocarpaceae (Sphaerosepalaceae)* endemic to Madagascar, has been compared with that of families, belonging to the orders *Bixales* and *Tiliales* (HUTCHINSON, 1973).

Considering the bark only, the two autonomous families possess affinities with the *Sterculiaceae*, *Bombacaceae* and to some extent with the *Tiliaceae* of the *Tiliales* (sensu HUTCHINSON, 1973) or *Malvales* (sensu TAKHTAJAN, 1969), not with the *Ochnales* in which they were placed by HUTCHINSON (1973).

So preference is given to TAKHTAJAN'S (1969) arrangement of the families within the *Malvales*; a position within the *Ochnales* (HUTCHINSON, 1973) seems doubtful.

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 separately in different orders, the *Sarcolaenaceae* in the *Malvales* and the *Rhopalocarpaceae* in the *Parietales (Violales, Cistales)*. Afterwards they were both arranged in the *Malvales* (for instance TAKHTAJAN, 1969) and recently together in the *Ochnales* (HUTCHINSON, 1973).

An investigation of the secondary phloem of some representatives of the two families and a comparison with some species from other families, might throw a new light on their mutual relation and systematic position.

Materials and methods

Bark samples used were from the Van Veenendaal/Den Outer collection, Madagascar (1978) and from the Versteegh/Den Outer collection, Ivory Coast, West Africa (1969). The collections are housed at the department of Botany, Agricultural University, Wageningen, The Netherlands. All the material studied is accompanied by herbarium vouchers. The samples were collected from tree stems at breast height and immediately fixed in F.A.A. Anatomical features were studied in transverse, radial and tangential sections and macerations. All sections were embedded in Kaiser's gelatin-glycerin (JOHANSEN, 1940).

Means and ranges of the length of sieve-tube members, parenchyma-cell strands and phloem fibres are based on at least twenty-five individual measurements. The ray type designations employed here are those of KRIBS (1935); the sieve-tube type, sieve-area type and companion-cell type were classified according to ZAHUR (1959), the bast type according to DEN OUTER and FUNDTER (1976).

RESULTS

The results are summarized in table 1.

The bark of the investigated *Sarcolaena multiflora* Dup.-Thou. is about 2.3 mm thick. It can be divided into three zones, i.e. the conducting secondary phloem immediately outside the cambial zone (380 µm), the nonconducting secondary phloem (ca. 1.9 mm) and finaly one periderm layer (100 µm) with U-shaped thickened phellem cell walls. The axial system of the conducting secondary phloem is composed of (2–) 3 (–5) cells wide tangential bands of phloem fibres, rather regularly alternated by (4–) 6 (–10) cells wide tangential bands of phloem-parenchyma cells, sieve tubes and companion cells.

The sieve tubes are never in contact with phloem fibres (bast type 4 mi; DEN OUTER and FUNDTER, 1976). In the nonconducting secondary phloem, the sieve tubes collapse and gradually more sclereids occur towards the periderm. Sieve tubes oval in cross-section, tangential diameter ca. 14 µm.

Sieve-tube member type I/II (ZAHUR, 1959), length (200–) 355 (–465) µm. Sieve plates compound (ca. 12 sieve areas), oblique. Sieve areas in radial walls, horizontal diameter 10 µm, type I rd (Zahur, 1959).

Companion cells type A (ZAHUR, 1959), tangential diameter 5 µm, usually situated along one of the radial walls of the sieve-tube member or in the corners.

Parenchyma cells rectangular in cross-section (tg 14, rd 9 µm), contents uniform light brown, sometimes a druse. Strands of 8 cells, length (315–) 380 (–465) µm.

Phloem fibres (680–) 820 (–970) µm long, thick walled (6 µm, hardly any lumina) with many, small, slightly bordered pits in the longitudinal walls.

Rays 14/tangential mm, uniseriate, usually composed of procumbent cells (tg 15, rd 45, lg 18 µm), marginal cells sometimes square or even upright, height (3–) 10 (–30) cells, no or hardly any dilatation in the nonconducting phloem. Cell contents uniform light brown, often a druse; when in contact with fibres secondary sclerosis of ray parenchyma cells regularly present in the nonconducting phloem.

Crystals druses, often in ray-parenchyma cells, less frequent in axial parenchym.

The following differences were found in the bark of *Sarcolaena oblongifolia* Gér., *Schizolaena hystrix* R.Cap. and *Leptolaena bojeriana* (H.Bn.) Cavaco, when compared with *Sarcolaena multiflora* Dup.-Thou. (see also table 1).

