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Studies in Annonaceae. VI
A leafanatomical survey of genera of Annonaceae in the Neotropics

By

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With 26 figures and 2 tables in the text

Abstract

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Within the scope of the multidisciplinary research project on systematics of Annonaceae, a survey of the leafanatomical features and their distribution in the neotropical Annonaceae is presented. The studied specimens form a rather homogeneous group, as may appear from the family description given here. A detailed study of the leafanatomical features reveals, that differences are mainly found in the indument, the position and contents of the idioblasts, the structure of the primary vein, the type of crystals in the epidermal cells, and the type of sclereids.

Based on character states, phenetic similarities and differences are discussed and compared with the classifications of Fries (1959) and Walker (1971).

Introduction

In 1982 a multidisciplinary research project on systematics of Annonaceae was started. For a survey of the scope and planning of this project, see Maas (1984). One of its objectives is to provide genus-descriptions which are based on as many features as possible. Among other subdisciplines of plant systematics, the leaf anatomy is a valuable source of information.

Although the Annonaceae are represented by many species in all tropical areas, thusfar few studies have been carried out with regard to the occurrence and variation of leafanatomical features and their taxonomic significance in

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Annonaceae. Some surveys (SOLEREDER 1899, 1908, METCALFE & CHALK 1950), though providing us with much information, are based upon material identification of which is difficult to verify, or the descriptions do not include all leafanatomical features which may be relevant. BEYER (1902) gives a description of the family, but this is mainly based on African genera. JOVET-AST (1942) lists in a summarizing chapter a number of taxonomically important characters, based on her study of genera of Indo-China. A world-wide survey of ROTH (1981) is restricted to epidermal characters. Other publications are restricted to smaller parts of the family: tribes (KRAMER 1969) or genera (for instance BLUNDEN & KYI 1973, PAVIANI & CAVALCANTI 1977). Some papers describe the occurrence of one or few features in a few genera (for instance PATEL 1971, RAO & CHIN 1966).

Summarizing: Leafanatomical data known from the literature so far, are insufficient as a base for a character survey, as a contribution to the generic revision of the Annonaceae intended in the project "Systematics of Annonaceae".

This paper deals with the leaf anatomy of the neotropical genera. The first part consists of a survey of the distribution and variation of the characters. A comparison of our conclusions and the literature with regard to the variability of characters within genera is given. In a last part, an attempt to arrange the neotropical genera in clusters on the base of similarity of leafanatomical characters is made.

Our study is based on specimens of all 38 neotropical genera. The specimens represent over 200 species. Most specimens were identified down to the species level (by P. J. M. MAAS, E. A. MENNEGA, and A. K. VAN SETTEN). However, as recent monographs are lacking for most genera and the delimitation of the genera is subject of our research, some specimens may turn out to be "wrongly placed" in a later stage.

Materials and methods

For sectioning, square centimeters were taken from mature leaves of herbarium specimens at ⅓ of the leaf length, counted from the petiole. These leaf parts and petioles were rehydrated by boiling in water and were used for the preparation of transverse microtome sections of lamina and petiole, of freehand paradermal section, and of cuticular macerations (in equal volumes of acetic acid and 30% hydrogen peroxide). All sections were bleached and stained with Astra-blue and Safranin. Cuticular macerations were stained with Sudan IV.

Of six genera (*Bocagea, Duckeanthus, Pseudephedranthus, Guatteriella, Reedrollinsia* and *Tridimeris*) only one specimen was studied because of the very small number of herbarium vouchers available. The monotypic genus *Deeringothamnus* (*D. pulchellus*) is treated here under *Asimina*. Of the other genera, three to forty specimens representing one to several species were studied (see list of material). In the presentation of the results, we have omitted character states which were found only once within a genus, except in the synoptical key and in Table 2. A discussion of such exceptional character states properly belongs in a monograph of the genera concerned.

Descriptive part

a) Description of the family, based on neotropical genera

1. in surface view:

Indument mostly present on the abaxial side, sometimes also, but less densely at the adaxial side, consisting of simple, 1 to more-cellular trichomes, rarely stellate tufts or scales; often the trichomes are easily shed.

Cuticle 0—6(—10) μm, with smooth outer surface; in some genera striations occur in radial or parallel arrangement round the stomata and trichome bases. Rarely reticulate or punctate structures covering the surface are found.

Unspecialized epidermal cells polygonal; adaxial cells 15—60 × 12—50 μm, abaxial cells 15—60 × 10—40 μm. The anticlinal cell walls are straight to undulate on both surfaces.

Stomata mostly restricted to the abaxial side and regularly distributed; rarely on the adaxial surface, and then less frequent, mostly restricted to a narrow zone along the primary vein; always paracytic or amphibrachy-paracytic with 2—6 subsidiary cells; length of the guard cells 15—40 μm; 10—30 per mm.

2. in transverse section:

Lamina mostly dorsiventral, rarely bilateral.

Epidermis 1—3-layered; in some genera oil cells occur in or immediately below the epidermis.

Stomata on the same level as the unspecialized epidermal cells or slightly sunken; often with outer cuticular ledges, sometimes also with inner ledges. Often the guard cells are included by the subsidiary cells, at least along the inner side.

Mesophyll composed of 1—2(—3)-layered palisade parenchyma and loosely packed to compact sponge parenchyma. Oil cells occur in all genera in the palisade parenchyma, in the sponge parenchyma, or in both tissues. Sclereids may occur, either as astrosclereids or as osteosclereids. They may run parallel to the epidermis only or they may also extend into the mesophyll.

Primary veins consisting nearly always of one vascular bundle surrounded by a continuous sclerenchyma cap. The vascular bundle is often arc-shaped with continuous or interrupted phloem tissue at the abaxial side of the xylem tissue; in about 25% of the genera the vascular bundle is more complex, with additional islands of sclerenchyma fibres and phloem tissue included in the xylem body.

Terminal veins collateral with narrow sclerenchymatic caps or sheaths; the sheaths sometimes connected with both abaxial and adaxial epidermis by collenchymatic or sclerenchymatic extensions.

Crystals may occur in the epidermal cells as crystal sand, druses, or rhombic crystals of varying shape and size; in the sponge- and palisade parenchyma nearly exclusively as druses.

In the petiole, the vascular bundles are arranged in one arc, or additional bundles are found in the centre of the petiole. Stone cells are always present, often in clusters. Crystals occur nearly always as druses, rarely as rhombic crystals. Oil cells occur often in varying size and frequency.

b) Description of the individual leafanatomical characters and a discussion of their taxonomic and/or diagnostic value

The indument

In nearly all neotropical genera, an indument of non-glandular trichomes can be found, be it sometimes in juvenile stages only. Usually the indument is restricted to, or dominant on, the abaxial surface. An abaxial indument was not found in *Cardiopetalum*, *Cremastosperma*, *Duckeanthus*, *Pseudephedranthus*, *Tridimeris*, and rarely in *Malmea* and *Porcelia* p.p. As trichomes are mostly easily shed, the frequency may vary considerably in leaves of one species or even of one specimen. However, high frequencies (more than 40 trichomes per mm^2) were always found in *Bocageopsis*, *Guatteriella*, *Onychopetalum*, *Ruizodendron*, and incidentally in several other genera p.p.

Adaxially, trichomes are more or less frequent in (most species of) *Annona*, *Raimondia*, *Rollinia*, *Rolliniopsis*, *Sapranthus*, and *Stenanona*, and incidentally in species of other genera.

The basic trichome type (at the same time the most simple and the most frequently occurring) is a trichome of one row of 1 to few cells; the basal cell is often surrounded by a cuticular rim. The top cell is elongated and often pointed. In many genera, trichomes consisting of more (up to 10) cells are found.

Duguetia is exceptional with its stellate to peltate trichomes which occur in all species studied (Fig. 1, 2). Tufts of trichomes are found in *Tetrameranthus* and in some species of *Annona* and *Rollinia* (Fig. 3). *Anaxagorea* is characterized by simple and branched to stellate trichomes with blunt, very thin-walled top cells (KOEK-NOORMAN & BERENDSEN 1985).

The length varies strongly within genera. Only in *Guatteriella*, *Guatteriopsis*, and *Stenanona* the trichomes are always more than 300 µm long. In *Bocageopsis*, *Ephedranthus*, *Onychopetalum*, and *Ruizodendron* the trichomes are always short (less than 100 µm), one- to two-celled and strongly appressed (Fig. 4). In these genera, but especially in *Ruizodendron*, transitions to a papillate epidermis (see paragraph on unspecialized epidermal cells) can be found.

In general, data from the literature are in accordance with our findings. BEYER (1902) also reports 2—3 cells long, simple hairs with a long, sharp top cell as the predominant type in the Asiatic Annonaceae, with the occurrence of tufted hairs, stellate hairs and scales in some genera. JOVET-AST (1942) found comparable hair types in the African genera. Both authors report the occurrence of hairs on the top of epidermal emergences in some genera. In our material, no emergences were observed: in all genera, the epidermis is flat, papillae excepted.

ROTH (1981), in his world-wide survey of epidermal features in Annonaceae, describes 16 trichome types. Apart from *Duguetia* ("bicellular stellate-peltate"), *Tetrameranthus* („multicellular, stellate tufts") and *Anaxagorea* ("clavate trichomes, single or in tufts"), the neotropical genera are grouped in about five categories, differing in number of cells per trichome and grouping of the trichomes in pairs, quartets, or tufts.

If we compare our results and conclusions with regard to the occurrence of an indument (see before) with the relevant literature, we may say that there is a general agreement about the value of the trichome type on the genus level. The occurrence of stellate-peltate scales is reported for some genera (this paper, JOVET-AST 1942, ROTH 1981, morphological descriptions of new species) and seems to be constant within these genera. The presence of scale-like trichomes in *Anaxagorea* reported by I. ROTH (1984) is without doubt due to an error, as *Anaxagorea* is characterized by simple or branched to stellate trichomes with peculiar, thin-walled, blunt top cells (JOVET-AST 1942, KOEK-NOORMAN & BERENDSEN 1985). Such a structure has not yet been found in other genera. Stellate trichomes, or "tufts", are also reported to be characteristic for a restricted number of genera (this paper, JOVET-AST 1942, ROTH 1981). In *Annona* and *Rollinia,* we found trichomes to be mostly single, but in a few species they are grouped in small tufts of two to several trichomes.

Contrary to the value that can be attributed to the trichome types, there seems to be hardly any taxonomic or diagnostic value on the genus level in the number of cells per trichome, the trichome length (in µm), and the frequency of trichomes on the abaxial surface. JOVET-AST suggests that the number of cells may have taxonomic value on the level of species, but mentions that even within species the number of cells may vary considerably. We have the same experience and therefore do not follow ROTH (1981) in distinguishing as many as 16 types of annonaceous trichomes, which are based a.o. on the number of cells per trichome.

Although in all genera the frequency of trichomes may vary strongly, high frequencies were always found in *Bocageopsis, Ephedranthus, Onychopetalum* and *Ruizodendron.* In these genera, the trichome frequency seems to be correlated with the small size of the epidermal cells and the transitions between trichomes and papillae. This combination of features results in a pattern which makes it possible to recognize these genera.

