

# Anatomical structure of barks in Neotropical genera of Annonaceae

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The bark anatomy of 32 Neotropical genera of Annonaceae was studied. A family description based on Neotropical genera and a discussion of individual bark components are presented. Selected character states at the family and genus levels are surveyed for identification purposes. This is followed by a discussion on the taxonomical and phylogenetic relevance of bark characters according to a phylogram in preparation based on molecular characters. Although the value of many bark anatomical characters turned out to be insignificant in systematic studies of the family, some features lend support to recent phylogenetic results based on morphological and molecular data sets. The taxonomically most informative features of the bark anatomy are sclerification of phellem cells, shape of fibre groups and occurrence of crystals in bark components.

**Key words:** anatomy, Annonaceae, bark, periderm, phloem, phylogeny, rhytidome, taxonomy

## Introduction

Woody members of the Annonaceae are one of the most species-rich components in the tropical rainforest. Since R.E. Fries, the foremost author on the taxonomy of the family published a series of revisions in the first half of the 20th century, many new genera and species have been collected and described from the New World tropics. The number of published species of Annonaceae worldwide exceeds 2500, with ca. 900 species in tropical and subtropical South and Central America. Because of ample new

collections and the development of some novel methods a multidisciplinary programme on Annonaceae was embarked on in 1983 at the University of Utrecht. The main goals of this project are to produce a series of new monographs for Flora Neotropica and to revise the family's classification. Within the scope of the project, a study on the surface patterns and the anatomical structure of the bark has been initiated. Only a few studies cover the variation of anatomical features and their taxonomical significance in the Annonaceae. Van Setten and Koek-Noorman (1986) investigated the leaf anatomy of the Neotropi-

cal genera. They surveyed all 38 Neotropical genera, together containing over 200 species, and showed that the family is rather homogeneous. Wood anatomy of Annonaceae has not yet been thoroughly studied. In a short note, ter Welle (1984) did stress the homogeneity of the family. However, some genera and genus groups can be distinguished based on vessel diameter, width and number of parenchyma bands and ray width (Westra & Koek-Noorman 2003).

In general, extensive anatomical surveys of bark are relatively rare compared with wood anatomical surveys, especially in the tropics. However, some studies have been published on, for instance, the family of Lauraceae (von Richter 1981). These results have been particularly beneficial at the genus level. Although the family Annonaceae is one of the most frequent arboreal groups in tropical forests and is also well-represented in wood collections, studies of its bark are fragmentary and its structure is poorly understood. Zahur (1959) surveyed barks of 423 North American woody dicotyledonous species, including three genera (five specimens) of the Annonaceae — all from the Hawaiian Islands. He focussed on the secondary phloem, paying special attention to the development and structure of sieve tube elements, companion cells and phloem fibres. Roth (1974) studied in detail four genera (five specimens) of the family Annonaceae, all from Venezuela, and showed that the phloem is very regular, strongly resembling the phloem in Boraginaceae. Roth (1981) summarised her pioneering and extensive studies on the bark and its taxonomical significance in ca. 280 species (47 families) of Neotropical origin, including four annonaceous genera. Rollet (1982) provided drawings of 14 transverse sections of bark of Annonaceae belonging to the genera *Anaxagorea*, *Cleistopholis*, *Annickia*, *Monocarpia*, *Monodora*, *Platymitra*, *Rollinia* (1 sp. each) and *Xylopia* (6 spp.). These sections clearly show the presence of funnel-formed dilatation tissue in members of the family Annonaceae. Other representative features (as viewed in transverse section) are regularly aligned square or rectangular fibre plates alternating with parenchyma, groups of sclereids, reduced formation of rhytidome and a strong smelling exudation (Roth 1974, 1981). Junikka (2003) described and analysed bark

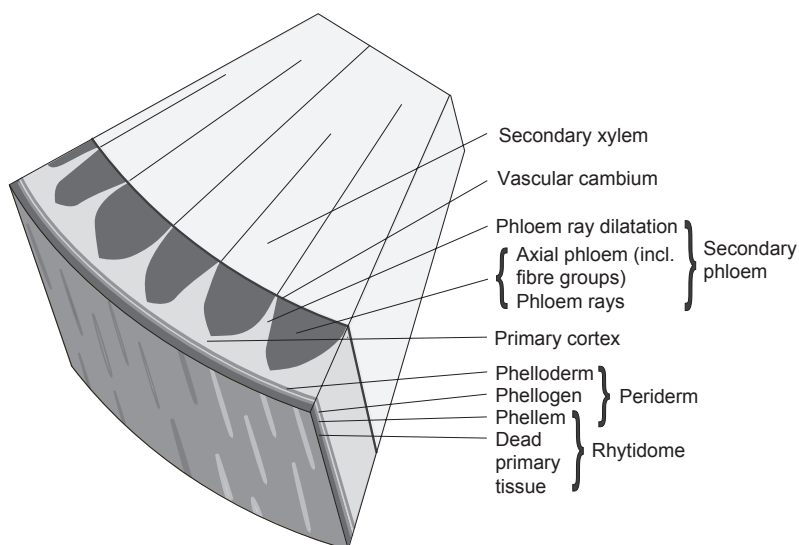
morphology and anatomy of the genus *Duguetia*, the results of which are included in this paper. The Annonaceae, although generally considered primitive in many features, offers a number of specialised anatomical features in both leaf and wood structure. The aim of this paper is to survey and describe the bark characters of the Neotropical Annonaceae and to assess their usefulness in the systematics of the family.

## Material and methods

Bark anatomical sections of 32 of the 41 genera currently recognised from the Neotropics were studied (Appendices 1 and 2). In total, 118 trees (99 species) were examined. Samples from nine genera, i.e. *Bocagea*, *Froesiodendron*, *Duckeanthus*, *Guatterrella*, *Pseudephedranthus*, *Raimondia*, *Stenanona*, *Rollinia*, and *Stenanona*, are missing. Identification of the specimens was checked by Professor Paul Maas and his co-workers. The number of studied specimens per genus varies considerably, from one (several genera) to 42 in *Duguetia*. This is partly due to much material of the last mentioned genus being recently collected in the course of a taxonomical revision of the group (Maas *et al.* 2003).

Bark material was mainly received from two sources. In 1996, the first author visited Reserva Ducke, near Manaus in Brazil, where he collected bark samples from tree trunks (RFD) and studied surface patterns in the field. Dry bark material was obtained from the National Herbarium of the Netherlands, Utrecht branch (Uw), except for one sample, which was from the Institute for Wood Biology and Wood Protection, Federal Research Centre of Forestry and Forest Products, Hamburg (RBHw).

Pieces of bark (usually including xylem) of 10 × 10 × 5 mm were placed in small glass tubes with perforated plastic caps and cooked for ca. two hours, after which the tubes were filled with polyethylene glycol (PEG 1500) and water in a 1:4 ratio. For harder bark tissues (sclereids) PEG 2000 was used. Tubes were kept in an oven at a temperature of 60 °C for three days, after which the PEG/water mixture was replaced with a pure PEG and the tubes were stored in the oven for one more day. PEG-impregnated bark samples



**Fig. 1.** Schematic drawing of part of a tree trunk showing the bark (all tissue outside the vascular cambium) and its components. Dead primary tissue consists of the remains of the primary cortex after the first periderm is formed.

were taken out from the glass tubes for sectioning. Transverse, radial and tangential sections were cut on a sliding microtome (Reichert), held together by adhesive tape to prevent fragmentation. Taped sections were rinsed with water to remove PEG and then double-stained in 1% aqueous solution of Astrablue and Acridin red-cryosidin for three to five minutes. After staining, the taped sections were transferred as such or the tape was removed using xylene and the sections were then shifted to slides. Sections were embedded in Canada balsam.

All slides are housed in the Botanical Museum, Finnish Museum of Natural History, University of Helsinki.

Terms used in the descriptions are in accordance with the terminology of the IAWA Committee (1989), Trockenbrodt (1990) and Junikka (1994). Some of the terms are indicated in Fig. 1. The data of individual specimens are given in Appendix 1.

Measurements of bark width were made at the point where the width was estimated to be average for the specimen. Often a part of the rhytidome was eroded, the result of either natural conditions or drying and storing.

Averages of values of each specimen were calculated from several measurements that included minimum and maximum values. Averages per genus were calculated by dividing the sum of minimum and maximum values of all specimens.

## Family description based on Neotropical genera

Bark surface smooth to rugose, usually with shallow fissures, rarely with scales. Lenticels frequent. Bark width 0.55–13.5 mm. Ratio of the radius of the trunk to bark width 1.2–31.8.

Rhytidome 0.09–1.75 mm thick, usually including one periderm (phellem, phellogen and phelloderm), rarely two or more. Periderm 0.05–1.30 mm thick.

Phellem mostly with more than 10 cell layers, 0.03–1.20 mm thick. Phellem of either thin-walled cells or thin-walled cells combined with U-shaped, reversely U-shaped or uniformly thickened cells, often completely sclerified — rarely with additional sclereids. Sclerified cells often in tangential bands, less often as solitary cells and/or small to large groups. Secretory cells frequent, usually as single cells or tangential bands, sometimes forming the main part of the phellem.

Phelloderm up to 0.30 mm thick, usually with 3–7 cell layers (up to 15). Mostly partly sclerified, sclereids as solitary cells or arranged in small groups, less often in tangential rows/bands. Secretory cells, when present, usually as solitary cells.

Phloem (*s. lato* incl. phelloderm, cortex and secondary phloem) 0.68–13.10 mm thick. Cortex mostly with sclereids, usually as solitary cells

and/or small to large groups, more rarely as tangential bands. Secretory cells common, less often lacking, usually as solitary cells and/or tangential bands.

Secondary phloem includes dilated rays and axial tissue with compact fibre groups in tangential bands, superposed to each other. Rays irregular to moderately straight, rarely straight or undulated, mainly irregularly dilated, more rarely funnel-formed, mostly homogeneous or obscurely heterogeneous, mainly > 1 mm high. In cross section, width of rays 2–8 cell layers, even up to 15, number of rays 1.7–6.8 mm<sup>-1</sup>; always some discontinuous rays present.

Sclereids usually present as solitary cells and/or small to large groups, rarely absent.

Secretory cells, when present, occurring as solitary cells, irregular groups or quite rarely tangential bands.

Fibre groups in the axial phloem tissue mostly wide ( $\geq 3$  cell layers) or combined with fibre groups < 3 cell layers wide; shape of fibre groups (in cross section) mostly oblong, less often a combination of square and oblong, seldom solely square; fibre groups sometimes arc-shaped. Fibre groups often accompanied by sclereids. Secretory cells, when present, occurring as solitary cells and sometimes as irregular groups or tangential bands.

Crystals of presumably calcium oxalate mostly present as prismatic crystals, rarely as spindle-shaped crystals, styloids, druses or other types, very rarely absent. Size 3–110  $\mu\text{m}$ , usually 10–30  $\mu\text{m}$ . Crystals common in all bark components, but rare in the cortex and lacking in the phellem; they are found in both sclereids and the parenchyma.

Crystals occur in association with fibre groups: around, or along the abaxial, adaxial or lateral side, more rarely between fibre groups; they are rarely found inside fibre groups. They are also seen bordering sclereid groups. Crystalliferous cells occur along fibre groups that are often chambered, usually one crystal/cell. If more, they are unequal, crystalliferous cells are rarely enlarged.

## Description of individual bark anatomical characters

### Surface patterns and bark width

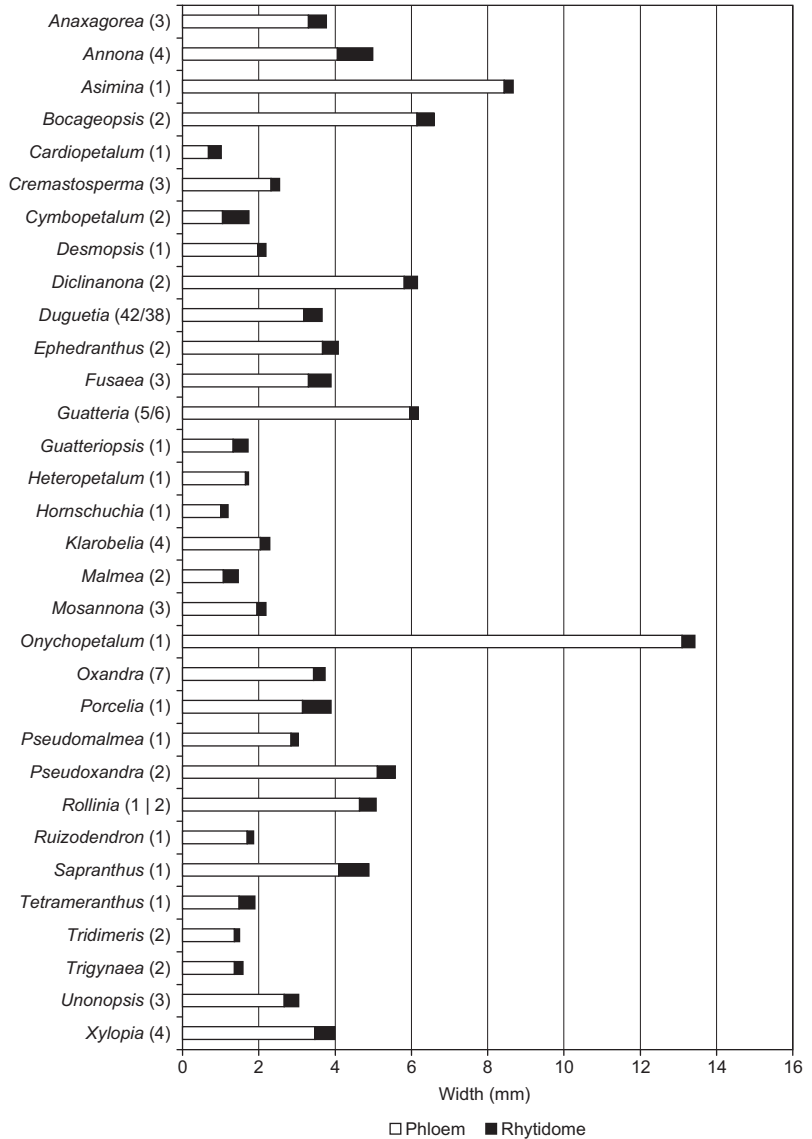
The surface pattern of the bark is the result of secondary growth, formation of phloem and external ecological factors.

In the field, the outer aspect is usually smooth to rugose. Most barks show shallow, simple, boat-shaped or oblique fissures. Rarely, barks have a scaly appearance and these scales are usually small. Lenticels are common. In some samples, the rhytidome was almost completely eroded, and the patterns consequently obscure.

A stem diameter of 10 cm is commonly regarded as an indicator of bark maturity, although variation certainly exists in the maturation process of barks of different taxa. In this study, about 30% of the specimens were collected from trunks or branches that were equal to or more than 10 cm in diameter. Another 30% of the samples were taken from stems or branches less than 5 cm in diameter.

The width of the bark, including both rhytidome and phloem, varies from 0.55 mm to 13.50 mm (Appendix 2A). This falls within all of Roth's (1981) categories, from "very thin" to "thick". Using this classification, based on 280 adult tree species from Venezuelan Guayana, almost half of the samples have a very thin bark (< 3.1 mm) and 1/3 have a thin bark (3.1–4.9 mm). Only one taxon in our study possesses a thick bark (10.1–15.0 mm) (Fig. 2). The average thickness of all sampled taxa is 3.73 mm. In 25 samples with a trunk diameter equal to or exceeding 10 cm, the average thickness of the bark is 5.14 (thick bark 5.0–10.0 mm), and in the rest ( $n = 57$ ) only 2.85. This correlation between sample diameter and bark width is mainly due to the width of the secondary phloem, as this is the main component of the bark.

The ratio of the radius of the sample to the bark width varies between 1.22 and 31.82 (Appendix 2A). The thickest barks relative to the diameter of the sample were encountered in the genera *Onychopetalum* and *Ruizodendron*, in which the ratio was smaller than 5 (Fig. 3). Relatively thin barks were found in, for instance, the genera *Anaxagorea*, *Guatteria* and *Mosannona*,



**Fig. 2.** Width of bark and its two main components in 32 Neotropical genera of Annonaceae. The number of samples studied is shown in parentheses. When two numbers are given, the first refers to the inner phloem, the second to the rhytidome.

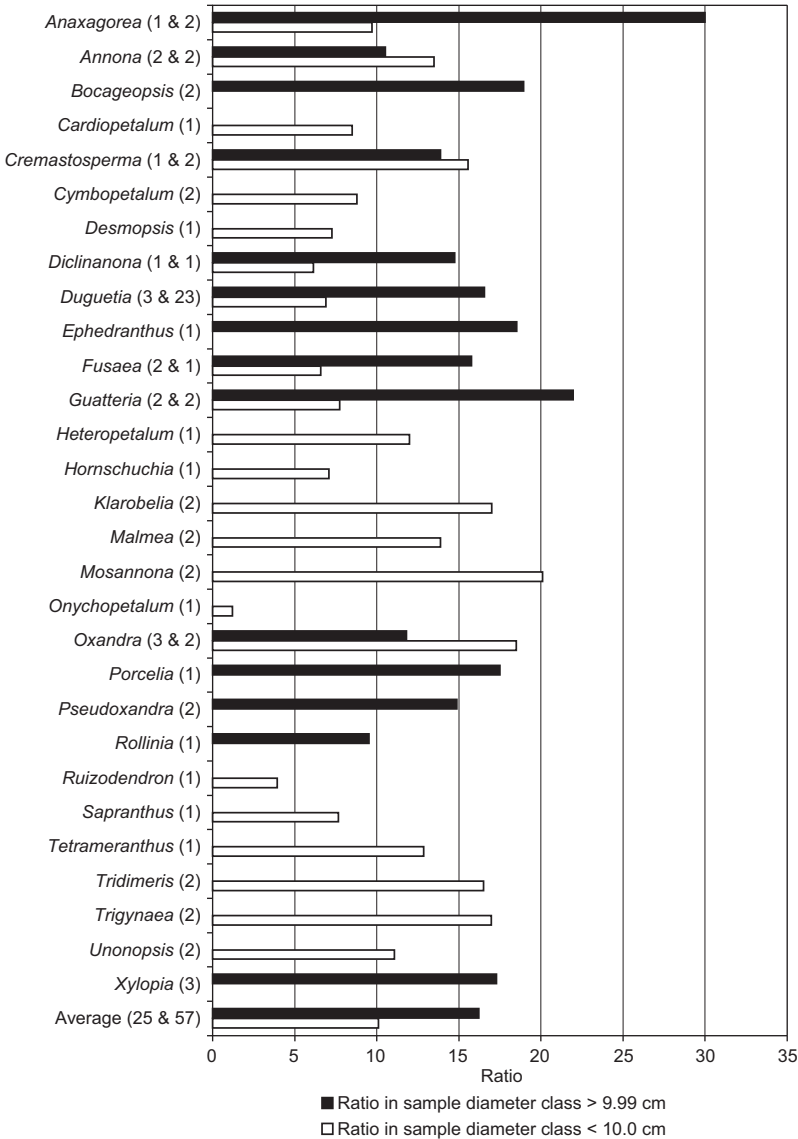
the calculated ratio lying between 20 and 30. Some values may be relatively low because the material studied is young or taken from understorey trees. The ratio tends to be higher with increasing diameter of the sample. However, no clear trend emerges.

### Rhytidome

The rhytidome is a minor component in the bark samples studied, the living part of the bark forming the major component, i.e. almost 90%

of the bark width (see Fig. 2). In only ca. 6.5% of the specimens is the rhytidome over 1 mm thick (medium-sized rhytidome, *sensu* Roth). The rhytidome is mostly composed of only one periderm with no dead phloem included. Only a few samples reveal traces of dead phloem and old phellem.

The rhytidome thickness ranges from 0.09 mm (*Heteropetalum*) to over 1.35 mm in the large trees of *Annona* (Fig. 4).



**Fig. 3.** Ratio of the radius of the sample to the bark width in two diameter classes (< 10 cm and > 10 cm) in 29 Neotropical genera of Annonaceae. The number of samples is shown in parentheses. When two numbers are given, the first refers to the upper horizontal bar, the second to the lower bar. Data for *Asimina*, *Guatteria* and *Pseudomalmea* are lacking, as the diameter of the samples is unknown.

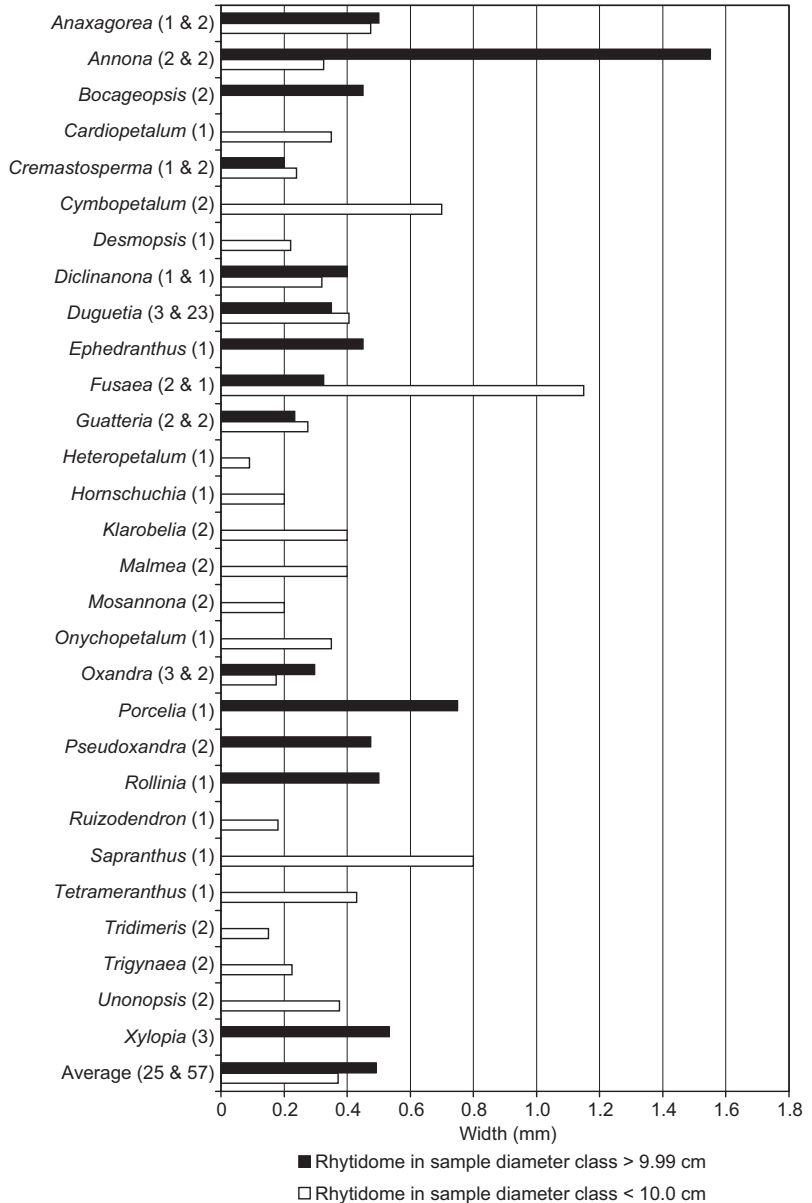
## Periderm and its components

The periderm was studied in all 32 genera. The periderm is very narrow in all genera (average 0.34 mm), varying from 0.1 in *Fusaea* and *Heteropetalum* to more than 0.6 mm for the genera of *Cymbopetalum*, *Porcelia* and *Sapranthus* (Fig. 5). However, individual samples of other genera exceeded this value: the periderm of *Annona impressivenia*, *Duguetia surinamensis* (some samples) and *Xylopia amazonica* exceeded 1 mm in width. Usually trunks of specimens with a thick periderm were over 10 cm in diameter.

However, the specimen of *Cymbopetalum brasiliense* was cut from a stem slightly over 30 mm thick, and the periderm, presumably not yet fully developed, was 1 mm thick.

The two derivatives of the phellogen are distinct when the sclerification of the cell walls is compared: in the phellem only sclerified cells (except in *Ruizodendron*) are found, whereas in the phelloderm sclereids are dominant and only rarely are sclerified cells present.

The phelloderm in all samples is less than 0.35 mm and 74.8% of the samples belong to thin phelloderms (0.01–0.09 mm, *sensu* Roth)



**Fig. 4.** Rhytidome width in 29 Neotropical genera of Annonaceae in two diameter classes (< 10 cm and > 10 cm). The number of samples is shown in parentheses. When two numbers are given, the first refers to the upper horizontal bar, the second to the lower bar. Data for *Asimina*, *Guatteria* and *Pseudomalmea* are lacking, as the diameter of the samples is unknown.

(Appendix 2C). Highest averages ( $\geq 0.10$  mm) were calculated in *Anaxagorea*, *Crematosperma*, *Diclinanona*, *Ephedranthus* and *Pseudoxandra*.

In only a few species, i.e. *Crematosperma cauliflorum*, *Duguetia calycina*, *Ephedranthus guianensis*, *Fusaea longifolia*, *Guatteria lehmannii*, *G. olivacea*, *Klarobelia cauliflora*, *Oxandra* sp. *Pseudomalmea* sp. and *Pseudoxandra lucida*, was the phellogen equal to or more developed than the phellem.

In the majority of the genera, however, it is the phellem that accounts for a considerable portion of the periderm (Fig. 5). On average, phellem of Neotropical genera are between 0.06 mm and 0.75 mm thick, and 75% of the samples belong to the class of medium-sized cork (0.10–0.50 mm, *sensu* Roth). Thick phellem, i.e. over 0.6 mm, was recorded in *Porcelia*, *Sapranthus* and *Cymbopetalum*.

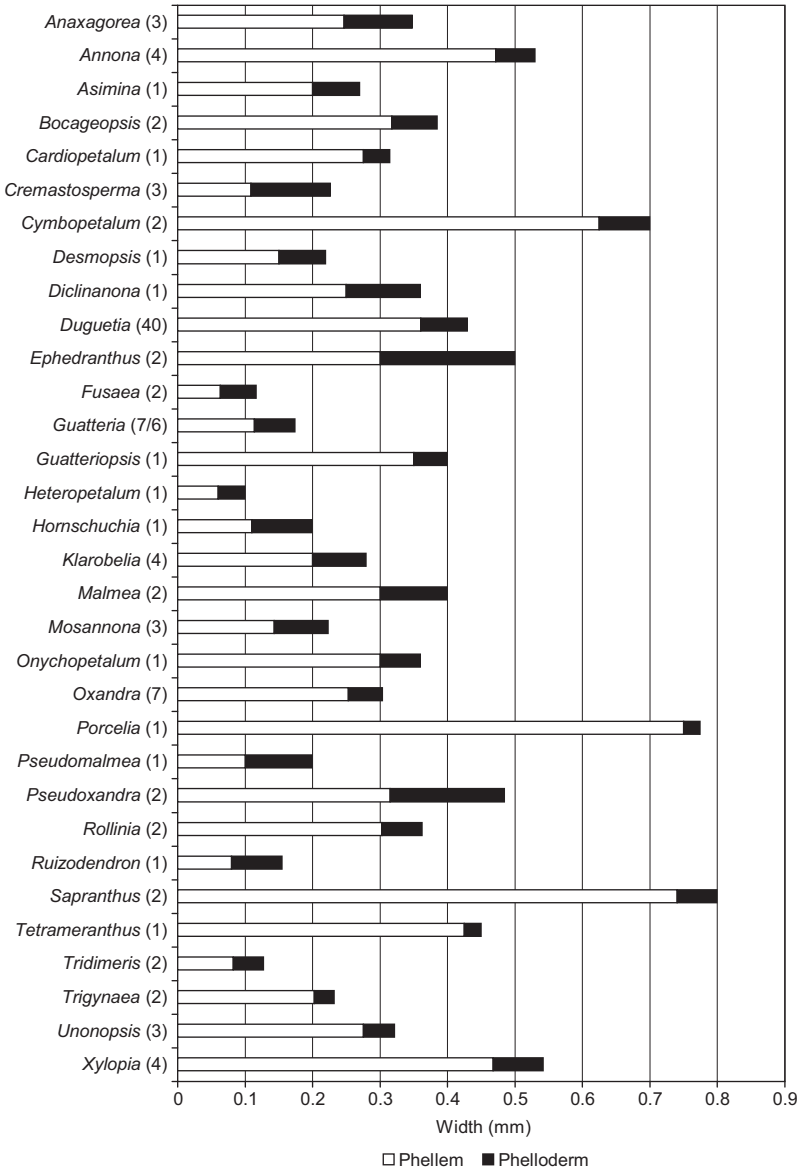


Fig. 5. Width of the periderm and its components in 32 Neotropical genera of Annonaceae. The number of samples is shown in parentheses. When two numbers are given, the first refers to the phellem, the second to the phelloderm.