Sarcolaena oblongifolia Gér.: the tangential fibre bands and bands of sieve tubes, companion cells and parenchyma cells, are both about 5 cells wide; the average length of sieve-tube members, parenchyma-cell strands and fibres are 290, 480 and 780 μm respectively; 18 rays/tangential mm, more square and upright cells; druses occur more often in axial parenchyma than in ray-parenchyma cells.

Schizolaena hystrix R. Cap.: sieve-tube members type II/I, average length 300 μm, ca. 8 sieve areas/sieve plate; companion-cells type B (A), tangential diameter 3 μm; parenchyma-cell strands ca. 340 μm long, 6 cells/strand, often chambered crystalliferous-cell strands composed of ca. 20 cells; fibre length ca. 580 μm; 23 rays/tangential mm, uniseriate but rather often 2-seriate; druses more often in axial parenchyma than in ray-parenchyma cells.

Leptolaena bojeriana (H. Bn.) Cavaco: sieve-tube member type II/I, average length 300 μm, ca. 10 sieve areas/sieve plate; companion-cells type B; parenchyma-cell strands ca. 415 μm long, 6 cells/strand; fibre length ca. 579 μm; 18 rays/tangential mm, much more square and upright cells present; the presence of druses, secondary sclerosis, sclereids, brown cell contents, is much less frequent than in the other three species.

The bark of the investigated *Rhopalocarpus lucidus* Bojer is about 3.6 mm thick, composed of conducting secondary phloem (280 μm), nonconducting secondary phloem (3.1 mm) and one periderm layer (250 μm).
Transverse sections show triangular fibrous portions with the apices directed outwards, alternated with triangular non-fibrous portions (rays) with the apices directed inwards: *Tilia*-dilatation type of the phloem rays. Sclereids absent or scarcely present. Storied structure present of all elements except rays.
The axial system of the conducting secondary phloem is composed of ca. 5 cells wide tangential bands of phloem fibres, regularly alternated by 5–8 cells wide tangential bands of phloem-parenchyma cells, sieve tubes and companion cells.

The sieve tubes are never in contact with the fibres (bast type 4 mr). In the nonconducting secondary phloem usually only one tangential layer of large parenchyma cells remain alive between the phloem-fibre layers; the other cells are collapsed. The phellem of the one periderm layer present is composed of bands of in cross-section rectangular cells with thick tangential walls, alternated with one cell wide tangential layers of rectangular, thin-walled cells with brown contents. The phelloderm cells are parenchymatous often containing a crystal. Sieve tubes rectangular or oval in cross-section (tg 25, rd 16 μm).

Sieve-tube member type II, length (215–) 240 (–265) μm. Sieve plates compound (ca. 5 sieve areas), oblique. Sieve areas in the radial walls, horizontal diameter 8 μm, type II rd.

Companion-cells type B, tangential diameter 7 μm, usually situated along one of the radial walls of the sieve-tube member or in the corners.

Parenchyma cells rectangular in cross section (tg 23, rd 10 μm). Strands of (2–)4(–7) cells, length ca. 250 μm. Contents often a styloid but also cubical crystals, in the dilatation area often with cubical crystals and sometimes brown substances.

Phloem fibres ca. 1640 μm long, with a gelatinous layer and some small simple pits with vertical inner apertures in the longitudinal walls of the middle thicker part of the fibre (storied structure).

Rays 3/tangential mm, (1–) 8 (–30) seriate, composed of procumbent cells with or without short uniseriate marginal parts of sometimes square cells; average width 125 µm, height 730 µm; aggregates regularly present; contents cubical crystals, very abundant in the dilatating parts. Cambium often bend outwards in large rays.

Crystals abundant, cubical in ray- and sometimes axial parenchyma cells, styloids in axial parenchyma.

Rhopalocarpus coriaceus (Sc. Elliot) R. Cap. differs from *R. lucidus* Bojer, on the following points.

Basttype 4 mi, in which every other (1–) 3 (–5) cells wide tangential fibre band is replaced by a 3 cells wide tangential band composed of large parenchyma cells with brown contents. The tangential bands parenchyma cells, sieve tubes and companion cells are arranged as follows: in the middle ca. 4 cell-layers sieve tubes and companion cells, flancked by 1–2 cells wide tangential layers small parenchyma cells against the fibres often with a styloid but without brown contents.

Sieve tubes smaller, irregular to oval in cross-section (tg 21, rd 13 µm); sieve-tube member length (225–) 265 (–300) µm. Sieve plates compound (ca. 4 sieve areas) or simple, almost horizontal. Sieve areas in the radial walls smaller, 4 µm.

