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FLOWERS OF ANNONACEAE:
MORPHOLOGY, CLASSIFICATION, AND EVOLUTION

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SUMMARY

The present paper describes the diversity in floral characters of Annonaceae and their distribution over the family, and discusses their value for classification and generic delimitation. Flower morphology predominated historical classifications of this family since Hooker & Thomson (1855) introduced floral characters to divide the Asiatic genera into a number of tribes. Since then, several taxonomists presented a classification of the Annonaceae using floral characters, which classifications, however, are generally felt as unnatural. A survey of the flower morphology of all genera reveals a reticulate distribution of floral character states. Classification of the genera, as presented in this study, learns that floral characters different from those in previous classifications should be used if one aims at a better correlation with non-floral features. The chromosome number in this respect turned out to be an important character. Classification of the neotropical genera is relatively easy compared with classification of the African and Asiatic genera. Current genus delimitations in many cases are disputable. The functional aspects of the flower morphology are discussed in connection with a literature survey of the results from field studies on flower biology of Annonaceae. Some remarks on evolutionary aspects are added.

1. INTRODUCTION

Preceding the revision of neotropical genera of Annonaceae, detailed studies of all parts of the plants of the whole family of Annonaceae were started. In a multidisciplinary project (Maas, 1983) specialists from various fields participate: flower morphology, fruit and seed morphology, wood anatomy, leaf anatomy, palynology, karyology, inflorescence morphology, and cladistics. These studies should provide new information about generic delimitations and affinities between genera. At the same time a character analytic study is severely handicapped by the absence of (recent) monographs.

The study presented here regards flower morphology. A comprehensive study of the flower morphology of the Annonaceae may provide basal information to those interested in pollination biology of Annonaceae or in the evolution of extant primitive Angiosperms.

The family of Annonaceae belongs to the order of the Magnoliales (e.g., Cronquist, 1981). It is generally considered to be a natural family and one of the most primitive families of the Angiosperms (Hutchinson, 1969). They comprise about 120–130 genera, occurring mainly in the lowland rain forests of both the Paleotropics and the Neotropics. Outside the tropics they are represented by only one species, *Asimina triloba*, occurring in North America up to the most southern part of Canada. Despite the large number of genera, the family is remarkably homogeneous. Within the Magnoliales it is the most successful family, not only because of its large number of genera, but also because several genera have a large number of species (highest in *Guatteria* with c. 250 species).

Great importance is attributed to the flower morphology in existing classifications of the family. Except for Dunal (1817), who used fruit characters to classify the eight annonaceous genera (and one non-annonaceous genus, *Kadsura*) known at that time, taxonomists mainly based their classifications on flower morphology. Hooker & Thomson (1855) in this respect were the first with their classification of the Asiatic

genera only. Bentham (1862, 1867) subsequently published a classification of the whole family, recognizing the same tribes as Hooker & Thomson (1855) although sometimes under different names and on different taxonomic levels. These tribes, Uvarieae, Unoneae, Mitrephoreae, Xylopieae, and Miliuseae return in nearly all subsequent classifications (e.g., Baillon, 1868; Prantl, 1888; Engler & Diels, 1900; Fries, 1959; Hutchinson, 1964) and in local floras. The Uvarieae were based on the imbricate aestivation of the petals; about this tribe there is most consensus between the various taxonomists. Only Engler & Diels (1900) and Diels (1932) attributed less importance to the aestivation of the petals. The delimitation of the remaining tribes with valvate petals generally gives more problems. The Unoneae are usually circumscribed as having equal-sized and spreading petals. The Mitrephoreae are characterized by connivent inner petals. The Xylopieae possess flowers with erect and thick outer petals which comprise the slightly smaller inner petals. The circumscription of the Miliuseae is more diverse: stamens imbricate (Hooker & Thomson, 1855), stamens of which the apex is not dilated above the anthers (Prantl, 1888), or outer petals reduced (Hutchinson, 1964). Fries (1959) did not recognize an equivalent of the Miliuseae. Keßler (1988) re-established this tribe under its older name Saccopetalae (Hooker & Thomson, 1855). The Miliuseae and the Mitrephoreae are difficult to separate as *Orophea* and *Platymitra* combine features of both tribes (Sinclair, 1955). *Isolona* (since 1897) and *Monodora* are in all classifications, except that of Bentham (1862, 1867), separated in a tribe Monodoreae or subfamily Monodoroideae. These two genera have one unilocular carpel, with ovules covering the whole ovary wall, which has, except by Dunal (1817), been considered as a syncarpous gynoecium with a parietal placentation.