**Phelloderm**

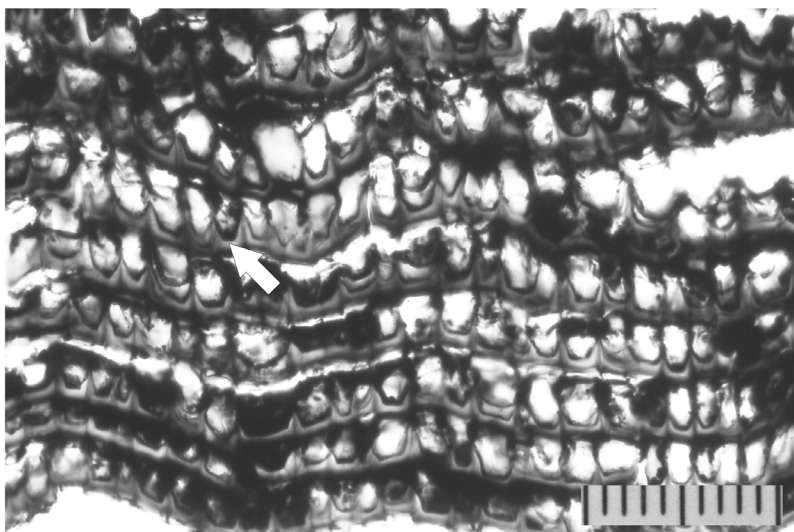
The phelloderm mostly comprises 3–7 cell layers (average 4.8). In 16 samples of various genera, the phelloderm was equal to or more than ten cell layers wide. By contrast, eight samples have only 1 or 2 cell layers. *Duguetia*, *Guatteria* and *Oxandra* showed the full range.

Sclereids are often common in phelloderm, being absent in less than 25% of the samples. Sclereids are visible as tangential bands or more often as small groups and/or solitary cells. Only

in the sample of *Onychopetalum* is the phelloderm totally sclerified. Sclerified tissue is lacking in almost all samples of *Cardiopetalum*, *Fusaea*, *Guatteria*, *Guatteriopsis*, *Hornschuchia*, *Klarobelia*, *Tetrameranthus* and *Trigynaea*. Four samples of *Diclinanona*, *Duguetia*, *Fusaea* and *Guatteria* have uniformly thickened phelloderm cells.

Secretory cells are present in more than 50% of the samples and found as solitary cells, small groups or tangential bands. Many samples have a mixed pattern. The phelloderm is





**Fig. 6.** *Ephedranthus guianensis*, cross-section. Phellem cells with U-shaped thickened cell walls (arrow). Scale bar = 100  $\mu\text{m}$ .

totally or largely impregnated with secretions in some samples of *Duguetia*, all *Fusaea* samples, many *Guatteria* samples, in *Guatteriopsis* and *Onychopetalum*. Secretory cells are lacking in 41 samples, including all species of *Anaxagorea*, *Annona* (except 1 sp.), *Cardiopetalum*, *Cymbopetalum*, *Ephedranthus*, *Heteropetalum*, *Hornschuchia*, *Porcelia*, *Tetrameranthus*, *Tridimeris* and *Trigynaea*. In *Onychopetalum*, with its totally sclerified phellogen, all sclereids are secretory cells as well.

### Phellem

The phellem consists chiefly of more than ten cell layers. In 50% of the material studied, it is formed by a combination of thin-walled and sclerified cells.

Thin-walled cells are lacking in *Bocageopsis*, *Onychopetalum*, *Oxandra*, *Pseudoxandra*, *Ruizodendron*, *Unonopsis* p.p. and *Xylopia* p.p. Sclerified cells are absent in 11 samples of *Duguetia* and 16 samples of other genera. In remainder of the samples cells have variously thickened cell walls.

Sclerified cells occur mostly in tangential bands and/or rows in *Diclinanona*, many samples in *Duguetia* and *Guatteria*, *Klarobelia*, *Pseudomalmea*, *Sapranthus*, *Tetrameranthus* and *Tridimeris*, and in nine samples of the other genera.

Sclerification is normally U-shaped (Fig. 6). Cells with reversibly U-shaped sclerified walls are found in *Pseudoxandra*, *Tetrameranthus* and *Unonopsis*, and in 11 samples of other genera. Uniformly thickened cells occur in 13 samples, eight of which belong to *Duguetia*.

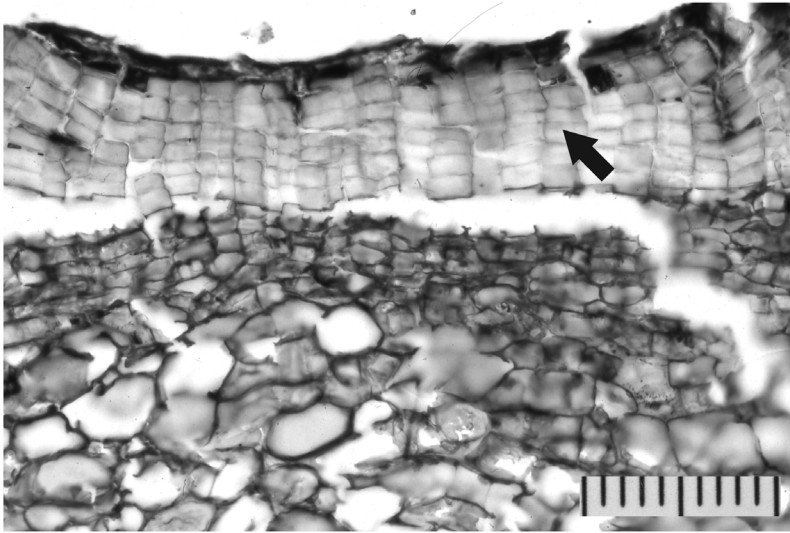
Only in *Ruizodendron* is the whole phellem formed by sclereids (Fig. 7). Sclereids can be found in other samples, but mostly they are absent or rare.

Secretory cells are present in the phellem of slightly less than 80% of the samples. They are particularly dominant in 16 genera, in which the whole tissue or the major part of it consists of secretory cells (although sclerified). In other samples they may occur as solitary cells, tangential bands or, rarely, radial rows or groups. Secretory cells are absent in *Asimina*, *Cardiopetalum* and *Desmopsis*, and in many samples of *Duguetia*, *Porcelia* and *Ruizodendron*.

### Primary cortex

The primary cortex was present in representatives of 29 genera (Appendix 2C). In 20 specimens, it could not be identified, i.e. was already removed by periderm formation.

In transverse section, sclereids form at least 50% of the primary cortex in *Bocageopsis*, *Heteropetalum*, *Onychopetalum* and *Tridimeris* as well as in 18 other samples. In most remaining



**Fig. 7.** *Ruizodendron ovale*, cross-section. Pheloderm with sclereids (arrow). Note the small-celled pheloderm vs. the large-celled cortex. Scale bar = 100  $\mu$ m.

samples, they are visible as solitary cells, as small or large groups or, more rarely, as tangential bands. Sclereids are completely absent in only a few samples.

Secretory cells are present in ca. 2/3 of the samples, including most samples of *Duguetia*. They dominate in only a few samples. Usually, they are solitary or arranged in tangential bands. In 34 samples, secretory cells are absent.

### Phloem and its components

The width of the phloem varies from < 1 mm (in *Cardiopetalum*) to > 5 mm (in *Asimina*, *Bocageopsis*, *Gutteria* (except one sample) and *Onychopetalum*) (Fig. 2; Appendix 2A). The average thickness of the phloem in the size class > 9.99 cm is 4.64 mm, which is nearly twice as high as in the samples of the size class < 10.0 cm (Fig. 8), in which the average is only 2.53 mm (*Onychopetalum* excluded because of its exceptionally high phloem width). This variation is comparable with the ratio of sample radius to bark width (see Fig. 3), as the phloem forms the main component of the bark.

When seen in transverse section, the phloem consists of parenchymatic rays and an axial ground tissue of parenchyma and fibres. Both tissues are intermingled with sclereids and secretory cells.

### Rays

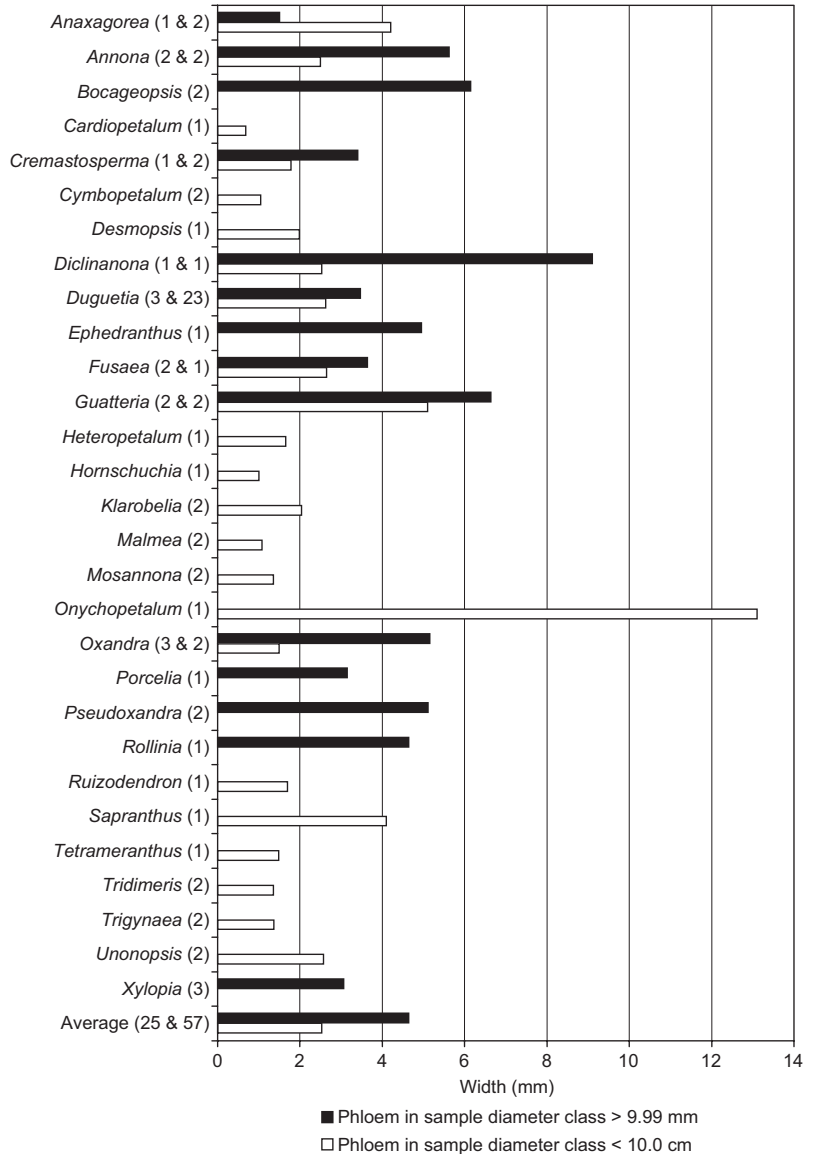
Rays are multiseriate (Fig. 9). Near the cambium, they are usually 4–7 cells wide at most (on average 5.67 for all samples). Rays equal to or less than 4 cells wide are present in *Cardiopetalum*, *Heteropetalum*, *Malmea*, *Pseudomalmea*, *Pseudoxandra* and *Xylopia*. Only a few samples have 1- or 2-seriate rays. Considerably wider rays are found in *Anaxagorea* (8–13), *Crematosperma* (7–11), *Tridimeris* (8–15) and *Unonopsis* (5–11) (Fig. 10).

Going outwards, the rays often strongly dilate, nearly always more or less irregularly. Funnel-formed dilatation occurs in *Gutteriopsis* and *Hornschuchia* and in some samples of *Duguetia*, *Klarobelia* and *Oxandra*. Discontinuous rays are invariably present

Rays are nearly always over 1 mm high, mostly homogeneous. Heterogeneous rays are seen in only 11 specimens. An exception is *Duguetia*, in which most samples show weakly heterogeneous rays. The presence of homocellular rays in bark samples is often difficult to determine and misinterpretations are possible.

No association was detected between homogeneity/heterogeneity and ray width.

Ray number measured in cross-section ranges between 1.7 and 6.8 per mm (average 3.7). Around 2/3 of samples fall within a range of 3 to 5. Fewer than 2 rays per mm is recorded in



**Fig. 8.** Phloem width in 29 Neotropical genera of Annonaceae in two diameter classes (< 10 cm and > 10 cm). The number of samples is shown in parentheses. When two numbers are given, the first refers to the upper horizontal bar, the second to the lower bar. Data for *Asimina*, *Guatteria* and *Pseudomalmea* are lacking, as the diameter of the samples is unknown.

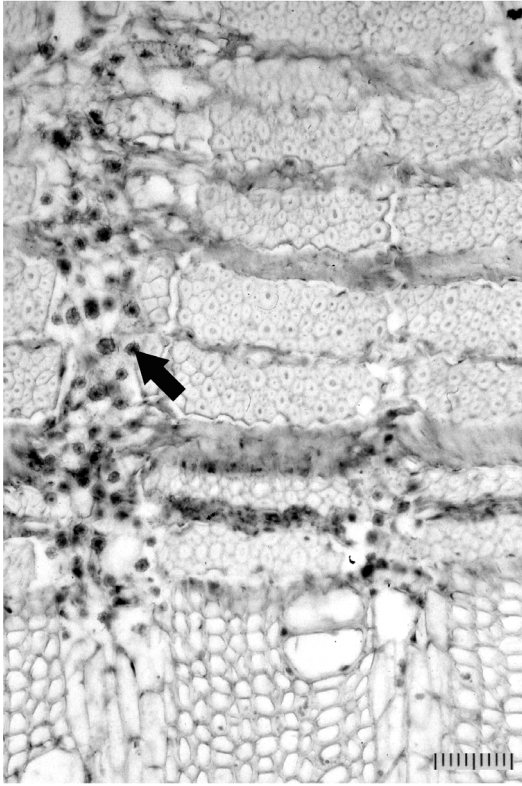
*Anaxagorea* and *Tetrameranthus*; more than 5 in *Xylopia* and many samples of *Oxandra* (Fig. 10).

In nearly all specimens, rays include sclereids, which are scattered as solitary cells or arranged in groups, rarely as tangential bands. Tangential bands are characteristic of *Heteropetalum*, *Trigynaea* and a few other specimens. Sclereids are missing in *Cardiopetalum*, *Duguetia* p.p. and *Hornschuchia* as well as in a few samples of other genera. We found no correlation with sample diameter or phloem thickness and occurrence of sclereids in rays.

Secretory cells are abundant, but occur mostly as solitary cells; only a few species have these as a dominant cell type. They were absent in 41 samples (totally lacking in 12 genera) (Appendix 2D).

#### Axial phloem

The term 'axial phloem' is used here to describe vertical system of tissues, i.e. fibres, sclereids and secretory cells, all embedded in axial parenchyma strands. Sieve tube members and com-



**Fig. 9.** *Anaxagorea dolichocarpa*, cross-section. Tangential fibre bands between the multiseriate phloem rays which include druses (arrow). Scale bar = 100  $\mu$ m.

panion cells were not investigated, because the sections were commonly too fragmented to discern reliably their structure and arrangement.

The single fibres are non-septate, composed of fibre groups which are distinctive of Annonaceae. The compact groups superpose each other and form tangential bands when viewed in cross-section (Figs. 9 and 11). The fibre groups are irregularly scattered in the axial phloem in *Tridimeris* sp. only.

Single fibre groups may be narrow (< 3 tangential cell layers) or wide. They are often alternating. Exclusively narrow groups are frequently found in *Duguetia* (22 out of 42 specimens) and in *Guatteria* (4 out of 7 specimens), but less so in other genera. Most of the genera have only wide fibre groups (Appendix 2E).

In transverse section fibre groups are mostly oblong, more rarely oblong to square. Only *Rollinia pittieri* has exclusively square-shaped fibre groups. Neither the number of tangential fibre

cell layers nor the shape of fibre groups is linked to sample radius.

Arc-shaped fibre groups are found in four genera: in 24 samples of *Duguetia*, in two samples of *Fusaea longifolia* and in all samples of *Guatteria* and *Diclinanona*.

In the axial phloem, sclereids are associated with fibre groups in ca. 43% of the specimens. A few taxa show a distinct pattern. Sclereids are restricted to the adaxial side of fibre groups in *Bocageopsis* p.p., *Unonopsis* and *Sapranthus*; they are found abaxially in nearly all samples of *Oxandra*. In *Malmea* p.p., they are only present on the radial side of fibre groups.

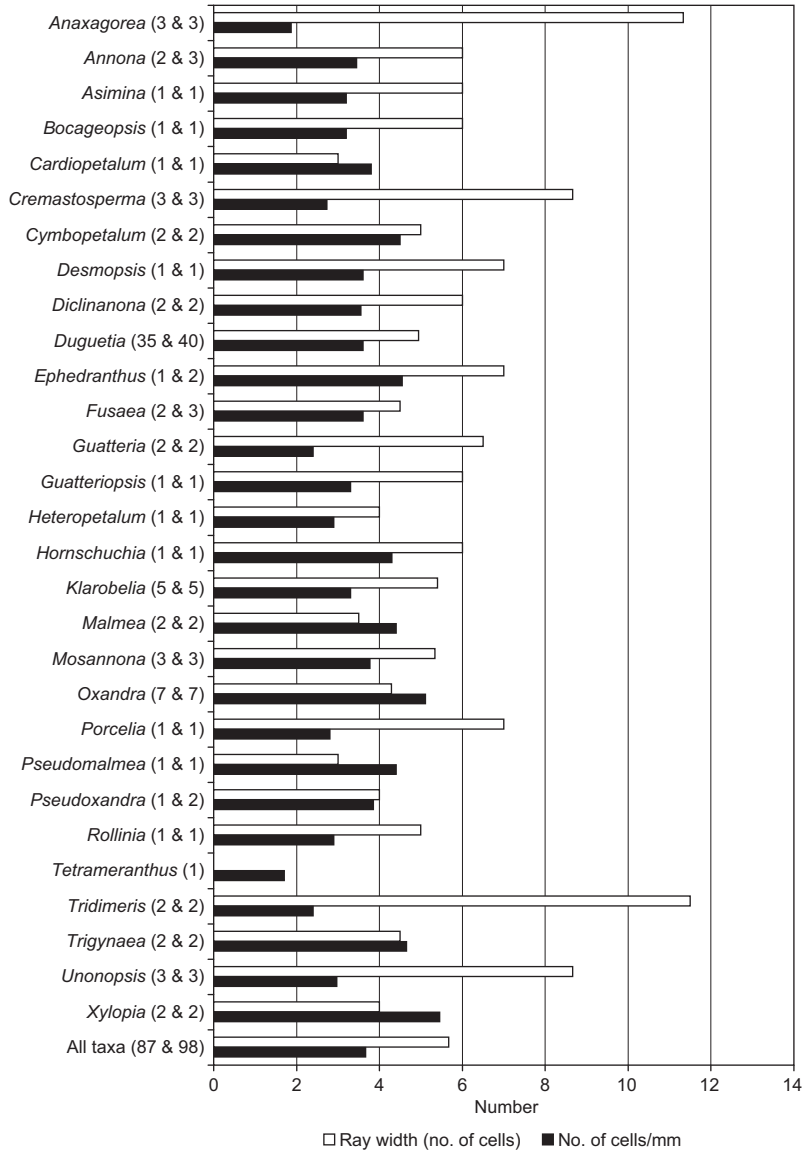
In the axial phloem tissue, secretory cells are present in ca. 60% of samples and are easy to detect (Fig. 11). They occur as solitary cells, irregular groups and/or tangential bands. They never form part of fibre groups. In *Bocageopsis*, *Fusaea* and some species of other genera, they are profuse. Some secretory cells can be larger than other cells; this was found in the axial phloem of *Bocageopsis*, *Tetrameranthus duckei* and *Unonopsis stipitata* and in the dilated rays of *Porcelia ponderosa*.

Often, however, only a few secretory cells are visible or they are completely lacking.

## Crystals

Crystals of presumably calcium oxalate occur in the majority of the Annonaceae investigated (Table 1, Fig. 12, Appendices 2F and 2G). They are totally lacking in *Diclinanona* and *Heteropetalum* and in a few samples of other genera. Prismatic crystals occur in all cell types. Other crystal types are mainly found in parenchyma cells.

Most crystals are prismatic, i.e. octahedral or rhombohedral (Fig. 13). Prismatic crystals were present in 68 of the 118 samples studied. Often, they are visible together with other types, i.e. elongated crystals (*Annona*, *Cymbopetalum*, *Oxandra* and *Trigynaea*), navicular crystals (*Cardiopetalum* and *Pseudoxandra*), spindle-shaped crystals (*Xylopia*) and styloids (*Annona*, *Asimina* and *Cymbopetalum*). In addition, more irregular forms are found with the above-mentioned types. An exception is *Anaxagorea*, in which all crys-



**Fig. 10.** Ray width and number of rays per millimetre in 29 Neotropical genera of Annonaceae. Width values are averages of maximum number of cell rows. The number of samples is shown in parentheses: the first number refers to ray width, the second to ray number.

tals are druses (Fig. 9). In *Duguetia*, the highest variation in crystal shape was recovered. In one sample of *Duguetia neglecta*, only rhombic crystals were distinguished, in contrast to the other sample, in which spindle-shaped forms were present.

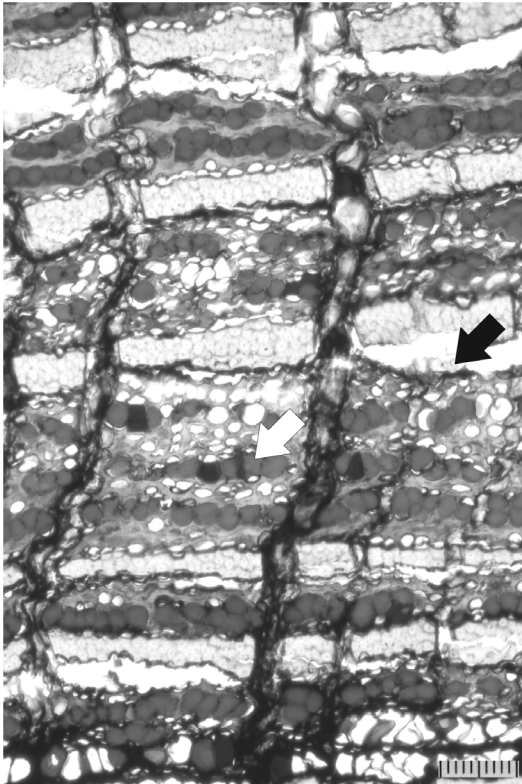
The size of prismatic crystals varies between 3  $\mu\text{m}$  and 110  $\mu\text{m}$ , usually their size lies between 10  $\mu\text{m}$  and 30  $\mu\text{m}$ . When two or more crystals occur in a single cell, they are clearly different-sized. In *Duguetia*, with its variety of crystal shapes, the size ranges from 3  $\mu\text{m}$  to 40  $\mu\text{m}$ , and occasionally larger. The smallest crystals

were found in *D. macrophylla* (3–7  $\mu\text{m}$ ). The largest crystals occur in *Annona*, particularly in *A. foetida* (50–110  $\mu\text{m}$ ). *A. ambotay*, *Cymbopetalum brasiliense*, *Pseudoxandra* sp. and *Trigynaea lagaropoda* also have large-sized crystals (Table 2).

With the exception of phellem, crystals occur in all bark tissues.

In ca. 30% of the samples, where the cortex was still present, crystals in this tissue were found, mainly in sclereids (Table 3 and Fig. 14).

Crystals are common in the phelloderm of *Cymbopetalum*, *Duguetia*, *Malmea*, *Mosannonna*,



**Fig. 11.** *Bocageopsis multiflora*, cross-section. Large secretory cells in axial phloem (white arrow) and crystals on adaxial side of fibre groups (black arrow). Scale bar = 100  $\mu$ m.

*Oxandra*, *Porcelia*, *Ruizodendron*, *Sapranthus* and *Tridimeris* (Table 3). Here, they were often difficult to distinguish, the phelloderm being only a few cell layers wide.

In 14 genera, crystals are visible exclusively in the sclereids of rays (Appendix 2G) and sometimes in both sclereids and the parenchyma. Exceptions to this rule are *Anaxagorea*, *Duguetia*, *Fusaea*, *Hornschuchia* and *Xylopia*, in which crystals are located in ray parenchyma cells only. Crystals were not found in the rays of *Bocageopsis*, *Guatteria*, *Guatteriopsis* or some species of other genera (Fig. 14 and Table 3). Sometimes ray crystals are formed only after dilatation begins and consequently, they are not found in the non-dilatated rays.

Instead of being located in solitary cells, crystals may border sclereid and/or fibre groups. The size of these sclereid groups varies, and they are situated in the phelloderm, the cortex

and/or rays. This feature in sclereid groups is not common; it was observed in only five species, namely in *Annona*, *Porcelia*, *Pseudomalmea* and *Pseudoxandra* (Table 4).

In the axial phloem, crystals are found in sclereids or parenchyma cells.

*Bocageopsis*, *Guatteria*, *Guatteriopsis*, *Oxandra*, *Sapranthus*, *Unonopsis* and some single species of other genera have crystals in sclereids of the axial phloem.

In *Annona*, *Cymbopetalum*, *Hornschuchia*, *Klarobelia*, *Mosannona*, *Porcelia*, *Rollinia*, *Ruizodendron*, *Tetrameranthus* and in a few other species crystals are either in the fibres or, as interpreted here, in parenchyma (Appendices 2F and 2G).

In *Asimina*, *Ephedranthus*, *Malmea* and *Pseudomalmea* crystals are also associated with fibre groups and localised in parenchyma and sclereids.

When flanking or surrounding fibre groups, crystals may occur in long axial chains (Fig. 13). They may be long (> 1 mm) or short when seen in radial section (Table 5). When seen in transverse section, crystals may form continuous or interrupted circles around fibre groups (Fig. 15) or they may be restricted to the abaxial, adaxial or lateral side of fibre groups. In *Oxandra*, crystals are frequently found on the abaxial side of fibre groups (Fig. 16). *Bocageopsis* and *Sapranthus*, by contrast, have crystals in cells attached to the adaxial side of fibre groups.