The cuticle

In the transverse sections of most specimens a cuticular layer can be seen on the abaxial and adaxial side. Even for those specimens in which no separate cuticular layer can be seen, a cuticle preparation can be made by maceration methods.

Commonly, the cuticle on the adaxial surface of the lamina is thicker than on the abaxial surface, but thinner than the cuticle of the petiole and over the primary veins. The differences, however, are seldom more than 1—3 µm. The thickness of the adaxial cuticle varies between 0—6(—10) µm and the overlap between genera is considerable.

When seen through a light-optical microscope, the outer surface of the cuticular layer is smooth. Alveolar material or wax is lacking. Striations, in radial or parallel arrangement around stomata or trichome bases (Fig. 5), occur in many species of *Anaxagorea*, *Annona*, *Asimina*, *Diclinanona*, and *Heteropetalum*; less regularly in *Fusaea*, *Guatteriella*, and *Rollinia*. In species of *Annona* and *Oxandra*, striations can be seen the position and orientation of which do not seem to be correlated with stomata or trichome bases. Thickened cuticular ledges following the anticlinal epidermal cell walls are often found (Figs. 6, 7). Besides, *Hornschuchia* shows incidentally a fine punctation on the abaxial surface.

Our findings given above are not always in agreement with data given by ROTH (1981). Apart from his remark, that many genera of Annonaceae show striations radiating from or perpendicular to the stomatal axis or trichome base, he reports striations in *Asimina* and *Heteropetalum* over (nearly) all of their abaxial or adaxial surface, and in *Ephedranthus* reticulate cuticular thickenings over the abaxial surface independent of stomata, anticlinal cell walls, or minor venations. Such discrepancies may be — at least partly — due to the fact that preparation methods and the use of light optical microscopes do not always guarantee that those fine cuticular structures are scored correctly. The discrepancy with regard to *Asimina* is most probably due to the fact that different species were studied: the illustrations of two species of *Asimina* (MORAWETZ & WAHA 1984) represent a variation comparable with the difference between our data and those of ROTH (1981).

In some genera we found that structures which at first view seem to be ornamentations of the outer surface of the cuticle, are in fact penetrations of the outer epidermal cell walls in the cuticle (specimens of *Anaxagorea*, *Annona*, *Cymbopetalum*, *Desmopsis*; unpublished data of SEM-research).

Although still much research work remains to be done, a few careful conclusions can be drawn about the diagnostic and taxonomic value of cuticular features in Annonaceae. Cuticular foldings are found in a restricted number of genera. However, within these genera they may vary from strongly to poorly developed or absent (synoptical key; MORAWETZ & WAHA 1984). As pointed out above, it is sometimes difficult to decide if the "striations", seen with a light optical microscope, are on the outer or inner side of the cuticle.

Unspecialized epidermal cells

The shape of the unspecialized epidermal cells is polygonal, isodiametric to oval, but more elongate over the primary and secondary veins.

Abaxially, the cells are often slightly longer and narrower than adaxially. The same shape of cells, both abaxially and adaxially, was found in *Bocagea*, *Cardiopetalum*, *Cymbopetalum*, *Malmea*, *Porcelia*, and *Sapranthus*.

The anticlinal cell walls can be straight (Fig. 7) or slightly to strongly undulated (Fig. 8). In some genera this feature is constant; in other genera it seems to vary between species. Often the anticlinal cell walls show the same degree of undulation on both abaxial and adaxial surfaces. We found undulating anticlinal cell walls in representatives of 23 genera. In *Anaxagorea*, *Diclinanona*, and *Tridimeris* we scored this feature for all specimens. Exclusively straight cell walls were found in *Bocagea*, *Bocageopsis*, *Cardiopetalum*, *Fusaea*, *Heteropetalum*, *Oxandra*, *Onychopetalum*, *Porcelia*, *Pseudoxandra*, *Raimondia*, *Ruizodendron*, *Tetrameranthus*, and *Trigynaea*.

In transverse sections, the epidermis is mostly one-layered. In one species of *Xylopia*, a three-layered epidermis was found adaxially. A two-layered adaxial epidermis (Fig. 9) occurs in species of *Annona*, *Asimina*, *Guatteria*, *Raimondia*, *Tetrameranthus*, and *Xylopia*. Sometimes, it is difficult to decide whether the inner layer of the epidermis is perhaps a hypodermis. As long as ontogenetic data are not available, we interpret all more-layered structures as epidermal layers.

With the exception of *Oxandra*, *Onychopetalum*, and *Stenanona*, the adaxial epidermis is thicker than the abaxial one, the values are between 8—25 µm. The variation within genera is large, and so is the overlap. Evidently, the highest values are found when the epidermis is more-layered or papillate.

Bocageopsis, *Ephedranthus*, *Onychopetalum*, and *Ruizodendron* are remarkable because of their circular abaxial epidermal cells, each with one papilla (Fig. 4), and smaller than or as large as the adaxial epidermal cells. (Transitions between papillae and simple trichomes may occur.) A papillate epidermis was also found in some species of *Annona* and *Rollinia* (Fig. 9).

Papillate epidermal cells are reported by several authors to be present in some annonaceous genera (JOVET-AST 1942, ROTH 1981). ROTH (1981) reports papillae in *Bocageopsis*, but only around the stomatal complex. We found them on the whole abaxial surface.

Many authors suggest that epidermal characters are highly influenced by ecological factors. For instance, it is often reported that the amplitude of the undulations of the anticlinal cell walls increases the more the leaves grow in shade. This fact, then, would ask for a very careful sampling of the leaf material. METCALFE & CHALK (1950) note that the abaxial epidermal cells are often more undulating than those of the adaxial side. We did not find such a trend, as in many specimens the cell wall undulations on both surfaces are comparable, and in some samples the degree of undulation can be even less abaxially than adaxially.

We have indications (unpublished data) that in at least some species the cell wall undulations increase with increasing age of the leaves. STACE (1965) also warns the reader: "Few other characters of the epidermis show as much variation as the cell wall undulation, and although this has been used taxonomically in a number of groups, its use requires the most extreme caution."

Even if the feature of cell wall undulation would prove to be rather constant and a reliable diagnostic tool on the level of species (as suggested by BEYER 1902), the variation within genera is so high that we disagree with ROTH (1981) who considers the degree of cell wall undulation "as a feature with taxonomic value in distinguishing between groups of genera".

Stomata

All stomatal complexes are variations of the paracytic type: the subsidiary cells are orientated parallel to the guard cells. Sometimes they include the guard cells completely (Fig. 5), but most often the polar zones border on unspecialized cells (Fig. 10). Within all specimens, the number of subsidiary cells varies from 2—4(—6).

The stomata are nearly always on the level of the unspecialized epidermal cells, or slightly sunken, with more or less prominent outer ledges covering a part of the guard cells. In *Ruizodendron* and *Annona* p.p. we observed sunken stomata covered by thick cutinized rims.

In a number of genera, species occur with stomata on the adaxial surface. These adaxial stomata are nearly always few, sometimes their distribution is restricted to narrow zones along the main veins; their size is very variable.

Abaxially, all specimens have stomata. They are almost always regularly distributed. The size and frequency per specimen is rather constant. Within genera, the variation and overlap is considerable, but in genera with small stomata (<20 µm) the frequency is often rather high (more than 20 per mm); in genera with exclusively large stomata (>35 µm) the frequency is moderate to low (less than 15 per mm). A comparable correlation is found between the frequency of stomata and the size of unspecialized epidermal cells: genera with small epidermal cells have moderate to high stomatal frequencies; genera with large epidermal cells have a moderate to low stomatal frequency.

As the stomatal type in Annonaceae is highly constant, whereas quantitative values (size, frequency) are highly variable on the genus level, stomata can hardly be used as a taxonomic or diagnostic tool, in contrast to, for instance, the related family of Myristicaceae, where structures of the stomatal complex distinguish between genera (KOSTER & BAAS 1981). The high uniformity of stomata within Annonaceae was already suggested by the data of other authors. The occurrence of sunken stomata in a few genera (*Ruizodendron, Annona* p.p.) and of stomatal vestibules formed by prominent outer ledges (*Anaxagorea* [ROTH 1981, KOEK-NOORMAN 1984, MORAWETZ 1984]; *Tetrameranthus* p.p. [v. SETTEN & KOEK-NOORMAN 1985] is known to be variable within these genera although it can be helpful in identifying leaf material. The occurrence of adaxial stomata is often thought to be correlated with an isobilateral structure of the mesophyll. In our material, we did not find such a correlation.

Mesophyll

By far the most Annonaceae have a dorsiventral lamina. However, in many genera some species with an isobilateral structure are found. In *Bocageopsis*, *Heteropetalum*, *Onychopetalum*, *Oxandra*, *Pseudoxandra*, and *Sapranthus*, (nearly) all species are isobilateral.

Although in most studied specimens the cells of the sponge parenchyma are transversely oblong, the sponge parenchyma can vary from loose to compact, even within specimens. In some specimens of *Annona*, *Raimondia*, *Rollinia*, *Rolliniopsis*, and *Tridimeris* the individual sponge parenchyma cells are flattened parallel to the epidermis (Fig. 11). In all specimens of *Bocagea*, *Hornschuchia*, and *Trigynaea* the cells are very thin-walled and bubble-like (Fig. 12).

The palisade parenchyma is mostly arranged in 1—2(—3) layers. Exclusively one-layered palisade parenchyma is found in *Anaxagorea*, *Bocagea*, *Cremastosperma*, *Duckeanthus*, *Froesiodendron*, *Guatteriopsis*, *Oxandra*, *Pseudephedranthus*, *Reedrollinsia*, and *Tridimeris*. In *Diclinanona*, *Fusaea*, *Heteropetalum*, *Onychopetalum*, and *Xylopia*, the palisade parenchyma always consists of more than one layer. Some specimens of *Anaxagorea*, *Cremastosperma*, and *Pseudoxandra* have intermediate forms, as some cells of the one-layered palisade parenchyma are divided. Three to four layers (Fig. 13) were found in specimens of *Annona*, *Asimina*, *Cymbopetalum*, *Guatteria*, *Heteropetalum*, *Tetrameranthus*, and *Xylopia*. *Duckeanthus* is exceptional because of its strongly stained, thick-walled sponge- and palisade parenchyma. The cell walls do not light-up, when seen in polarized light.

In part of the studied specimens (of 12 genera) the palisade parenchyma seems to be compressed perpendicular to the surface of the lamina, resulting in concertina-shaped cells (Fig. 14). This might be an artefact.

Because of the variation and transitional forms, we do not attribute any taxonomic value to the number of layers of palisade parenchyma, although it can be helpful in identifying leaf material. (This seems to fit with a suggestion of JOVET-AST 1942, who attributes diagnostic value to the height of palisade parenchyma/height of sponge parenchyma ratio in two genera.)

The same can be said for the thickness of the lamina. This feature varies between 80—300 µm, except in *Annona coriacea*, where values of 600—650 µm were scored.

JOVET-AST (1942) indicates, that the thickness of the lamina in a few genera or species is constant, also when specimens of varying habitats are measured. The selection of our material does not allow us to draw conclusions regarding this point.