With Fries (1959) the criteria for classification became more diverse. By then the number of genera had increased to nearly 120. He introduced the position of the inflorescence as an important character, while *Tetrameranthus* was separated from the other genera in a tribe Tetramerantheae, because of the spiral arrangement of the leaves (in all other genera they are distichous). Beside the traditional criteria, the presence or absence of bracts and some new floral characters, like the aestivation of the sepals, the number of the ovules per carpel, and the arrangement of the petals in one or two whorls, were added.

Thus far, surveys on the flower morphology are usually given in connection with general classifications, e.g., by Baillon (1868) and Fries (1959), for the African genera by Le Thomas (1969), and for the Asiatic genera by Sinclair (1955). Flower morphological trends are discussed by Sinclair (1955) and, in connection with trends in pollen morphology, by Le Thomas (1981). These trends refer to the number of ovules, to the size, shape, and arrangement of the petals, and to the fusion of carpels. Le Thomas (1981) found a high ovule number to be most primitive. More recent developments in studies on the flower morphology of Annonaceae are (a) field observations as part of studies on the flower biology and (b) the use of SEM-techniques in studies on flower structures in Magnoliidae. For instance, Morawetz (1988) gives a subdivision of development types of the flowers of Annonaceae based on field observations, whereas Endress & Hufford (1989) show SEM-photographs of several stamen structures and dehiscence types in Magnoliidae, among which Annonaceae.

The aims of the present (herbarium) study are:

1) to present a survey of the flower morphology of the Annonaceae and the distribution of floral character states over the family;
2) to examine generic delimitations and to indicate affinities between genera;
3) to indicate the importance and the limitations of the flower morphology in generic and supra-generic classification of the Annonaceae;
4) to indicate some morphological trends within the flowers of Annonaceae.

2. MATERIAL AND METHODS

2.1. MATERIAL

Material was studied mainly from the following herbaria: B, BM, BR, K, L, P, U, and WAG. Some additional specimens were studied from: A, C, CEPEC, COL, E, F, G, GOET, LE, M, MICH, MO, NY, OXF, RB, S, SP, UC, US, VEN, and W. Material preserved in spirit was available from B, BRI, K, L, OSA, U, WAG, and WU.

2.2. CIRCUMSCRIPTION OF TAXA

Usually the generic classification of Fries (1959) (table 1) is followed. Exceptions are made with regard to recently published genera and when the author had doubts about the inclusion of some genera in usually larger ones by Fries or other taxonomists: in such cases genera are treated separately. For instance, *Ancana, Mitrella,* and *Pyramidanthe* are included in *Fissistigma* by Fries, but are kept separate in the present study. *Friesodielsia* was included in *Richella,* but the two are treated here as distinct genera. *Sphaerothalamus* is treated here as distinct from *Polyalthia,* and *Mezzettiopsis* as distinct from *Orophea.* On the other hand, *Drepananthus* is included in *Cyathocalyx,* like Sinclair (1955) did. *Rolliniopsis* is included in *Rollinia* because of problems with a correct identification since the two genera cannot be distinguished on the basis of their flowers. *Pseudannona* is included in *Xylopia* (Keraudren-Aymonin, 1980). *Enneastemon* and the African species of *Popowia* are included in *Monanthotaxis,* following the genus-concept of Verdcourt (1971b). *Ararocarpus* is excluded, as this genus was based solely on an anomalous specimen of *Meiogyne* (Sinclair, 1958). Fries (1959) overlooked *Phoenicanthus*; although the available material was very poor, also this genus was studied. Rauschert (1982) proposed new names, *Dendrokingstonia* and *Woodiellantha,* for *Kingstonia* and *Woodiella* respectively, as their names already applied to other taxa. Genera, published after Fries's generic revision in Die natürlichen Pflanzenfamilien (1959), are also studied: *Ambavia, Balonga, Boutiquea, Chieniodendron, Enicosanthellum, Greenwayodendron, Mkilua, Pseudephedranthus,* and *Reedrollinsia.*

2.3. METHODS

The flower morphology of a genus was studied using a representative number of species, and usually including the type of the genus. Descriptions of the genera are exclusively based on the cited specimens. Additional information from literature is mentioned in the notes on the genera or in Chapter 3 with a reference to the author.