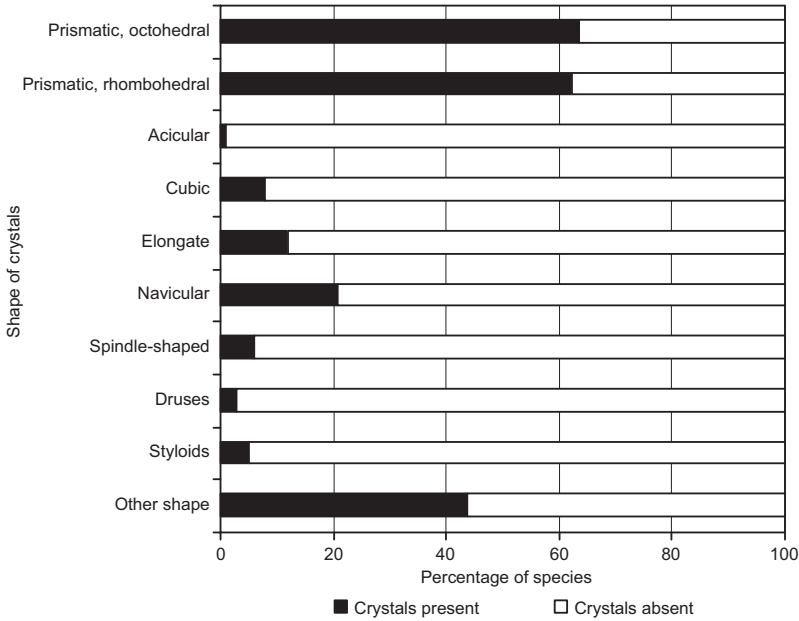
In *Guatteria*, *Guatteriopsis* and *Hornschuchia*, crystals seem to occur along the radial (lateral) side of fibre groups (Table 4), but they are few and scattered. In *Hornschuchia*, many crystals are on the lateral side of fibre groups in parenchyma cells, but in *Guatteria* and *Guatteriopsis* only a few crystals are found in slightly sclerified cells.

In *Cymbopetalum* and *Trigynaena*, crystals are clustered in the cells between fibre groups (Fig. 17). In one species of *Annona*, long radial rows of crystals can be detected in transverse section (Fig. 18, Table 5, Appendix 2F).

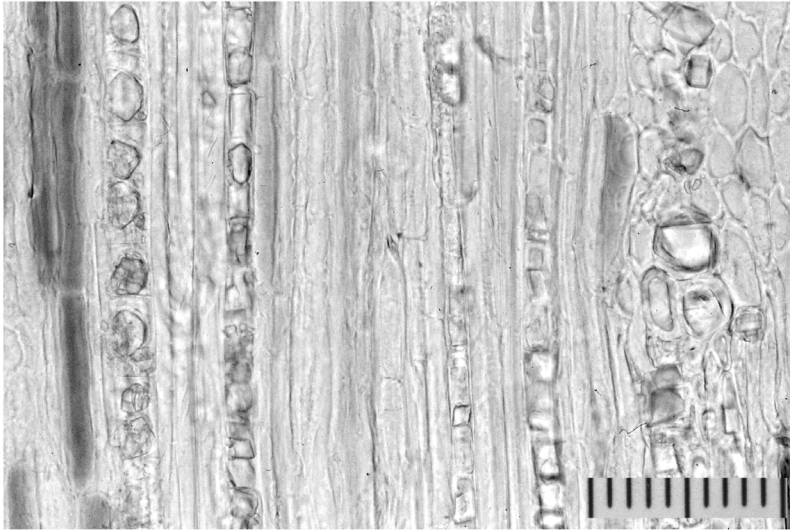
Cells containing crystals are usually not enlarged, but in *Malmea dielsiana*, *Malmea surinamensis* and *Mosannona depressa* subsp. *ascondita*, the crystal-containing sclereids laterally associated with fibre groups are clearly

**Table 1.** Types of crystals found in Neotropical Annonaceae. Numbers indicate the number of specimens in which the crystal type was found. Numbers in parentheses in the left column indicate the number of investigated species.

Genus	Crystals										
	Octohedral	Rhombohedral	Acicular	Cubic	Druses	Elongated	Navicular	Spindle-shaped	Like styloids	Other shape	Not present
<i>Anaxagorea</i> (3)					3						
<i>Annona</i> (4)		2				3			3		1
<i>Asimina</i> (1)	1	1							1	1	
<i>Bocageopsis</i> (2)	2	2									
<i>Cardiopetalum</i> (1)	1	1					1				
<i>Crematosperma</i> (3)	3	3									
<i>Cymbopetalum</i> (2)	2	2				2			1		
<i>Desmopsis</i> (1)	1	1									
<i>Diclinanona</i> (2)											2
<i>Duguetia</i> (28)	1		1	10		4	24	5		41	
<i>Ephedranthus</i> (2)	2	2									
<i>Fusaea</i> (2)	3	3									
<i>Guatteria</i> (7)	7	5								4	
<i>Guatterioopsis</i> (1)	1	1									
<i>Heteropetalum</i> (1)											1
<i>Hornschurchia</i> (1)	1	1									
<i>Klarobelia</i> (5)	4	4								2	1
<i>Malmea</i> (2)	2	2								2	
<i>Mosannonna</i> (3)	3	3								1	
<i>Onychopetalum</i> (1)	1	1									
<i>Oxandra</i> (7)	8	8				1				2	
<i>Porcellia</i> (1)	1	1									
<i>Pseudomalmea</i> (2)	2	2									
<i>Pseudoxandra</i> (3)	3	3					1			1	
<i>Rollinia</i> (2)	2	2								1	
<i>Ruizodendron</i> (1)	1	1									
<i>Sapranthus</i> (1)	1	1								1	
<i>Tetrameranthus</i> (1)	2	2									
<i>Tridimeris</i> (2)	2	2								1	
<i>Trigynaea</i> (2)	2	2				2					
<i>Unonopsis</i> (3)	3	3								1	
<i>Xylopia</i> (4)	4	4						1			
In genera found	28	28	1	1	1	5	3	2	3	12	4



**Fig. 12.** Types of crystals found in Neotropical Annonaceae. The horizontal bars indicate the percentage of species in which crystals were found.



**Fig. 13.** *Cymbopetalum longipes*, radial section. Crystals located around and between fibre groups. Scale bar = 100  $\mu\text{m}$ .

enlarged (Appendix 2G).

In virtually all cases, crystals occurring along fibre groups are situated in chambered cells, each crystal filling its compartment almost completely. More than one crystal in a cell was found in *Duguetia* (with a few exceptions), *Hornsuchia* and *Porcelia* and in some species of other genera. Some other taxa have only a few crystals in the axial phloem, and chambered crystalliferous cells are not distinct.

## Discussion

Bark is a complex tissue, the taxonomic value of which can be compared with wood and leaf anatomy in many respects. However, bark in its young stage may lack some of the most important features apparent upon maturity, such as fully developed sclerenchyma, dilatation growth and crystals. Thickness growth of the stem and secondary growth of the phloem forge in bark its typical outer pattern and anatomy. This “matura-



tion process" is dependent on the growth rate and thickness of the stem.

In this study, we mostly made use of bark material which was available in wood collections. Most wood/bark samples are extracted from trees with a slender stem and branches. Therefore, not all of the barks studied were fully developed. This can be easily estimated from the amount of cortex in the samples, as in older bark subsequent periderms usually cut-off the cortex and older parts of the phloem, converting them into dead rhytidome (cf. Fig. 1). However, according to our experience, this did not greatly affect the anatomy after the initial phase of bark formation. We found no correlation between the diameter of trunk/thickness of the bark and patterns of the inner bark (cf. Figs. 4 and 8).

Similarly, exposure of the bark to climate and other site factors, such as altitude and soil fertility, may affect periderm formation, amount of dead rhytidome and bark thickness. Moreover, handling of bark samples in the herbarium easily erodes the fragile surface of the rhytidome. A section was typically cut from the thickest part of the bark to improve the quality of the section and the visibility of different components.

Bark material was available in only a fraction of the samples preserved in the wood collections. Only the genus *Duguetia* was quite well represented, while bark of several noteworthy genera was lacking. Moreover, bark samples are usually poorer in their quality than wood, because dissimilarity of tissues and particularly the abundance of sclereids easily fragments sections, even those cut whilst held together with tape.

Bearing this in mind, we will first compare some aspects of our findings with other anatomical studies of bark (Zahur 1959, Roth 1974, 1981, Rollet 1982) and wood (ter Welle 1984). Because we will frequently cite Roth's (1981) publication, the year of publication is not mentioned unless needed. Phenetic similarities and differences will be discussed in view of some recent results on the phylogeny of Neotropical Annonaceae (Koek-Noorman *et al.* 1997, Chatrou *et al.* 2003, Sauquet *et al.* 2003; L. W. Chatrou pers. comm.).

The surface structure of the bark in our material is quite homogeneous with a few distinct patterns, which should be studied from

more specimens in the field. Typically, barks in Annonaceae are completely smooth or have shallow boat-shaped to oblique fissures.

Unfortunately, many of our samples are thin (84.4 mm on average) and lack data on exposure. Therefore, the description presumably does not give a full picture of the variation in outer bark patterns.

Barks are mostly "very thin" (< 3.0 mm) or "thin" (> 5 mm) according to Roth's classification. "Thick bark" (13.5 mm) was found in the genus *Onychopetalum* (Fig. 2), which was surprising, as the diameter of the tree was, in comparison, rather small (33 mm) (Appendix 2A). Four of the five Annonaceae samples studied by

**Table 2.** Variation in the size of crystals. In the right columns, minimum and maximum sizes are given. Numbers in parentheses following the generic names indicate the number of investigated species.

Genera	Size (m <sup>-6</sup> )
<i>Anaxagorea</i> (3)	8–25
<i>Annona</i> (3)	15–110
<i>Asimina</i> (1)	15–25
<i>Bocageopsis</i> (1)	15–30
<i>Cardiopetalum</i> (1)	20–25
<i>Cremastris</i> (3)	5–45
<i>Cymbopetalum</i> (2)	10–50
<i>Desmopsis</i> (1)	10–30
<i>Diclinanona</i> (2)	–
<i>Duguetia</i> (27)	3–72
<i>Ephedranthus</i> (2)	10–25
<i>Fusaea</i> (2)	15–30
<i>Guatteria</i> (7)	5–25
<i>Guatterioopsis</i> (1)	12–25
<i>Heteropetalum</i> (1)	–
<i>Hornschuchia</i> (1)	10–35
<i>Klarobelia</i> (4)	10–25
<i>Malmea</i> (2)	10–50
<i>Mosannonna</i> (3)	5–45
<i>Onychopetalum</i> (1)	25–30
<i>Oxandra</i> (8)	5–45
<i>Porcelia</i> (1)	15–40
<i>Pseudomalmea</i> (2)	10–25
<i>Pseudoxandra</i> (3)	10–50
<i>Rollinia</i> (2)	15–30
<i>Ruizodendron</i> (1)	7–25
<i>Sapranthus</i> (1)	10–30
<i>Tetrameranthus</i> (2)	12–50
<i>Tridimeris</i> (2)	10–30
<i>Trigynaea</i> (2)	15–60
<i>Unonopsis</i> (3)	10–45
<i>Xylopia</i> (4)	12–35

Roth had “medium-sized barks” (5.0–10.0 mm). However, the diameter of these trees varied from 20 cm to 45 cm, being substantially thicker than our samples.

In an inventory of 1800 trees over 40 cm in diameter in Venezuelan Guayana, Rollet (1980) measured the average thickness of the bark to be 8.7 mm. The ratio of the width of the bark to the radius of the trunk varied from 1:30 ( $\varnothing$  40–60 cm) to 1:50 ( $\varnothing$  60–100 cm). Although the size classes distinguished by him are different from ours, his findings of the proportion of the bark

generally diminishing with a larger tree diameter is congruent with ours. However, we did not observe this trend in all genera (cf. in *Annona*, *Crematosperma* and *Oxandra*) (Fig. 3).

### Rhytidome (incl. periderm)

The rhytidome — or outer bark — is mostly thin, exceeding 1 mm thickness in only a small proportion of the specimens (Fig. 4), and is composed of one periderm. The low number of

**Table 3.** Presence of crystals in bark tissues in Neotropical Annonaceae. Numbers indicate the number of samples in which crystals were found. Numbers in parentheses indicate the number of investigated species. par. = parenchyma; scl. = sclereids.

Genus	Phelloderm		Cortex		Rays		Axial phloem	
	Par.	Scl.	Par.	Scl.	Par.	Scl.	Par.	Scl.
<i>Anaxagorea</i> (3)					3			
<i>Annona</i> (4)		1		1	1	1	3	
<i>Asimina</i> (1)				1		1	1	1
<i>Bocageopsis</i> (1)								2
<i>Cardiopetalum</i> (1)					1			
<i>Crematosperma</i> (3)		1		1	3	1		
<i>Cymbopetalum</i> (2)		2	2	2	2	2	2	
<i>Desmopsis</i> (1)		1				1		
<i>Diclinanona</i> (2)	–	–	–	–	–	–	–	–
<i>Duguetia</i> (28)	39				42		1	
<i>Ephedranthus</i> (2)		1		2		2	2	1
<i>Fusaea</i> (2)					3			
<i>Guatteria</i> (7)								7
<i>Guatterriopsis</i> (1)								1
<i>Heteropetalum</i> (1)	–	–	–	–	–	–	–	–
<i>Hornschuchia</i> (1)					1		1	
<i>Klarobelia</i> (5)	1	1	1		1	2	4	
<i>Malmea</i> (2)		2		2		2	2	2
<i>Mosannonna</i> (3)	3	3	1	2	3	3	2	1
<i>Onychopetalum</i> (1)				1		1		
<i>Oxandra</i> (7)	2	6		7		6		7
<i>Porcelia</i> (1)		1		1		1	1	
<i>Pseudomalmea</i> (2)				1		1	2	1
<i>Pseudoxandra</i> (3)		1		3		2		
<i>Rollinia</i> (2)	1	1	2	2	2	2	2	
<i>Ruizodendron</i> (1)		1		1		1	1	
<i>Sapranthus</i> (1)		1				1	1	
<i>Tetrameranthus</i> (1)				2		2	2	
<i>Tridimeris</i> (2)		2		1		2		2
<i>Trigynaea</i> (2)					2	2	2	
<i>Unonopsis</i> (3)		1		3		3		3
<i>Xylopia</i> (4)					4			
Number of genera	5	16	4	17	13	21	16	11

samples, i.e. 11 (Appendix 2A), with more than one periderm suggests that the rhytidomes of most samples are still young. Roth found two out of five annonaceous specimens to have more than one periderm. She also suggested that more periderms are formed in very thick rhytidomes.

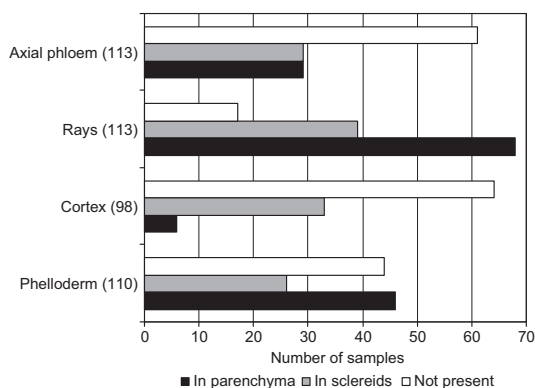
Phellem is formed at an early phase in branches and young trunks to form an initial protective layer against desiccation, fire, pests and diseases. Mostly, phellem of our material falls into “medium-sized corks” (0.10–0.50 mm), which agrees well with the measurements in Roth’s annonaceous taxa and in Venezuelan trees in general. In the majority of our material, the phellem consists of more than ten cell layers.

Phelloderm is mostly “thin” (0.01–0.09 mm) (Fig. 5); only in a few species is it more than 0.20 mm thick. Zahur (1959) demonstrated that the phelloderm of the five species of Hawaiian Annonaceae is only 1–5 cell layers thick. Three out of the five Annonaceae specimens in Roth’s study have a phelloderm equal to or less than 0.10 mm, the fourth one being 0.15 mm. A “very thick phelloderm” (0.26–1.50 mm) occurred in Roth’s specimen of *Rollinia exsucca*, which had also a very thick bark. By contrast, the phelloderm of our two *Rollinia* specimens is thin (0.05–0.07 mm). These examples show that phelloderm is not always thin in trees of humid tropics.

Roth mentioned a “rule of economy”, in which phelloderm/phellem usually partly substitute for each other. In the thickest periderms found in our samples, the phellem clearly dominates, although in other samples the role of the phelloderm may be even more developed than the phellem; i.e. substitution is not coherent with the “rule of economy” in all samples (cf. Fig. 5).

### Inner bark

In general, phloem structure has been reported to be homogeneous in Annonaceae, although Zahur (1959) noted two types of phloem rays in Hawaiian Annonaceae. In our material, no distinct disparity in medullary rays was detected. In wood anatomical studies, the distinction between homo- and heterocellular rays is often indicated. In phloem, however, this feature seems to be



**Fig. 14.** Occurrence of crystals in different bark components in Neotropical Annonaceae. Numbers indicate the number of samples in which crystals were found. Numbers in parentheses in the left column indicate the total number of samples investigated.

obscure and may cause misinterpretations. We recommend, therefore, that it not be used in bark anatomical observations.

Near the cambium, most rays are 3–8 seriate (Fig. 10), which confirms Roth’s observations. However, the full range in our material is higher (2–15) (Appendix 2D).

Dilatation of phloem parenchyma is a common phenomenon in tropical trees (cf. Roth 1981). It is easily detected by the presence of fissures at the outer surface of the bark. Dilatation growth in Annonaceae may result in very regular funnels (*Tilia* type) or in irregular dilatation patterns. In our material, straight, funnel-formed rays are rare and, when found, are inconsistent with Roth’s findings.

### Sclerenchyma

A common character in Annonaceae is the presence of sclereids (Roth 1974). They are found in both outer and inner bark. Roth (1981) distinguished between “hard bast sclereids” and the secondarily formed sclereids found in the dilating zones. We do not follow that distinction and refer to both cell types as sclereids.

Sclereids were often found in dilated rays. The few specimens in which we discerned no sclereids, are quite thin. Sclereids were also very frequent in both the cortex and the phelloderm. Uniformly thickened cells sometimes dominate

**Table 4.** Presence of crystals in association with sclerenchyma in Neotropical genera of Annonaceae. Numbers indicate the number of samples in which crystals were found. Numbers in parentheses indicate the number of investigated species.

Genus	Crystals							
	associated with all sclerenchyma	associated with sclereid groups only	associated with fibre groups only	around fibre groups	associated with abaxial side of fibre groups	associated with adaxial side of fibre groups	associated with lateral side of fibre groups	not associated with sclerenchyma
<i>Anaxagorea</i> (3)								3
<i>Annona</i> (3)	1		2	3				
<i>Asimina</i> (1)			2					1
<i>Bocageopsis</i> (2)			2		2			1
<i>Cardiopetalum</i> (1)								1
<i>Crematosperma</i> (3)								3
<i>Cymbopetalum</i> (2)			2	2				
<i>Desmopsis</i> (1)			2	1				1
<i>Duguetia</i> (28)			2	2				40
<i>Ephedranthus</i> (2)			2					
<i>Fusaea</i> (2)			7				6	3
<i>Guatteria</i> (7)			1				1	
<i>Guatterlopsis</i> (1)			1				1	
<i>Hornschurchia</i> (1)			4	4				1
<i>Klarobelia</i> (4)			2	1				
<i>Malmea</i> (2)			3	3				
<i>Mosannonna</i> (3)			7					1
<i>Onychopetalum</i> (1)					7			1
<i>Oxandra</i> (7)			1	1				
<i>Porcella</i> (1)	1		1	2				
<i>Pseudomalmea</i> (2)	1		2					1
<i>Pseudoxandra</i> (3)		2						
<i>Rollinia</i> (2)			2					
<i>Ruizodendron</i> (1)			1					
<i>Sapranthus</i> (1)			1			1		
<i>Tetrameranthus</i> (1)			2	2				
<i>Tridimeris</i> (2)			1					1
<i>Trigynaea</i> (2)			3					2
<i>Unonopsis</i> (3)			3					
<i>Xylopia</i> (4)			19	10	1	2	3	4
Number of genera	3	1	19	10	1	2	3	14

in the phelloderm. These cells are presumably in the process of sclerification. As sclereids are formed secondarily, external factors may have an impact on their formation.

The common stratification of the phellem is caused by layers of thin-walled cells alternating with cells with U-shaped thickenings, rarely reversed U-shaped thickenings or sclereids. Roth also distinguished similar patterns in five taxa she studied, but her findings are not fully congruent with our results.

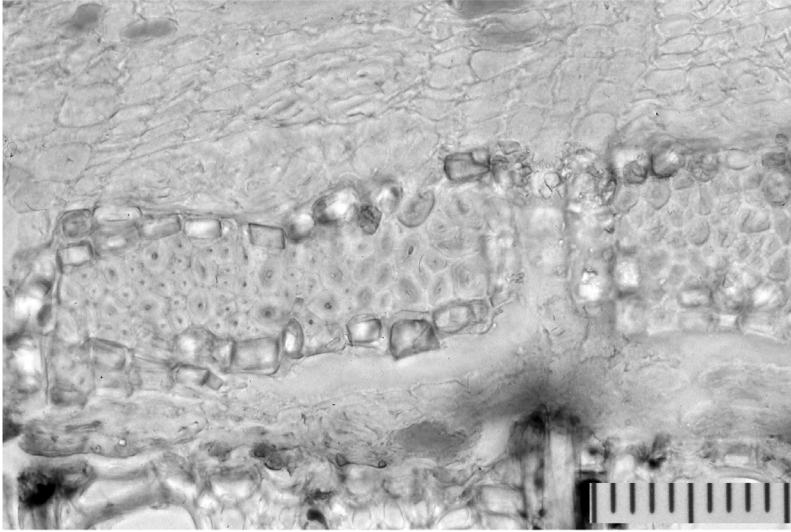
Sclereids were quite often associated with one or two fibre groups. In some other genera, sclereids accompany almost every fibre group,

sometimes forming a characteristic pattern together with fibre groups, as with the presence of sclereids on the abaxial side of fibre groups in *Oxandra*. In contrast to our findings, Roth did not describe sclereids as being associated with fibres in the barks of Annonaceae — a pattern which she did record in other families.

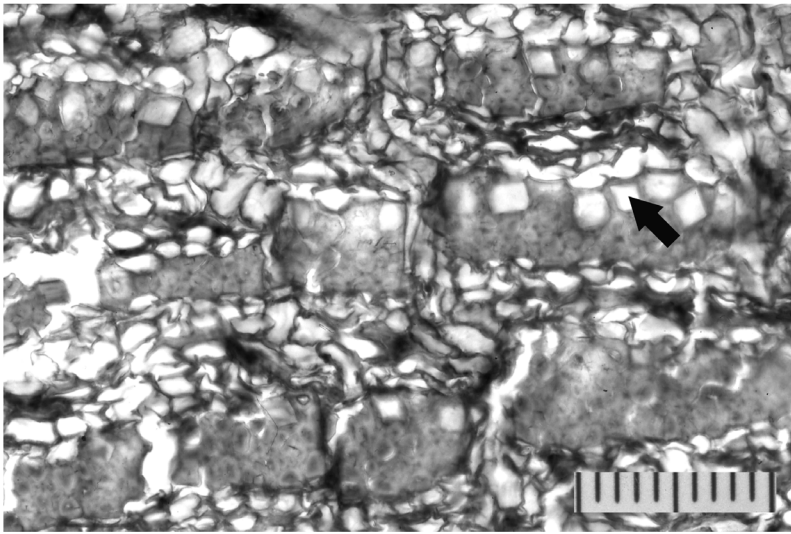
In the inner phloem, fibre groups are differentiated early in the non-collapsed secondary phloem outside the cambium. They are arranged in very regular, square to oblong fibre groups in tangential zones, thus forming a regular web-like pattern with the rays. According to Zahur (1959), the first-formed fibre groups are thicker and

**Table 5.** Pattern of crystals in axial phloem in Neotropical Annonaceae. Numbers in parentheses indicate the number of investigated species.

Genus	Crystals			
	in short vertical chains	in long vertical chains	in tangential chains between fibre groups	in long radial chains
<i>Anaxagorea</i> (3)				
<i>Annona</i> (3)	2	1		1
<i>Asimina</i> (1)	1			
<i>Bocageopsis</i> (2)	2			
<i>Cardiopetalum</i> (1)				
<i>Crematosperma</i> (3)				
<i>Cymbopetalum</i> (2)		2	2	
<i>Desmopsis</i> (1)				
<i>Diclinanona</i> (2)				
<i>Duguetia</i> (28)		2		
<i>Ephedranthus</i> (2)		2		
<i>Fusaea</i> (2)				
<i>Guatteria</i> (7)				
<i>Guatterriopsis</i> (1)				
<i>Heteropetalum</i> (1)				
<i>Hornschuchia</i> (1)	1			
<i>Klarobelia</i> (5)		4		
<i>Malmea</i> (2)				
<i>Mosannonna</i> (3)	1	2		
<i>Onychopetalum</i> (1)				
<i>Oxandra</i> (8)	1	6		
<i>Porcelia</i> (1)		1		
<i>Pseudomalmea</i> (2)		2		
<i>Pseudoxandra</i> (3)				
<i>Rollinia</i> (2)	2			
<i>Ruizodendron</i> (1)	1			
<i>Sapranthus</i> (1)				
<i>Tetrameranthus</i> (1)	1			
<i>Tridimeris</i> (2)	1			
<i>Trigynaea</i> (2)			2	
<i>Unonopsis</i> (3)	2			
<i>Xylopia</i> (4)				
Number of genera	11	9	2	1



**Fig. 15.** *Cymbopetalum longipes*, crystals located around and between fibre groups (c.s.). Scale bar = 100  $\mu$ m.



**Fig. 16.** *Oxandra espin-tana*, cross-section. Crystals encased in sclereids flanking the abaxial side of fibre groups (arrow). Scale bar = 100  $\mu$ m.

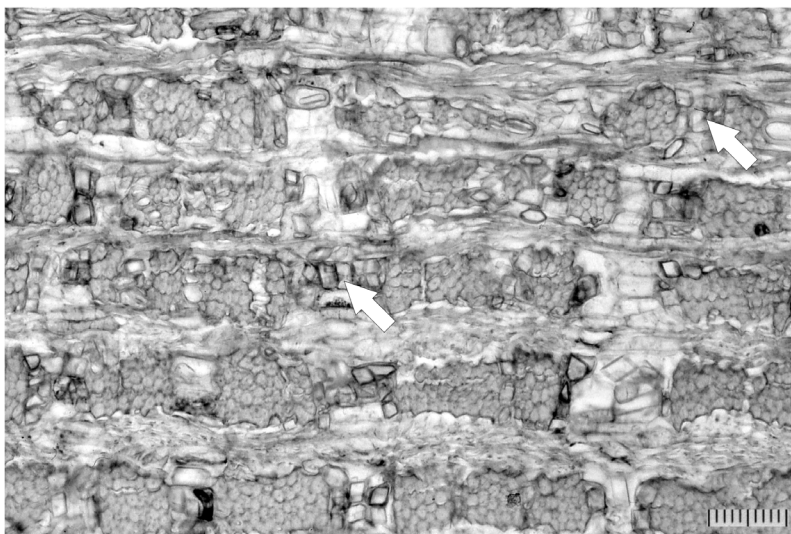
better developed than later-formed groups. Both referred to growth rings detected in the phloem of Annonaceae specimens. Two to six layers of “hard and soft bast” compose a growth ring which is separated by a wide zone of soft tissue. Hence, one could count the age of the bark. In our material, this is not a prominent character, as our barks are relatively thin. Furthermore, some bark samples are poor and tangential alignment of fibre groups is distorted. However, quite often some relatively wide tangential rows of fibre groups alternate with thinner ones and, therefore, may be a sign of annual growth. Mostly fibre

groups are over two cell rows wide, sometimes combined with narrow fibre groups. In a few genera, we found groups of arc-shaped fibres, which is, as in other taxa (Roth 1981), a rare feature in inner phloem.