Oil cells and mucilageous cells

For Annonaceae, oil cells and mucilageous cells have been reported to occur in the lamina. As pointed out in a literature study of BAAS & GREGORY

(1986), both types of secretory cells occur in mutually related species of several families. Although the structure of typical oil- and mucilageous cells is different in a number of features, transitions occur (WEST 1969). Sometimes it appears difficult to indicate which type of idioblast is present, and then authors report "secretory cells". It must be emphasized here, that the taxonomic value of the occurrence of oil- and mucilage cells can only be judged when more is known about the ontogeny and possible relation between both cell types.

In this survey, we restrict ourselves to a description of the occurrence and position of these idioblasts and refer to them as oil cells.

In all specimens round to oval oil cells occur with a diameter between 25—100 µm. Although in some genera the diameter is always less than 40 µm or more than 60 µm, the large variation blurs differences between genera.

The oil cells may be „empty" or filled with yellow to brown contents. It is possible that in the case of empty cells the oil disappeared during the preparation of the slides. It is, however, remarkable that coloured contents were found in representatives of 17 genera only.

Mostly the oil cells occur in the sponge parenchyma (Fig. 6), occasionally also in the transitional zone between sponge- and palisade parenchyma. In specimens of some genera, oil cells occur also (or exclusively) in the palisade parenchyma (Figs. 11, 13). In *Asimina* and *Tetrameranthus* oil cells are lacking in the sponge parenchyma. *Hornschuchia* is the only genus where no oil cells were recorded. This may be due to the bubble-like, large oil cells of the sponge parenchyma which could easily be confused with occasionally present small-"empty" oil cells.

Comparable idioblasts, without contents, were found in or immediately below the epidermis in *Bocageopsis* p.p., *Onychopetalum*, and *Unonopsis* p.p. They seem to communicate with the open air by a narrow aperture (Fig. 15), surrounded by radially orientated epidermal cells.

In specimens of 15 genera, another type of idioblasts occurs. The cells are large, mostly angular, and for the main part filled with an amorphic substance (Fig. 16), colouring blue or yellow when stained with Safranin and Astra-blue. The amorphic substance proved to consist mainly of silica (when studied with a SEM with a linked microröntgen analytic system; Fig. 17, 18). Most often these idioblasts are found in the sponge parenchyma near the (end of the) smallest veinlets, but in *Cremastosperma* also along the larger veins. In *Cremastosperma* they occur both in sponge- and palisade parenchyma.

Although the taxonomic significance of the oil-, mucilage- and silica-containing idioblasts is uncertain, they have some diagnostic value because of their restricted occurrence and varying location in the mesophyll.

Sclereids

In about 50% of the genera sclereids occur in the lamina. However, they are rarely present in all specimens of those genera.

As pointed out by METCALFE (1979), for instance, the terminology with regard to sclerenchymatic cells, used in the literature, is confusing. He advises, as long as a uniform typology for sclerenchymatic cells is lacking, to use the terminology proposed by TSCHIRCH (1889). Following this advice, we can classify the sclereids found in the leaves of neotropical Annonaceae as brachysclereids (stone cells, frequently found in the ground tissue of petioles and primary veins), osteosclereids (poorly branched sclereids with thick, multi-layered cell walls (Fig. 19)), and astrosclereids (branched to stellate sclereids, which are mostly longer and thinner than the osteosclereids, and often connected with terminal veins). In some cases, astrosclereids occur as a continuous layer under the epidermis (Fig. 20).

Notwithstanding the high degree of variation in size, shape, and frequency of the astro- and osteosclereids found in our samples (which in some cases made us hesitate as to which type we actually saw), it seems that within genera either filiform, uni-layered, branched astrosclereids or multi-layered, often poorly branched osteosclereids occur.

Astrosclereids are found in *Anaxagorea*, *Annona*, *Desmopsis*, *Heteropetalum*, and *Tetrameranthus*; osteosclereids are the dominant type in *Cymbopetalum*, *Fusaea*, *Guatteriella*, *Guatteriopsis*, *Hornschuchia*, *Onychopetalum*, *Oxandra*, *Pseudoxandra*, *Trigynaea*, and *Unonopsis*. *Guatteria* is the only genus in which both sclereid types are a common phenomenon.

It is perhaps due to the sometimes vague demarcation line between the types of sclereids, that various authors express different opinions about the distribution of the types of sclereids over genera, and thus about their taxonomic value. According to JOVET-AST (1942) and VAN DER WIJK (1950), several sclereid types may occur within one genus. RAO & CHIN (1966) report that four out of sixteen annonaceous genera from the Singapore islands show sclereids, and that in only one species both astro- and osteosclereids occur.

Our results indicate that, with the exception of *Guatteria*, all genera can be grouped according to the presence of absence of either astro- or osteosclereids. However, as sclereids may be lacking in part of the specimens, their diagnostic value is restricted.

Perhaps it is not to be ruled out that further study will reveal differences between (groups of) species in more detail.

Crystals

Crystals in epidermal cells

Crystals occur in several types. Often, they are present as druses (Fig. 7), varying from 4—12 μm. In other genera, rhombic crystals of varying size and shape (Figs. 21, 22), or crystal sand is found. Nearly always the abaxial and adaxial crystals are of the same type, although they may vary in size.

Generally, one crystal per epidermis cell is found on the adaxial side. Abaxially, the crystal frequency is lower, but in *Bocageopsis*, *Cardiopetalum*, *Cymbopetalum*, and *Froesiodendron*, the abaxial crystals outnumber the adaxial ones. In nearly all genera specimens or species are found where crystals are lacking. In *Anaxagorea* and *Guatteriella* they are rarely present.

Small, acicular crystals are found in *Diclinanona*. Banana-shaped crystals (which are coloured when seen with polarized light) occur in the adaxial epidermis of one species of *Desmopsis*. In *Sapranthus* large, hexangular, often coloured rhombic crystals occur. Book-shaped crystals are seen in some specimens of genera, which have rhombic crystals in other species: *Annona*, *Desmopsis*, *Ephedranthus*, *Fusaea*, *Malmea*, *Oxandra*, *Ruizodendron*, *Sapranthus*, and *Stenanona*. In some species of *Ephedranthus*, *Fusaea*, *Malmea*, *Ruizodendron*, and *Sapranthus*, the rhombic crystals are coloured when seen in polarized light.

In general, either druses or rhombic crystals are found within a genus. *Annona*, *Duguetia*, and *Rollinia* are exceptional, as these genera, though in most species showing druses or crystal sand, include a few species with small or large rhombic crystals.

If druses are found in specimens of a genus, quite often other specimens without any crystals or with only some crystal sand in the epidermal cells are found. In contrast, if rhombic crystals are found in species of a genus, they are almost always present in the other specimens of that genus as well.

Reports in the literature are in agreement with our findings with only few contradictions. BEYER (1902) writes that druses are present in all cells of *Anaxagorea*. KRAMER (1969) reports "druses primarily above and below veins" in *Anaxagorea*. This was found by us in *Anaxagorea acuminata*. In all other species of *Anaxagorea* crystals are lacking. KRAMER's observation of "prisms" in *Diclinanona* was not confirmed by us (see above).

Crystals in the mesophyll

In the sponge- and palisade parenchyma, crystals occur nearly exclusively as druses. Only in some specimens of *Duguetia* acicular crystals were found; in species of *Cymbopetalum* coloured rhombic crystals occur.

In *Cardiopetalum*, *Cymbopetalum*, *Froesiodendron*, and *Porcelia*, the druses are only found in the sponge parenchyma. In all other genera, they are found either in the sponge parenchyma, the palisade parenchyma, or in both. This variation seems to be unrelated to the generic limits.

All publications dealing with crystals in annonaceous leaves indicate that the occurrence of special types of crystals, in particular in the epidermal cells, has a strong taxonomic or diagnostic value. VAN DER WIJK (1950) and JOVET-AST (1942) arrange genera according to the crystal type. These groupings, however, are not similar to the classification based on morphological features (FRIES 1959) or palynological data (WALKER 1971). Within genera, however, the crystal types are very constant and have proven to be a reliable diagnostic feature.

Primary vein

Abaxially, the primary vein is always raised. Adaxially, it may be raised, flat, or concave. Although this feature seems to be fairly constant within species, there are only few genera to which this feature applies as a whole. With some caution we can say that in the following genera most species show raised primary veins on the adaxial side: *Bocagea, Bocageopsis, Cardiopetalum, Cremastosperma, Cymbopetalum, Duckeanthus, Ephedranthus, Froesiodendron, Hornschuchia, Malmea, Onychopetalum, Oxandra, Porcelia, Pseudephedranthus, Pseudoxandra, Ruizodendon, Trigynaea,* and *Unonopsis* (Fig. 23).

The vascular system mostly consists of one continuous or interrupted arc of phloem which abaxially borders the xylem body. Both phloem and xylem are surrounded by a sheath of sclerenchyma (Fig. 23). This type of vascular system is similar to the "*Uvaria*"-type of JOVET-AST (1942). She indicates that also in Asiatic taxa this type is the most frequently occurring vascular structure.

In specimens of *Anaxagorea, Annona,* and *Rollinia,* we found structures which can be thought to be derived from the simple type described above: the phloem tissue has extended along the adaxial side of the xylem body, in *Anaxagorea* also in the centre (Fig. 24; cf. the description of the primary vein of *Anaxagorea acuminata* given by JOVET-AST 1942 and KOEK-NOORMAN 1984).

The second main type of a complex vascular structure does not show adaxial phloem, but additional sclerenchyma and phloem tissues are found as islands or zones penetrating in the xylem body. The most simple form of this type is found in specimens of *Guatteria, Guatteriella,* and *Guatteriopsis.* More complex mixtures of xylem, phloem and sclerenchyma are found in other specimens of the same three genera, and in *Bocageopsis, Fusaea, Heteropetalum, Onychopetalum, Ruizodendron,* and *Unonopsis* (Fig. 25). The most complex structures are found in *Tetrameranthus* (Fig. 26). JOVET-AST describes comparable structures for *Melodorum,* and indicates that this type also occurs in *Bocageopsis.*

Our results confirm the generally accepted idea, that the histology of the primary vein is rather constant on the generic level, and thus a reliable diagnostic tool.

The ground tissue of the primary veins consists of parenchyma, changing in collenchyma towards the epidermis. In this transitional zone, in particular at the abaxial side, one may find a zone of flattened parenchyma cells in *Asimina, Cremastosperma, Desmopsis, Raimondia, Sapranthus, Stenanona,* and *Tetrameranthus.*

Like in the mesophyll, most genera have species with oil cells and druses in the primary veins and also species without such idioblasts. Oil cells are completely lacking in *Bocagea* and *Trigynaea.* Druses are (nearly) always lacking in

Bocageopsis, *Duguetia*, *Fusaea*, *Guatteriella*, *Guatteriopsis*, and *Heteropetalum*. Because of the varying occurrence in the other genera the absence of these structures has no taxonomic or diagnostic value. Isolated or clustered stone cells are found in all genera. In *Heteropetalum* and *Guatteriopsis* they are arranged in a continuous layer under the abaxial epidermis.