Table 1. The classification of Fries (1959).

Genera published after 1959 or overlooked by Fries are marked with an asterisk (*). Genera not recognized as such by Fries are placed between brackets. Two genera changed names and one genus was misspelled by Fries. See text for more information.

Annonoideae:

Uvarieae:

Uvaria-gruppe: *Uvaria, Anomianthus, Tetrapetalum, Ellipeia, Ellipeiopsis, Stenanona, Sapranthus, *Reedrollinsia, Desmopsis, Afroguatteria, Mischogyne, Toussaintia.*

Duguetia-gruppe: *Duguetia, Duckeanthus, Fusaea, Letestudoxa, Pachypodanthium, Malmea.*

Asimina-gruppe: *Cremastosperma, Pseudoxandra, Ruizodendron, *Balonga, Oxandra, Ephedranthus, *Pseudephedranthus, Enicosanthum, Cleistopholis, Asimina, Deeringothamnus, Tridimeris, Sageraea, Fitzalania, Stelechocarpus, Cyathostemma, *Phoenicanthus.*

Hexalobus-gruppe: *Hexalobus, Asteranthe, Ophrypetalum, Lettowianthus, Cleistochlamys.*

Guatteria-gruppe: *Guatteria, Guatteriella, Guatteriopsis, Heteropetalum.*

Unoneae:

Desmos-gruppe: *Desmos, Alphonsea, Rauwenhoffia, Monocarpia, Dasoclema, Meiocarpidium.*

Polyalthia-gruppe: *Cananga, Polyalthia* (including *Sphaerothalamus*), *Greenwayodendron, Sphaerocoryne, Meiogyne, Mezzettia, (Dendro)Kingstonia, Fenerivia, Papualthia, Woodiella(ntha), Miliusa.*

Unonopsis-gruppe: *Unonopsis, Bocageopsis, Onychopetalum, Uvariodendron, Uvariastrum, Polyceratocarpus, Dennettia, Neo-uvaria, Dielsiothamnus.*

Xylopia-gruppe: *Xylopia, Pseudannona, Dicinanona, Ararocarpus, Polyaulax, Dasymaschalon, Piptostigma, Anaxagorea, Fissistigma* (including *Ancana, Mitrella,* and *Pyramidanthe*), *Oncodostigma, *Chieniodendron, Guamia.*

Artabotrys-gruppe: *Artabotrys, Pseudartabotrys, *Boutiquea, Neostenanthera, Marsypopetalum, Drepananthus, Cyathocalyx, Enantia, Disepalum, *Enicosanthellum.*

Orophea-gruppe: *Orophea* (including *Mezzettiopsis*), *Platymitra, Petalo(lo)phus, Oreomitra, Schefferomitra, Goniothalamus, Pseuduvaria, Exellia, Mitrephora, Popowia* (African & Asiatic species), *Ambavia, Richella* (including *Friesodielsia*), *Phaeanthus, Trivalvaria, Atopostema.*

Annona-gruppe: *Annona, Raimondia, Rollinia, Rolliniopsis, Anonidium.*

Trigynaea-gruppe: *Trigynaea, Bocagea, Hornschuchia, Cardiopetalum, Froesiodendron, Cymbopetalum, Porcelia, *Mkilua.*

Monanthotaxis-gruppe: *Monanthotaxis, Gilbertiella, Enneastemon, Monocyclanthus, Haplostichanthus, Uvariopsis.*

Tetramerantheae: *Tetrameranthus.*

Monodoroideae: *Monodora, Isolona.*

Bibliographic data on genera and their types are taken from Index Nominum Genericorum (Farr et al., 1979), although in a number of cases corrections were necessary [see also Van Setten & Maas (1990) for a revised list of generic names of Annonaceae]. The number of species studied per genus varies from 100% in genera with very few species to c. 20% in genera with a large number of species. Counts of the number of ovules are often based on few specimens as less material was available or suitable for examination. The number of species per genus is only an estimate, as recent revisions of genera are scarce. For the same reason misidentifications on the species level may occur.