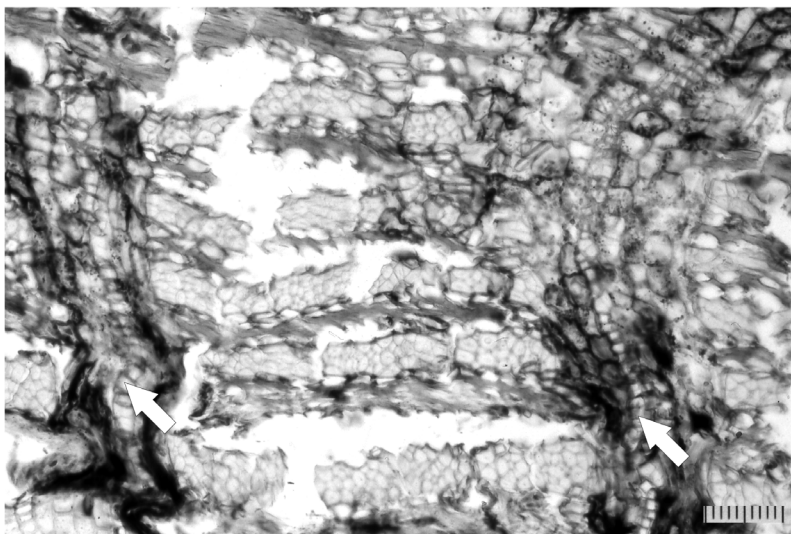
### Secretory cells

Many tropical trees have a well-developed secretory system in their bark. One of the features typifying an Annonaceae tree in the field is the characteristic odour when the bark is slashed.

**Fig. 17.** *Trigynaea lagaropoda*, cross section. Crystals clustered in the phloem cells between fibre groups (arrows). Scale bar = 100  $\mu$ m.



**Fig. 18.** *Annona foetida*, cross-section. Radial rows of crystals in phloem rays (arrows). Scale bar = 100  $\mu$ m.



The odour comes from secretory cells, which, in the majority of the samples, are present in all bark components. They are found least in the phelloderm and axial phloem tissue, but even there they are present in well over half of the specimens, usually as scattered cells or cell groups or tangential rows. We found secretory cells to be most common in phellem.

In our material, almost every specimen has at least some secretory cells in one of its bark components, even the youngest samples. Thus, secretory cells, like sclereids, seem to be a feature characterising Annonaceae.

Roth (1974) reports secretory cells in the

phloem of *Unonopsis glaucopetala*, but it is uncertain, whether they existed in the other four taxa. Metcalfe (1987) surveyed literature in which secretory cells in wood of many South-American genera (*Annona*, *Bocageopsis*, *Cymbopetalum*, *Diclinanona*, *Duguetia*, *Hornschuchia*, *Oxandra*, *Rollinia*, *Unonopsis* and *Xylopia* p.p.) are referred to as oil or mucilage cells. The first author here observed in the field (French Guiana) bark of a tree called *Annona paludosa* Aubl., which oozed on the first or second day after wounding a large amount of red, non-sticky liquid resembling mucilage. We did not identify the chemical components. How-

ever, in the scope of this study, the distinction between the two types of idioblasts does not seem relevant. Bakker's conclusion (1992) after intensive ultrastructural studies (Bakker & Gerritsen 1990, 1992) is that oil and mucilage cells in *Annona* are homologous cell types. At least below the genus level, the significance as taxonomical markers is very restricted.

## Crystals

Although the wood of the family is reported to generally lack crystals, some genera form an exception to this rule. In 15 genera of the Old and New World, crystals were found, usually small, square to round. Small druses have been detected in *Anaxagorea* (ter Welle 1984). Rhombic crystals in the marginal ray cells and elongate crystals in parenchyma cells of wood have been recorded for some *Rollinia* species. Shape and distribution of crystals are assumed to be taxonomically important (ter Welle 1992). Also in the wood of *Fusaea* spp. small rhombic crystals are observed (ter Welle 1999). Small crystals are found in the wood rays of Neotropical genera, such as *Trigynaea* and *Xylophia*, and in the parenchyma of *Hornschuchia*. Large crystals are sporadic in *Rollinia membranacea* (as *R. rensoniana*). Axially elongated crystals are connected to phloem fibres in *Annona coriacea* (Metcalf 1987). Ter Welle (1998) and ter Welle and Du (2003) reported an absence of crystals in the wood of *Desmopsis*, *Duguetia*, *Klarobelia*, *Malmea*, *Mosannonna*, *Pseudomalmea*, *Raimondia*, *Stenanona*, *Sapranthus* and *Tetrameranthus*.

Leaves mostly have druses, but rhombic crystals of varying size and shape and crystal sand also occur. Crystals in leaves have been shown to have diagnostic and taxonomical value (van Setten & Koek-Noorman 1986).

In bark tissue, we found crystals to occur commonly (Table 1). Although quite a few samples had only a few crystals, which were not always easy to discern, only in *Diclinanona* and *Heteropetalum* were crystals totally lacking. This seems to contradict Roth (1974), who did not report any crystals in the barks of *Anaxagorea*, *Rollinia*, *Unonopsis* or *Xylophia*.

In almost all genera studied, with the exception of *Duguetia* and *Anaxagorea*, the crystals are prismatic (Fig. 12 and Table 1). *Duguetia* shows a wide variety of crystal shapes. Prismatic crystals were found in only one sample. This, however, may be an artefact, as another sample of the same species lacks prismatic crystals and shows some other anatomical differences as well. In *Anaxagorea*, only druses occur in the parenchyma of dilated rays. Some other types of crystals are also confined to one or a few genera, but these crystals are usually scarce and difficult to distinguish, except for the styloids in *Annona*, *Asimina* and *Cymbopetalum*.

In addition to shape, crystal size varies between and within genera, but this cannot be used like the shape as a diagnostic character (Table 2).

Crystals occur mostly in dilated rays, less often in other bark components (Fig. 14). They may be present in parenchyma cells or sclereids. Crystal-containing sclereids are common in all bark components. Particularly, in the cortex of the investigated samples (and also in the pheloderm, if *Duguetia* is excluded), sclereids dominate. The quantity of crystal-containing parenchyma cells, however, varies in different bark components (Fig. 14 and Table 3). In phloem rays, crystals are more frequently present in parenchyma cells. This may be a consequence of the greater age of the tissue in the cortex. Cells have had time to thicken their cell walls and finally convert into sclereids because they are initiated earlier than cells in (dilating) rays and axial phloem. Sometimes sclerification is typical of a genus, as it is for *Oxandra*, in which crystals are exclusively present in sclereids in all tissues. More than one crystal per cell was found particularly in *Duguetia* and occasionally in other genera, but this feature was not thoroughly explored.

For Annonaceae, the occurrence of crystals in sclereids or parenchyma cells, which accompany fibre groups, is a very distinctive feature. Crystals apparently are initiated close to fibre groups in axial phloem parenchyma. The fusiform phloem parenchyma cells may turn into sclereids or may undergo transverse divisions. As a result, crystalliferous sclereids or chambered parenchyma cells with crystals in short or



long chains flank or surround fibre groups. We sometimes also detected some single crystals inside fibre groups, which may be a sign of fibres failing to develop and being replaced by crystal cells (cf. Evert 1960).

The way in which crystalliferous cells flank fibre groups is diagnostic in Neotropical Annonaceae (Figs. 13, 15–18). The most striking pattern, crystals more or less completely surrounding the fibre groups, is seen in ten genera (Fig. 15 and Table 4). Roth (1981) described this pattern for *Agonandra brasiliensis* (Opiliaceae), in which crystalliferous parenchymatic sheaths surround the roundish or oval fibre groups. When crystal chains occur on one side of the fibre groups, she classified these as “septate crystal bands”. She reports these septate crystal bands as a constant feature in some families, such as Leguminosae. She did not, however, distinguish the location, i.e. abaxial, adaxial or lateral to the fibre groups. For Annonaceae, we regard the different crystal locations as highly diagnostic since they are restricted to a few genera.

Where crystals accompany fibre groups, these long/short crystal chains may be parenchymatic or more or less sclerified.

*Cymbopetalum* and *Trigynaea* stand out because of the occurrence of tangential bands of crystals between fibre groups (cf. Table 5). Roth (1981) recognised a comparable pattern in two *Terminalia* species. In that genus, crystalliferous cells formed continuous bands, whereas in our samples tangential bands are interrupted by fibre groups.

An exceptional finding is radial rows of crystals in a few larger rays in one sample of *Annona*. No similar pattern was seen in any other sample.

Crystals may border sclereid groups in dilated phloem rays, but this is rare and does not seem to be of any taxonomical value.

### Distribution of character states

As shown above, the Neotropical members of Annonaceae are quite uniform in their bark structure. However, some quantitative and qualitative variation can be distinguished that might be useful for identification purposes. As we studied only one or two specimens per species, our

material does not allow a well-founded interpretation. Although in *Duguetia*, the genus in which 42 specimens covering 28 species were studied, marked variation seems to be present at or below the species level, in the discussion of the distribution of the character states we confine ourselves to the genus level. As far as we know, the variation of all other characters or character states not mentioned here is independent of the generic limits.

**Features characterising the family: common in (nearly) all species of the genera studied**

**FIBRES.** Compose compact groups which are square to tangentially oblong; formed in tangential bands superposing each other in a regular manner.

**RAYS.** Dilate more or less regularly; multiseptate; some are discontinuous.

**Characters present in all specimens in at least some genera (indicated with asterisk) and also found in a part of the specimens of other genera (without asterisk)**

**PHELLEM.** Type of phellem cells: only parenchymatic cells in *Anaxagorea*, *Asimina*\*, *Cardiopetalum*\*, *Crematosperma*, *Cymbopetalum*\*, *Duguetia*, *Fusaea*, *Guatteria*, *Guatteriopsis*\*, *Heteropetalum*\*, *Hornschuchia*\*, *Porcelia*\*, *Rollinia*\*, *Trigynaea*.

**SCLEREIDS.** *Annona*, *Duguetia*, *Fusaea*, *Klarobelia*, *Ruizodendron*\*. Type of sclerified cells: U-shaped in *Annona*, *Bocageopsis*\*, *Crematosperma*, *Desmopsis*\*, *Diclinanona*, *Duguetia*, *Ephedranthus*\*, *Guatteria*, *Klarobelia*\*, *Malmea*\*, *Mosannonna*\*, *Onychopetalum*\*, *Oxandra*\*, *Pseudomalmea*\*, *Sapranthus*\*, *Tridimeris*\*, *Xylopia*\*; reversely U-shaped in *Anaxagorea*, *Annona*, *Diclinanona*, *Duguetia*, *Guatteria*, *Pseudoxandra*\*, *Tetrameranthus*\*, *Unonopsis*\*; only non-secretory cells in *Anaxagorea*, *Asimina*\*, *Cardiopetalum*\*, *Cymbopetalum*, *Desmopsis*\*, *Duguetia*, *Ephedranthus*, *Fusaea*, *Klarobelia*, *Malmea*, *Porcelia*\*, *Rollinia*, *Ruizodendron*\*, *Trigynaea*.

**PHELLODERM.** Type of phellogen cells: only parenchymatic cells in *Bocageopsis*, *Cardiope-*

*talum\**, *Duguetia*, *Ephedranthus*, *Fusaea*, *Guatteria*, *Guatteriopsis\**, *Hornschurchia\**, *Klarobelia*, *Mosannona*, *Oxandra*, *Rollinia*, *Tetrameranthus\**, *Trigynaea\**; only non-secretory cells in *Anaxagorea\**, *Annona*, *Cardiopetalum\**, *Crematosperma*, *Cymbopetalum\**, *Diclinanona*, *Duguetia*, *Ephedranthus\**, *Guatteria*, *Heteropetalum\**, *Hornschurchia\**, *Klarobelia*, *Mosannona*, *Oxandra*, *Porcelia\**, *Rollinia*, *Tetrameranthus\**, *Tridimeris\**, *Trigynaea\**, *Xylopia*.

CORTEX. Type of cortex cells: only parenchymatic cells in *Cardiopetalum\**, *Klarobelia*, *Unonopsis*; only non-secretory cells in *Anaxagorea\**, *Annona*, *Asimina\**, *Bocageopsis\**, *Crematosperma\**, *Cymbopetalum*, *Duguetia*, *Ephedranthus*, *Guatteria*, *Guatteriopsis\**, *Heteropetalum\**, *Hornschurchia\**, *Malmea*, *Mosannona*, *Oxandra*, *Pseudoxandra*, *Rollinia*, *Ruizodendron\**, *Tetrameranthus\**, *Tridimeris\**, *Unonopsis*, *Xylopia*.

RAYS. Type of dilatation: funnel-form in *Duguetia*, *Guatteriopsis\**, *Hornschurchia\**, *Klarobelia*, *Oxandra*; cellular composition weakly heterocellular in *Annona*, *Bocageopsis*, *Duguetia*, *Ephedranthus*, *Guatteria*, *Porcelia\**, *Pseudomalmea*, *Xylopia*. Types of cells: only parenchymatic cells in *Annona*, *Cardiopetalum\**, *Duguetia*, *Hornschurchia\**, *Klarobelia*; only non-secretory cells in *Anaxagorea*, *Annona*, *Asimina\**, *Cardiopetalum\**, *Crematosperma\**, *Desmopsis\**, *Diclinanona*, *Duguetia*, *Ephedranthus\**, *Guatteria*, *Heteropetalum\**, *Hornschurchia\**, *Mosannona*, *Oxandra*, *Pseudoxandra*, *Rollinia*, *Ruizodendron\**, *Tetrameranthus\**, *Tridimeris\**, *Trigynaea\**, *Unonopsis\**, *Xylopia*.

AXIAL PHLOEM. (<sup>1</sup> = one exception). Fibre groups only wide (<sup>3</sup> 3 cell layers): *Anaxagorea\**, *Annona\**, *Bocageopsis*, *Cardiopetalum\**, *Crematosperma\**, *Cymbopetalum\**, *Duguetia*, *Guatteria*, *Klarobelia*, *Onychopetalum\**, *Oxandra*<sup>1</sup>, *Porcelia\**, *Pseudomalmea\**, *Pseudoxandra*, *Rollinia\**, *Ruizodendron\**, *Sapranthus\**, *Tetrameranthus*, *Trigynaea\**, *Unonopsis*, *Xylopia\**. Fibre groups arc-shaped: *Diclinanona\**, *Duguetia*, *Fusaea\**, *Guatteria\**. Association of sclereids with fibre groups frequent: *Duguetia*, *Ephedranthus*, *Malmea\**, *Onychopetalum\**, *Oxandra\**, *Pseudomalmea*, *Sapranthus\**, *Tridimeris*, *Unonopsis*. Completely lacking: *Annona\**, *Cardiopetalum\**, *Crematosperma*,

*Cymbopetalum\**, *Diclinanona\**, *Duguetia*, *Ephedranthus*, *Fusaea\**, *Guatteria*, *Guatteriopsis\**, *Heteropetalum\**, *Hornschurchia\**, *Klarobelia\**, *Mosannona\**, *Porcelia\**, *Pseudomalmea*, *Rollinia*, *Ruizodendron\**, *Tetrameranthus\**, *Tridimeris*, *Trigynaea\**, *Xylopia\**. Types of cells: only non-secretory cells in *Anaxagorea*, *Annona*, *Asimina\**, *Cardiopetalum\**, *Crematosperma\**, *Desmopsis\**, *Duguetia*, *Ephedranthus\**, *Guatteria*, *Guatteriopsis\**, *Heteropetalum\**, *Hornschurchia\**, *Mosannona*, *Oxandra*, *Pseudoxandra*, *Rollinia*, *Ruizodendron\**, *Sapranthus\**, *Tetrameranthus\**, *Tridimeris\**, *Trigynaea\**, *Unonopsis*, *Xylopia*.

CRYSTALS: (<sup>1</sup> = one exception, probably an artefact; <sup>2</sup> = one exception, phloem is too young). Crystals not present in *Annona*, *Diclinanona\**, *Heteropetalum\**, *Klarobelia*<sup>2</sup>. Type of crystals: only non-prismatic in *Anaxagorea\**, *Annona*, *Duguetia*<sup>\*1</sup>; styloid-like in *Annona*, *Asimina\**, *Cymbopetalum*; elongate in *Annona*, *Cymbopetalum\**, *Duguetia*, *Oxandra*, *Trigynaea\**. Pattern of crystals: bordering sclereid groups in *Annona*, *Porcelia\**, *Pseudomalmea*, *Pseudoxandra*; not bordering any sclerenchyma in *Anaxagorea\**, *Cardiopetalum\**, *Crematosperma\**, *Desmopsis\**, *Duguetia*<sup>\*1</sup>, *Fusaea\**, *Hornschurchia\**, *Onychopetalum\**, *Oxandra*, *Pseudoxandra*, *Tridimeris*, *Trigynaea\**, *Xylopia\**; around fibre groups in *Annona*, *Cymbopetalum\**, *Duguetia*<sup>1</sup>, *Ephedranthus\**, *Klarobelia*<sup>\*2</sup>, *Malmea*, *Mosannona\**, *Porcelia\**, *Pseudomalmea\**, *Tetrameranthus\**; short vertical chains (< 1 mm) in *Annona*, *Asimina\**, *Bocageopsis\**, *Mosannona*, *Oxandra*, *Rollinia\**, *Ruizodendron\**, *Tetrameranthus\**, *Tridimeris*, *Unonopsis*; long vertical chains (> 1 mm) in *Annona*, *Cymbopetalum\**, *Duguetia*<sup>1</sup>, *Ephedranthus\**, *Klarobelia*<sup>\*2</sup>, *Mosannona*, *Oxandra*, *Porcelia\**, *Pseudomalmea\**.

OCCURRENCE OF CRYSTALS. (<sup>1</sup> = no information on cortex, <sup>2</sup> = also in parenchyma). Only in ray parenchyma in *Anaxagorea\**, *Cardiopetalum\**, *Crematosperma*, *Duguetia*, *Fusaea\**, *Xylopia\**; only along fibres (in parenchyma or sclereids) in *Annona*, *Bocageopsis*<sup>\*1</sup>, *Guatteria\**, *Guatteriopsis\**, *Klarobelia*<sup>1</sup>; in sclerenchyma in every bark component in *Cymbopetalum*<sup>\*2</sup>, *Ephedranthus*, *Malmea*<sup>\*2</sup>, *Mosannona*<sup>2</sup>, *Oxandra*, *Rollinia*<sup>2</sup>, *Sapranthus*<sup>\*1</sup>, *Tridimeris*<sup>\*1</sup>, *Unonopsis*; more than one per cell (crystals of unequal size) in

*Annona*, *Cymbopetalum*, *Duguetia* (almost in every specimen), *Hornschuchia*\*, *Mosannona*, *Oxandra*, *Porcelia*\*, *Pseudomalmea*; in enlarged cells in *Malmea*\*, *Mosannona*.

Characters present in all (indicated with asterisk) or in part of the specimens in one or a few genera (without asterisk)

(<sup>1</sup> = one exception, sample is poor).

Phelloderm impregnated with sclereids: *Onychopetalum*\*.

Rays less than 1 mm high in tangential section: *Oxandra*, *Pseudomalmea*.

Fibre groups in irregular tangential bands: *Tridimeris*.

Fibre groups only narrow: *Duguetia*, *Fusaea*, *Guatteria*, *Mosannona*, *Pseudoxandra*, *Tridimeris*.

Crystals as druses: *Anaxagorea*\*.

Pattern of crystals: adaxial side of fibre groups: *Bocageopsis*\*, *Sapranthus*\*; lateral side of fibre groups: *Guatteria*<sup>1</sup>\*, *Guatteriopsis*\*; between fibre groups: *Cymbopetalum*\*, *Trigynaena*\*.

Crystals in long radial chains: *Annona*.

## Phenetic similarity of bark characters

In the last decade, several contributions to the classification of Annonaceae have been pub-

lished. Some of these concentrate on phenetics, others, mainly molecular studies, focus on phylogenetic relationships.

We will concentrate on the possible contribution of bark anatomical characters to phenetic grouping, focussing at the genus level. Restricting ourselves to the Neotropical genera, we shall compare our results with a preliminary grouping of annonaceous genera (Koek-Noorman *et al.* 1997; Table 6), which was based on flower and fruit morphology. The question of whether these characters have diagnostic or taxonomical value at the species level, falls beyond the scope of this paper.

For a discussion of the phylogenetic signal of bark anatomical data, we deem our bark anatomical data alone to be insufficient. We will return to this topic in the last paragraph of this paper.

Group 1 (the “*Duguetia* group”) is represented by *Duguetia* and *Fusaea*. In both genera, secretory cells, often present in most tissues, are, at least partly, arranged in tangential rows and/or bands. Similar bands are found in other genera, mostly so in members of the “*Crematosperma* group” (Group 4) and *Xylopia*, however, not in all tissues.

Fibre groups are characteristically arch-shaped. This feature is only found in the genera *Diclinanona* and *Guatteria*.

Crystals occur only in ray parenchyma, however, never associated with fibre groups. This combination is found only in *Anaxagorea*, *Crematosperma* and *Xylopia*.

**Table 6.** List of studied Neotropical genera of Annonaceae and their grouping according to Koek-Noorman *et al.* (1997).

Groups	Genus and number of species
Group 1 (“ <i>Duguetia</i> group”)	<i>Duguetia</i> (28), <i>Fusaea</i> (1)
Group 2 (“ <i>Annona</i> group”)	<i>Annona</i> (4), <i>Rollinia</i> (2)
Group 3 (“ <i>Guatteria</i> group”)	<i>Guatteria</i> (7), <i>Guatteriopsis</i> (1), <i>Heteropetalum</i> (1)
Group 4 (“ <i>Crematosperma</i> group”)	<i>Ephedranthus</i> (2), <i>Malmea</i> (2), <i>Klarobelia</i> (5), <i>Mosannona</i> (3), <i>Pseudomalmea</i> (2), <i>Oxandra</i> (7), <i>Ruizodendron</i> (1), <i>Crematosperma</i> (2), <i>Pseudoxandra</i> (3)
Group 5 (“ <i>Ambavia</i> group”)	<i>Tetrameranthus</i> (1)
Group 6 (“ <i>Cardiopetalum</i> group”)	<i>Cardiopetalum</i> (1), <i>Cymbopetalum</i> (2), <i>Hornschuchia</i> (1), <i>Trigynaena</i> (2)
Group 7 (“ <i>Annickia</i> group”)	<i>Bocageopsis</i> (2), <i>Onychopetalum</i> (1), <i>Unonopsis</i> (3)
Group 8 (“ <i>Ancana</i> group”)	<i>Desmopsis</i> (1)
Group 12 (“ <i>Alphonsea</i> group”)	<i>Porcelia</i> (1), <i>Sapranthus</i> (1), <i>Tridimeris</i> (2)
Genera in isolated position	<i>Anaxagorea</i> (3), <i>Xylopia</i> (4)
Genera with intermediate positions	<i>Asimina</i> (1), <i>Diclinanona</i> (2)

Group 2 (the “*Annona* group”) consists of *Annona* and *Rollinia*. In the available material, all fibre groups are more than 3 cell layers wide, without accompanying sclereids. Wide fibre groups are common in the Annonaceae studied, but this combination was only found in the “*Ambavia* group” (group 5), “*Cardiopetalum* group” (group 6), *Klarobelia*, *Anaxagorea*, *Xylopia* and some single specimens.

Group 3 (the “*Guatteria* group”, consisting of *Guatteria* and some small satellite genera) is characterised by crystals occurring exclusively in sclerified cells on the lateral side of fibre groups. With the sole exception of *Hornschnuchia*, this feature is unique to this group. All phellem cells are secretory cells. This is also found in *Tetrameranthus* (group 5), in the “*Annickia* group” (group 7) and in some other genera and specimens. However, in the “*Guatteria* group”, this feature is in sharp contrast to the axial phloem, where secretory cells are absent or very rare. Apart from *Tetrameranthus* and part of the “*Cardiopetalum* group” (group 6), this last feature is shared with the “*Annona* group”, and some other genera.

The well-represented “*Crematosperma* group” (group 4) seems to be highly diverse. A very conspicuous and constant feature is formed by the U-shaped cell walls in the phellem, which are only lacking in *Pseudoxandra* (reversely U-shaped cell walls) and *Klarobelia lucida* (uniformly thickened cell walls). This feature is, however, shared with many other genera, i.e. *Bocageopsis*, *Desmopsis*, *Onychopetalum*, *Sapranthus*, *Tridimeris*, *Xylopia* and some single samples of other genera.

*Tetrameranthus* is the only genus representing group 5 (the “*Ambavia* group”). In contrast to the phellem, which consists exclusively of secretory cells, these cells are lacking in the phelloderm, cortex, rays and axial phloem. This combination was also found in *Hornschnuchia*, *Tridimeris* and some other specimens.

Group 7 (the “*Annickia* group”), represented by *Bocageopsis*, *Onychopetalum* and *Unonopsis*, is difficult to typify on the basis of bark characters. The group, which is quite variable, shows only characters that are present in many other genera.

The same can be said of *Cardiopetalum* and

*Cymbopetalum*, which represent group 6, the “*Cardiopetalum* group”. An exception may be the phellem cells, of which are all parenchymatic (except in one sample, where they are slightly thickened). This feature is not very common, being present in the monotypic genera *Asimina*, *Guatterioopsis*, *Heteropetalum*, *Porcelia*, *Rollinia* and some single specimens.

*Desmopsis* is the only genus representing the mainly paleotropical group 8 (the “*Ancana* group”), which does not show typical characters or any remarkable combinations of features.

The mainly paleotropical “*Alphonsea* group” (group 12) is represented by *Porcelia*, *Sapranthus* and *Tridimeris*. Crystals are located only in sclereids in all bark components (except the phellem). The absence of crystals in parenchyma cells resembles *Oxandra*.

*Xylopia* was loosely clustered with *Desmopsis* and 12 paleotropical genera and not included in any group by Koek-Noorman *et al.* (1997). Likewise, *Anaxagorea*, which was placed at the base of their main cluster. *Anaxagorea* is outstanding, as crystals are only present as druses.

## Phylogenetic signals in bark anatomy

As mentioned previously, the bark anatomical data, as given in the descriptions and Appendices 2A–2G, do not provide us with a strong phylogenetic hypothesis. An explanation may be found in the noise arising from data collection since we strove more for completeness than for “taxonomically important” characters. Furthermore, a disproportion exists in the material studied, due to the incidental availability of samples.

Another way to answer the question of whether phylogenetic signals are present in bark structure is to start from a phylogeny based on another character set, preferably obtained from molecular data.