Terminal veins

The smallest veins, situated in the sponge parenchyma, are accompanied by a sclerenchymatic sheath. This sheath consists of two caps or a narrow ring (Fig. 12). Sheath extensions connecting the vascular bundle with the palisade parenchyma are often found. Sheath extensions connecting both abaxial and adaxial epidermis are found in *Ephedranthus*, *Ruizodendron*, and *Xylopia* (Fig. 13); and in part of the specimens of *Annona*, *Asimina*, *Duguetia*, *Rollinia*, and *Rolliniopsis*. In these last five genera the parts of the extension which are nearest to the epidermis are often collenchymatic instead of sclerenchymatic.

Beyer (1902) already considered sheath-extensions as a useful feature: in some cases on the generic level, but sometimes as a feature distinguishing between species.

The petiole

The vascular system of the petiole in Annonaceae shows less variation than that of the primary vein. This fact, together with the fact that in many specimens the small bundles in the petiole are difficult to distinguish from the ground tissue, makes it difficult to use the structure of the vascular system in the petiole as a separate taxonomic criterium.

In genera with a simple vascular system in the primary vein (Fig. 23), the vascular bundles in the basal part of the petiole are nearly always arranged in a single arc. In the petioles of the genera in which a more complex structure of the primary veins is found, the vascular bundles of the petiole are arranged in a circle, or in two or more concentric arcs. The individual bundles are collateral, except in *Duguetia*, where the xylem is included in a ring of phloem.

Jovet-Ast (1942) describes a comparable variation and correlation between structure of primary veins and petioles in Indo-Chinese genera.

The ground tissue is parenchymatic to collenchymatic and includes many stone cells. Near these stone cells, large prismatic crystals occur in specimens of *Annona*, *Hornschuchia*, *Malmea*, *Oxandra*, *Rollinia*, *Ruizodendron*, and *Unonopsis*. Druses are found in varying quantities in all genera, except in *Diclinanona* and *Fusaea*, where rhombic crystals occur. Oil cells are mostly present, varying from few to many, but they are lacking of very scanty in the specimens of *Anaxagorea*, *Heteropetalum*, and *Trigynaea*.

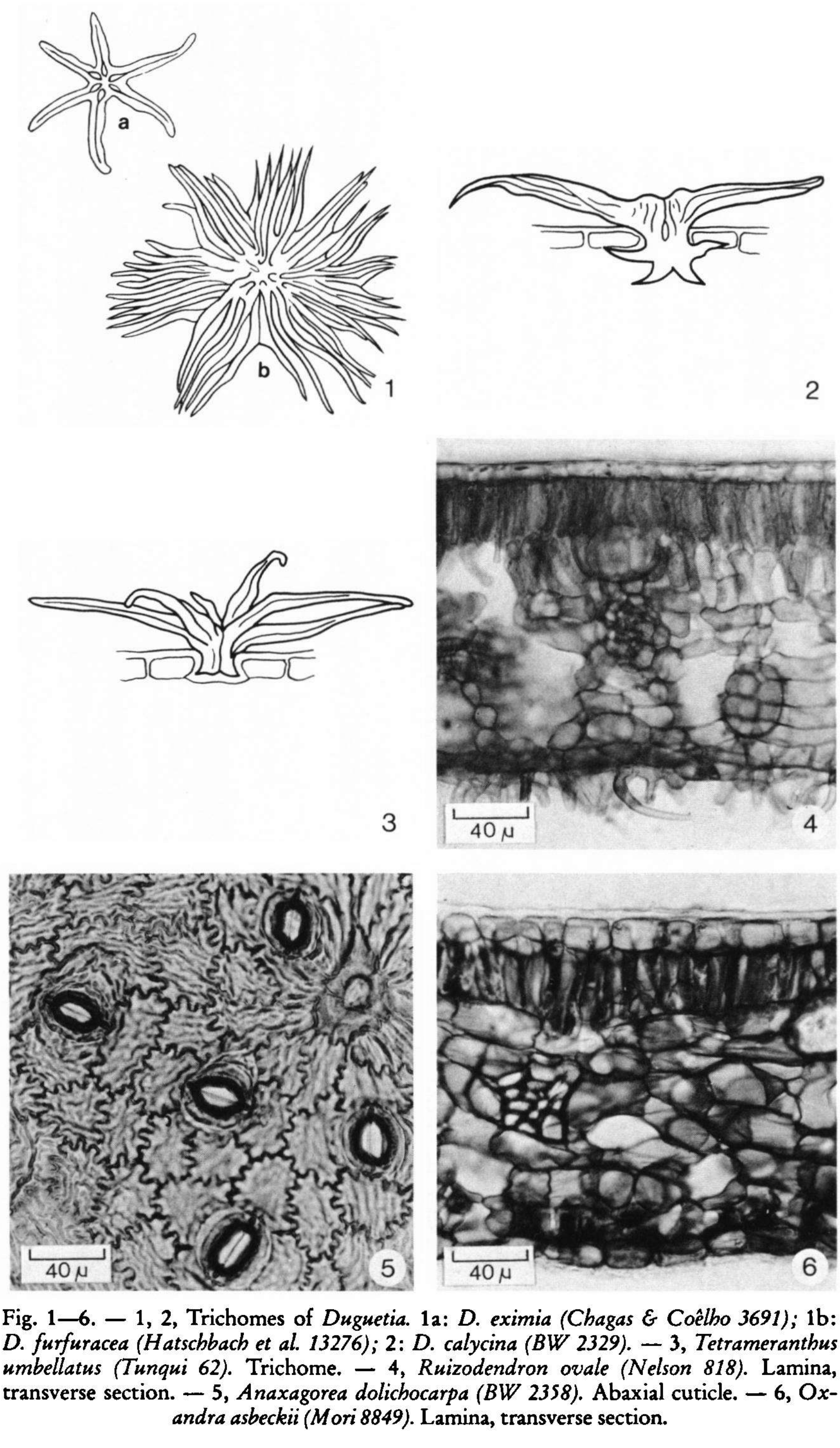


Fig. 1—6. — 1, 2, Trichomes of *Duguetia.* 1a: *D. eximia (Chagas & Coêlho 3691);* 1b: *D. furfuracea (Hatschbach et al. 13276);* 2: *D. calycina (BW 2329).* — 3, *Tetrameranthus umbellatus (Tunqui 62).* Trichome. — 4, *Ruizodendron ovale (Nelson 818).* Lamina, transverse section. — 5, *Anaxagorea dolichocarpa (BW 2358).* Abaxial cuticle. — 6, *Oxandra asbeckii (Mori 8849).* Lamina, transverse section.

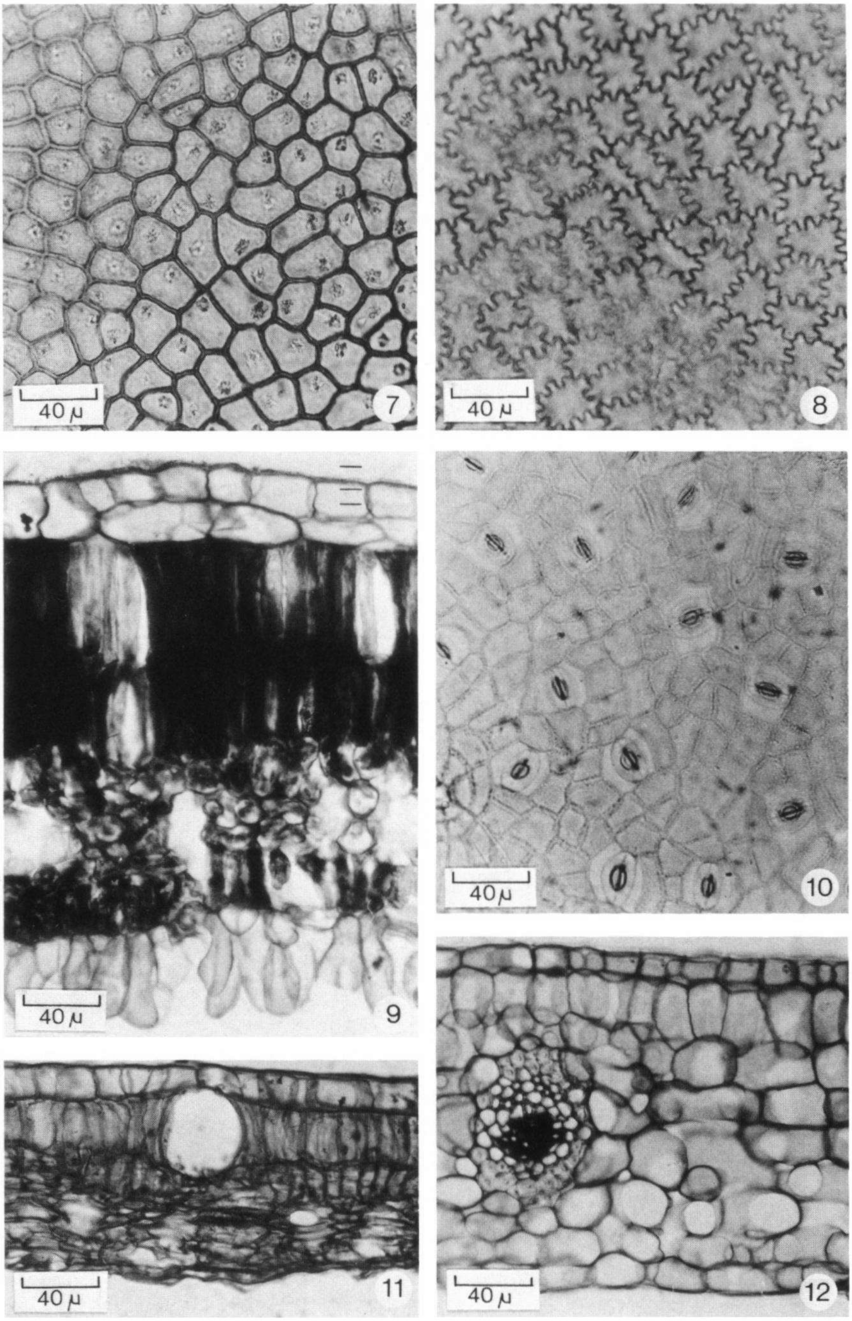
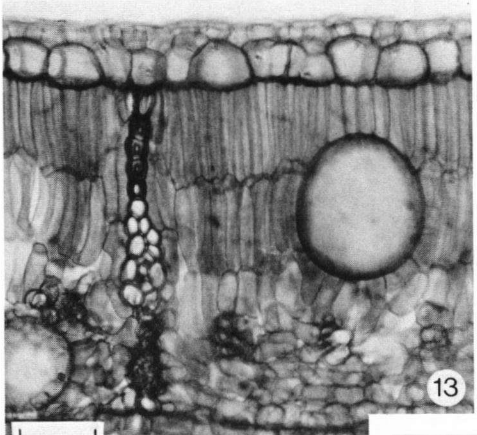
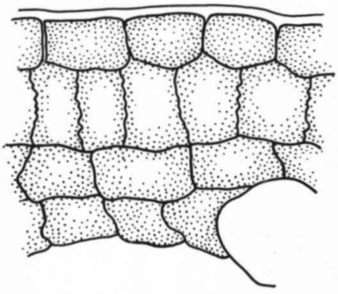
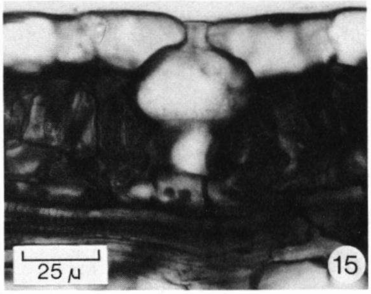
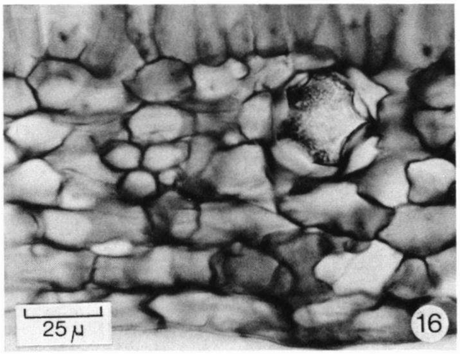