2.4. Terminology

Usually the terminology proposed by Radford et al. (1974) is used. Some features, however, need further explanation.

The shape of the bud may be defined by the sepals or the petals. In the latter case the sepals are small and do not or hardly enclose the buds.

The aestivation is defined at the apex of the sepals and petals, as in some cases apex and base are different in this respect.

For description of the indument, the type of hairs (simple, stellate, or scales) and their distribution (present or absent, margins ciliate or not) are indicated. The density, length, and exact distribution of hairs over the various flower parts may vary both between and within genera. A specialized study of all hair types within the Annonaceae seems promising.

When calculating the ratio length of petals/length of sepals, the length of the longest petals is used in cases of a difference in length between outer and inner whorl. The same applies to the ratio length/width of the petals.

Data regarding the colours of the petals are taken from the labels of the herbarium specimens.

With regard to the torus, a distinction is made between the general outline of the whole torus and the apex of the torus.

The number of stamens and carpels varies gradually. A subdivision in categories, admittedly, is arbitrary, but for practical reasons the following terminology is used:

stamens	few:	up to 20	**carpels**	few:	up to 10
	numerous:	more than 20		numerous:	more than 10

3. Morphology of the flowers

3.1. Flowers

3.1.1. General characteristics

Flowers in Annonaceae are generally actinomorphic. Within the Magnoliales they are recognized by a (normally) 3-merous perianth more or less clearly differentiated into sepals and petals. Sepals and petals show a whorled arrangement, whereas stamens and carpels are usually spirally arranged. The perianth parts alternate, the inner petals being opposite the sepals. Only in *Toussaintia* occasionally the (up to 10) petals are placed in 2 or 3 irregular whorls (Le Thomas, 1969; Verdcourt, 1971a).

Flower diagrams of some genera are provided by, for instance, Baillon (1868) and Le Thomas (1969).

The flowers may be borne on leafy branches, on leafless parts of the branches, on the trunk, or on shoots departing from the trunk. The latter situation is found in, e.g., *Duguetia* sect. *Geanthemum* and in some species of *Uvariopsis*. In *Annona* (one species), *Asimina* (one species), *Cleistochlamys*, and *Hexalobus* (one species) flowers are occasionally found on leafless branches, due to seasonal circumstances. The flowers are solitary or placed in few- to many-flowered inflorescences. As far as known in most genera the (mature) flowers are pendulous or nodding. In *Cleistochlamys*, *Hexalobus*, *Haplostichanthus* (Morawetz, 1988), *Tetrameranthus* p.p., *Trigynaea*, and *Xylopia* (the latter two genera according to Gottsberger, 1990), however, the flowers are erect. The flowers may be hidden by the leaves or exposed, sometimes pending on a long pedicel. The latter situation is present in *Cymbopetalum*, *Dasymaschalon* p.p., *Desmos* p.p., *Monodora* p.p., and in many species of various genera from New Guinea.

3.1.2. Maturation

The duration of the period of maturation from bud break to the end of the anthesis when the perianth-parts and the stamens are shed off is insufficiently known. Anthesis is defined here as the period that carpels and/or stamens are mature. In one species of *Monodora* the maturation period lasts 25 days (Lamoureux, 1975); anthesis lasts about 12 days. Conspicuous differences, however, exist between and within genera. Most literature on flower biology on Annonaceae report short periods for anthesis (1–3 days). Maturation is independent from the size of the flower. Observations in the greenhouse at Utrecht learned that large *Annona*-flowers are short-lived, whereas a much smaller *Polyalthia*-flower lived for many weeks. Backer & Bakhuizen van den Brink (1963) mentioned that flower buds of *Marsypopetalum* remain dormant for a long time. The same applies to flower buds of *Cleistochlamys* and one species of *Hexalobus* (Coates Palgrave, 1977; Codd, 1951; White, 1962).