Sauquet *et al.* (2003) in a phylogenetic analysis of Magnoliales and Myristicaceae based on morphological data and multiple molecular data sets found *Anaxagorea* at the base of the monophyletic Annonaceae. The other 12 annonaceous genera studied were distributed in three clades: an ambavioid clade (not represented in our study), a malmeoid-piptostigmoid-miliusoid

Genera/ Characters	1	2	3	4	5	6	7	8	9
Desmopsis	0	0	1	0	0	1	0	3	
Sapranthus	0	0	3	3	4	1	1	3	
Tridimeris	0	0	0	0	4	1	1	3	
Crematosperma	0	1	1	0	3	1	1	2	
Pseudoxandra	0	0	1	0	3	2	0	3	
Malmea	0	0	3	1	0-4	1	1	2	
Klarobelia	0	0	0	1	0-3	1	1	2	
Pseudomalmea	0	0	1	1	4	1	1	2	
Oxandra	0	0	3	2	2-4	1	0	3	
Ephedranthus	0	0	2	1	0-3	1	1	2	
Ruizodendron	0	0	0	0	0	3	0	2	
Mosanona	0	0	0	1	2-4	1	1	2	
Bocageopsis	0	0	1	3	4	1	0	3	x
Onychopetalum	0	0	3	0	4	1	0	3	
Unonopsis	0	0	3	0	3-4	2	1	3	
Annona	0	0	0	1	1-3	1-2	1	2	
Rollinia	0	0	1	0	0-2	0	2	2	
Asimina	0	0	1	0	0	0	2	2	
Diclinanona	2	n	0	n	1-2	1-2	1	0	
Duguettia	1	2	1	0	0-3	1(0-2)	1	1	
Fusaea	1	2	0	0	0-3	0-1	1	1	
Xylopia	0	2	0	0	3-4	1	2	1	
Guatteria	2	0	1	4	4	0-1	1	(3)	x
Guatteropsis	0	0	0	4	4	0	2	(3)	x
Heteropetalum	0	n	0	n	4	0	2	0	n
Cymbopetalum	0	0	0	1	0-1	0	2	2	
Porcellia	0	0	0	1	0	0	2	2	
Trigynaea	0	0	0	0	0-1	3	1	2	
Hornsuchia	0	2	0	4	4	0	2	1	
Cardiopetalum	0	2	0	0	0	0	2	1	
Tetrameranthus	0	0	0	1	4	2	1	2	
Anaxagorea	0	2	1	0	0-4	2	1	1	

**Fig. 19.** Relative position of Neotropical genera deduced from phylogram in preparation (Chatrou *et al.* 2003, **pers. comm?**). Differences in branch length are omitted. Only the branches that are well-supported by molecular data are shown. The bark data have been extracted from Appendices 2A–G. With the exception of character 5, data are estimated averages per genus. For detailed explanation, see text. Character explanations: 1: Arc-shaped fibre groups: 0 = absent; 1 = present, but not all arc-shaped; 2 = all fibre groups arc-shaped. 2: Crystals in rays only present in parenchyma cells: 0 = no; 1 = often; 2 = always. 3: Sclereids in wide fibre groups: 0 = absent; 1 = sporadic; 2 = present; 3 = frequent. 4: Location of crystals in relation to fibre groups: 0 = absent; 1 = around (on every side); 2 = abaxial; 3 = adaxial; 4 = lateral. 5: Secretory cells in phellem: 0 = absent; 1 = few; 2 = abundant; 3 = bulk; 4 = full. 6: Type of sclerification of phellem cells. 0 = absent; 1 = U-shaped; 2 = reversely U-shaped; 3 = thickened. 7: Parenchymatic phellem cells. 0 = absent; 1 = partly present; 2 = exclusively present. 8: Presence of crystals. 0 = absent; 1 = in parenchyma only; 2 = in parenchyma and sclereids; 3 = in sclereids only. 9: Crystals lacking in rays.

(MPM) clade and a large clade including the genera with inaperturate pollen.

Chatrou *et al.* (2003, pers. comm.) studying several cpDNA markers (*rbcL*, *trnT-L* intergenic spacer, *trnL* intron, *trnL-F* intergenic spacer, *psbA-trnH* intergenic spacer, and partial *matK*) constructed a phylogram of 148 species of Annonaceae, representing 67 genera. With the exception of a few basal lineages formed by *Tetrameranthus* and *Anaxagorea*, the majority of the species diverge into two major sister clades, distinct on the basis of pollen morphology, geographical distribution and patterns of

molecular evolution. One clade includes, in addition to many genera from the Paleotropics, all genera from the “*Crematosperma* group” and the “*Annickia* group”, together with some genera from the “*Alphonsea* group”. This clade is characterised by monosulcate and disulcate pollen. The other clade includes the genera with inaperturate pollen. Here, all other Neotropical genera studied can be found.

No discrepancy exists between the results of Sauquet *et al.* (2003) and those of Chatrou *et al.* (2003). The relative position of the Neotropical genera deduced from the phylogram of Chatrou

*et al.* (2003, pers. comm.) is given in Fig. 19, together with some features discussed under “Phenetic similarity of bark characters”. Differences in branch length are neglected here. Only the well-supported branches are given; others have been supposed to be still unresolved. For *Cardiopetalum*, no molecular data were available. Its position in the clade representing the “*Cardiopetalum* group” seems, however, undisputed.

The following tentative conclusions are drawn:

The upper half of Fig. 19, including the genera with monosulcate and disulcate pollen, differs in some respects from the lower half. It includes most genera with U-shaped cell walls in the phellem (character 6), *Xylopia* in the lower half being the only other genus, in which this is a constant feature. Cell wall thickenings found in the basal genus *Anaxagorea* are reversely U-shaped.

In the genera of the upper half, crystals are always found in sclerenchymatic tissue (character 8). This, too, is in contrast to the lower half of the phylogram including *Anaxagorea*, in which crystals are nearly always found in parenchymatic cells.

The wide fibre groups (character 3) have no or few sclereids in the genera of the lower half, in contrast to those of the upper half. This feature seems to connect the “*Cardiopetalum* group” to the “*Annona* group” and *Xylopia*. This combination of characters occurs, however, in some genera of the upper half as well. Since scanty sclereids are found in the basal genus *Anaxagorea*, it is impossible to determine the plesiomorphic state of this feature.

There are no bark characters that support any further subdivision within the upper half.

The lower half of the phylogram, including the genera with inaperturate pollen, shows a second bipartition separating the “*Cardiopetalum* group”. This bipartition is hardly supported. The “*Cardiopetalum* group” shares the fully parenchymatic phellem cells (character 7) with genera from the “*Guatteria* group” and the “*Annona* group”. However, this feature occurs elsewhere as well. In *Anaxagorea*, both parenchymatic and sclerenchymatic phellem cells were observed.

The arc-shaped fibre groups (character 1)

characterising the “*Duguetia* group” seem to be apomorphic, as they also occur in *Diclinanona* and *Guatteria*, but are lacking in the basal genera *Anaxagorea* and *Tetrameranthus*.

Another character found to be constant in the “*Duguetia* group” is the absence of crystals in sclerenchymatic ray cells (character 2). This feature is present in *Anaxorea* as well, which diminishes its phylogenetic value.

The best characters to distinguish the “*Guatteria* group” are the absence of crystals in the rays (character 9) and the lateral location along the fibre groups (character 4).

Like character 4, character 5 (abundance of secretory cells in phellem) is shared with *Hornschurchia*. Character 5, however, is present in many specimens from the upper half. The absence in some specimens of *Anaxagorea*, however, suggests that these features may have at least some phylogenetic relevance.

## Concluding remark

Notwithstanding that the bark anatomical dataset alone does not yet permit conclusions about the phylogeny of the Annonaceae to be drawn, comparison with molecular data does show that the shape of the fibre groups, the distribution of crystals and the nature of the phellem cells are phylogenetically relevant in Annonaceae.

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**Appendix 1.** List of voucher specimens for bark morphological and anatomical studies. Bark samples are listed by their collection number according to the Index Xylarium (Stern 1988). Samples of morphological bark descriptions collected from the Reserva Florestal Ducke (near Manaus, Brazil) are abbreviated to RFD, and the collection number of the project is used to refer to trees.

### **Anaxagorea**

- A. brevipes* Benth.: Sothers 611 (RFD 3239).  
*A. dolichocarpa* Sprague & Sandwith: Maas *et al.* 7894 (Uw 33 681).  
*A. manausensis* Timmerman: Miralha *et al.* 301 (RFD 3405).

### **Annona**

- A. ambotay* Aubl.: Sothers 528 (RFD 3015).  
*A. foetida* Mart.: Miralha *et al.* 293 (RFD 3402).  
*A. impressivenia* Saff. ex R.E. Fr. (RFD 3716).  
*A. sp. nov. aff. excellens* (RFD 2810).

### **Asimina**

- A. triloba* (L.) Dunal: Smiths. Inst. W-3427 (Uw 7318).

### **Bocageopsis**

- B. multiflora* (Mart.) R.E. Fr.: Hopkins 1507 (RFD 2189).  
*B. pleiosperma* Maas: Sothers 513 (RFD 2978).

### **Cardiopetalum**

- C. surinamense* R.E. Fr.: de Granville 6273 (Uw 29 923).

### **Crematosperma**

- C. brevipes* (DC.) R.E. Fr.: de Granville *et al.* 7672 (Uw 31 466).  
*C. cauliflorum* R.E. Fr.: Maas *et al.* 6271 (Uw 30 306);  
 Maas *et al.* 4592 (Uw 26 252).

### **Cymbopetalum**

- C. brasiliense* (Vell.) Benth. ex Baill.: Maas *et al.* 6185 (Uw 30 267).  
*C. longipes* Benth. ex Diels: Maas *et al.* 6024 (Uw 30 244).

### **Desmopsis**

- D. sp.*: van Rooden 760 (Uw 26 195).

### **Diclinanona**

- D. calycina* (Diels) R.E. Fr.: (RFD 2853).  
*D. tessmannii* Diels: Maas 6318 *et al.* (Uw 30 328).

### **Duguetia**

- D. argentea* (R.E. Fr.) R.E. Fr.: Krukoff 7000 (Uw 8094).  
*D. bahiensis* Maas: Maas *et al.* 6987 (Uw 31 902).  
*D. cadaverica* Huber: Florschütz & Maas 2767 (Uw 11 096); de Granville *et al.* 6301 (Uw 29 933); Polak 381 (Uw 34 284).  
*D. calycina* Benoist: Lindeman 5838 (Uw 3989); Lindeman, Görts van Rijn *et al.* 566 (Uw 26 506); Lindeman, de Roon *et al.* 833 (Uw 27 467); Maguire 24820 (Uw 2570).  
*D. cauliflora* R.E. Fr.: Jansen-Jacobs *et al.* 1441 (Uw 33158).  
*D. eximia* Diels: de Granville 6265 (Uw 29917); de Granville 6433 (Uw 29971); de Granville 7308 (Uw 31411).  
*D. furfuracea* (A. St.-Hil.) Saff.: Simonis *et al.* 85 (Uw 29 402).  
*D. granvilleana* Maas: de Granville 6134 (Uw 29888).

- D. hadrantha* (Diels) R.E. Fr.: Maas *et al.* 6304 (Uw 30323).  
*D. inconspicua* Sagot: Maas *et al.* 5897 (Uw 27373).  
*D. lanceolata* A. St.-Hil.: Reitz 14 225 (Uw 6328).  
*D. latifolia* R.E. Fr.: Maas *et al.* 6254 (Uw 30298).  
*D. macrocalyx* R.E. Fr.: Jansen-Jacobs *et al.* 3011 (Uw 34510).  
*D. macrophylla* R.E. Fr.: Davidse & Miller 26 775 (Uw 31207).  
*D. neglecta* Sandw.: Lindeman, de Roon *et al.* 722 (Uw 27412); Maas *et al.* 7433 (Uw 32602).  
*D. odorata* (Diels) J.F. Macbr.: Krukoff 5112 (Uw 19766).  
*D. pauciflora* Rusby: Forest Dept. Brit. Guiana 3692 (Uw 762).  
*D. pycnastera* Sandw.: Florschütz & Maas 3091 (Uw 11121); Lindeman 6975 (Uw 4691).  
*D. quitarensis* Benth.: Ellenberg 2500 (Uw 8703); Jansen-Jacobs *et al.* 416 (Uw 30627); Krukoff 5556 (Uw 20029).  
*D. riparia* Huber: Oldenburger *et al.* 1404 (Uw 17969).  
*D. spixiana* Mart.: Krukoff 5738 (Uw 20158); Maas *et al.* 6296 (Uw 30318).  
*D. stelechantha* (Diels) R.E. Fr.: Maguire *et al.* 56 608 (Uw 16453).  
*D. stenantha* R.E. Fr.: Krukoff 8582 (Uw 16138); Maas *et al.* 6325 (Uw 30330).  
*D. surinamensis* R.E. Fr.: Jansen-Jacobs *et al.* 376 (Uw 30612); Jansen-Jacobs *et al.* 377 (Uw 30613); Jansen-Jacobs *et al.* 2202 (Uw 33906).  
*D. ulei* (Diels) R.E. Fr.: Miralha *et al.* 231 (Uw 33456).  
*D. uniflora* (DC.) Mart.: Miralha *et al.* 232 (Uw 33457).  
*D. yeshidan* Sandw.: Jansen-Jacobs *et al.* 374 (Uw 30610); Jansen-Jacobs *et al.* 1458 (Uw 33175).

### **Ephedranthus**

- E. columbianus* Maas & van Setten: Rentería A. 2364 (Uw 31299).  
*E. guianensis* R.E. Fr.: Schulz 8568 (Uw 6856).

### **Fusaea**

- F. longifolia* (Aubl.) Saff.: Lindeman 5801 (Uw 3955); Lindeman 6742 (Uw 4559), Maas *et al.* 6320 (Uw 30329).

### **Guatteria**

- G. citriodora* Ducke: Ribeiro 1595 (RFD 2624).  
*G. discolor* R.E. Fr.: Assunção 205 (RFD 1397).  
*G. foliosa* Benth.: Vicentini 638 (RFD 1817).  
*G. lehmannii* R.E. Fr.: Cuatrecasas 15507 (Uw 25052).  
*G. megalophylla* Diels: Ribeiro 1608 (RFD 2809).  
*G. olivacea* R.E. Fr.: Vicentini 621 (RFD 1807).  
*G. scytophylla* Diels: Vicentini 694 (RFD 2062).

### **Guatteriopsis**

- G. hispida* R.E. Fr.: (RFD 3591).

### **Heteropetalum**

- H. sp.*: Stevenson 1115 (Uw 33073).



**Hornschuchia**

*H. polyantha* Maas: Amorim & Maas 827 (Uw 35426).

**Klarobelia**

*K. candida* Chatrou: Chatrou *et al.* 35 (Uw 34868).

*K. cauliflora* Chatrou: Chatrou *et al.* 6 (Uw 34863).

*K. lucida* (Diels) Chatrou & Montero 85303 (Uw 35428).

*K. inundata* Chatrou: Chatrou *et al.* 4 (Uw 34862).

*K. stipitata* Chatrou: Jiménez *et al.* 667 (Uw 36709).

**Malmea**

*M. dielsiana* R.E. Fr.: Maas *et al.* 6026 (Uw 30246).

*M. surinamensis* Chatrou: Daniëls & Jonker 859 (Uw 8543).

**Mosannonna**

*M. depressa* (Baill.) Chatrou subsp. *abscondita* Chatrou: S.S. Colin *et al.* 369 (Uw 31041).

*M. aff. discolor* Chatrou: Lindeman, Görts-van Rijn *et al.* 283 (Uw 26395).

*M. raimondii* (Diels) Chatrou: Schunke V. 10899

**Onychopetalum**

*O. amazonicum* R.E. Fr.: Rodrigues W. 3326 (Uw 23662).

**Oxandra**

*O. asbeckii* (Pulle) R.E. Fr.: Lanjouw & Lindeman 2165 (?Uw 1637); Polak 397 (Uw 34292).

*O. espintana* (Benth.) Baill.: Maas *et al.* 5956 (Uw 30229).

*O. lanceolata* (Sw.) Baill.: Maas *et al.* 6395 (Uw 31209).

*O. laurifolia* (Sw.) A. Rich.: Sintenis 6121 (Uw 29376).

*O. riedeliana* R.E. Fr.: Rodrigues & Mello 2373 (Uw 33451).

*O. sphaerocarpa* R.E. Fr.: Maas *et al.* 8226 (Uw 34859).

*O. sp.*: Maas *et al.* 8297 (Uw 34861).

**Porcelia**

*P. ponderosa* (Rusby) Rusby: Maas *et al.* 6137 (Uw 30259).

**Pseudomalmea**

*P. diclina* (R.E. Fr.) Chatrou: Chatrou *et al.* 21 (Uw 34866).

*P. sp.*: Rentería A. *et al.* 1726.

**Pseudoxandra**

*P. lucida* R.E. Fr.: Maas *et al.* 6289 (Uw 30312).

*P. obscurinervis* Maas R.E. Fr.: Vicentini 703 (RFD 2010).

*P. sp.*: (RFD 2804).

**Rollinia**

*R. insignis* R.E. Fr.: Miralha *et al.* 265 (RFD 3282).

*R. pittieri* Saff.: Chatrou 18 (Uw 34865).

**Ruizodendron**

*R. ovale* (Ruiz & Pav.) R.E. Fr.: Maas *et al.* 8600 (Uw 35948).

**Sapranthus**

*S. palanga* R.E. Fr.: van Rooden 868 (Uw 26216).

**Tetrameranthus**

*T. duckei* R.E. Fr.: Maas 230 (Uw 33455); Coêlho *s.n.* (Uw 26747).

**Tridimeris**

*T. baillonii* G.E. Schatz: Schatz *et al.* 1198 (Uw 31206).

*T. sp.*: S.S. Colin *et al.* 367 (Uw 31039).

**Trigynaea**

*T. lagaropoda* D.M. Johnson & N.A. Murray: Maas *et al.* 6280 (Uw 30308).

*T. guianensis* (R.E. Fr.) R.E. Fr.: Maas *et al.* 7739 (Uw 32 595).

**Unonopsis**

*U. stipitata* Diels: Miralha *et al.* 281 (RFD 3289).

*U. veneficiorum* (Mart.) R.E. Fr.: Maas *et al.* 6361 (Uw 30339).

*U. quatterioides* (A. Dc.) R.E. Fr.: Chatrou *et al.* 16 (Uw 34864).

**Xylopia**

*X. amazonica* R.E. Fr.: Maguire 51917 (RFD 2817).

*X. aromatica* (Lam.) Mart.: 51917 Belem (Uw 9119).

*X. nitida* Dunal: (RFD 2794).

*X. parviflora* Spruce: (RFD 2802).

**Appendix 2(A–G).** Bark anatomical characters of 32 Neotropical genera (99 species) of Annonaceae. Rows set in boldface show (average) values for the genus. Principal symbols used in the table: + = present; – = not applicable; ! = lacking information due to poor section or absence of tissue; ~0 = layer very thin; ? = impossible to determine or uncertain. <sup>1</sup> = Crystals along fibre groups, but not visible in a longitudinal section. Fibre groups are bordered by thick-walled cells which are also visible in longitudinal section. <sup>2</sup> = Very young phloem with long tangential rows of sclereids — a pattern that has not been found in any other species.

**A.** Explanations for collection no.: RFD = tree no. in Reserva Florestal Ducke; Uw = Xylarium of Utrecht branch of National Herbarium of the Netherlands; RA = Rentería, A. *et al.* 1726, a specimen of Utrecht branch of National Herbarium of the Netherlands.

Taxa	Collection no.	Diameter of sample (cm)	Bark width (mm)	Ratio of radius of the sample to bark width	Rhytidome width (mm)	Phloem width (mm)	Periderm width (mm)	Phellem width (mm)	Phelloderm width (mm)	No. of periderms
<i>Anaxagorea brevipes</i>	RFD 3239	12.00	2.00	30.00	0.50	1.50	0.40–0.60	0.28–0.35	0.10–0.25	1
<i>Anaxagorea dolichocarpa</i>	Uw 33681	9.70	6.30	7.70	0.70	5.60	0.35	0.30	0.05	>1
<i>Anaxagorea manausensis</i>	RFD 3405	7.00	3.00	11.70	0.25	2.80	0.20–0.30	0.10–0.15	0.06–0.10	1
<b><i>Anaxagorea</i></b>		<b>9.57</b>	<b>3.77</b>	<b>16.47</b>	<b>0.48</b>	<b>3.30</b>	<b>0.35</b>	<b>0.25</b>	<b>0.10</b>	
<i>Annona ambotay</i>	RFD 3015	6.00	2.75	10.91	0.35	2.45	0.10–0.15	0.09–0.13	0.01–0.03	1
<i>Annona foetida</i>	RFD 3402	15.00	6.25	12.00	1.75	4.50	0.28–0.50	0.20–0.45	0.05–0.08	2
<i>Annona impressivenia</i>	RFD 3716	15.00	8.30	9.04	1.35	6.75	1.00–1.75	0.80–1.60	0.05–0.15	1
<i>Annona</i> sp. nov. aff. <i>excellens</i>	RFD 2810	9.00	2.80	16.07	0.30	2.55	0.25–0.35	0.20–0.30	0.05	1
<b><i>Annona</i></b>		<b>11.25</b>	<b>5.03</b>	<b>12.00</b>	<b>0.94</b>	<b>4.06</b>	<b>0.53</b>	<b>0.47</b>	<b>0.06</b>	
<b><i>Asimina triloba</i></b>	<b>Uw 7318</b>	<b>!</b>	<b>8.70</b>	<b>–</b>	<b>0.25</b>	<b>8.43</b>	<b>0.27</b>	<b>0.20</b>	<b>0.07</b>	<b>1</b>
<i>Bocageopsis multiflora</i>	RFD 2189	30.00	6.00	25.00	0.20	6.00	0.20	0.15	0.05	1
<i>Bocageopsis pleiosperma</i>	RFD 2978	18.00	7.00	12.90	0.70	6.30	0.60–0.80	0.32–0.65	0.07–0.10	1
<b><i>Bocageopsis</i></b>		<b>24.00</b>	<b>6.50</b>	<b>18.95</b>	<b>0.45</b>	<b>6.15</b>	<b>0.39</b>	<b>0.32</b>	<b>0.07</b>	
<b><i>Cardiopetalum surinamense</i></b>	<b>Uw 29923</b>	<b>1.70</b>	<b>1.00</b>	<b>8.50</b>	<b>0.35</b>	<b>0.68</b>	<b>0.32</b>	<b>0.28</b>	<b>0.04</b>	<b>1</b>
<i>Crematosperma brevipes</i>	Uw 31466	7.50	1.90	19.74	0.18	1.72	0.18	0.13	0.05	1
<i>Crematosperma cauliflorum</i>	Uw 26252	5.00	2.20	11.36	0.30	1.85	0.20–0.35	0.10–0.15	0.15–0.20	1
<i>Crematosperma cauliflorum</i>	Uw 30306	10.00	3.60	13.89	0.20	3.40	0.20	0.07	0.13	1
<b><i>Crematosperma</i></b>		<b>7.50</b>	<b>2.57</b>	<b>15.00</b>	<b>0.23</b>	<b>2.32</b>	<b>0.23</b>	<b>0.11</b>	<b>0.12</b>	
<i>Cymbopetalum brasiliense</i>	Uw 30267	3.10	1.90	8.16	1.00	0.90	1	0.90	0.10	1
<i>Cymbopetalum longipes</i>	Uw 30 244	3.20	1.70	9.41	0.40	1.20	0.30–0.50	0.25–0.45	0.05	1
<b><i>Cymbopetalum</i></b>		<b>3.15</b>	<b>1.80</b>	<b>8.78</b>	<b>0.70</b>	<b>1.05</b>	<b>0.70</b>	<b>0.63</b>	<b>0.08</b>	
<b><i>Desmopsis</i> sp.</b>	<b>Uw 26195</b>	<b>3.20</b>	<b>2.20</b>	<b>7.27</b>	<b>0.22</b>	<b>1.98</b>	<b>0.22</b>	<b>0.15</b>	<b>0.07</b>	<b>1</b>
<i>Diclinanona calycina</i>	RFD 2853	28.00	9.50	14.74	0.40	9.10	0.40	0.30	0.10	1
<i>Diclinanona tessmannii</i>	Uw 30328	3.50	2.85	6.14	0.32	2.53	0.32	0.20	0.12	1
<b><i>Diclinanona</i></b>		<b>15.75</b>	<b>6.18</b>	<b>10.44</b>	<b>0.36</b>	<b>5.82</b>	<b>0.36</b>	<b>0.25</b>	<b>0.11</b>	
<i>Duguetia argentea</i>	Uw 8094	!	1.40	–	0.70	0.70	0.70	0.65	0.05	1
<i>Duguetia bahiensis</i>	Uw 31902	!	4.50	–	0.80	3.70	0.80	0.60	0.20	1
<i>Duguetia cadaverica</i>	Uw 11096	3.00	2.60	5.77	0.20	2.40	0.20	0.14	0.06	1
<i>Duguetia cadaverica</i>	Uw 29933	3.00	2.60	5.77	0.47	2.13	0.47	0.35	0.12	1
<i>Duguetia cadaverica</i>	Uw 34284	2.00	2.00	5.00	0.20	1.80	0.20	0.12	0.08	1
<i>Duguetia calycina</i>	Uw 3989	!	1.30	–	0.22	1.08	0.22	0.10	0.12	1
<i>Duguetia calycina</i>	Uw 27467	11.00	4.10	13.41	0.45	3.65	0.45	0.38	0.07	1
<i>Duguetia cauliflora</i>	Uw 33158	12.00	2.30	26.09	0.20	2.10	0.20	0.15	0.05	1
<i>Duguetia eximia</i>	Uw 29917	5.00	3.20	7.81	0.31	2.89	0.31	0.28	0.03	1
<i>Duguetia eximia</i>	Uw 29971	3.00	3.10	4.84	0.28	2.82	0.28	0.25	0.03	1
<i>Duguetia eximia</i>	Uw 31411	4.00	3.80	5.26	0.26	3.55	0.26	0.23	0.03	1
<i>Duguetia furfuracea</i>	Uw 29402	2.00	2.20	4.55	0.10	2.10	0.10	0.08	0.02	1
<i>Duguetia granvilleana</i>	Uw 29888	2.00	1.70	5.88	0.45	1.25	0.45	0.38	0.07	1
<i>Duguetia hadrantha</i>	Uw 30323	4.00	2.50	8.00	0.70	1.80	0.70	0.65	0.05	1
<i>Duguetia inconspicua</i>	Uw 27373	1.00	1.35	3.70	0.40	0.95	0.40	0.35	0.05	1
<i>Duguetia lanceolata</i>	Uw 6328	5.00	–	–	!	2.65	–	!	0.05	1
<i>Duguetia latifolia</i>	Uw 30298	4.00	2.40	8.33	0.20	2.20	0.20	0.16	0.04	1
<i>Duguetia macrocalyx</i>	Uw 34510	!	1.60	–	0.45	1.15	0.43	0.35	0.08	1
<i>Duguetia macrophylla</i>	Uw 31207	2.00	2.45	4.08	0.25	2.20	0.25	0.20	0.05	1

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## A. Continued.