Parenchyma cells with brown contents rectangular to oval in cross-section (tg 23, rd 15 µm), those without brown contents but with styloids, smaller.

Rays (1–)6(–15) seriate, average width 100 µm, height 480 µm; contents many styloids and some cubical crystals. Cambium not undulated.

Crystals abundant, styloids in ray- and axial parenchyma cells; cubical crystals less frequent in rays.

Discussion

The *Sarcolaenaceae* is represented by 8 genera with 33 species (Cavaco, 1952), or by 10 genera with 34 or 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 systematic position of the family is still uncertain. Dupetit-Thouars (1806) considered the family to be allied to the *Malvaceae* or *Tiliaceae*. Cavaco (1952) states that the heterogeneous polyphyletic family derived from the *Theaceae* and *Tiliaceae*. Carlquist (1964) concludes that the group is probably related to the *Tiliaceae* and that palynological evidence does not support the suggestion of Cavaco (1952) of polyphyletic origins of the family. Hutchinson's (1969) opinion is that the family shows no very close relationship with any other, except *Dipterocarpaceae* (also Metcalfe and Chalk, 1950) and that anatomy helps little in determining the taxonomic position of this peculiar small family. CAPURON (1970) suggests that the homogeneous monophyletic family is derived from mutual ancestors of the *Malvales*, *Theales*, *Guttiferales*, *Terebinthales* and *Parietales (Violales, Cistales)*. STRAKA (1963 and 1971) gives a relationship outline of the family and associates himself with TAKHTAJAN (1969) who arranged the family in the *Malvales*.

The *Rhopalocarpaceae* are represented by 2 genera, viz. *Rhopalocarpus* with 13 species and *Dialyceras* with one species.

The systematic position of this family too still seems uncertain. Under the name *Sphaerosepalum* it was formerly placed in the *Guttiferae* by BAKER, transferred to the *Bixaceae* by WARBURG (1895) and still later to the *Cochlospermaceae* of the order *Parietales* by PILGER (1925). CAPURON (1952) was the first one who mentioned the *Rhopalocarpaceae* as a separate autonomous family. BOUREAU (1958) concludes after wood-anatomical studies of *Rhopalocarpus louvelii* (A. Danguy) R. Cap. and *Cochlospermum*, that the two are phylogenetic independent. Even if one considers only the orientation of the excretion canals, vertical and traumatic in *Rhopalocarpus* and horizontal in *Cochlospermum*, it seems justified to group the *Rhopalocarpus* species into an autonomous family (BOUREAU, 1958). CAPURON'S revision (1962) of the *Rhopalocarpaceae* reveals that the characteristics of the family are sufficient to place it within the *Malvales* (*Tiliales* and *Malvales* sensu HUTCHINSON, 1973). On the other hand the affinity with the *Bixaceae* and *Cochlospermaceae* is also present and if these two families stay close to the *Flacourtiaceae* and can be placed close to the *Malvales*, this is an other possibility (CAPURON, 1962). HUARD (1965 a and b) from a wood-anatomical point of view, also places the family close to the *Sterculiaceae* (and *Tiliaceae*) in the *Malvales* (*Tiliales* and *Malvales* sensu HUTCHINSON, 1973), although affinities remain existent with the *Ochnales* (HUTCHINSON, 1973), but above all with the *Bixaceae*.

Both the *Sarcolaenaceae* and the *Rhopalocarpaceae* are placed in the *Malvales* by TAKHTAJAN (1967). This order, evidently derived from early *Violales (Parietales)*, exhibits many features in common with the *Flacourtiaceae* of the *Violales*. Last mentioned order encloses among others the families *Bixaceae* closely related to the *Flacourtiaceae* and the *Cochlospermaceae* very near to the *Bixaceae*. Finally HUTCHINSON (1973) placed both the *Sarcolaenaceae* and *Rhopalocarpaceae* together with for instance the *Ochnaceae* and *Dipterocarpaceae* in the *Ochnales*.

It is obvious from table 1 that the investigated species of the families *Bixaceae*, *Tiliaceae*, *Sterculiaceae* and *Bombacaceae* possess many features in common; they differ clearly from the species belonging to the *Flacourtiaceae* and *Ochnaceae* (DEN OUTER, 1977). In spite of HUTCHINSON'S opinion (1967) that there is tangible difference between the *Tiliaceae* and *Sterculiaceae* and a future monographer might combine them into one, the *Tiliaceae* is undoubtedly the most primitive of the alliance. It is probably possible to distinguish two groups, viz. the *Bixaceae* and *Tiliaceae* along with the *Sterculiaceae* and *Bombacaceae*. The last mentioned more homogeneous group differs from the *Bixaceae* and *Tiliaceae*,

on the following points:
the rays are wider, with an abundance of druses; crystalliferous cells with cubical crystals against the tangential fibre layers, seldom occur; usually sieve-area type II instead of III; the average length of the axial elements is somewhat shorter.