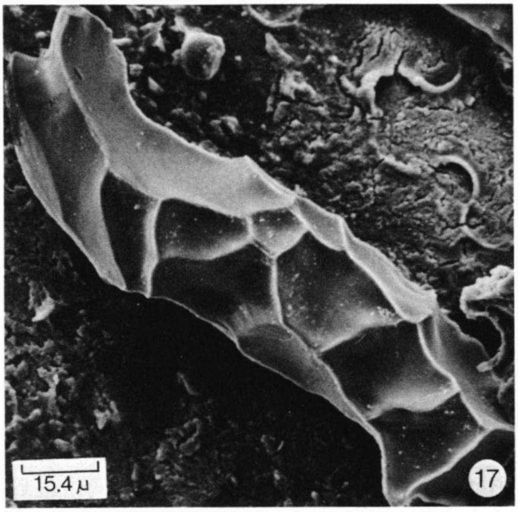
Fig. 7—12. — 7, *Oxandra asbeckii (Mori 8849).* Adaxial cuticle. — 8, *Anaxagorea dolichocarpa (BW 2358).* Adaxial cuticle. — 9, *Annona cornifolia (Irwin et al. 25241).* Lamina, transverse section. — 10, *Bocagea viridis (de Saint-Hilaire 119).* Abaxial cuticle. — 11, *Rollinia mucosa (Asplund 14594).* Lamina, transverse section. — 12, *Hornschuchia bryotrophe (Mori et al. 9368).* Lamina, transverse section.











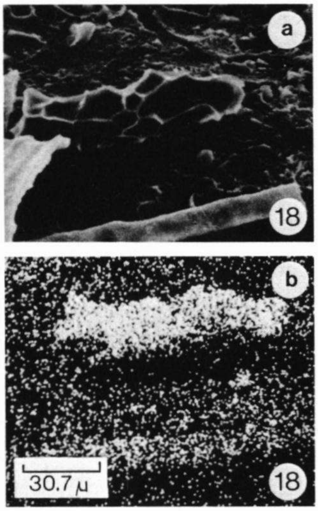


Fig. 13—18. — 13, *Xylopia aromatica (Nee 7446)*. Lamina, transverse section. — 14, *Trigynaea caudata (Wessels Boer 1595)*. Lamina, transverse section, with concertina-shaped cells in the palisade parenchyma. — 15, *Unonopsis* cf. *glaucopetala (Lanjouw & Lindeman 2503)*. Lamina, transverse section. — 16, *Guatteria trichoclonia (Schunke V. 7427)*. Sponge parenchyma, transverse section. — 17, 18, *Guatteria boliviana (Krukoff 11089)*. 17, 18a: SEM-photographs of silica body; 18b: as 18a, but seen with a SEM-linked microröntgen analytic system.

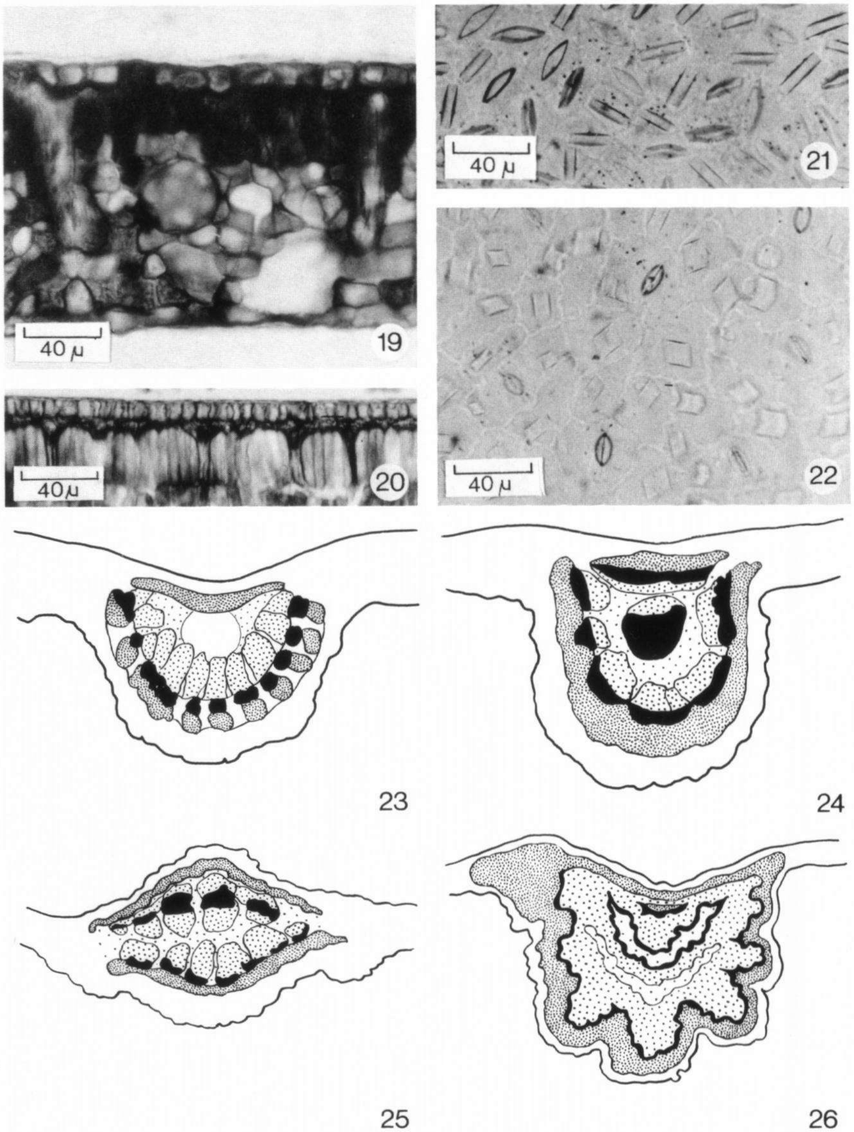


Fig. 19—26. — 19, *Fusaea longifolia (Nascimento 435)*. Lamina, transverse section with osteosclereids. — 20, *Heteropetalum spruceanum (Spruce 3184)*. Astrosclereids forming a continuous layer under the epidermis. — 21, 22, *Desmopsis stenopetala (Schipp 698)*. Epidermis with rhombic crystals; 21: adaxial, 22: abaxial. — 23—26, Topographical drawings of transverse sections of primary veins. 23: *Annona montana (Froes 11532)*. 24: *Anaxagorea dolichocarpa (BW 2358)*. 25: *Unonopsis* cf. *glaucopetala (Lanjouw & Lindeman 2503)*. 26. *Tetrameranthus umbellatus (Tunqui 62)*.

(▨ = sclerenchyma; ■ = phloem; ▦ = xylem, ⬚ = parenchymatic tissue)

Discussion

a) Distribution of leafanatomical characters over the neotropical genera

Most leafanatomical characters vary within rather narrow limits within Annonaceae. Our own data combined with the results of other papers give us the impression that the Annonaceae form a rather homogeneous group of plants.

Yet, we found some qualitative or quantitative variation for nearly all features. The distribution of the character states over the neotropical genera is such, that quite often exceptions on the "rules" are found, either in individual specimens or in species. In some cases such exceptions were found in our material. For other genera, discrepancies with data from the literature were found.

A survey of a selection of the leafanatomical characters is given in Table 2 and in the synoptical key. Here we will confine ourselves to a discussion of general trends as found for genera. A discussion of exceptions found in individual specimens, as well as considerations of the value of leafanatomical characters on the species level, has to wait for generic revisions to come.

Following hereafter, we give some lists of character states according to their degree of constancy within the studied genera.

Characters restricted to one or few genera

— Type of trichomes
stellate-peltate scales: *Duguetia;*
stellate tufts: *Tetrameranthus;*
trichomes with clavate top cells: *Anaxagorea;*
short, appressed trichomes on papillate epidermis: *Bocageopsis, Ephedranthus, Onychopetalum, Ruizodendron;*
— Type of primary vein
most complex: *Tetrameranthus;*
phloem and sclerenchyma penetrating into the xylem tissue but absent on its adaxial side: *Bocageopsis, Fusaea, Guatteria, Guatteriella, Guatteriopsis, Heteropetalum, Onychopetalum, Ruizodendron, Unonopsis.*

Characters present in all species in at least some genera, and also found in a part of the species of other genera (only those genera are printed in italics)

— Type of crystals in epidermal cells
acicular crystals: Diclinanona;
rhombic or book-shaped crystals: *Annona,* Desmopsis, Duckeanthus, *Duguetia,* Ephedranthus, Fusaea, Malmea, Pseudephedranthus, Reedrollinsia, *Rollinia,* Ruizodendron, Sapranthus, Stenanona, Tridimeris;

— Presence of a bundle sheath extension up to the epidermis
Annona, Asimina, Duguetia, Ephedranthus, *Rollinia, Rolliniopsis,* Ruizodendron, Xylopia;
— Presence of idioblasts in the epidermis
Onychopetalum, *Bocageopsis, Unonopsis;*
— Primary vein raised adaxially
Asimina, Bocagea, Bocageopsis, Cardiopetalum, *Cremastosperma,* Cymbopetalum, Duckeanthus, *Ephedranthus,* Froesiodendron, *Hornschuchia, Malmea,* Onychopetalum, *Oxandra, Porcelia,* Pseudephedranthus, Pseudoxandra, Ruizodendron, *Sapranthus, Trigynaea,* Unonopsis;
— Type of sclereids in the mesophyll
astrosclereids: *Anaxagorea, Annona, Desmopsis, Guatteria,* Heteropetalum, Tetrameranthus;
osteosclereids: *Cymbopetalum, Fusaea, Guatteria,* Guatteriella, Guatteriopsis, *Hornschuchia,* Onychopetalum, *Oxandra,* Pseudoxandra, Trigynaea, Unonopsis;
(Guatteria is the only genus where astrosclereids as well as osteosclereids occur, though not both in the same species.)
— Presence of an adaxial indument
Annona, Asimina, Cymbopetalum, Duguetia, Froesiodendron, Guatteria, Porcelia, Raimondia, Rollinia, Rolliniopsis, Ruizodendron, Sapranthus, Stenanona, *Tetrameranthus, Unonopsis, Xylopia;*
— Presence of yellow to brown contents in the oil cells
Bocageopsis, *Cymbopetalum, Desmopsis, Diclinanona,* Duckeanthus, *Ephedranthus, Froesiodendron, Malmea, Onychopetalum, Oxandra,* Porcelia, Pseudephedranthus, Reedrollinsia, Ruizodendron, *Sapranthus, Stenanona, Unonopsis;*
— Presence of angular idioblasts with amorphic silica contents
Bocageopsis, Cremastosperma, *Duguetia, Ephedranthus, Guatteria,* Guatteriella, *Guatteriopsis, Heteropetalum, Malmea, Onychopetalum, Oxandra, Pseudoxandra,* Reedrollinsia, *Unonopsis.*