Taxa	Collection no.	Diameter of sample (cm)	Bark width (mm)	Ratio of radius of the sample to bark width	Rhytidome width (mm)	Phloem width (mm)	Periderm width (mm)	Phellem width (mm)	Phelloderm width (mm)	No. of periderms
<i>Duguetia neglecta</i>	Uw 27412	!	8.00	–	0.33	7.67	0.33	0.22	0.11	1
<i>Duguetia neglecta</i>	Uw 32602	!	3.60	–	0.60	3.00	0.60	0.52	0.08	1
<i>Duguetia odorata</i>	Uw 19766	4.00	1.85	10.81	0.25	1.60	0.24	0.17	0.07	1
<i>Duguetia pauciflora</i>	Uw 762	!	3.00	–	1.55	2.53	0.47	0.40	0.07	2
<i>Duguetia pycnastera</i>	Uw 4691	10.00	4.90	10.20	0.25	4.65	0.25	0.20	0.05	1
<i>Duguetia pycnastera</i>	Uw 11121	7.00	7.00	5.00	!	7.00	–	0.90	!	1
<i>Duguetia quitarensis</i>	Uw 20029	6.00	3.25	9.23	0.47	2.78	0.47	0.40	0.07	1
<i>Duguetia quitarensis</i>	Uw 8703	!	3.00	–	0.20	2.80	0.20	0.15	0.05	1
<i>Duguetia quitarensis</i>	Uw 30627	5.00	3.00	8.33	0.40	2.60	0.40	0.30	0.10	1
<i>Duguetia riparia</i>	Uw 17969	4.00	1.75	11.43	0.25	1.50	0.25	0.20	0.05	1
<i>Duguetia spixiana</i>	Uw 20158	6.00	3.60	8.33	0.42	3.22	0.42	0.35	0.07	1
<i>Duguetia spixiana</i>	Uw 30318	!	10.40	–	0.70	9.70	0.70	0.65	0.05	1
<i>Duguetia stelechantha</i>	Uw 16453	!	3.35	–	0.22	3.13	0.22	0.15	0.07	1
<i>Duguetia stenantha</i>	Uw 16138	!	6.00	–	0.90	5.10	0.40	0.33	0.07	4
<i>Duguetia stenantha</i>	Uw 30330	4.00	4.80	4.17	1.70	3.10	0.50	0.40	0.10	2
<i>Duguetia surinamensis</i>	Uw 30612	!	4.20	–	0.85	3.35	0.85	0.80	0.05	1
<i>Duguetia surinamensis</i>	Uw 30613	!	10.10	–	1.10	9.00	1.10	1.00	0.10	1
<i>Duguetia surinamensis</i>	Uw 33906	4.00	2.15	9.30	0.40	1.75	0.40	0.33	0.07	1
<i>Duguetia ulei</i>	Uw 33456	!	4.10	–	0.32	3.78	0.32	0.20	0.12	1
<i>Duguetia uniflora</i>	Uw 33457	!	4.00	–	0.70	3.30	0.70	0.65	0.05	1
<i>Duguetia yeshidan</i>	Uw 30610	8.00	4.50	8.89	0.35	4.15	0.34	0.27	0.07	1
<i>Duguetia yeshidan</i>	Uw 33175	5.00	3.10	8.06	!	3.10	–	!	!	1
<i>Duguetia</i> sp.	Uw 4706	5.00	4.00	6.25	0.45	3.53	0.47	0.40	0.07	1
<b><i>Duguetia</i></b>		<b>4.85</b>	<b>3.63</b>	<b>8.02</b>	<b>0.50</b>	<b>3.18</b>	<b>0.42</b>	<b>0.36</b>	<b>0.07</b>	
<i>Ephedranthus columbianus</i>	Uw 31299	!	2.80	–	0.40	2.40	0.40	0.30	0.10	1
<i>Ephedranthus guianensis</i>	Uw 6856	20.00	5.40	18.52	0.45	4.95	0.45	0.25–0.35	0.30	1
<b><i>Ephedranthus</i></b>		<b>20.00</b>	<b>4.10</b>	<b>18.52</b>	<b>0.43</b>	<b>3.68</b>	<b>0.50</b>	<b>0.30</b>	<b>0.20</b>	
<i>Fusaea longifolia</i>	Uw 3955	11.00	3.70	14.86	0.45	3.27	0.05	0.03	0.02	2
<i>Fusaea longifolia</i>	Uw 4559	14.00	4.20	16.67	0.20	4.00	0.15	0.06	0.09	1
<i>Fusaea longifolia</i>	Uw 30329	5.00	3.80	6.58	1.15	2.65	0.15	0.10	0.05	2
<b><i>Fusaea</i></b>		<b>10.00</b>	<b>3.90</b>	<b>12.70</b>	<b>0.60</b>	<b>3.31</b>	<b>0.12</b>	<b>0.06</b>	<b>0.05</b>	
<i>Guatteria citriodora</i>	RFD 2624	20.00	–	–	0.20	!	0.10–0.30	0.06–0.25	0.01–0.05	1
<i>Guatteria discolor</i>	RFD 1397	35.00	5.50	31.82	0.10	5.40	0.05–0.15	0.10	~0	1
<i>Guatteria foliosa</i>	RFD 1817	!	6.40	–	0.14	6.30	0.10–0.18	0.07–0.15	0.05	1
<i>Guatteria lehmannii</i>	RFD 25052	7.20	6.10	5.90	0.30	5.80	0.10	0.06	0.04	2
<i>Guatteria megalophylla</i>	RFD 2809	9.00	4.70	9.57	0.25	4.40	0.15–0.35	0.15–0.35	~0	1
<i>Guatteria olivacea</i>	RFD 1807	20.00	8.25	12.12	0.40	7.88	0.15–0.30	0.03–0.05	0.15–0.30	>1
<i>Guatteria scytophylla</i>	RFD 2062	20.00	–	–	!	!	0.08–0.13	0.06–0.10	0.20–0.30	1
<b><i>Guatteria</i><sup>1</sup></b>		<b>18.53</b>	<b>6.19</b>	<b>14.85</b>	<b>0.23</b>	<b>5.96</b>	<b>0.17</b>	<b>0.11</b>	<b>0.06</b>	
<b><i>Guatteriopsis hispida</i></b>	<b>RFD 3591</b>	<b>!</b>	<b>3.70</b>	<b>–</b>	<b>0.40</b>	<b>1.33</b>	<b>0.40</b>	<b>0.35</b>	<b>0.05</b>	<b>1</b>
<b><i>Heteropetalum</i> sp.</b>	<b>Uw 33073</b>	<b>4.20</b>	<b>1.75</b>	<b>12.00</b>	<b>0.09</b>	<b>1.65</b>	<b>0.10</b>	<b>0.06</b>	<b>0.04</b>	<b>1</b>
<b><i>Hornschieuchia polyantha</i></b>	<b>Uw 35426</b>	<b>1.70</b>	<b>1.20</b>	<b>7.08</b>	<b>0.20</b>	<b>1.00</b>	<b>0.20</b>	<b>0.11</b>	<b>0.09</b>	<b>1</b>
<i>Klarobelia candida</i>	Uw 34868	!	3.25	–	0.25	3.00	0.25	0.20	0.05	1
<i>Klarobelia cauliflora</i>	Uw 34863	!	1.70	–	0.20	1.48	0.22	0.10	0.12	1
<i>Klarobelia inundata</i>	Uw 34862	!	2.70	–	0.20	2.50	0.20	0.12	0.08	1
<i>Klarobelia lucida</i> <sup>2</sup>	Uw 35428	3.20	0.55	29.09	!	0.55	–	!	!	!
<i>Klarobelia stipitata</i>	Uw 36709	3.20	3.25	4.92	0.40	2.65	0.20–0.60	0.15–0.60	0.01–0.10	1
<b><i>Klarobelia</i></b>		<b>3.20</b>	<b>2.29</b>	<b>17.01</b>	<b>0.26</b>	<b>2.04</b>	<b>0.28</b>	<b>0.20</b>	<b>0.08</b>	
<i>Malmea dielsiana</i>	Uw 30246	4.00	1.25	16.00	0.40	0.85	0.40	0.30	0.10	1
<i>Malmea surinamensis</i>	Uw 8543	4.00	1.70	11.76	0.40	1.30	0.40	0.30	0.10	1
<b><i>Malmea</i></b>		<b>4.00</b>	<b>1.48</b>	<b>13.88</b>	<b>0.40</b>	<b>1.08</b>	<b>0.40</b>	<b>0.30</b>	<b>0.10</b>	
<i>Mosannonna depressa</i> subsp. <i>abscondita</i>	Uw 31041	6.00	1.30	23.08	0.20	1.12	0.18	0.14	0.04	1

continued

## A. Continued.

Taxa	Collection no.	Diameter of sample (cm)	Bark width (mm)	Ratio of radius of the sample to bark width	Rhytidome width (mm)	Phloem width (mm)	Periderm width (mm)	Phellem width (mm)	Pheloderm width (mm)	No. of periderms
<i>Mosannona discolor</i>	Uw 26395	6.00	1.75	17.14	0.20	1.60	0.10–0.25	0.05–0.18	0.05–0.10	1
<i>Mosannona raimondii</i>	Schunke 10899	!	3.50	–	0.33	3.15	0.35	0.15–0.20	0.10–0.15	1
<b>Mosannona</b>		<b>6.00</b>	<b>2.18</b>	<b>20.11</b>	<b>0.24</b>	<b>1.96</b>	<b>0.22</b>	<b>0.14</b>	<b>0.08</b>	
<b><i>Onychopetalus amazonicum</i></b>	<b>Uw 23662</b>	<b>3.30</b>	<b>13.50</b>	<b>1.22</b>	<b>0.35</b>	<b>13.10</b>	<b>0.36</b>	<b>0.30</b>	<b>0.06</b>	<b>1</b>
<i>Oxandra asbeckii</i>	Uw 1637	!	2.50	–	0.15	2.30	0.14–0.20	0.09–0.13	0.05	1
<i>Oxandra asbeckii</i>	Uw 34292	12.00	4.60	13.04	0.20	4.40	0.12–0.25	0.10–0.23	0.02–0.05	1
<i>Oxandra espintana</i>	Uw 30229	10.50	5.50	9.55	0.45	5.05	0.45	0.40	0.05	1
<i>Oxandra lanceolata</i>	Uw 31209	5.20	1.40	18.57	0.25	1.18	0.10–0.40	0.10–0.40	~0	1
<i>Oxandra laurifolia</i>	Uw 29376	7.00	1.90	18.42	0.10	1.80	0.10	0.07–0.08	0.01–0.03	1
<i>Oxandra riedeliana</i>	Uw 33451	!	4.10	–	0.75	3.35	0.75	0.68	0.07	1
<i>Oxandra sphaerocarpa</i>	Uw 34859	!	–	–	!	!	–	!	!	!
<i>Oxandra</i> sp.	Uw 34861	16.00	6.25	12.80	0.24	6.00	0.18–0.30	0.06–0.12	0.10–0.17	1
<b>Oxandra</b>		<b>10.14</b>	<b>3.75</b>	<b>14.48</b>	<b>0.31</b>	<b>3.44</b>	<b>0.30</b>	<b>0.25</b>	<b>0.05</b>	
<b><i>Porcelia ponderosa</i></b>	<b>Uw 30259</b>	<b>14.00</b>	<b>4.00</b>	<b>17.50</b>	<b>0.75</b>	<b>3.15</b>	<b>0.78</b>	<b>0.75</b>	<b>0.03</b>	<b>1</b>
<i>Pseudomalmea diclina</i>	Uw 34866	!	–	–	!	!	–	!	!	!
<i>Pseudomalmea</i> sp.	RA 1726	!	3.00	–	0.20	2.85	0.15–0.25	0.05–0.15	0.10	1
<b>Pseudomalmea</b>			<b>3.00</b>	–	<b>0.20</b>	<b>2.85</b>	<b>0.20</b>	<b>0.10</b>	<b>0.10</b>	
<i>Pseudoxandra lucida</i>	Uw 30312	13.00	4.20	15.48	0.35	3.83	0.37	0.13	0.24	1
<i>Pseudoxandra obscurinervis</i>	RFD 2010	20.00	7.00	14.29	0.60	6.40	0.50–0.60	0.45–0.55	0.05–0.15	1
<i>Pseudoxandra</i> sp.	RFD 2804	23.00	–	–	!	!	–	!	!	!
<b>Pseudoxandra</b>		<b>18.67</b>	<b>5.60</b>	<b>14.88</b>	<b>0.48</b>	<b>5.12</b>	<b>0.49</b>	<b>0.32</b>	<b>0.17</b>	
<i>Rollinia insignis</i>	RFD 3282	10.00	5.25	9.52	0.50	4.64	0.20–0.45	0.15–0.40	0.05	2
<i>Rollinia pittieri</i>	Uw 34865	!	–	–	0.40	!	0.40	0.33	0.07	1
<b>Rollinia</b>		<b>10.00</b>	<b>5.25</b>	<b>9.52</b>	<b>0.45</b>	<b>4.64</b>	<b>0.36</b>	<b>0.30</b>	<b>0.06</b>	
<b><i>Ruizodendron ovale</i></b>	<b>Uw 35948</b>	<b>1.50</b>	<b>1.90</b>	<b>3.95</b>	<b>0.18</b>	<b>1.70</b>	<b>0.16</b>	<b>0.08</b>	<b>0.08</b>	<b>1</b>
<b><i>Sprantijus palanga</i></b>	<b>Uw 26216</b>	<b>7.50</b>	<b>4.90</b>	<b>7.65</b>	<b>0.80</b>	<b>4.10</b>	<b>0.80</b>	<b>0.74</b>	<b>0.06</b>	<b>1</b>
<i>Tetrameranthus duckei</i>	Uw 33455	3.50	–	–	!	!	–	!	!	!
<i>Tetrameranthus duckei</i>	Uw 26747	4.50	1.75	12.86	0.43	1.48	0.30–0.55	0.30–0.55	0.01–0.04	1
<b>Tetrameranthus</b>		<b>4.00</b>	<b>1.75</b>	<b>12.86</b>	<b>0.43</b>	<b>1.48</b>	<b>0.45</b>	<b>0.43</b>	<b>0.03</b>	
<i>Tridimeris baillonii</i>	Uw 31206	2.50	1.15	10.87	0.15	1.00	0.10–0.15	0.05–0.10	0.05	1
<i>Tridimeris</i> sp.	Uw 31039	8.20	1.85	22.16	0.15	1.72	0.13	0.09	0.04	1
<b>Tridimeris</b>		<b>5.35</b>	<b>1.50</b>	<b>16.52</b>	<b>0.15</b>	<b>1.36</b>	<b>0.13</b>	<b>0.08</b>	<b>0.05</b>	
<i>Trigynaëa guianensis</i>	Uw 32595	6.00	1.90	15.79	0.35	1.18	0.25–0.45	0.18–0.40	0.05–0.07	1
<i>Trigynaëa lagaropoda</i>	Uw 30308	6.00	1.65	18.18	0.10	1.55	0.08–0.15	0.08–0.15	~0	1
<b>Trigynaëa</b>		<b>6.00</b>	<b>1.78</b>	<b>16.99</b>	<b>0.23</b>	<b>1.37</b>	<b>0.23</b>	<b>0.20</b>	<b>0.03</b>	
<i>Unonopsis stipitata</i>	RFD 3289	9.00	4.50	10.00	0.45	4.05	0.25–0.35	0.15–0.35	0.05	2
<i>Unonopsis veneficorum</i>	Uw 30339	3.40	1.40	12.14	0.30	1.10	0.20–0.35	0.20–0.35	~0	1
<i>Unonopsis</i> sp.	Uw 34864	!	3.25	–	0.40	2.86	0.39	0.30	0.09	1
<b>Unonopsis</b>		<b>6.20</b>	<b>3.05</b>	<b>11.07</b>	<b>0.38</b>	<b>2.67</b>	<b>0.32</b>	<b>0.28</b>	<b>0.05</b>	
<i>Xylopia amazonica</i>	RFD 2817	13.00	4.00	16.25	1.10	2.90	1.10	0.90	0.20	1
<i>Xylopia aromatica</i>	Uw 9119	!	5.25	–	0.55	4.70	0.30–0.80	0.25–0.75	0.05–0.10	1
<i>Xylopia nitida</i>	RFD 2794	12.00	3.50	17.14	0.30	3.20	0.30	0.30	~0	1
<i>Xylopia parviflora</i>	RFD 2802	12.00	3.25	18.46	0.20	3.08	0.10–0.30	0.07–0.27	0.02–0.03	1
<b>Xylopia</b>		<b>12.33</b>	<b>4.00</b>	<b>17.28</b>	<b>0.54</b>	<b>3.47</b>	<b>0.54</b>	<b>0.47</b>	<b>0.08</b>	

B. Phellem. Explanations: Cell type: S = sclerified cells; Tw = thin-walled cells; Pattern of thin-walled cells: T = tangential; Type of sclerified cells: H = uniformly thickened, U = U-shaped, R = rev. U-shaped; Sclerified cells/Sclereids/Secretory cells: 0 = not present, 1 = few, 2 = abundant, 3 = bulk, 4 = only sclerified cells/sclereids/secretory cells present.

Taxon	No. of cells (radial direction)	Cell type	Pattern of thin-walled cells	Type of sclerified cells	Sclerified cells	Sclerified cells solitary	Sclerified cells in small groups	Sclerified cells in large groups	Sclerified cells in tangential rows/bands	Sclereids	Sclereids solitary	Sclereids in small groups	Sclereids in large groups	Sclereids in tangential rows/bands	Secretory cells	Secretory cells solitary	Secretory cells in irregular groups	Secretory cells in radial rows	Secretory cells in tangential rows/bands
<i>Anaxagorea brevipes</i>	> 10	S	-	R	4	-	-	-	0?	-	-	-	-	1	+	-	-	-	+
<i>Anaxagorea dolichocarpa</i>	6	Tw	-	-	0	-	-	-	0	-	-	-	-	0	-	-	-	-	-
<i>Anaxagorea manausensis</i>	7-8	S	-	R	4	-	-	-	0	-	-	-	-	4	-	-	-	-	-
<b>Anaxagorea</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Annona ambotay</i>	> 10	Tw&S	-	R	3	-	+	-	0	-	-	-	-	1	+	-	-	-	+
<i>Annona foetida</i>	> 10	Tw&S	-	U	2	-	-	-	1	-	+	-	+	3	-	-	-	-	+
<i>Annona impressivenia</i>	> 10	Tw&S	-	R	3	-	-	+	0	-	-	-	-	1	+	-	-	-	-
<i>Annona</i> sp. nov. aff. <i>excellens</i>	> 10	Tw&S	-	R	3	-	-	+	1	+	-	-	-	2	+	+	-	-	-
<b>Annona</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Asimina triloba</b>	> 10	Tw	-	-	0	-	-	-	-	0	-	-	-	0	-	-	-	-	-
<i>Bocageopsis multiflora</i>	7	S	-	U	4	-	-	-	0	-	-	-	-	4	-	-	-	-	-
<i>Bocageopsis pleiosperma</i>	> 10	S	-	U	4	-	-	-	0	-	-	-	-	4	-	-	-	-	-
<b>Bocageopsis</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Cardiopetalum surinamense</b>	> 8	Tw	-	-	0	-	-	-	-	0	-	-	-	0	-	-	-	-	-
<i>Cremaosperma brevipes</i>	> 8	Tw&S	T	U	2	-	-	-	+	0	-	-	-	4	-	-	-	-	-
<i>Cremaosperma cauliflorum</i>	2-10	Tw&S	T	U	2	-	-	-	+	0	-	-	-	2	-	-	-	-	+
<i>Cremaosperma cauliflorum</i>	> 4	Tw	-	-	0	-	-	-	+	0	-	-	-	4	-	-	-	-	-
<b>Cremaosperma</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cymbopetalum brasiliense</i>	> 10	Tw	-	-	0	-	-	-	-	0	-	-	-	1	+	-	-	-	+
<i>Cymbopetalum longipes</i>	> 10	Tw	-	-	0	-	-	-	-	0	-	-	-	0	-	-	-	-	-
<b>Cymbopetalum</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Desmopsis</b> sp.	> 8	S	-	U	4	-	-	-	-	0	-	-	-	0	-	-	-	-	-
<i>Diclinanona calycina</i>	> 10	Tw&S	-	R	3	-	-	-	+	0	-	-	-	1	+	-	-	-	+
<i>Diclinanona tessmannii</i>	8	Tw&S	T	U	2	-	-	-	+	0	-	-	-	2	+	-	-	-	+
<b>Diclinanona</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Duguetia argentea</i>	> 10	Tw&S	-	H	1	+	-	-	-	0	-	-	-	1	-	-	+	-	+
<i>Duguetia bahiensis</i>	> 10	Tw	-	-	0	-	-	-	-	0	-	-	-	1	+	-	-	-	+
<i>Duguetia cadaverica</i>	> 10	Tw&S	T	R	2	-	-	-	+	0	-	-	-	1	-	-	-	-	+
<i>Duguetia cadaverica</i>	> 10	Tw&S	-	R	2	-	-	-	+	0	-	-	-	1	+	-	-	-	+
<i>Duguetia cadaverica</i>	> 10	Tw&S	-	R	1	-	-	-	+	0	-	-	-	1	+	-	-	-	+
<i>Duguetia calycina</i>	> 10	Tw&S	T	U	2	-	-	-	+	0	-	-	-	2	-	-	-	-	+
<i>Duguetia calycina</i>	> 10	Tw&S	-	U	1	+	-	-	-	0	-	-	-	1	-	-	+	-	+
<i>Duguetia cauliflora</i>	> 10	Tw&S	T	U	2	-	-	-	+	0	-	-	-	3	-	-	-	-	+
<i>Duguetia eximia</i>	> 10	Tw	-	-	0	-	-	-	-	0	-	-	-	2	+	-	-	-	+
<i>Duguetia eximia</i>	> 10	Tw	-	-	0	-	-	-	-	0	-	-	-	2	+	-	-	-	+
<i>Duguetia eximia</i>	> 10	Tw	-	-	0	-	-	-	-	0	-	-	-	2	+	-	-	-	+
<i>Duguetia furturacea</i>	> 10	Tw&S	T	U	1	-	-	-	+	0	-	-	-	1	+	-	-	-	+
<i>Duguetia granvilleana</i>	> 10	Tw&S	-	H	1	-	+	-	-	0	-	-	-	1	+	-	-	-	+
<i>Duguetia hadrantha</i>	> 10	Tw	-	-	0	-	-	-	-	0	-	-	-	1	+	-	+	-	+
<i>Duguetia inconspicua</i>	> 10	Tw&S	-	?	1	+	-	-	1	+	-	-	-	2	+	-	-	-	+
<i>Duguetia lanceolata</i>	!	Tw&S	T	U	0	-	-	-	-	3	-	-	-	+	0	-	-	-	-
<i>Duguetia latifolia</i>	> 10	Tw	-	-	0	-	-	-	-	0	-	-	-	1	-	-	-	-	+
<i>Duguetia macrocalyx</i>	> 10	Tw	-	-	0	-	-	-	-	0	-	-	-	2	+	-	+	-	+
<i>Duguetia macrophylla</i>	> 10	Tw&S	-	H	1	+	-	-	1	+	+	-	-	2	+	-	+	-	+
<i>Duguetia neglecta</i>	> 10	Tw&S	T	H	2	-	-	-	+	1	-	-	-	4	-	-	-	-	-
<i>Duguetia neglecta</i>	> 10	Tw&S	T	H	2	-	-	-	+	0	-	-	-	1	+	-	-	-	+
<i>Duguetia odorata</i>	> 10	Tw&S	T	U	0	-	-	-	-	1	-	-	-	+	1	+	-	-	-

continued

## B. Continued.

Taxon

	No. of cells (radial direction)	Cell type	Pattern of thin-walled cells	Type of sclereified cells	Sclerified cells	Sclerified cells solitary	Sclerified cells in small groups	Sclerified cells in large groups	Sclerified cells in tangential rows/bands	Sclereids	Sclereids solitary	Sclereids in small groups	Sclereids in large groups	Sclereids in tangential rows/bands	Secretory cells	Secretory cells solitary	Secretory cells in irregular groups	Secretory cells in radial rows	Secretory cells in tangential rows/bands
<i>Duguetia pauciflora</i>	> 10	Tw	- -	0	-	-	-	-	0	-	-	-	-	2	-	-	-	+	+
<i>Duguetia pycnastera</i>	> 10	Tw	- -	0	-	-	-	-	0	-	-	-	-	0	-	-	-	-	-
<i>Duguetia pycnastera</i>	> 10	Tw&S	H	1	+	-	-	-	0	-	-	-	-	0	-	-	-	-	-
<i>Duguetia quitarensis</i>	> 10	Tw&S	T U	2	-	-	-	+	0	-	-	-	-	1	-	+	-	-	-
<i>Duguetia quitarensis</i>	> 10	Tw&S	T U	2	-	-	-	+	0	-	-	-	-	2	+	-	-	-	+
<i>Duguetia quitarensis</i>	> 10	Tw&S	T U	2	-	-	-	+	1	+	-	-	-	1	-	-	-	-	+
<i>Duguetia riparia</i>	> 10	Tw	- -	0	-	-	-	-	0	-	-	-	-	1	+	-	-	-	+
<i>Duguetia spixiana</i>	> 10	Tw&S	T U	1	-	-	-	+	3	-	-	-	-	0	-	-	-	-	-
<i>Duguetia spixiana</i>	> 10	Tw&S	T U	1	-	-	-	+	2	-	-	-	-	2	+	+	-	-	-
<i>Duguetia stelechantha</i>	> 10	Tw&S	T U	1	-	-	-	+	0	-	-	-	-	2	+	+	-	-	+
<i>Duguetia stenantha</i>	> 10	Tw&S	U	3	-	-	-	+	1	+	-	-	-	3	-	-	-	-	+
<i>Duguetia stenantha</i>	> 10	Tw&S	U	1	-	-	-	+	0	-	-	-	-	3	+	-	+	-	+
<i>Duguetia surinamensis</i>	> 10	Tw&S	T U	2	-	-	-	+	3	-	-	-	-	0	-	-	-	-	-
<i>Duguetia surinamensis</i>	> 10	Tw&S	T U	2	-	-	-	+	2	-	-	-	-	0	-	-	-	-	-
<i>Duguetia surinamensis</i>	> 10	Tw&S	T U	2	-	-	-	+	0	-	-	-	-	1	+	+	-	-	-
<i>Duguetia ulei</i>	> 10	Tw	- -	0	-	-	-	-	0	-	-	-	-	0	-	-	-	-	-
<i>Duguetia uniflora</i>	> 10	Tw&S	T U	2	-	-	-	+	0	-	-	-	-	0	-	-	-	-	-
<i>Duguetia yeshidan</i>	> 10	Tw&S	T H	2	-	-	-	+	0	-	-	-	-	1	-	-	+	-	-
<i>Duguetia yeshidan</i>	!	!	!	!	!	-	-	-	-	!	-	-	-	-	!	-	-	-	-
<i>Duguetia</i> sp.	> 10	Tw&S	T H&U	3	-	-	-	+	0	-	-	-	-	0	-	-	-	-	-
<b>Duguetia</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ephedranthus columbianus</i>	> 10	Tw&S	T U	2	-	-	-	+	0	-	-	-	-	3	-	-	-	-	+
<i>Ephedranthus guianensis</i>	> 10	S	- U	4	-	-	-	-	0	-	-	-	-	0	-	-	-	-	-
<b>Ephedranthus</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Fusaea longifolia</i>	4	Tw	- -	0	-	-	-	-	0	-	-	-	-	3	-	-	-	-	+
<i>Fusaea longifolia</i>	F	Tw	- -	0	-	-	-	-	0	-	-	-	-	3	-	-	-	-	+
<i>Fusaea longifolia</i>	> 10	S	- H	4	-	-	-	-	1	+	-	-	-	0	-	-	-	-	-
<b>Fusaea</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Guatteria citriodora</i>	> 4	Tw&S	- U	2	-	-	-	+	0	-	-	-	-	4	-	-	-	-	-
<i>Guatteria discolor</i>	5	S	- H	4	-	-	-	-	0	-	-	-	-	4	-	-	-	-	-
<i>Guatteria foliosa</i>	7	Tw&S	R	1	-	-	-	+	0	-	-	-	-	4	-	-	-	-	-
<i>Guatteria lehmannii</i>	3-5	Tw	- -	0	-	-	-	-	0	-	-	-	-	4	-	-	-	-	-
<i>Guatteria megalophylla</i>	> 10	Tw&S	H&U	2	+	-	-	+	0	-	-	-	-	4	-	-	-	-	-
<i>Guatteria olivacea</i>	5	Tw&S	R	1	+	-	-	+	0	-	-	-	-	4	-	-	-	-	-
<i>Guatteria scytophylla</i>	8	Tw&S	H?	4	-	-	-	-	0	-	-	-	-	4	-	-	-	-	-
<b>Guatteria</b> <sup>1</sup>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Guatteropsis hispida</i>	> 10	Tw	- -	0	-	-	-	-	0	-	-	-	-	4	-	-	-	-	-
<i>Heteropetalum</i> sp.	7	Tw	- -	0	-	-	-	-	0	-	-	-	-	4	-	-	-	-	-
<b>Hornsuchia polyantha</b>	2-3	Tw	- -	0	-	-	-	-	0	-	-	-	-	4	-	-	-	-	-
<i>Klarobelia candida</i>	> 10	Tw&S	U	3	-	-	-	+	0	-	-	-	-	3	-	-	-	-	+
<i>Klarobelia cauliflora</i>	> 7	Tw&S	T U	2	-	-	-	+	0	-	-	-	-	2	-	-	-	-	+
<i>Klarobelia inundata</i>	> 7	Tw&S	U	2	-	-	-	+	2	-	-	-	-	3	-	-	-	-	+
<i>Klarobelia lucida</i> <sup>2</sup>	!	!	!	!	!	-	-	-	!	-	-	-	-	!	-	-	-	-	-
<i>Klarobelia stipitata</i>	> 10	Tw&S	T U	3	-	-	-	+	0	-	-	-	-	1	+	+	-	-	+
<b>Klarobelia</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Malmea dielsiana</i>	> 10	Tw&S	U	3	-	-	-	+	0	-	-	-	-	4	-	-	-	-	-
<i>Malmea surinamensis</i>	> 10	S	- U	4	-	-	-	-	0	-	-	-	-	0	-	-	-	-	-
<b>Malmea</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

continued



C. Phelloderm. Explanations: Cell type: Tw = thin-walled; S = sclereids; H = uniformly thickened; Sclereids/uniformly thickened cell walls/Secretory cells: 0 = not present; 1 = few; 2 = abundant; 3 = bulk; 4 = only sclerified/secretory cells present; \*Cortex. Explanations: Sclereids/Secretory cells: 0 = not present; 1 = few; 2 = abundant; 3 = bulk; 4 = only sclereids/secretory cells present.