Within the *Sterculiaceae*, *Buettneria* and *Dombeya* are different because they usually possess uniseriate rays (or He I which are much higher) joining the storied structure and crystalliferous cells with cubical crystals are present against the tangential fibre layers. Also *Scaphopetalum*, *Theobroma* and *Waltheria* deviate because the tangential layering of the bark is very irregular, storied structure is absent, compound sieve plates are present (*Scaphopetalum* and *Theobroma*) or He I-rays (*Waltheria*).

Within the *Bombacaceae*, *Ochroma* deviates because storied structure is absent, sieve plates are compound (sieve-tube type II/I) and the sieve areas in the longitudinal walls belong to type I.

The *Rhopalocarpaceae* could be easily arranged closely to the *Sterculiaceae* and *Bombacaceae*, however compound sieve plates occur, like homogeneous rays and cubical crystals or styloids instead of druses.

The *Sarcolaenaceae* also has similarities with the *Sterculiaceae* (especially *Scaphopetalum* and *Theobroma* of the more advanced tribe *Theobromeae*, HUTCHINSON, 1967) and *Bombacaceae* (especially *Ochroma* belonging to the more primitive tribe *Matisieae*, closely related to the *Sterculiaceae*, HUTCHINSON, 1967). But possibly also some affinities are present via the *Tiliaceae* (small rays; regularly without a storied structure) with the *Flacourtiaceae*. Common characteristics of *Sarcolaenaceae* and *Flacourtiaceae* are absence of a storied structure, compound sieve plates, rather small rays which do not dilatate according to the *Tilia*-type; on the other hand the bast type is totally different.

So considering the secondary phloem only, both the autonomous families *Rhopalocarpaceae* and *Sarcolaenaceae* possess affinities with *Sterculiaceae* and *Bombacaceae*, possibly *Tiliaceae* of the *Tiliales* (HUTCHINSON, 1973) or *Malvales* (TAKHTAJAN, 1969); but also, the *Sarcolaenaceae* may be more than the *Rhopalocarpaceae*, in some extent with the *Bixaceae* and *Flacourtiaceae* of the *Bixales* (HUTCHINSON, 1973) or *Violales* (*Cistales;* TAKHTAJAN, 1969). A position of the families within the *Ochnales*, as proposed by HUTCHINSON (1973), seems doubtful from a bark anatomical standpoint. Preference is given to TAKHTAJAN'S (1969) arrangement within the *Malvales*.

References

CAPURON, R. (1952). Rhopalocarpacées. In H. Humbert: Flore de Madagascar et des Comores **127**: 1–42. Paris.

CAPURON, R. (1962). Révision des Rhopalocarpacées. Adansonia **2** (2): 228–267.

CAPURON, R. (1970). Observations sur les Sarcolaenacées. Adansonia **10** (2): 247–265.

CARLQUIST, S. (1964). Pollen morphology and evolution of Sarcolaenaceae (Chlaenaceae). Brittonia **16** (3): 231–254.

CAVACO, A. (1952). Recherches sur les Chlaenacées, famille endemique de Madagascar Mém. Inst. Sc. Madagascar, sér. B, **4**: 52–92.

BOUREAU, E. (1958). Contribution a l'étude anatomique des espèces actuelles de Rhopalocarpaceae. Bull. Mus. Hist. Nat., 2e ser., **30** (2): 213–221.

DUPETIT-THOUARS, A. DU (1806). Chlaenaceae. In: Histoire des végétaux recueillis dans les îles australes d'Afrique: 32–48. Levrault, Schoell et Co., Paris.

HUARD, J. (1965a). Anatomie des Rhopalocarpacées. Adansonia **5** (1): 103–123.

HUARD, J. (1965b). Remarques sur la position systématique des Rhopalocarpacées d'après leur anatomie et leur morphologie pollinique. Bull. Soc. Bot. Fr. **112**: 252–254.

JOHANSEN, D. A. (1940). Plant microtechnique. McGraw-Hill Book Company Inc., New York and London, 523 p.

KRIBS, D. A. (1935). Salient lines of structural specialization in the wood rays of dicotyledons. Bot. Gaz. **96**: 547–557.