Characters occurring in a restricted number of genera, though not in all species

— Adaxial epidermis more-layered
Asimina, Annona, Guatteria, Raimondia, Tetrameranthus, Xylopia;
— Type of primary vein: phloem tissue surrounding but not penetrating the xylem tissue
Anaxagorea, Annona, Rollinia;
— Palisade parenchyma 3(—4)-layered
Annona, Asimina, Cymbopetalum, Guatteria, Heteropetalum, Tetrameranthus, Xylopia;
— A continuous layer of sclerenchyma cells under the abaxial epidermis of the primary vein
Guatteriopsis, Heteropetalum;

As far as we know now, the variation of all other characters or character states is independent of the generic limits. The question, whether these other characters may have diagnostic or taxonomic value on the species level or not, falls beyond the scope of this paper.

b) Phenetic similarity in leaf anatomy and the classification of genera

Our observations with regard to similarities and differences in leaf anatomy between annonaceous genera are hindered by two factors, which — for the time being — can not be avoided. First: as long as no good recent monographs of genera are available, we remain in doubt about the correct identification of some of our specimens or about the correct place of certain species in genera to which they are now assigned. Secondly: our material represents only a small percentage of the tremendous amount of available (herbarium) specimens. Although we have aimed at a representative sampling, we are aware that many species (even sections of genera) are not included in this study.

Keeping these two restrictions in mind, we will comment on the phenetic similarities and differences, following the classification of FRIES (1959) and commenting WALKER's classification based on pollen morphology (1971). Their grouping of genera is given in Table 1.

The *Uvaria* -group has rhombic crystals in the epidermal cells (which may sometimes be very slender, tending to the acicular type); the oil cells often have coloured contents. This combination of features is elsewhere only found in *Ephedranthus* and *Ruizodendron* (see under *Asimina*-group).

The *Guatteria* -group is characterized by the presence of a complex structure of the primary vein, a frequent occurrence of angular silicabodies, and (astro- and osteo-)sclereids; adaxial stomata occur, except in *Heteropetalum.*

A comparable structure of the primary vein and the presence of silica bodies are also found in the *Unonopsis*- group. Here, however, idioblastic (oil) cells occur in the epidermis. In *Bocageopsis* and *Onychopetalum* the epidermis is papillate, with short trichomes. In this feature they resemble *Ephedranthus* and *Ruizodendron* of the *Asimina*-group.

The genera of the *Asimina*-group are rather heterogeneous. The papillate epidermis in *Ephedranthus* and *Ruizodendron* reminds of the *Unonopsis*-group. The combination of osteosclereids, silicabodies and adaxial stomata in *Oxandra* and *Pseudoxandra* reminds of the *Guatteria*-group. *Asimina, Cremastosperma, Pseudephedranthus* and *Tridimeris* can not easily be grouped with one of those two pairs. WALKER (1971) suggests for *Asimina* an isolated position; the other genera of FRIES' *Asimina*-group are combined by him in one group together with *Malmea* and the three genera of the *Unonopsis*-group. Leafanatomically, this does not result in a more satisfactory classification for *Cremastosperma, Oxandra, Pseudoxandra,* and *Pseudephedranthus.* The combination of *Ephedranthus* and *Ruizodendron* together with *Malmea* and the *Unonopsis*-group can be confirmed.

Table 1. List of studied neotropical genera. The sequence is alphabetical with the exception of the genera 34—38. Abbreviations in the second column refer to the groups of genera as recognized by FRIES. The third column refers to the classification given by WALKER.

column I	II	III	column I	II	III
1. *Anaxagorea*	Xy	— Fu	20. *Onychopetalum*	Un	— Ma
2. *Annona*	An	— An	21. *Oxandra*	As	— Ma
3. *Asimina*	As	— As	22. *Porcelia*	Tr	— Cy
4. *Bocageopsis*	Un	— Ma	23. *Pseudoxandra*	As	— Ma
5. *Cardiopetalum*	Tr	— Cy	24. *Raimondia*	An	— An
6. *Cremastosperma*	As	— Ma	25. *Rollinia*	An	— An
7. *Cymbopetalum*	Tr	— Cy	26. *Rolliniopsis*	An	— An
8. *Desmopsis*	Uv	— Uv	27. *Ruizodendron*	As	— Ma
9. *Diclinanona*	Xy	— He	28. *Sapranthus*	Uv	— Uv
10. *Duguetia*	Du	— Uv	29. *Stenanona*	Uv	— Uv
11. *Ephedranthus*	As	— Ma	30. *Tetrameranthus*	Te	— Uv
12. *Froesiodendron*	Tr	— Cy?	31. *Trigynaea*	Tr	— Cy
13. *Fusaea*	Du	— Fu	32. *Unonopsis*	Un	— Ma
14. *Guatteria*	Gu	— Gu	33. *Xylopia*	Xy	— Fu
15. *Guatteriella*	Gu	— Gu?	34. *Bocagea*	Tr	— ?
16. *Guatteriopsis*	Gu	— Gu	35. *Duckeanthus*	Du	— Fu
17. *Heteropetalum*	Gu	— Gu	36. *Pseudephedranthus*	As	— Ma
18. *Hornschuchia*	Tr	— Cy	37. *Reedrollinsia*	Uv	— Uv
19. *Malmea*	Du	— Ma	38. *Tridimeris*	As	— ?

column II:
An = *Annona*-group
As = *Asimina*-group
Du = *Duguetia*-group
Gu = *Guatteria*-group
Tr = *Trigynaea*-group
Un = *Unonopsis*-group
Uv = *Uvaria*-group
Xy = *Xylopia*-group
Te = tribe Tetramerantheae

column III:
An = *Annona*-tribe
As = *Asimina*-tribe
Cy = *Cymbopetalum*-tribe
Gu = *Guatteria*-tribe
He = *Hexalobus*-tribe
Ma = *Malmea*-tribe
Uv = *Uvaria*-tribe
Fu = *Fusaea*-subfamily

Explanations to Table 2.
+: present; ±: present in part of the specimens;
a: type of trichomes; 1: peltate to stellate scales; 2: tufts of simple trichomes; 3: simple to branched trichomes with blunt top cells; 4: trichomes short with transitions to papillae; 5: trichomes simple, 100—1000 μm with acute top cell.
b: indument present; 1: adaxial; 2: abaxial.
c: adaxial epidermis more-layered.
d: adaxial stomata.
e: lamina isobilateral.
f: cells of sponge parenchyma; 1: bubble-like; 2: elongated parallel to the epidermis.
g: palisade parenchyma 3—4-layered.
h: cells of palisade parenchyma concertina-shaped.
i: oil cells; s: in sponge parenchyma (and in the transitional zone between sponge- and palisade parenchyma); p: in palisade parenchyma (and in the transitional zone between sponge- and palisade parenchyma); e: in or immediately below epidermis.

Table 2. The occurrence of some leafanatomical characters in neotropical Annonaceae.

	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p
1. *Anaxagorea*	3	2						±	s,p		1			2		
2. *Annona*	2,5	1,2	±		±	2	±	±	s,p		1	4		2	±	
3. *Asimina*	5	1,2	±	±			±	±	p				±		±	
4. *Bocageopsis*	4	2			±				s,e	c,si	2		+	1		
5. *Cardiopetalum*	—	—		±	±			+	s				+			
6. *Cremastosperma*	—	—							s	si	2		±			
7. *Cymbopetalum*	5	1,2		±			±	±	s,p	c	1,2		+			
8. *Desmopsis*	5	2							s,p	c	1	1,4				
9. *Diclinanona*	5	2			±				s,p	c		2				
10. *Duguetia*	1	1,2							s,p	si		2,4			±	
11. *Ephedranthus*	4	2			±				s	c,si	1	4	±		+	
12. *Froesiodendron*	5	1,2		±				+	s,p	c			+			
13. *Fusaea*	5	2							s		2	4		1		
14. *Guatteria*	5	1,2	±	±	±		±		s	si	1,2	2		1		
15. *Guatteriella*	5	2		+					s	si	1,2			1		
16. *Guatteriopsis*	5	2		±					s	si	1,2			1		±
17. *Heteropetalum*	5	2			±		±		s,p	si	1			1		+
18. *Hornschuchia*	5	2				1		±	—		2		±			
19. *Malmea*	5	—			±			±	s	c,si		4	±			
20. *Onychopetalum*	4	2			+				s,e	c,si	2		+	1		
21. *Oxandra*	5	2		±	+				s	c,si	2		±			
22. *Porcelia*	—	—		±	±			±	s	c			+			
23. *Pseudoxandra*	5	2		±	±				s,p	si	2		+			
24. *Raimondia*	5	1,2	±			2		+	s							
25. *Rollinia*	2,5	1,2				2		±	s,p			4		2	±	
26. *Rolliniopsis*	5	1,2			±	2			s						±	
27. *Ruizodendron*	4	1,2							s	c		4	+	1	+	
28. *Sapranthus*	5	1,2			±				s	c	2	3,4			±	
29. *Stenanona*	5	1,2			±				s	c		4				
30. *Tetrameranthus*	2	1,2	±				±		p		1			1		
31. *Trigynaea*	5	2				1		±	s,p		1,2		±			
32. *Unonopsis*	5	1,2							s,e	c,si	2		+	1		
33. *Xylopia*	5	1,2	±	±			±		s							+
34. *Bocagea*	5	2				1			s				+			
35. *Duckeanthus*	—	—							s			4	+			
36. *Pseudephedranthus*	—	—							s	c		4	+			
37. *Reedrollinsia*	5	2							s	c		4				
38. *Tridimeris*	—	—				2			s			4				

j: idioblasts; c: with coloured oil; si: with silica bodies.
k: sclereids; 1: astrosclereids; 2: osteosclereids.
l: crystals; 1: banana-shaped; 2: acicular; 3: large, hexangular; 4: rhombic; no indication: druses or absent.
m: primary vein adaxially raised.
n: histology of primary vein; 1: phloem and/or sclerenchyma intruding the xylem body; 2: phloem surrounding the xylem body (abaxially and adaxially), sometimes also intruding the xylem body.
o: sheath extensions of small veins reaching up to the epidermis.
p: a continuous sclerenchyma layer at the abaxial side of the primary vein.

The *Trigynaea*-group is also heterogeneous in its leaf anatomy. *Bocagea*, *Trigynaea* and *Hornschuchia* are recognizable by the thin-walled, bubble-like, sponge parenchyma (not found anywhere else within the studied Annonaceae). In the slides of *Cymbopetalum*, *Froesiodendron* and *Porcelia* we recorded adaxial stomata and coloured contents in the oil cells. These genera are similar in several other aspects as well. *Cardiopetalum* does not fit in one of these two subgroups; its structure seems to be intermediate.

All seven genera of the *Trigynaea*-group show the phenomenon of "concertina-shaped" cells in the palisade parenchyma. Even when this phenomenon should prove to be an artefact, it points towards a comparable cell wall structure in this group.