Taxa	No. of cells (radial direction)	Cell type	Sclereids/uniformly thickened cell walls	Sclereids solitary	Sclereids in small groups	Sclereids in large groups	Sclereids in tangential rows/bands	Secretory cells	Secretory cells solitary	Secretory cells in irregular groups	Secretory cells in radial rows	Secretory cells in tangential rows/bands	*Sclereids	*Sclereids solitary	*Sclereids in small groups	*Sclereids in large groups	*Sclereids in tangential rows/bands	*Secretory cells	*Secretory cells solitary	*Secretory cells in irregular groups	*Secretory cells in radial rows	*Secretory cells in tangential rows/bands
<i>Anaxagorea brevipes</i>	4–7	Tw&S	3		+	+	0	-	-	-	-	-	!	-	-	-	-	!	-	-	-	-
<i>Anaxagorea dolichocarpa</i>	3–4	Tw&S	1	+	+	-	0	-	-	-	-	-	2	+	+	+	0	-	-	-	-	-
<i>Anaxagorea manausensis</i>	6–7	Tw&S	2	+	+	-	0	-	-	-	-	-	2	+	+	+	0	-	-	-	-	-
<b>Anaxagorea</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Annona ambotay</i>	1–2	Tw&S	2	+			0	-	-	-	-	-	2	+	+			1	+			
<i>Annona foetida</i>	3–4	Tw&S	1	+			0	-	-	-	-	-	2	+	+			0	-	-	-	-
<i>Annona impressivenia</i>	4–8	Tw&S	1	+			1	+					3	+	+			1	+	+		
<i>Annona</i> sp. nov. aff. <i>excellens</i>	2–3	Tw&S	1	+			0	-	-	-	-	-	2	+	+	+	0	-	-	-	-	-
<b>Annona</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Asimina triloba</b>	7–10	Tw&S	1	+			2	+			+	2	+	+	+	0	-	-	-	-	-	-
<i>Bocageopsis multiflora</i>	4–5	Tw&S	2	+	+		1	+					3	+	+	+	0	-	-	-	-	-
<i>Bocageopsis pleiosperma</i>	5–7	Tw	0	-	-	-	1	+					3	+	+	+	0	-	-	-	-	-
<b>Bocageopsis</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Cardiopetalum surinamense</b>	2–4	Tw	0	-	-	-	0	-	-	-	-	-	0	-	-	-	-	1	+			
<i>Crematosperma brevipes</i>	3–4	Tw&S	1	+			0	-	-	-	-	-	2	+	+		0	-	-	-	-	-
<i>Crematosperma cauliflorum</i>	>10	Tw&S	3	+	+		2	+	+		+	1	+				0	-	-	-	-	-
<i>Crematosperma cauliflorum</i>	8–10	Tw&S	2	+			0	-	-	-	-	-	2	+	+	+	0	-	-	-	-	-
<b>Crematosperma</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cymbopetalum brasiliense</i>	4–6	Tw&S	2	+	+		0	-	-	-	-	-	2	+	+		0	-	-	-	-	-
<i>Cymbopetalum longipes</i>	3–6	Tw&S	1	+			0	-	-	-	-	-	2	+	+	+	1	+				
<b>Cymbopetalum</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Desmopsis</b> sp.	4	Tw&S	2	+		+	1	+	+			!	-	-	-	-	!	-	-	-	-	-
<i>Diclinanona calycina</i>	1–7	H&Tw&S	2	+	+		0	-	-	-	-	-	2	+	+	+	2	+	+			
<i>Diclinanona tessmannii</i>	4–8	Tw&S	1	+	+		1	+			+	2	+	+			1	+				
<b>Diclinanona</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Duguetia argentea</i>	2	Tw&S	1	+			2	+					2	+	+		3					+
<i>Duguetia bahiensis</i>	6–10	Tw&S	1	+			0	-	-	-	-	-	1	+			1	+				
<i>Duguetia cadaverica</i>	4–5	Tw&S	1	+	+		0	-	-	-	-	-	2	+	+	+	1	+				
<i>Duguetia cadaverica</i>	>10	Tw&S	2	+			0	-	-	-	-	-	2	+	+		1					+
<i>Duguetia cadaverica</i>	3–4	Tw&S	1	+			0	-	-	-	-	-	2	+	+		1	+				+
<i>Duguetia calycina</i>	F	Tw&S	3			+	0	-	-	-	-	-	3	+	+		1					+
<i>Duguetia calycina</i>	F	Tw&S	2	+	+		2				+	1	+			+	1					+
<i>Duguetia cauliflora</i>	3	Tw&S	1	+			2					1	+				2					+
<i>Duguetia eximia</i>	2–4	Tw&S	1	+			0	-	-	-	-	-	1	+			1					+
<i>Duguetia eximia</i>	1–2	Tw	0	-	-	-	0	-	-	-	-	-	1	+	+		1	+				
<i>Duguetia eximia</i>	2–3	Tw&S	1	+	+		0	-	-	-	-	-	1	+	+		1	+				+
<i>Duguetia furfuracea</i>	2	Tw	0	-	-	-	0	-	-	-	-	-	1	+			0	-	-	-	-	
<i>Duguetia granvilleana</i>	5–6	Tw&S	1	+	+		0	-	-	-	-	-	2	+	+		0	-	-	-	-	-
<i>Duguetia hadrantha</i>	3	Tw&S	1	+			1	+				!	-	-	-	-	!	-	-	-	-	-
<i>Duguetia inconspicua</i>	3–4	Tw	0	-	-	-	0	-	-	-	-	-	1	+			0	-	-	-	-	-
<i>Duguetia lanceolata</i>	3–4	Tw&S	1	+	+		1	+				2			+		2	+				+
<i>Duguetia latifolia</i>	3	Tw&S	1	+			0	-	-	-	-	-	2	+	+		1	+				+
<i>Duguetia macrocalyx</i>	4–8	Tw&S	1	+	+		0	-	-	-	-	-	2	+		+	1	+				+
<i>Duguetia macrophylla</i>	3–4	Tw&S	1	+			0	-	-	-	-	-	2	+	+		1	+				+
<i>Duguetia neglecta</i>	3–4	Tw&S	2	+			4	-	-	-	-	3			+		2	+	+			
<i>Duguetia neglecta</i>	4	Tw&S	3			+	0	-	-	-	-	-	3	+	+		1	+				+
<i>Duguetia odorata</i>	4	Tw&S	2	+			1				+	3	+	+		+	2	+				+

continued



## C. Continued.

Taxa	No. of cells (radial direction)	Cell type	Sclereids/uniformly thickened cell walls	Sclereids solitary	Sclereids in small groups	Sclereids in large groups	Sclereids in tangential rows/bands	Secretory cells	Secretory cells solitary	Secretory cells in irregular groups	Secretory cells in radial rows	Secretory cells in tangential rows/bands	*Sclereids	*Sclereids solitary	*Sclereids in small groups	*Sclereids in large groups	*Sclereids in tangential rows/bands	*Secretory cells	*Secretory cells solitary	*Secretory cells in irregular groups	*Secretory cells in radial rows	*Secretory cells in tangential rows/bands
<i>Duguetia pauciflora</i>	4–6	Tw&S	2	+				1	+				2	+				2	+			+
<i>Duguetia pycnastera</i>	2–3	Tw&S	1	+				0	-	-	-	-	2	+	+	+		1	+			+
<i>Duguetia pycnastera</i>	4	Tw&S	3				+	0	-	-	-	-	3	+	+	+		1	+			
<i>Duguetia quitarensis</i>	4	Tw&S	1	+	+			1	+	+			2	+	+			2		+		+
<i>Duguetia quitarensis</i>	4	H&Tw&S	2	+				2				+	2	+	+	+	+	2				+
<i>Duguetia quitarensis</i>	3–4	Tw&S	1	+				1	+				2	+	+			1				+
<i>Duguetia riparia</i>	4	Tw&S	1	+	+			1				+	3	+	+			2	+			+
<i>Duguetia spixiana</i>	5–6	Tw&S	3	+	+			0	-	-	-	-	3	+	+	+		2	+			+
<i>Duguetia spixiana</i>	3–4	Tw&S	1	+	+			1	+	+			3	+	+	+		2	+			+
<i>Duguetia stelechantha</i>	>10	Tw&S	2	+	+	+		3	+	+			!	-	-	-	!	-	-	-	-	-
<i>Duguetia stenantha</i>	4–5	Tw&S	1	+				3	+			+	2	+	+	+		3	+	+		+
<i>Duguetia stenantha</i>	4	Tw&S	2	+		+		3	+			+	!	-	-	-	!	-	-	-	-	-
<i>Duguetia surinamensis</i>	3–5	Tw&S	1	+				0	-	-	-	-	!	-	-	-	!	-	-	-	-	-
<i>Duguetia surinamensis</i>	4–6	Tw&S	2	+				1	+	+			2	+	+			2	+	+		+
<i>Duguetia surinamensis</i>	4	Tw&S	1	+				1				+	!	-	-	-	!	-	-	-	-	-
<i>Duguetia ulei</i>	6	Tw&S	1	+				2	+	+			1	+				1	+			
<i>Duguetia uniflora</i>	3–4	Tw&S	2	+				2	+	+			2	+	+	+		2	+	+		+
<i>Duguetia yeshidan</i>	4–5	Tw&S	1	+				2	+				1	+	+			2	+	+		
<i>Duguetia yeshidan</i>	F	Tw&S	2	+				3	+			+	!	-	-	-	!	-	-	-	-	-
<i>Duguetia</i> sp.	4	Tw	0	-	-	-	-	2	+	+			!	-	-	-	!	-	-	-	-	-
<b>Duguetia</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ephedranthus columbianus</i>	>10	Tw&S	3			+		0	-	-	-	-	3	+	+	+	0	-	-	-	-	-
<i>Ephedranthus guianensis</i>	>10	Tw	0	-	-	-	-	0	-	-	-	-	2	+	+		2	+	+			
<b>Ephedranthus</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Fusaea longifolia</i>	>10	H&Tw	1	+				3		+	+	+	1	+		+		2	+	+		+
<i>Fusaea longifolia</i>	1–4	Tw	0	-	-	-	-	4	-	-	-	-	!	-	-	-	!	-	-	-	-	-
<i>Fusaea longifolia</i>	4–6	Tw	0	-	-	-	-	4	-	-	-	-	!	-	-	-	!	-	-	-	-	-
<b>Fusaea</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Guatteria citriodora</i>	1–6	Tw	0	-	-	-	-	4	-	-	-	-	2	+	+	+		1	+			
<i>Guatteria discolor</i>	1?	Tw	0	-	-	-	-	4	-	-	-	-	!	-	-	-	!	-	-	-	-	-
<i>Guatteria foliosa</i>	1–2	Tw	0	-	-	-	-	0	-	-	-	-	2		+		0	-	-	-	-	-
<i>Guatteria lehmannii</i>	1–3	Tw	0	-	-	-	-	4	-	-	-	-	1	+			2					+
<i>Guatteria megalophylla</i>	1–2	Tw	0	-	-	-	-	1	+				1	+	+		0	-	-	-	-	-
<i>Guatteria olivacea</i>	>10	H&Tw&S	3			+	+	1	+	+			2	+	+	+		1	+			
<i>Guatteria scytophylla</i>	!	!	!	-	-	-	-	!	-	-	-	-	!	-	-	-	!	-	-	-	-	-
<b>Guatteria</b> <sup>1</sup>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Guatteropsis hispida</i>	1–3	Tw	0	-	-	-	-	4	-	-	-	-	1	+	+		0	-	-	-	-	-
<b>Heteropetalum</b> sp.	4	Tw&S	1	+				0	-	-	-	-	3			+	0	-	-	-	-	-
<b>Hornsuchia polyantha</b>	0–3	Tw	0	-	-	-	-	0	-	-	-	-	1	+			0	-	-	-	-	-
<i>Klarobelia candida</i>	5–6	Tw	0	-	-	-	-	1	+				1	+			1	+	+			+
<i>Klarobelia cauliflora</i>	>3	Tw	0	-	-	-	-	1	+				!	-	-	-	!	-	-	-	-	-
<i>Klarobelia inundata</i>	7–8	Tw&S	1	+				2	+	+			!	-	-	-	!	-	-	-	-	-
<i>Klarobelia lucida</i> <sup>2</sup>	!	!	!	-	-	-	-	!	-	-	-	-	!	-	-	-	!	-	-	-	-	-
<i>Klarobelia stipitata</i>	0–6	Tw	0	-	-	-	-	0	-	-	-	-	0	-	-	-		1	+			
<b>Klarobelia</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Malmea dielsiana</i>	4–5	Tw&S	3	+	+		+	1	+				1	+	+			1	+			
<i>Malmea surinamensis</i>	3–6	Tw&S	2				+	1	+				1	+	+			0	-	-	-	-
<b>Malmea</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

continued



D. Rays. Explanations: Width (no. of cells): F = few, impossible to determine the number; Shape in cross section: IR = irregular course or moderately straight, ST = straight, UN = undulated; Dilatation: ID = irregularly dilatated, FF = funnel form; Ray height: H ≥ 1 mm, L ≤ 1 mm; Sclereids/Secretory cells: 0 = not present, 1 = few, 2 = abundant, 3 = bulk, 4 = only sclereids/secretory cells present.

Taxa	Width	No./mm	Shape in cross section	Dilatation	Ray height	Homocellular/heterocellular (* = weakly)	Sclereids	Sclereids solitary	Sclereids in small groups	Sclereids in large groups (> 10 cells)	Sclereids in tangential rows/bands	Secretory cells	Secretory cells solitary	Secretory cells in irregular groups	Secretory cells in radial rows	Secretory cells in tangential rows/bands
<i>Anaxagorea brevipes</i>	!	1.70	IR	ID	!	HO	2	+	+	+	+	0	-	-	-	-
<i>Anaxagorea dolichocarpa</i>	13	1.90	IR	ID	H	HO	1	+	+	+	+	1	+	-	-	-
<i>Anaxagorea manausensis</i>	13	2.00	IR	ID	H	HO	1	+	+	+	+	0	-	-	-	-
<b>Anaxagorea</b>	<b>13.00</b>	<b>1.87</b>														
<i>Annona ambotay</i>	6	3.90	IR	ID	H	HE	0	-	-	-	-	1	+	-	-	-
<i>Annona foetida</i>	6	3.75	IR	ID	H	HO	2	+	+	+	+	1	+	+	+	-
<i>Annona impressivenia</i>	!	2.70	IR	ID	H	HO	3	+	+	+	+	1	+	-	-	-
<i>Annona</i> sp. nov. aff. <i>excellens</i>	!	!	IR	ID	!	HO	2			+		0	-	-	-	-
<b>Annona</b>	<b>6.00</b>	<b>3.45</b>														
<i>Asimina triloba</i>	6	3.20	IR	ID	H	HO	1		+			0	-	-	-	-
<i>Bocageopsis multiflora</i>	6	3.20	IR	ID	H	HE	2		+	+		1	+	-	-	-
<i>Bocageopsis pleiosperma</i>	!	!	IR	ID	H	HO	2	+	+			1	+	-	-	-
<b>Bocageopsis</b>	<b>6.00</b>	<b>3.20</b>														
<i>Cardiopetalum surinamense</i>	3.00	3.80	IR	ID	H	HO	0	-	-	-	-	0	-	-	-	-
<i>Crematosperma brevipes</i>	7	3.20	IR	ID	H	HO	1	+	+	+		0	-	-	-	-
<i>Crematosperma cauliflorum</i>	11	2.40	IR	ID	H	HO	1	+	+			0	-	-	-	-
<i>Crematosperma cauliflorum</i>	8	2.60	IR	ID	H	HO	2	+	+	+		0	-	-	-	-
<b>Crematosperma</b>	<b>8.67</b>	<b>2.73</b>														
<i>Cymbopetalum brasiliense</i>	4	3.80	IR	ID	H	HO	2	+	+	+		1	+	-	-	-
<i>Cymbopetalum longipes</i>	6	5.20	IR	ID	!	HO	2	+	+	+		1	+	-	-	-
<b>Cymbopetalum</b>	<b>5.00</b>	<b>4.50</b>														
<i>Desmopsis</i> sp.	7	3.60	IR	ID	H	HO	2	+	+	+		0	-	-	-	-
<i>Diclinanona calycina</i>	6	3.10	IR	ID	H	HO	2	+	+	+		2	+	+	-	+
<i>Diclinanona tessmannii</i>	6	4.00	IR	ID	H	HO	1	+	+			0	-	-	-	-
<b>Diclinanona</b>	<b>6.00</b>	<b>3.55</b>														
<i>Duguetia argentea</i>	2	4.40	IR	FF	H	HE*	1		+			2				
<i>Duguetia bahiensis</i>	5	3.40	IR	FF	H	HE*	1			+		1	+			+
<i>Duguetia cadaverica</i>	4	3.40	IR	ID	H	HE*	1	+		+		1	+			
<i>Duguetia cadaverica</i>	7	3.20	IR	ID	H	HE*	2	+	+	+		1	+			
<i>Duguetia cadaverica</i>	7	3.00	IR	ID	H	HE*	1		+			1	+			
<i>Duguetia calycina</i>	5	2.40	IR	FF	H	HO	2	+	+			2				+
<i>Duguetia calycina</i>	5	3.00	IR	ID	H	HE*	1	+	+			2	+			+
<i>Duguetia cauliflora</i>	3	3.60	IR	FF	H	HO	0	-	-	-	-	1	+			+
<i>Duguetia eximia</i>	5	3.6	IR	ID	H	HE*	0	-	-	-	-	1	+			
<i>Duguetia eximia</i>	5	3.20	IR	ID	H	HE*	0	-	-	-	-	0	-	-	-	-
<i>Duguetia eximia</i>	5	4.60	IR	ID	H	HE*	0	-	-	-	-	1	+			
<i>Duguetia furfuracea</i>	8	4.20	IR	ID	H	HE*	0	-	-	-	-	0	-	-	-	-
<i>Duguetia granvilleana</i>	5	2.60	IR	ID	H	HE*	1	+				1	+			+
<i>Duguetia hadrantha</i>	4	3.40	IR	ID	H	HE*	2	+	+			2				+
<i>Duguetia inconspicua</i>	5	4.40	IR	ID	H	HE*	1		+			1	+			
<i>Duguetia lanceolata</i>	5	3.00	IR	ID	H	HE*	2			+		1	+			+
<i>Duguetia latifolia</i>	4	4.80	IR	ID	H	HE*	2	+	+	+		1	+			+
<i>Duguetia macrocalyx</i>	5	3.20	IR	ID	H	HE*	1	+				1	+			
<i>Duguetia macrophylla</i>	!	2.40	IR	FF	H	HE*	1	+	+			1	+			+
<i>Duguetia neglecta</i>	!	!	!	!	H	!	3	+	+	+		2	+	+		
<i>Duguetia neglecta</i>	3	4.40	IR	ID	H	HE*	2	+	+			1	+			

continued

## D. Continued

Taxa

	Width	No./mm	Shape in cross section	Dilatation	Ray height	Homocellular/heterocellular (* = weakly)	Sclereids	Sclereids solitary	Sclereids in small groups	Sclereids in large groups (> 10 cells)	Sclereids in tangential rows/bands	Secretory cells	Secretory cells solitary	Secretory cells in irregular groups	Secretory cells in radial rows	Secretory cells in tangential rows/bands
<i>Duguetia odorata</i>	5	3.20	IR	ID	H	HE*	1	+				1	+			+
<i>Duguetia pauciflora</i>	F	2.80	IR	ID	H	HE*	1	+				2	+			+
<i>Duguetia pycnastera</i>	3	4.40	IR	ID	H	HE*	2	+	+	+		1	+			+
<i>Duguetia pycnastera</i>	!	4.00	IR	ID	H	HE*	2	+	+	+		1	+			+
<i>Duguetia quitarensis</i>	4	4.80	IR	FF	H	HE*	1		+	+		2	+	+		+
<i>Duguetia quitarensis</i>	!	!	IR	ID	H	HE*	2	+	+	+		1	+			+
<i>Duguetia quitarensis</i>	3	2.00	IR	FF	H	HE*	1	+	+			2	+			+
<i>Duguetia riparia</i>	6	3.40	IR	FF	H	HO	1	+		+		2	+			+
<i>Duguetia spixiana</i>	5	3.80	IR	ID	H	HE*	2	+		+		1	+			+
<i>Duguetia spixiana</i>	4	4.00	IR	ID	H	HE	2		+	+		1	+	+		+
<i>Duguetia stelechantha</i>	5	4.40	IR	FF	H	HE*	2	+	+	+		3	+	+		+
<i>Duguetia stenantha</i>	7	3.60	IR	ID	H	HO	2	+	+	+		3	+			+
<i>Duguetia stenantha</i>	6	2.60	IR	ID	H	HO	2	+	+	+		2	+			+
<i>Duguetia surinamensis</i>	6	3.80	UN	ID	H	HO	2	+	+	+		1	+			+
<i>Duguetia surinamensis</i>	6	3.00	IR	FF	H	HE	2		+	+		1	+			+
<i>Duguetia surinamensis</i>	7	4.00	IR	ID	H	HE*	1		+	+		1	+			+
<i>Duguetia ulei</i>	6	4.60	IR	ID	H	HE*	1	+	+	+		1	+			+
<i>Duguetia uniflora</i>	F	4.40	IR	ID	H	HE*	2	+	+	+		2	+	+		+
<i>Duguetia yeshidan</i>	5	4.00	IR	ID	H	HE*	0	-	-	-	-	1	+			+
<i>Duguetia yeshidan</i>	3	4.20	IR	FF	H	HE*	2	+	+			1	+			+
<i>Duguetia</i> sp.	F	2.80	IR	ID	H	HE	1	+	+			2	+	+		+
<b><i>Duguetia</i></b>	<b>4.94</b>	<b>3.60</b>														
<i>Ephedranthus columbianus</i>	!	4.00	IR	ID	H	HO	3	+	+	+		0	-	-	-	-
<i>Ephedranthus guianensis</i>	7	5.10	IR	ID	H	HE	1		+			0	-	-	-	-
<b><i>Ephedranthus</i></b>	<b>7.00</b>	<b>4.55</b>														
<i>Fusaea longifolia</i>	5	4.00	IR	ID	H	HO	1	+				3	+	+		+
<i>Fusaea longifolia</i>	4	3.20	IR	ID	H	HO	1	+				3	+	+		+
<i>Fusaea longifolia</i>	F	3.60	IR	ID	H	HO	1	+	+			2	+	+		+
<b><i>Fusaea</i></b>	<b>4.50</b>	<b>3.60</b>														
<i>Guatteria citriodora</i>	!	!	IR	ID	H	HO	2	+	+	+		0	-	-	-	-
<i>Guatteria discolor</i>	!	!	IR	ID	H	HE	1	+	+			1	+			+
<i>Guatteria foliosa</i>	!	!	IR	ID	H	HO	2	+	+	+		0	-	-	-	-
<i>Guatteria lehmannii</i>	8	2.00	IR	ID	H	HO	1	+				2	+			+
<i>Guatteria megalophylla</i>	5	2.80	IR	ID	H	HO	1	+	+			0	-	-	-	-
<i>Guatteria olivacea</i>	!	!	!	ID	H	HE	2	+	+	+		1	+			+
<i>Guatteria scytophylla</i>	!	!	IR	ID	H	HO	2	+	+	+		0	-	-	-	-
<b><i>Guatteria</i><sup>1</sup></b>	<b>6.50</b>	<b>2.40</b>														
<b><i>Guatterioopsis hispida</i></b>	<b>6</b>	<b>3.30</b>	<b>IR</b>	<b>FF</b>	<b>H</b>	<b>HO</b>	<b>1</b>	<b>+</b>	<b>+</b>			<b>1</b>	<b>+</b>	<b>+</b>		
<b><i>Heteropetalum</i> sp.</b>	<b>4</b>	<b>2.90</b>	<b>IR</b>	<b>ID</b>	<b>H</b>	<b>!</b>	<b>2</b>	<b>+</b>			<b>+</b>	<b>0</b>	<b>-</b>	<b>-</b>	<b>-</b>	<b>-</b>
<b><i>Hornschurchia polyantha</i></b>	<b>6</b>	<b>4.30</b>	<b>IR</b>	<b>FF</b>	<b>H</b>	<b>HO</b>	<b>0</b>	<b>-</b>	<b>-</b>	<b>-</b>	<b>-</b>	<b>0</b>	<b>-</b>	<b>-</b>	<b>-</b>	<b>-</b>
<i>Klarobelia candida</i>	7	4.00	IR	FF	H	HO	0	-	-	-	-	1	+			+
<i>Klarobelia cauliflora</i>	6	4.80	IR	FF	H	HO	1		+			1	+	+		+
<i>Klarobelia inundata</i>	9	3.40	IR	ID	H	HO	1	+	+			2	+			+
<i>Klarobelia lucida</i> <sup>2</sup>	3	3.50	ST	ID	L	HO	1				+	0	-	-	-	-
<i>Klarobelia stipitata</i>	6	4.20	IR	ID	H	HO	2		+		+	1	+			+
<b><i>Klarobelia</i></b>	<b>6.20</b>	<b>3.98</b>														
<i>Malmea dielsiana</i>	3	4.00	IR	ID	H	HO	2	+	+	+		1	+	+		+
<i>Malmea surinamensis</i>	4	4.80	IR	ID	H	HO	1		+			1	+			+
<b><i>Malmea</i></b>	<b>3.50</b>	<b>4.40</b>														

continued



E. Axial phloem. Explanations: Fibre groups (1): R = regular tangential bands, I = irregular tangential bands; Fibre groups (2): N = mostly narrow (< 3 cell layers), W = wide; Fibre groups (3): O = mostly oblong, S = square; Fibre groups (4): A = arc-shaped; Sclereids associated with fibre groups: FR = frequent, SP = sporadic, 0 = not exist; Secretory cells: 0 = not present, 1 = few, 2 = abundant, 3 = bulk, 4 = only secretory cells present.