METCALFE, C. R. & L. CHALK (1950). Anatomy of the dicotyledons. I. Clarendon Press, Oxford.

OUTER, R. W. DEN (1977). The secondary phloem of some Ochnaceae and the systematic position of Lophira lanceolata v. Tieghem ex Keay. Blumea **23**: 439–447.

OUTER, R. W. DEN & J. M. FUNDTER (1976). The secondary phloem of some Combretaceae and the systematic position of Strephonema pseudocola A. Chev. Acta Bot. Neerl. **25** (6): 481–493.

PILGER, R. (1925). Cochlospermaceae. In A. Engler und K. Prantl: Die natürlichen Pflanzenfamilien, ed. 2, **21**: 320. Leipzig.

HUTCHINSON, J. (1967). The genera of flowering plants. Dicotyledons, Vol. II. Clarendon Press, Oxford, 659 p.

HUTCHINSON, J. (1969). Evolution and phylogeny of flowering plants. Academic Press, London and New York, 717 p.

HUTCHINSON, J. (1973). The families of flowering plants. Third edition. Clarendon Press, Oxford, 968 p.

STRAKA, H. (1963). Betrachtungen zur Phylogenie der Sarcolaenaceae (Chlaenaceae) Ber. Dtsch. Bot. Ges. **76**: 55–62.

STRAKA, H. (1971). Über das System der madagassichen Sarcolaenaceae. Ber. Dtsch. Bot. Ges. **84**: 731–735.

TAKHTAJAN, A. (1969). Flowering plants, origin and dispersal. Oliver and Boyd, Edenburgh, 310 p.

WARBURG, O. (1895). Bixaceae. In A. Engler und K. Prantl: Die natürlichen Pflanzenfamilien, ed. 1, **III**, 6: 307–314. Leipzig.

ZAHUR, S. (1959). Comparative study of secondary phloem of 423 species of woody dicotyledons belonging to 85 families. Agr. Exp. St. Mem. 358, 160 p.

Legends to table 1.

V & O No.	=	number of the bark sample and corresponding herbarium material of the Van Veenendaal and Den Outer collection, Madagascar, 1978, and the Versteegh and Den Outer collection, Ivory Coast, 1969.
dbh	=	diameter at breast height of trees, or diameter of basal parts of shrubs
bast type 4 mr	=	orderly sequence in four, multiseriate, regular: fibres-parenchyma cells – sieve tubes – parenchyma cells – fibres...
4 mi	=	orderly sequence in four, multiseriate, irregular: fibres – parenchyma cells – sieve tubes – parenchyma cells... fibres...
4 m$\underline{i}$	=	4 mi, but very irregular
2 ui	=	orderly sequence in two, uniseriate, irregular: parenchyma cells – sieve tubes – parenchyma cells...
s	=	sieve tubes scattered in ground tissue of parenchyma cells
g	=	sieve-tube groups scattered in ground tissue of parenchyma cells
r	=	rays
m.r.	=	multiseriate rays
+	=	present
–	=	absent

sieve-tube type, classified according to Zahur (1959):

I	=	sieve tubes are essentially long (> 500 μm), with very oblique sieve plates with 10 or more sieve areas. When the number of sieve areas is extremely variable, or when the sieve areas are very closely placed, the plate length and the angle of inclination were relied upon as defining features
II	=	intermediate between types I and III
III	=	sieve tubes are short (100–300 μm) with slightly oblique to transverse, simple sieve plates
obl. c–4 and s	=	oblique sieve plates, compound, with 4 closely placed sieve areas but also simple sieve plates present

sieve-area type, classified according to Zahur (1959):

I	=	many, well developed sieve areas on the side walls, equally spaced. They are well developed when they are rounded and of approximately the same shape and size as the sieve areas on the sieve plate
II	=	a small number rather poorly developed sieve areas on the tangential (tg) or radial (rd) side walls, unequally spaced or diffuse
III	=	sieve areas on the side walls entirely absent or obscure

companion-cell type, classified according to Zahur (1959):

A	=	the companion cells are much shorter than the sieve-tube elements and usually occur single
B	=	the companion cells are as long as the sieve-tube elements they accompany
C	=	the companion cells are as long as the sieve-tube elements, but are septated to form a strand of cells so that more than one companion cell accompanies each sieve-tube member
crystals (cr.)		c = cubical; dr = druse; st = styloid

phloem-ray type, classified according to Kribs (1935):

He	=	heterogeneous phloem rays, procumbent and upright cells are present
Ho	=	homogeneous phloem 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

PC	=	parenchyma cell
Ph F	=	phloem fibre
Ph R	=	phloem ray

TABLE 1. Secondary phloem characters of the investigated species.