Within the two large genera *Annona* and *Rollinia* of the *Annona*-group, we found a wide variation in many features. Remarkable in both *Annona* p.p. and *Rollinia* p.p. is the presence of complex vascular bundles in the primary vein with adaxial phloem- and sclerenchyma layers (like in *Anaxagorea*) and the occurrence of sheath extensions (like in the *Asimina*-group p.p. and in *Xylopia*). Due to the high variability in *Annona* and *Rollinia*, the genera *Raimondia* and *Rolliniopsis* can not be separated.

As for the *Duguetia*-group: the samples of *Malmea* are comparable with some representatives of the *Asimina*-group. *Fusaea* shows some features which are also found in the *Guatteria*- and *Unonopsis*-group. *Duguetia* can easily be recognized by its scale-like trichomes and does not show a close resemblance with other genera of FRIES' *Duguetia*-group. *Duckeanthus* comes closest to *Malmea*.

WALKER accomodates *Duguetia* in one group with *Tetrameranthus*, *Desmopsis*, *Sapranthus* and *Stenanona*. The leaf anatomy does not suggest such a combination of genera. Neither is his grouping of *Fusaea* with *Anaxagorea* and *Xylopia* confirmed.

Anaxagorea and *Tetrameranthus* are characterized each by an unique trichome-type. At first view, their other leafanatomical characters do not reveal a close resemblance with other genera. In the case of *Tetrameranthus*, this fits with the isolated position in an own tribe (FRIES 1959). *Anaxagorea* is clearly deviating from all other Annonaceae by the structure of its monocarps (see, for instance, MAAS & WESTRA 1984). Nevertheless, both FRIES and WALKER accommodate *Anaxagorea* in one group with some other genera (FRIES: *Xylopia*-group with a.o. *Diclinanona* and *Xylopia*; WALKER: *Fusaea*-subfamily with a.o. *Duckeanthus*, *Fusaea*, and *Xylopia*). The leafanatomical phenology does not support either of those classifications.

From the foregoing it will be evident, that the leaf anatomy does not support FRIES' or WALKER's grouping of genera in all aspects. On the other hand, it does not seem possible to present an alternative, all-encompassing classification on the base of our present knowledge of leafanatomical features and their distribution within Annonaceae.

A report on further analyses of our data falls beyond the scope of this preliminary survey of leafanatomical characters in neotropical Annonaceae. We hope to return with a cladistic approach in another paper.

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List of material

All cited material is located in U, unless indicated otherwise.

Anaxagorea

A. acuminata (Dunal) A.DC.: *Steyermark & Lorreno 105877.*
A. dolichocarpa Sprague & Sandw.: *BW 2358; Maas & Tawjoeran 3179.*
A. phaeocarpa Mart.: *Lleras et al., P17415; Prance et al. 24259.*
A. prinoides (Dunal) A.DC.: *de Granville B4529; Prance & Pennington 1925.*
A. silvatica R.E. Fr.: *Mexia 4696, 5053.*

Annona

A. ambotay Aubl.: *Krukoff 5294; Smith 2542.*
A. aurantiaca Barb. Rodr.: *Hatschbach et al. 36071.*
A. cherimola Mill.: *van Rooden 192, s.n.; Yuncker et al. 5555.*
A. coriacea Mart.: *Irwin et al. 30970, 32466.*
A. cornifolia Mart.: *Irwin et al. 25241.*
A. crotonifolia Mart.: *Irwin & Soderstrom 6949.*
A. echinata Dunal: *Lindeman, Mennega et al. 222.*
A. foetida Mart.: *de Granville 598; Schulz 8168.*
A. glabra L.: *Lanjouw & Lindeman 1237; Lindeman 6640.*
A. haematantha Miq.: *van Donselaar 3804.*
A. hypoglauca Mart.: *Jimenez-Saa 1537; Prance et al. 13376.*
A. jahnii Saff.: *Breteler 3895.*
A. montana Macfad: *Fróes 11532; Krukoff 5652.*

A. muricata L.: *Gentry et al. 22198; Lanjouw 129.*
A. phaeoclados Mart.: *Hassler 8361.*
A. reticulata L.: *Opler 690.*
A. sericea Dunal: *Kramer & Hekking 2528; Oldenburger et al. 1148; Prance et al. 2673.*
A. squamosa L.: *Stoffers 3431.*
A. spec.: *Gentry & Troth 24768.*

Asimina (*Deeringothamnus* included)
A. longifolia Kral: *Genelle & Fleming 2052.*
A. parviflora (Michaux) Dunal: *Bozeman & Logue 9179.*
A. pulchella Small: *Small et al. 10925.*
A. tetramera Small: *Small s.n.*
A. triloba (L.) Dunal: *Bartholomew Ra-5; Hekking 1617; Kramer 521.*

Bocagea
B. viridis St. Hil.: *de Saint-Hilaire 119* (P).

Bocageopsis
B. canescens (Spruce) R.E. Fr.: *Prance et al. 5049.*
B. mattogrossensis (R.E.Fr.) R.E. Fr.: *Dziewa 18; Prance et al. 19240.*
B. multiflora (Mart.) R.E. Fr.: *Maas & Tawjoeran, LBB 10736; Prance et al. 10812, 22714.*

Cardiopetalum
C. calophyllum Schlechtend.: *Hatschbach & Ramamoorthy 38194; Irwin et al. 31731; Santos et al. 60.*

Cremastosperma
C. cauliflorum R.E. Fr.: *Prance et al. 23783.*
C. leiophyllum (Diels) R.E. Fr.: *Krukoff 10556.*
C. microcarpum R.E. Fr.: *Krukoff 4975.*
C. pedunculatum (Diels) R.E. Fr.: *Prance et al. 7885.*

Cymbopetalum
C. baillonii R.E. Fr.: *Calzada 342.*
C. brasiliense (Vell. Conc.) Benth.: *BW 2567; Lindeman, Stoffers et al. 343; Schulz 8591; Schunke V. 9592.*
C. odoratissimum Barb. Rodr.: *Krukoff 4646.*
C. stenophyllum J.D. Smith: *Hinton 15893.*

Desmopsis
D. bibracteata (Robinson) Saff.: *Shimek & Smith 232* (F).

D. galeottiana (Baill.) Saff.: *Liebmann 152.5* (C), *152.6* (L).
D. lanceolata Lundell: *Matuda 6145* (MICH).
D. maxonii Saff.: *Standley 36834* (US).
D. neglecta (A. Rich.) R.E. Fr.: *Ekman 17499* (S).
D. panamensis (Robinson) Saff.: *Gentry 6294* (MO).
D. stenopetala (J.D. Smith) R.E. Fr.: *Schipp 698* (S); *Steyermark 45573* (F).
D. spec. nov.: *Cedillo & Calzada 7* (F); *Sousa 3051* (MEXU).

Diclinanona

D. calycina (Diels) R.E. Fr.: *Berry 2194; Krukoff 8346.*
D. spec.: *Silva & Souza 2552.*

Duckeanthus

D. grandiflorus R.E. Fr.: *Prance et al. 15696.*

Duguetia

D. asterotricha (Diels) R.E. Fr.: *Campbell et al. P21255.*
D. calycina Benoist: *BW 2329, 3130; Lindeman 6414.*
D. cauliflora R.E. Fr.: *Lindeman 6991.*
D. eximia Diels: *Chagas & Coêlho 3691.*
D. flagellaris Huber: *Plowman & Schunke V. 11477.*
D. friesii Jansen-Jacobs: *Daniëls & Jonker 1159.*
D. furfuracea (St. Hil.) Benth. & Hook. f.: *Hatschbach et al. 13276; Mori et al. 9437.*
D. lanceolata St. Hil.: *Reitz & Klein 3044.*
D. neglecta Sandw.: *Maas & Tawjoeran, LBB 10791.*
D. pycnastera Sandw.: *Florschütz & Maas 3091; Lindeman, Stoffers et al. 575.*

Ephedranthus

E. amazonicus R.E. Fr.: *Prance et al. 18787.*
E. guianensis R.E. Fr.: *Irwin et al. 55720; Maas & Tawjoeran, LBB 11029; Schulz 8568.*
E. parviflorus S. Moore: *Krukoff 1597.*

Froesiodendron

F. amazonicum R.E. Fr.: *Gentry et al. 25887; Schulz 7396.*
F. surinamense (R.E. Fr.) R.E. Fr.: *Cid et al. 1925; Lindeman 6947.*
F. spec.: *Lleras et al., P17155.*

Fusaea

F. decurrens R.E. Fr.: *Schultes & Cabrera 16039.*
F. longifolia (Aubl.) Saff.: *Hekking 1198, Lindeman 6957; Nascimento 435.*
F. peruviana R.E. Fr.: *Huashikat 880.*

Guatteria

G. australis St. Hil.: *Reitz & Klein 1408.*
G. boliviana H. Winkler: *Krukoff 11089, 11108.*
G. buchtienii R.E. Fr.: *Krukoff 11027.*
G. chrysopetala (Steud.) Miq.: *Albuquerque L. et al. 10, 17; de Granville 4322, B4561; Hekking 1203; Irwin et al. 54863; Lindeman 6809; Maas et al. 2181; Schulz 8250.*
G. discolor R.E. Fr.: *Krukoff 7047.*
G. foliosa Benth.: *Prance & Berg 17959.*
G. cf. *glauca* Ruiz & Pavón: *Ellenberg 2459.*
G. gracilipes R.E. Fr.: *Lindeman, Stoffers et al. 580.*
G. kuhlmannii R.E. Fr.: *Prance et al. 2277.*
G. maypurensis Kunth: *Prance et al. 3504.*
G. megalophylla Diels: *Prance et al. 25643.*
G. nigrescens Mart.: *Maas & Martinelli 3222.*
G. olivacea R.E. Fr.: *Prance & Pennington 23035.*
G. oliviformis J.D. Smith: *J. & K. Utley 2608.*
G. scandens Ducke: *van Donselaar 2696; Pulle 107.*
G. schomburgkiana Mart.: *BW 3650, 6409.*
G. trichoclonia R .E. Fr.: *Schunke V. 6440, 7427.*
G. villosissima St. Hil.: *Irwin et al. 20165; Mexía 5277.*

Guatteriella

G. tomentosa R.E. Fr.: *Krukoff 8765.*

Guaterriopsis

G. blepharophylla (Mart.) R.E. Fr.: *Fróes 22108; Pennington & Monteiro, P22652; Vieira et al. 745, 939.*
G. friesiana W. Rodrigues: *Campbell et al., P21896.*
G. sessiliflora (Benth.) R.E. Fr.: *Spruce 1668* (P).

Heteropetalum

H. brasiliense Benth.: *Madison et al. 6142; Maguire et al. 36371; Nascimento 591.*
H. spruceanum R.E. Fr.: *Huber & Medina 5818; Spruce 3184* (P).