## Taxa

Taxa	Fibre groups (1)	Fibre groups (2)	Fibre groups (3)	Fibre groups (4)	Sclereids associated with fibre groups	Secretory cells	Secretory cells solitary	Secretory cells in irregular groups	Secretory cells in radial rows	Secretory cells in tangential rows/bands
<i>Anaxagorea brevipes</i>	R	W	O		SP	1	+			
<i>Anaxagorea dolichocarpa</i>	R	W	O		SP	1	+	+		
<i>Anaxagorea manausensis</i>	R	W	O		SP	0	-	-	-	-
<b>Anaxagorea</b>	-	-	-	-	-	-	-	-	-	-
<i>Annona ambotay</i>	R	W	O		0	1	+			
<i>Annona foetida</i>	R	W	O		0	1	+			
<i>Annona impressivenia</i>	R	W	O		0	0	-	-	-	-
<i>Annona sp. nov. aff. excellens</i>	R	W	O		0	0	-	-	-	-
<b>Annona</b>	-	-	-	-	-	-	-	-	-	-
<b>Asimina triloba</b>	R	N&W	O&S		SP	0	-	-	-	-
<i>Bocageopsis multiflora</i>	R	N&W	O		SP	3	+	+		+
<i>Bocageopsis pleiosperma</i>	R	W	O		SP	3	+	+		+
<b>Bocageopsis</b>	-	-	-	-	-	-	-	-	-	-
<b>Cardiopetalum surinamense</b>	R	W	O		0	0	-	-	-	-
<i>Crematosperma brevipes</i>	R	W	O		0	0	-	-	-	-
<i>Crematosperma cauliflorum</i>	R	W	O&S		0	0	-	-	-	-
<i>Crematosperma cauliflorum</i>	R	W	O&S		SP	0	-	-	-	-
<b>Crematosperma</b>	-	-	-	-	-	-	-	-	-	-
<i>Cymbopetalum brasiliense</i>	R	W	O		0	2	+	+		
<i>Cymbopetalum longipes</i>	R	W	O		0	1	+	+		
<b>Cymbopetalum</b>	-	-	-	-	-	-	-	-	-	-
<b>Desmopsis</b> sp.	R	N&W	O		SP	0	-	-	-	-
<i>Diclinanona calycina</i>	R	N&W	O	A	0	2	+	+		
<i>Diclinanona tessmannii</i>	R	N&W	O	A	0	1	+			
<b>Diclinanona</b>	-	-	-	-	-	-	-	-	-	-
<i>Duguetia argentea</i>	R	N	O	A	SP	2				+
<i>Duguetia bahiensis</i>	R	N	O	A	SP	1	+			
<i>Duguetia cadaverica</i>	R	N	O		0	0	-	-	-	-
<i>Duguetia cadaverica</i>	R	N	O		SP	0	-	-	-	-
<i>Duguetia cadaverica</i>	R	N	O		0	0	-	-	-	-
<i>Duguetia calycina</i>	R	N&W	O		0	2				+
<i>Duguetia calycina</i>	R	N	O		0	2				+
<i>Duguetia cauliflora</i>	R	W	O&S		0	1	+			
<i>Duguetia eximia</i>	R	N&W	O		0	0	-	-	-	-
<i>Duguetia eximia</i>	R	N&W	O		0	0	-	-	-	-
<i>Duguetia eximia</i>	R	N	O		0	0	-	-	-	-
<i>Duguetia furfuracea</i>	R	W	O&S	A	0	0	-	-	-	-
<i>Duguetia granvilleana</i>	R	N	O	A	0	2	+			
<i>Duguetia hadrantha</i>	R	N	O		0	2	+			
<i>Duguetia inconspicua</i>	R	N	O		0	0	-	-	-	-
<i>Duguetia lanceolata</i>	R	N	O	A	SP	2				+
<i>Duguetia latifolia</i>	R	N	O	A	SP	0	-	-	-	-
<i>Duguetia macrocalyx</i>	R	N	O		SP	1	+			
<i>Duguetia macrophylla</i>	R	N	O	A	0	0	-	-	-	-
<i>Duguetia neglecta</i>	!	!	!	!	FR	4	-	-	-	-
<i>Duguetia neglecta</i>	R	W	O	A	0	2	+			+

continued

## E. Continued.

Taxa

	Fibre groups (1)	Fibre groups (2)	Fibre groups (3)	Fibre groups (4)	Sclereids associated with fibre groups	Secretory cells	Secretory cells solitary	Secretory cells in irregular groups	Secretory cells in radial rows	Secretory cells in tangential rows/bands
<i>Duguetia odorata</i>	R	N&W	O&S	A	SP	2	+			
<i>Duguetia pauciflora</i>	R	N&W	O	A	0	2	+			+
<i>Duguetia pycnastera</i>	R	N	O	A	SP	1	+			
<i>Duguetia pycnastera</i>	R	N&W	O	A	SP	1	+			
<i>Duguetia quitarensis</i>	R	N	O		SP	2	+			
<i>Duguetia quitarensis</i>	R	N&W	O	A	0	1	+			
<i>Duguetia quitarensis</i>	R	N	O	A	0	2	+			
<i>Duguetia riparia</i>	R	N	O		0	2	+			
<i>Duguetia spixiana</i>	R	W	O	A	SP	1	+			
<i>Duguetia spixiana</i>	R	W	O	A	SP	1	+			
<i>Duguetia stelechantha</i>	R	N&W	O	A	SP	3	+			+
<i>Duguetia stenantha</i>	R	N&W	O	A	SP	1	+			
<i>Duguetia stenantha</i>	R	N	O	A	SP	2	+	+		
<i>Duguetia surinamensis</i>	R	N&W	O&S		SP	1	+			
<i>Duguetia surinamensis</i>	R	N&W	O	A	SP	1	+			
<i>Duguetia surinamensis</i>	R	N&W	O&S	A	0	1	+			
<i>Duguetia ulei</i>	R	N	O		0	1	+			
<i>Duguetia uniflora</i>	R	N&W	O	A	SP	1	+			
<i>Duguetia yeshidan</i>	R	N	O		0	1	+			
<i>Duguetia yeshidan</i>	R	N	O	A	0	1	+			
<i>Duguetia</i> sp.	R	W	O	A	0	1	+			
<b>Duguetia</b>	–	–	–	–	–	–	–	–	–	–
<i>Ephedranthus columbianus</i>	R	N&W	O		FR	0	–	–	–	–
<i>Ephedranthus guianensis</i>	R	N&W	O		0	0	–	–	–	–
<b>Ephedranthus</b>	–	–	–	–	–	–	–	–	–	–
<i>Fusaea longifolia</i>	R	N&W	O	A	0	3				+
<i>Fusaea longifolia</i>	R	N&W	O	A	0	3				+
<i>Fusaea longifolia</i>	R	N	O		0	3				+
<b>Fusaea</b>	–	–	–	–	–	–	–	–	–	–
<i>Guatteria citriodora</i>	R	W	O	A	SP	0	–	–	–	–
<i>Guatteria discolor</i>	R	N&W	O	A	0	1	+			
<i>Guatteria foliosa</i>	R	N	O	A	0	0	–	–	–	–
<i>Guatteria lehmannii</i>	R	N	O	A	0	0	–	–	–	–
<i>Guatteria megalophylla</i>	R	N	O	A	SP	0	–	–	–	–
<i>Guatteria olivacea</i>	R	N	O	A	0	0	–	–	–	–
<i>Guatteria scytophylla</i>	R	N&W	O	A	0	0	–	–	–	–
<b>Guatteria</b> <sup>1</sup>	–	–	–	–	–	–	–	–	–	–
<i>Guatterioopsis hispida</i>	R	N&W	O		0	0	–	–	–	–
<i>Heteropetalum</i> sp.	R	N&W	O&S		0	0	–	–	–	–
<b>Hornschurchia polyantha</b>	R	N&W	O		0	0	–	–	–	–
<i>Klarobelia candida</i>	R	N&W	O		0	1	+			
<i>Klarobelia cauliflora</i>	R	W	O		0	1	+			
<i>Klarobelia inundata</i>	R	W	O		0	1	+			
<i>Klarobelia lucida</i> <sup>2</sup>	R	W	O		0	0	–	–	–	–
<i>Klarobelia stipitata</i>	R	W	O&S		0	1	+	+		+
<b>Klarobelia</b>	–	–	–	–	–	–	–	–	–	–
<i>Malmea dielsiana</i>	R	N&W	O		FR	1	+			
<i>Malmea surinamensis</i>	R	N&W	O		FR	1	+			
<b>Malmea</b>	–	–	–	–	–	–	–	–	–	–

continued





F. Crystals. Explanations: Crystals: 0 = not present, 1 = few, 2 = abundant; Bordering: F = fibre groups, S = sclereid groups, 0 = no special pattern; Pattern: AR = around fibre groups, AB = abaxial side of fibre groups, AD = adaxial side of fibre groups, LA = lateral side of fibre groups, SV = in short vertical chains, LV = in long vertical chains, BF = in tangential chains between fibre groups, LR = in long radial rows.

Taxa	Crystals	Prismatic, octohedral	Prismatic, rhombohedral	Navicular	Acicular	Cubic	Elongated	Druses	Spindle-shaped	Like styloids	Other crystals	Bordering (*weakly)	Pattern		
													AR	LV	BF
<i>Anaxagorea brevipes</i>	2							+				0	-	-	-
<i>Anaxagorea dolichocarpa</i>	2							+				0	-	-	-
<i>Anaxagorea manausensis</i>	1							+				0	-	-	-
<b>Anaxagorea</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Annona ambotay</i>	2						+			+		F	AR	LV	
<i>Annona foetida</i>	2		+				+			+		F	AR	SV	LR
<i>Annona impressivenia</i>	2		+				+			+		F&S	AR	SV	
<i>Annona sp. nov. aff. excellens</i>	0	-	-	-	-	-	-	-	-	-	-	0	-	-	-
<b>Annona</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Asimina triloba</b>	<b>1</b>	<b>+</b>	<b>+</b>							<b>+</b>	<b>+</b>	<b>F</b>		<b>SV</b>	
<i>Bocageopsis multiflora</i>	1	+	+									F	AD	SV	
<i>Bocageopsis pleiosperma</i>	1	+	+									F	AD	SV	
<b>Bocageopsis</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Cardiopetalum surinamense</b>	<b>1</b>	<b>+</b>	<b>+</b>	<b>+</b>								<b>0</b>	-	-	-
<i>Crematosperma brevipes</i>	1	+	+									0	-	-	-
<i>Crematosperma cauliflorum</i>	1	+	+									0	-	-	-
<i>Crematosperma cauliflorum</i>	1	+	+									0	-	-	-
<b>Crematosperma</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cymbopetalum brasiliense</i>	2	+	+				+			+		F	AR	LV	BF
<i>Cymbopetalum longipes</i>	2	+	+				+					F	AR	LV	BF
<b>Cymbopetalum</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Desmopsis sp.</b>	<b>1</b>	<b>+</b>	<b>+</b>									<b>0</b>	-	-	-
<i>Diclinanona calycina</i>	0	-	-	-	-	-	-	-	-	-	-	0	-	-	-
<i>Diclinanona tessmannii</i>	0	-	-	-	-	-	-	-	-	-	-	0	-	-	-
<b>Diclinanona</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Duguetia argentea</i>	1			+								0	-	-	-
<i>Duguetia bahiensis</i>	2			+		+					+	0	-	-	-
<i>Duguetia cadaverica</i>	2								+		+	0	-	-	-
<i>Duguetia cadaverica</i>	2			+							+	0	-	-	-
<i>Duguetia calycina</i>	1			+							+	0	-	-	-
<i>Duguetia calycina</i>	2					+					+	0	-	-	-
<i>Duguetia cauliflora</i>	1			+							+	0	-	-	-
<i>Duguetia eximia</i>	2			+							+	0	-	-	-
<i>Duguetia eximia</i>	2								+		+	0	-	-	-
<i>Duguetia eximia</i>	2			+							+	0	-	-	-
<i>Duguetia furfuracea</i>	1					+					+	0	-	-	-
<i>Duguetia granvilleana</i>	2			+							+	0	-	-	-
<i>Duguetia hadrantha</i>	2					+					+	0	-	-	-
<i>Duguetia inconspicua</i>	2			+							+	0	-	-	-
<i>Duguetia lanceolata</i>	2			+							+	0	-	-	-
<i>Duguetia latifolia</i>	2			+							+	0	-	-	-
<i>Duguetia macrocalyx</i>	2								+		+	0	-	-	-
<i>Duguetia macrophylla</i>	1								+		+	0	-	-	-
<i>Duguetia neglecta</i>	1	+									+	F	AR	LV	
<i>Duguetia neglecta</i>	1								+		+	0	-	-	-
<i>Duguetia odorata</i>	2					+					+	0	-	-	-
<i>Duguetia pauciflora</i>	1			+							+	0	-	-	-
<i>Duguetia pycnastera</i>	2			+							+	0	-	-	-
<i>Duguetia pycnastera</i>	2					+	+				+	0	-	-	-
<i>Duguetia quitarensis</i>	2					+					+	0	-	-	-
<i>Duguetia quitarensis</i>	2					+	+				+	0	-	-	-

continued

## F. Continued.

Taxa	Crystals	Prismatic, octohedral	Prismatic, rhombohedral	Navicular	Acicular	Cubic	Elongated	Druses	Spindle-shaped	Like styloids	Other crystals	Bordering (*weakly)	Pattern		
<i>Duguetia quitarensis</i>	2					+					+	0	-	-	-
<i>Duguetia riparia</i>	2										+	0	-	-	-
<i>Duguetia spixiana</i>	2			+							+	0	-	-	-
<i>Duguetia spixiana</i>	2			+							+	0	-	-	-
<i>Duguetia stelechantha</i>	1						+				+	0	-	-	-
<i>Duguetia stenantha</i>	1			+							+	0	-	-	-
<i>Duguetia stenantha</i>	1					+					+	0	-	-	-
<i>Duguetia surinamensis</i>	2				+						+	0	-	-	-
<i>Duguetia surinamensis</i>	2			+							+	0	-	-	-
<i>Duguetia surinamensis</i>	2			+							+	0	-	-	-
<i>Duguetia ulei</i>	2			+							+	0	-	-	-
<i>Duguetia uniflora</i>	1						+				+	0	-	-	-
<i>Duguetia yeshidan</i>	1			+							+	0	-	-	-
<i>Duguetia yeshidan</i>	1			+							+	0	-	-	-
<i>Duguetia</i> sp.	2			+							+	0	-	-	-
<b>Duguetia</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ephedranthus columbianus</i>	2	+	+									F*	AR	LV	
<i>Ephedranthus guianensis</i>	2	+	+									F*	AR	LV	
<b>Ephedranthus</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Fusaea longifolia</i>	1	+	+									0	-	-	-
<i>Fusaea longifolia</i>	1	+	+									0	-	-	-
<i>Fusaea longifolia</i>	1	+	+									0	-	-	-
<b>Fusaea</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Guatteria citriodora</i>	1	+	+									F	LA		
<i>Guatteria discolor</i>	1	+									+	F*	LA		
<i>Guatteria foliosa</i>	1	+									+	F*	LA		
<i>Guatteria lehmannii</i>	1	+	+								+	F*	LA		
<i>Guatteria megalophylla</i>	2	+	+									F	?	?	?
<i>Guatteria olivacea</i>	2	+	+								+	F*	LA		
<i>Guatteria scytophylla</i>	2	+	+									F*	LA		
<b>Guatteria<sup>1</sup></b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Guatteriopsis hispida</i>	1	+	+									F*	LA		
<b>Heteropetalum</b> sp.	0	-	-	-	-	-	-	-	-	-	-	0	-	-	-
<b>Hornschurchia polyantha</b>	2	+	+									F	LA	SV	
<i>Klarobelia candida</i>	2	+	+								+	F	AR	LV	
<i>Klarobelia cauliflora</i>	2	+	+									F	AR	LV	
<i>Klarobelia inundata</i>	2	+	+								+	F	AR	LV	
<i>Klarobelia lucida<sup>2</sup></i>	0	-	-	-	-	-	-	-	-	-	-	0	-	-	-
<i>Klarobelia stipitata</i>	2	+	+									F	AR	LV	
<b>Klarobelia</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Malmea dielsiana</i>	2	+	+								+	F*	?	?	?
<i>Malmea surinamensis</i>	1	+	+								+	F*	AR		
<b>Malmea</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Mosannonna depressa</i> subsp. <i>abscondita</i> <sup>2</sup>	2	+	+								+	F	AR	SV	
<i>Mosannonna discolor</i>	2	+	+									F	AR	LV	
<i>Mosannonna raimondii</i>	2	+	+									F	AR	LV	
<b>Mosannonna</b>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<b>Onychopetalum amazonicum</b>	1	+	+									0	-	-	-
<i>Oxandra asbeckii</i>	2	+	+									F*	AB	LV	
<i>Oxandra asbeckii</i>	2	+	+									F*	AB	LV	
<i>Oxandra espintana</i>	2	+	+								+	F*	AB	LV	
<i>Oxandra lanceolata</i>	1	+	+									F*	AB	SV	
<i>Oxandra laurifolia</i>	2	+	+									F*	AB	LV	
<i>Oxandra riedeliana</i>	2	+	+								+	F*	AB	LV	
<i>Oxandra sphaerocarpa</i>	2	+	+									F*	AB	LV	

continued



G. Crystals. Explanations: Occurrence: Phelloderm/Cortex/Rays/Axial phloem: 0 = not present, P = parenchyma, S = sclereids.

Taxa	Occurrence				Other features				
	Phelloderm	Cortex	Rays	Axial phloem	Size (µm)	No./cell	Crystals unequal/cell	In enlarged cells	Cells chambered (crystals in axial parenchyma strand cells)
<i>Anaxagorea brevipes</i>	0	!	P	0	10–23	1			–
<i>Anaxagorea dolichocarpa</i>	0	0	P	0	13–25	1			–
<i>Anaxagorea manausensis</i>	0	0	P	0	8–12	1			–
<b>Anaxagorea</b>	–	–	–	–	–	–	–	–	–
<i>Annona ambotay</i>	0	0	0	P	25–60	1			+
<i>Annona foetida</i>	0	0	P	P	50–110	1			+?
<i>Annona impressivenia</i>	S	S	S	P	15–35	> 1	+		+
<i>Annona</i> sp. nov. aff. <i>excellens</i>	0	0	0	0	–	–	–	–	–
<b>Annona</b>	–	–	–	–	–	–	–	–	–
<b>Asimina triloba</b>	0	S	S	P&S	15–25	1			+
<i>Bocageopsis multiflora</i>	0	0	0	S	15–25	1			+
<i>Bocageopsis pleiosperma</i>	0	0	0	S	20–30	1			+
<b>Bocageopsis</b>	–	–	–	–	–	–	–	–	–
<b>Cardiopetalum surinamense</b>	0	0	(P)	0	20–25	1			–
<i>Crematosperma brevipes</i>	0	0	P	0	(5–)10–20	1			–
<i>Crematosperma cauliflorum</i>	S	S	P&S	0	15–45	1			–
<i>Crematosperma cauliflorum</i>	0	0	P	0	(5–)20–30	1			–
<i>Crematosperma</i>	–	–	–	–	–	–	–	–	–
<i>Cymbopetalum brasiliense</i>	S	P&S	P&S	P(S)	10–50	> 1	+		+
<i>Cymbopetalum longipes</i>	S	P&S	P&S	P(S)	10–30	1			+
<b>Cymbopetalum</b>	–	–	–	–	–	–	–	–	–
<b>Desmopsis</b> sp.	S	!	S	0	(10–)15–30	1			–
<i>Diclinanona calycina</i>	0	0	0	0	–	–	–	–	–
<i>Diclinanona tessmannii</i>	0	0	0	0	–	–	–	–	–
<b>Diclinanona</b>	–	–	–	–	–	–	–	–	–
<i>Duguetia argentea</i>	0	0	P	0	7–10	> 1	+		–
<i>Duguetia bahiensis</i>	P	0	P	0	10–35	> 1	+		–
<i>Duguetia cadaverica</i>	P	0	P	0	5–20	> 1	+		–
<i>Duguetia cadaverica</i>	P	0	P	0	10–20	> 1	+		–
<i>Duguetia cadaverica</i>	P	0	P	0	10–15	> 1	+		–
<i>Duguetia calycina</i>	P	0	P	0	5–10	> 1	+		–
<i>Duguetia calycina</i>	P	0	P	0	5–15	> 1	+		–
<i>Duguetia cauliflora</i>	P	0	P	0	5–15	> 1	+		–
<i>Duguetia eximia</i>	P	0	P	0	5–30	> 1	+		–
<i>Duguetia eximia</i>	P	0	P	0	5–25	> 1	+		–
<i>Duguetia eximia</i>	P	0	P	0	10–20	> 1	+		–
<i>Duguetia furfuracea</i>	P	0	P	0	5–15	> 1	+		–
<i>Duguetia granvilleana</i>	P	0	P	0	5–13	> 1	+		–
<i>Duguetia hadrantha</i>	P	!	P	0	5–15	> 1	+		–
<i>Duguetia inconspicua</i>	P	0	P	0	(5–)10	> 1	+		–
<i>Duguetia lanceolata</i>	P	0	P	0	10–30	> 1	+		–
<i>Duguetia latifolia</i>	P	0	P	0	5–25	> 1	+		–
<i>Duguetia macrocalyx</i>	P	0	P	0	5–10	> 1	+		–
<i>Duguetia macrophylla</i>	P	0	P	0	3–7	> 1	+		–
<i>Duguetia neglecta</i>	0	0	P	P(S)	15–25	1			+
<i>Duguetia neglecta</i>	P	0	P	0	10–40	> 1	+		–
<i>Duguetia odorata</i>	P	0	P	0	10–30	> 1	+		–
<i>Duguetia pauciflora</i>	P	0	P	0	5–10	> 1	+		–
<i>Duguetia pycnastera</i>	P	0	P	0	15–30	> 1	+		–
<i>Duguetia pycnastera</i>	P	0	P	0	15–30	> 1	+		–

continued

## G. Continued.

Taxa	Occurrence				Other features				
	Pheloderm	Cortex	Rays	Axial phloem	Size (µm)	No./cell	Crystals unequal/cell	In enlarged cells	Cells chambered (crystals in axial parenchyma strand cells)
<i>Duguetia quitarensis</i>	P	0	P	0	12–25	> 1	+		–
<i>Duguetia quitarensis</i>	P	0	P	0	10–30	> 1	+		–
<i>Duguetia quitarensis</i>	P	0	P	0	10–20	> 1	+		–
<i>Duguetia riparia</i>	P	0	P	0	7–15	> 1	+		–
<i>Duguetia spixiana</i>	P	0	P	0	10–25	> 1	+		–
<i>Duguetia spixiana</i>	P	0	P	0	10–15	> 1	+		–
<i>Duguetia stelechantha</i>	0	!	P	0	15–28	1?	?		–
<i>Duguetia stenantha</i>	P?	0	P	0	15–35(–72)	> 1	+		–
<i>Duguetia stenantha</i>	P	!	P	0	15–20	1?	?		–
<i>Duguetia surinamensis</i>	P	!	P	0	15–30	> 1	+		–
<i>Duguetia surinamensis</i>	P	0	P	0	15–35(–40)	> 1	+		–
<i>Duguetia surinamensis</i>	P	!	P	0	10–35(–40)	> 1	+		–
<i>Duguetia ulei</i>	P	0	P	0	12–20(–25)	> 1	+		–
<i>Duguetia uniflora</i>	P?	0	P	0	12–20(–25)	> 1	+		–
<i>Duguetia yeshidan</i>	P	0	P	0	5–10	> 1	+		–
<i>Duguetia yeshidan</i>	P	!	P	0	5–15	> 1	+		–
<i>Duguetia</i> sp.	P	!	P	0	12–20	> 1	+		–
<b>Duguetia</b>	–	–	–	–	–	–	–	–	–
<i>Ephedranthus columbianus</i>	S	S	S	P&S	10–25	1			+
<i>Ephedranthus guianensis</i>	0	S	S	P	10–25	1			+
<b>Ephedranthus</b>	–	–	–	–	–	–	–	–	–
<i>Fusaea longifolia</i>	0	0	P	0	20–30	1			–
<i>Fusaea longifolia</i>	0	!	P	0	15–25	1			–
<i>Fusaea longifolia</i>	0	!	P	0	15–20	1			–
<b>Fusaea</b>	–	–	–	–	–	–	–	–	–
<i>Guatteria citriodora</i>	0	0	0	S	5–10	?	?		–
<i>Guatteria discolor</i>	0	!	0	S	5–25	?	?		–
<i>Guatteria foliosa</i>	0	0	0	S	5–10	?	?		–
<i>Guatteria lehmannii</i>	0	0	0	S	5–10	1			–
<i>Guatteria megalophylla</i>	0	0	0	S	12–25	1			–
<i>Guatteria olivacea</i>	0	0	0	S	5–12	?	?		–
<i>Guatteria scytophylla</i>	0	!	0	S	5–12	?	?		–
<b>Guatteria</b> <sup>1</sup>	–	–	–	–	–	–	–	–	–
<b>Guatterioopsis hispida</b>	0	0	0	S	12–25	1			–
<b>Heteropetalum</b> sp.	0	0	0	0	–	–	–	–	–
<b>Hornsuchia polyantha</b>	0	0	P	P	10–35	> 1	+		–
<i>Klarobelia candida</i>	S	0	P&S	P	7–15	1			+
<i>Klarobelia cauliflora</i>	0	!	0	(P)	10–20	1			+
<i>Klarobelia inundata</i>	0	!	0	P	7–15	1			+
<i>Klarobelia lucida</i> <sup>2</sup>	!	!	0	0	–	–	–	–	–
<i>Klarobelia stipitata</i>	P	P	S	P	10–25	1			+
<b>Klarobelia</b>	–	–	–	–	–	–	–	–	–
<i>Malmea dielsiana</i>	S	S	S	P&S	20–40; 10–15	1		+	–
<i>Malmea surinamensis</i>	S	S	S	P&S	20–50; 10–15	1		+	–
<b>Malmea</b>	–	–	–	–	–	–	–	–	–
<i>Mosannonna depressa</i> subsp. <i>abscondita</i>	P&S	S	P&S	S	5–40	1		+	+
<i>Mosannonna discolor</i>	P&S	P&S	P&S	P	10–45	1			+
<i>Mosannonna raimondii</i>	P&S	!	P&S	P	10–40	> 1	+		+
<b>Mosannonna</b>	–	–	–	–	–	–	–	–	–
<b>Onychopetalum amazonicum</b>	0	S	S	0	25–30				–

continued