Specimen studied	V & O No.	dbh cm	bast type	storied structure	sieve tube					comp. cell
					type	av. member length µm	sieve plates	hor. diam. s.a. in lg. walls µm	type sieve area	type
Rhopalocarpaceae										
Rhopalocarpus coriaceus (Sc. Elliot) R. Cap.	1168	40	4 mi	+ (r. exc.)	II	265	obl. c-4 and s	4	IIrd	B
Rhopalocarpus lucidus Bojer	1090	25	4 mr	+ (r. exc.)	II	240	obl. c-5	8	IIrd	B
Sarcolaenaceae										
Leptolaena bojeriana (H. Bn.) Cavaco	1012	15	4 mi	–	II(I)	300	obl. c-10	8	Ird	B
Sarcolaena multiflora Dup.-Thou.	1167	10	4 mi	–	I(II)	355	obl. c-12	10	Ird	A
Sarcolaena oblongifolia Gér.	1171	6	4 mi	–	I(II)	290	obl. c-12	11	Ird	A (B)
Schizolaena hystrix R. Cap.	1173	20	4 mi	–	II(I)	300	obl. c-8	9	Ird	B (A)
Bombacaceae										
Adansonia digitata L.	301	150	4 mr	+ (r. exc.)	III(II)	420	± hor. s	8	II	B
Adansonia fony H. Bn.	1091	100	4 mi	+ (r. exc.)	III(II)	440	± hor. s	9	IIrd	B
Bombax glabra (Pasq.) Robyns	401	30	4 mi	+ (r. ±)	III(II)	470	± hor. s	8	II	B
Ceiba pentandra (L.) Gaertn.	161	40	4 mi	± (r. exc.)	III(II)	295	± hor. s	10	II	B
Ochroma lagopus Sw.	683	80	4 mr	–	II(I)	530	obl. c-8	13	I	B
Sterculiaceae										
Buettneria biloba H. Bn.	1011	3	4 mi	+ (r. ±)	III	250	± hor. s	5	II	B
Cola buntingii Bak. f.	777	10	4 mi	± (r. exc.)	III	305	± hor. s	6	IIrd	B
Cola caricaefolia (G. Don) K. Schum.	546	7	4 mi	+ (r. exc.)	III	360	± hor. s	6	IIrd	B
Cola clamydantha K. Schum.	676	20	4 mi	+ (r. exc.)	III	230	± hor. s	6	IIrd	B
Cola gigantea A. Chev.	299	40	4 mi	+ (r. exc.)	III	290	± hor. s	9	II	B
Cola cf. gigantea A. Chev. var. glabrescens Brenan et Keay	498	20	4 mi	+ (r. exc.)	III	320	± hor. s	9	II	B
Cola lateritia K. Schum. var. maclaudii Brenan et Keay	697	30	4 mi	± (r. exc.)	III	320	± hor. s	6	II	B
Cola laurifolia Mast.	362	60	4 mi	+ (r. exc)	III	245	hor. s	6	II	B
Cola millenii K. Schum.	331	10	4 mi	+ (r. exc.)	III	335	± hor. s	6	II	B
Cola nitida (Vent.) Schott. et Endl.	20	40	4 mi	+ (r. exc.)	III	350	hor. s	6	II	B
Cola reticulata A. Chev.	660	2	4 mi	± (r. exc.)	III	260	± hor. s	6	IIrd	C ?
Dombeya mandenensis J. Ar.	1146	10	4 mi	+ (r. ±)	III	270	± hor. s	4	II	B
Heritiera utilis (Sprague) Sprague	781	60	4 mi	+ (r. exc.)	III	290	hor. s	9	IIrd	B
Mansonia altissima (A. Chev.) A. Chev.	591	25	4 mi	+	III	305	± hor. s	6	IIrd	B
Scaphopetalum amoenum A. Chev.	738	6	4 mi	–	II	435	obl. c-4 and s	3	II-III	B-A
Sterculia setigera Del.	340	25	4 mi	+ (r. exc.)	III	335	hor. s	3	II	B
Sterculia tragacantha Lindley	336	25	4 mi	+ (r. exc.)	III	360	hor. s	9	II	B
Theobroma cacao L.	256	15	4 mi	–	II	405	obl. c-2 and s	6	II	B
Triplochiton scleroxylon K. Schum.	129	200	4 mi	+ (r. exc.)	III	275	± hor. s	17	IIrd	C