Hornschuchia

H. alba (St. Hil.) R.E. Fr.: *de Saint-Hilaire 566* (P).
H. bryotrophe Nees: *Mori et al. 9368.*
H. spec. nov.: *dos Santos 3099.*

Malmea

M. depressa (Baill.) R.E. Fr.: *Dorantes et al. 958; Trigos 297.*

M. diclina R.E. Fr.: *Krukoff 5644.*
M. aff. *lucida* Diels: *Foster 5118.*
M. obovata R.E. Fr.: *Daniëls & Jonker 1178.*

Onychopetalum

O. amazonicum R.E. Fr.: *Fróes 32206* (P).
O. krukoffii R.E. Fr.: *Cordiero 1065.*
O. lanceolatum R.E. Fr.: *Krukoff 6909.*

Oxandra

O. acuminata Diels: *Krukoff 6096.*
O. asbeckii (Pulle) R.E. Fr.: *Lindeman 6988; Lindeman, Stoffers et al. 346; Mori 8849.*
O. lanceolata (Sw.) Baill.: *Shafer 12007.*
O. laurifolia (Sw.) A. Rich.: *Beard 460.*
O. riedeliana R.E. Fr.: *Krukoff 5331.*

Porcelia

P. macrocarpa (Warm.) R.E. Fr.: *Lourteig 2354* (P).
P. nitidifolia Ruiz & Pavón: *Schunke V. 5763, 7832.*
P. venezuelensis Pittier: *Steyermark & Bunting 101369.*

Pseudephedranthus

P. fragrans (R.E. Fr.) Aristeguieta: *Maguire et al. 60189.*

Pseudoxandra

P. coriacea R.E. Fr.: *Prance et al. 11468.*
P. guianensis R.E. Fr.: *A. C. Smith 2665.*
P. lucida R.E. Fr.: *Berg et al., P18462.*
P. polyphleba (Diels) R.E. Fr.: *Krukoff 4882; Revilla et al. 2552.*

Raimondia

R. quinduensis (Kunth) Saff. var. *latifolia* R.E. Fr.: *Triana s.n.* (P).
R. tenuiflora (Mart.) R.E. Fr.: *Poeppig 2845* (P).
R. spec.: *Breteler 4469.*

Reedrollinsia

R. spec.: *Walker 357.*

Rollinia

R. centrantha R.E. Fr.: *Krukoff 8488* (BR).
R. dolabripetala (Raddi) St. Hil.: *Mosén 3778* (S).

R. *emarginata* Schlechtend.: *Fiebrig 180* (E).
R. *exsucca* (Dunal) A.DC.: *BW 3785; Gardner 1914* (NY).
R. *jimenezii* Saff.: *Contreras 4507* (S).
R. *membranacea* Triana & Planchon: *Little 7564* (S).
R. *mucosa* (Jacq.) Baill.: *Asplund 14594* (S).
R. *pachyptera* Diels: *Croat 19351* (MO).
R. *peruviana* Diels: *Schunke V. 2182* (G).
R. *silvatica* (St. Hil.) Mart.: *Loefgren & Edwall 17881* (S).
R. *uniflora* R.E. Fr.: *Krukoff 6181.*
R. *williamsii* Rusby: *Fleischmann 433* (S).

Rolliniopsis

R. *discreta* Saff.: *Rose & Russell 19963* (GH).
R. *ferruginea* R.E. Fr.: *Gaudichaud 801* (G).
R. *leptopetala* (R.E. Fr.) Saff.: *Blanchet 3101* (G); *Irwin et al. 30681* (NY).
R. *parviflora* (St. Hil.) Saff. var. *latifolia* (Mart.) R.E. Fr.: *Glaziou 6077 (C).*
R. *parviflora* (St. Hil.) Saff. var. *parviflora*: *de Saint-Hilaire 824* (LE).

Ruizodendron

R. *ovale* (Ruiz & Pavón) R.E. Fr.: *Krukoff 10669; Meneces & Terceros 473; Nelson 818; Steinbach 7248.*

Sapranthus

S. *borealis* R.E. Fr.: *Ortega 6619, 6695* (US).
S. *campechianus* (Kunth) Standley: *Enriquez 196* (MEXU).
S. *chiapensis* Standley (ined.): *Matuda 16466* (MEXU).
S. *foetidus* (Rose) Saff.: *Palmer 394* (GH).
S. *ligularis* Saff. ex R.E. Fr.: *Heyde & Lux 4508* (GH, US).
S. *longepedunculatus* R.E. Fr.: *Hinton et al. 10344* (NY).
S. *microcarpus* (J.D. Smith) R.E. Fr.: *Standley 21817* (NY).
S. *nicaraguensis* Seemann: *van Rooden 200.*
S. *oxypetalus* Standley & L. Williams: *Carlson 2140* (F, NY).
S. *palanga* R.E. Fr.: *van Rooden 868.*
S. spec. nov.: *van Rooden 850.*

Stenanona

S. *costaricensis* R.E. Fr.: *Davidson & Donahue 8886* (LA); *Wilbur & Stone 10215, 10706* (DUKE).
S. *panamensis* Standley: *Cooper 427* (US).

Tetrameranthus

T. *duckei* R.E. Fr.: *Liesner 7590, 8598* (MO); *Rodrigues 8742* (INPA); *Steyermark & Bunting 102721* (NY, US).

T. umbellatus Westra: *Tunqui 62.*

Tridimeris

T. hahniana (Baill.) Baill.: *Hahn 239* (P).

Trigynaea:

T. caudata (R.E. Fr.) R.E. Fr.: *Wessels Boer 1595.*
T. duckei (R.E. Fr.) R.E. Fr.: *Foster 5460; Hartshorn 2428.*
T. guianensis (R.E. Fr.) R.E. Fr.: *Oldenburger et al. 489, 580* (cf.).

Unonopsis

U. angustifolia (Benth.) R.E. Fr.: *Rimachi Y. 2224* (US).
U. floribunda Diels.: *Krukoff 4806, 5992.*
U. glaucopetala R.E. Fr.: *van Donselaar 3782; Lanjouw & Lindeman 2503.*
U. guatterioides (DC.) R.E. Fr.: *BW 2060; Prance & Silva 58562.*
U. lindmanii R.E. Fr.: *Mexía 5030.*
U. rufescens (Baill.) R.E. Fr.: *Schulz 9314.*
U. stipitata Diels: *van Donselaar 3513; Prance et al. 2171.*

Xylopia

X. amazonica R.E. Fr.: *Maguire 24818; Prance & Silva 59162.*
X. aromatica (Lam.) Mart.: *BW 6321; Davidse & Gonzalez 16080; Grenand 574; Labourieau 807; Liesner 7562, 8723; Nee 7440; Silva & Rosario 3663; Vieira et al. 997.*
X. benthamii R.E. Fr.: *Krukoff 6426; Maas & Tawjoeran, LBB 10763.*
X. emarginata Mart. var. *duckei* R.E. Fr.: *Pires 51820.*
X. frutescens Aubl.: *Pires 51832; Stevens 7765.*
X. frutescens var. *ferruginea* R.E. Fr.: *BW 6887.*
X. muricata L.: *Proctor 28858, 29190.*
X. obtusifolia (A. DC.) A. Rich.: *Howard 5129.*
X. sericea St. Hil.: *Mori et al. 10958; Pinheiro 292.*

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Synoptical key to the neotropical genera

Numbers refer to the genera as listed in Table 1. When a number is underlined, the character (state) was only found in a part of that genus. Brackets indicate that the character (state) was found in a single specimen of the material studied. The genera 34—38 are never underlined or between brackets, as only one specimen per genus was studied.

Indument

1. Type of trichomes (Figs. 1, 2, 3)
   a. scales: 10
   b. stellate or tufted: 1—30 (—2—25)
   vs. simple, single trichomes or absent
2. Length of trichomes
   a. < 100 µm: 2—4—11—20—27 (—8—32)
   b. >700 µm: 2—14—15—28—33 (—16—25—26—29)
   vs. between 100—700 µm
3. Top cells of trichomes
   a. clavate: 1
   vs. more or less acute with normal cell walls
4. Number of trichomes on abaxial surface
   a. > 40 per mm²: 1—2—4—11—14—15—20—27 (—24)
   vs. less than 40 per mm² or absent

Epidermis

5. Number of epidermal layers (Figs. 9, 11, 12, 13)
   a. consisting of 2—3 layers: 2—3—14—24—30—33
   vs. one layer
6. Striations (Fig. 5)
   a. present on adaxial or abaxial surface: 1—2—3—9—13—15—17—21—25
   vs. absent
7. Crystals in adaxial epidermal cells (Figs. 7, 21, 22)
   a. banana-shaped: (8)
   b. acicular: 9 (—10—14)
   c. large, hexangular, along the veins: 28
   d. rhombic, multi-coloured in polarized light: 11—27—28 (—13—19)
   e. rhombic, white in polarized light: 2—8—11—13—19—25—27—28—29—35—36—37—38
   vs. druses or absent
8. Stomata on adaxial surface
   a. present: 3—5—7—12—14—15—16—21—22—23—33
   vs. absent
9. Length of abaxial stomata
   a. < 20 µm: 2—4—11—20—23—27—32
   b. > 35 µm: 1—2—3—10—14—17—25—30
   vs. between 20—35 µm
10. Length of unspecialized epidermal cells on adaxial surface
    a. ⩾ 50 µm: 2—7—14 (—8—12—25)
    vs. less than 50 µm
11. Outer wall of epidermal cells (Figs. 4, 9)
    a. papillate: 2—4—11—20—25—27
    vs. flat

Lamina

12. Structure of the lamina
    a. isobilateral: 2—4—5—9—11—14—17—19—20—21—22—23—26—28—29
    vs. dorsiventral
13. Palisade parenchyma (Figs. 9, 11, 13)
    a. adaxially in more than 2 layers: 2—3—7—14—17—30—33
    vs. in 1—2 layers

Veins

14. Histology of primary vein (Figs. 23, 24, 25, 26)
    a. complex, with phloem at the adaxial side of the xylem body: 1—2—25
    b. complex, with xylem forming the adaxial side of the vascular bundle: 4—13—14—15—16—17—20—27—30—32
    vs. phloem in one interrupted or continuous arc.
15. Primary vein at adaxial surface (Figs. 23, 24, 25, 26)
    a. raised: 3—4—5—6—7—11—12—18—19—20—21—22—23—27—31—32—34—35—36
    vs. flat or impressed
16. Sheath extensions of small veins (Figs. 12, 13)
    a. connecting the abaxial and adaxial epidermis: 2—3—10—11—25—26—27—28—33
    vs. restricted to a narrow zone

Ideoblasts

17. Type of sclereids (Figs. 19, 20)
    a. astrosclereids: 1—2—8—14—17—30 (—7—11—15—16—31)
    b. osteosclereids: 7—13—14—15—16—18—20—21—23—31—32 (—4—6—28)
    vs. absent
18. Oil cells present (Figs. 4, 11, 13, 15, 19)
    a. in palisade parenchyma only: 1—2—3—7—8—9—10—12—17—18—23—25—30
    b. in or immediately below the epidermis: 4—20—32
    vs. in sponge parenchyma or absent
19. Coloured contents in oil cells
    a. present: 4—7—8—9—11—12—19—20—21—22—27—28—29—32—36—37
    vs. not recorded
20. Angular silica bodies (Fig. 16)
    a. present in palisade parenchyma: 6 (—10)
    b. present in sponge parenchyma only: 4—11—14—15—16—17—19—20—21—23—32
    vs. absent