nechanical tissue				phloem-parenchyma cell		phloem-ray		further information
iv. ibre ength im	stone cells	crys-tals	crystal-cell strand µm; number	av. length of strand µm	av. number cells per strand	type	max. number of rows (av.)	
950	±	st&c	var.	265	4	HoII	15 (6)	r. cells procumbent; st. in PhR and PC, c. in PhR
640	±	st&c	var.	250	4	HoII	30 (8)	r. cells procumbent; st. in PC, c. in PhR and PC
570	+	dr	var.	415	6	HeIII	1	r. cells often upright; dr. not abundant in PhR and PC
820	+	dr	var.	380	8	He(Ho)III	1	r. cells usually procumbent; dr. abundant in PhR, sometimes in PC
780	+	dr	var.	480	8	He(Ho)III	1	r. cells usually procumbent; dr. in PC, less often in PhR
580	+	dr	380; 20	340	6	He(Ho)III	2 (1)	r. cells usually procumbent; dr. in PC, less often in PhR
100	?	dr	var.	490	4	HeII	8 (6)	r. cells often procumbent
120	?	dr	var.	440	4	HeII	12 (8)	
360	+	dr	var.	490	8	HeII	6 (3)	r. cells often procumbent; stone cells in dilatating PhR
450	+	dr	var.	380	8	HoII	12 (6)	r. cells procumbent; marginal cells ± upright; stone cells in dilatating PhR
270	±	dr	var.	795	8	HeII	11 (6)	slime cells in PhR
10	–	c	270; 18	265	4(–6)	HeI(III)	5 (1)	c. crystals in PC; many slime tubes
95	+	dr	var.	320	4	HeII	11	r. cells often procumbent; very much dr. in PhR
05	±	dr	var.	390	4	HeII	9	r. cells often procumbent; many dr. in PhR
85	±	dr	var.	350	4	HeII	13	r. cells often procumbent with dr.; brown cont. in some PC; slime cells
95	–	dr	var.	305	4	HeII	12	idem; brown cont. in PC; slime cells
95	–	dr	var.	320	4(–6)	HeII	11	idem; brown cont. in PC; slime lumina
40	–	dr	var.	350	4	HeII	11	idem; brown cont. in PC; slime lumina
60	–	c&dr	var.	260	4	HeII	12	r. cells often procumbent with c. cr. and some dr.; brown cont. in PC; slime lumina
95	±	dr	var.	350	4	HeII	11	r. cells often procumbent with dr.; slime lumina
75	–	dr	var.	350	4	HeII	12	r. cells often procumbent with dr.; brown cont. in PC; slime lumina
95	–	dr	var.	275	4	HeII	10	large gum- or slime cells
20	–	c	265; 17	270	4	HeI(III)	3 (1)	c. cr. in PC.
50	–	c	var.	290	4(–6)	HeII	13	r. cells often procumbent; c. cr. or brown cont. in PC; slime cells
60	–	dr	var.	335	4	HeII	4	dr. in PhR; a few slime cells
75	–	c	var.	520	4	HeII	10	
40	±	c&dr	340; 10	350	4	HeII	18	r. cells often procumbent with a few cr.; PC with c. cr., sometimes brown cont.
05	+	dr	var.	375	4(–6)	HeII	13	r. cells often procumbent with dr.; a few dr. and some brown cont. in PC
60	–	c&dr	var.	435	4	HeII	10	r. cells often procumbent with cr.; PC with cr. and brown cont.
70	–	c&dr	var.	320	4	HeII	9	many dr., some c. cr. in PhR; large gum- or slime cells

TABLE 1. Secondary phloem characters of the investigated species

Specimen studied	V & O No.	dbh cm	bast type	storied structure	sieve tube type	sieve tube av. member length µm	sieve tube sieve plates	sieve tube hor. diam. s.a. in lg. walls µm	sieve tube type sieve area	comp. cell type
Waltheria indica L.	149	5	4 mi	–	III	290	± hor. s	3	II	B
Tiliaceae										
Christiana africana DC.	214	6	4 mr	+	III	305	obl. s	3	IItg	B
Clappertonia ficifolia (Willd.) Decne	159	5	4 mr	–	II-III	405	± hor. s	4	II	B
Desplatsia chrysochlamys Mildbr. et Burret	114	5	4 mr	±	III	350	± hor. s	–	III	B-A
Duboscia viridifolia (K. Schum.) Mildbr.	578	50	4 mr	+	III	350	± hor. s	–	III	B
Glyphaea brevis (Spreng.) Monachino	12	5	s	–	III	320	± hor. s	–	III	B
Grewia carpinifolia Juss.	289	3	4 mr	+ (r. exc.)	III	260	± hor. s	–	III	B-A
Grewia hookerana Exell et Mendonca	662	6	4 mi	–	II	550	obl. c-3	6	II	B
Grewia malacocarpa Mast.	264	5	4 mi	± (r. exc.)	II	420	obl. c-3 and s	6	IItg	B
Grewia mollis Juss.	298	10	4 mi	+ (r. exc.)	III	205	± hor. s	–	III	B
Nesogordonia papaverifera (A. Chev.) R. Cap.	243	30	4 mi	+	III	305	± hor. s	–	III	B
Flacourtiaceae										
Caloncoba brevipes Gilg	753	10	s	–	II	420	obl. c-4	6	IItg	A
Caloncoba echinata (Oliv.) Gilg	670	8	s/2ui	–	III	350	± hor. s	6	IItg	A ?
Casearia inaequalis Hutch. et Dalz.	644	20	s	–	I	785	obl. c-10	–	III	C
Dasylepis cf. brevipedicellata Chipp	225	10	s/2ui	–	II	495	obl. c-6 and s	–	III	C
Flacourtia flavescens Willd.	288	7	g	–	III	260	± hor. s and c	–	III	A
Homalium patoklaense Aubrév. et Pellegr.	203	20	g	–	I	740	obl. c-10	7	IItg	C
Lindackeria dentata (Oliv.) Gilg	16	15	s/2ui	–	III	380	± hor. s	–	III	A
Oncoba spinosa Forsk.	499	?	g	–	III	350	± hor. s	9	IItg	A
Trichostephanus acuminatus Gilg	deW. 8000	?	g/s	–	I	455	obl. c-9	–	III	C?
Bixaceae										
Bixa orellana L.	692	8	4 mi	+ (m.r. exc.)	III	235	± hor. s	2	III	B (

v. bre ngth m	stone cells	crys- tals	crystal- cell strand µm; number	av. length of strand µm	av. number cells per strand	type	max. number of rows (av.)	further information
echanical tissue				phloem-parenchyma cell		phloem-ray		
150	–	c&dr	var.	350	4(–6)	HeI	7	r. cells often upright with brown cont.; a few cr. in PhR and PC
150	–	dr	var.	305	4(–5)	HeII	4 (2)	r. cells often upright; with dr.
20	–	dr	var.	405	6	HeII	4 (1)	r. cells often upright and brown cont.; a few dr.; PC often with brown cont.
75	–	c&dr	var.	360	4	HeII	5 (1)	r. cells often upright, with cr.
150	+	c&dr	var.	360	6	HeII	5	r. cells often procumbent, with brown cont. and dr.; c. cr. in PC against PhF
?	–	dr	var.	375	4	HeII	5	r. cells often upright, with dr.; a few PhF
65	–	c	var.	275	4	HeII	5	r. cells often upright; c. cr. in PC against PhF; many large slime lumina
35	+	dr	var.	580	9	HeII	9	r. cells often upright, with dr.
10	+	c	var.	435	8	HeII	8	PhR high, with c. cr.
15	–	c	205; 12	205	4(–5)	HeII	7	r. cells with c. cr.; c. cr. in PC against PhF, brown cont.; many large slime lumina
10	±	c	305; 16	305	4(–6)	HeII	4	r. cells often procumbent; c. cr. in PC against PhF, brown cont.; slime lumina
05	+	c&dr	var.	640	5	He(Ho)II	3	r. cells upright, with dr.; PC with c.cr. and often brown cont.
60	+	dr	var.	520	5	HeI	4	r. cells often upright, often with dr.
–	+	c&dr	var.	840	8	HeI	5	dr. in r. cells, c.cr. or brown cont. in PC.
–	+	c&dr	var.	695 (580)	6(3)	HeII	5	dr. in r. cells, c. cr. in PC against stone cells; orange cont. in shorter PC.
–	+	c	var.	300	4	HeI	3	r. cells often upright, very many c. cr.; in PC sometimes a cr.
–	+	c&dr	var.	770	13	HeI	5	r. cells often procumbent, often a dr.; in PC sometimes a c. cr.
–	+ (ag-gr.)	dr	var.	520	4	HeI	7	dr. often in r. cells, sometimes in PC.
–	+ (ag-gr.)	c.	var.	520	7	HeI	3	
±	+	c	var.	880	6	HoII	6	r. often 1- or 3-seriate, upright cells, cr.; some PC with cr. or brown cont.
0	–	–	–	290	4	HeI	5(1)	r. cells often with red-brown cont.