Flower break may occur in mature flowers at the onset of the anthesis or in juvenile flowers. The latter situation is observed in *Desmopsis*, *Desmos*, *Guatteria*, *Polyalthia*, *Sapranthus*, and *Stenanona*. Also cleistopetalous flowers are reported to occur within the Annonaceae (Burck, 1890, 1906): these flowers do not open their petals before or during anthesis. This seems to occur in, for example, species of *Artabotrys*, *Cleistopholis* (fig. 4d), *Cyathocalyx*, *Dasymaschalon* (fig. 2n), *Friesodielsia* p.p., *Goniothalamus*, *Mitrella*, *Pachypodanthium*, and one species of *Toussaintia*.

As far as known, all Annonaceae are protogynous. Anthesis is usually associated with discoloration of the perianth and emission of odours.

3.2. Buds

The shape of the closed flower buds varies from ellipsoid via spheroid to transversely ellipsoid, from lanceoloid to depressed ovoid, and from triangular-lanceoloid to deltoid-ovoid. Field observations learn that also 'open' flower buds exist. The shape of the bud is usually characteristic for a genus (compare figs. 1f, i, k, n).

Ovoid shapes are most common. Lanceoloid buds are characteristic for *Annona* p.p., *Greenwayodendron, Hornschuchia, Pyramidanthe, Raimondia* p.p., and *Xylopia* p.p. (fig. 1f). Triangular shapes (fig. 3i, p) are found, e.g., in *Annona* p.p., *Dasymaschalon, Enantia, Heteropetalum, Mitrella, Phaeanthus, Raimondia* p.p., and *Uvariastrum.*

In most genera the shape of the flower buds is mainly defined by the petals. The sepals (or calyx) enclose the buds only in a very early stage of their development. This is also observed in Winteraceae (e.g., Sampson & Tucker, 1978). Only in genera with relatively large sepals, the shape of the bud is determined by the sepals (compare figs. 1i and 3l and figs. 1m and 3e).

In a few genera closed flower buds are not seen, although ample material was investigated, e.g., *Desmos, Desmopsis,* and most species of *Isolona* and *Polyalthia.*

3.3. Sepals

3.3.1. Aestivation

Within the Annonaceae several aestivation types are recognized in the sepals: valvate, reduplicate-valvate, imbricate, and apert.

Valvate sepals are found in the majority of the genera. Reduplicate-valvate sepals (fig. 1i, l) are common in genera with middle-sized to large flower buds. In several genera both species with reduplicate-valvate sepals and with valvate sepals are found.

Imbricate sepals are present in a minority of genera: *Cleistopholis, Dendrokingstonia, Enicosanthum, Greenwayodendron, Lettowianthus, Malmea, Mezzettia, Mkilua, Oxandra,* some species of *Polyalthia, Porcelia, Pseudephedranthus,* and *Pseudoxandra.*

An apert aestivation is noted for genera with very small sepals and for genera of which only open flowers could be studied.

3.3.2. Number

The number of sepals is usually 3 (fig. 1d), but in a few genera 2 or 4 are counted. *Disepalum* (fig. 1h), *Tetrapetalum,* and *Tridimeris* always have 2 sepals, whereas in *Anaxagorea, Dennettia,* and *Uvariopsis* both species with 2 and 3 sepals exist. *Deeringothamnus, Lettowianthus, Reedrollinsia,* and *Tetrameranthus* have 4 sepals.

3.3.3. Fusion

Both free and connate sepals occur in the family. In many genera both conditions are found. In some genera the sepals are connate at the base only, whereas in other genera the sepals are distinctly fused. The latter case is found, for instance, in *Dennettia, Duguetia* sect. *Synsepalantha, Hornschuchia, Monocyclanthus, Polyceratocarpus, Pyramidanthe, Reedrollinsia, Uvaria,* and *Xylopia* (fig. 1f).

In most genera with connate sepals, the sepals eventually separate into three equal parts when the bud matures. However, in some genera the calyx, which is in this case often apiculate, ruptures circumferentially or irregularly when the bud matures. This is observed in *Fusaea, Letestudoxa,* some species of *Uvaria,* and in one species of *Duguetia* and *Guatteria.*

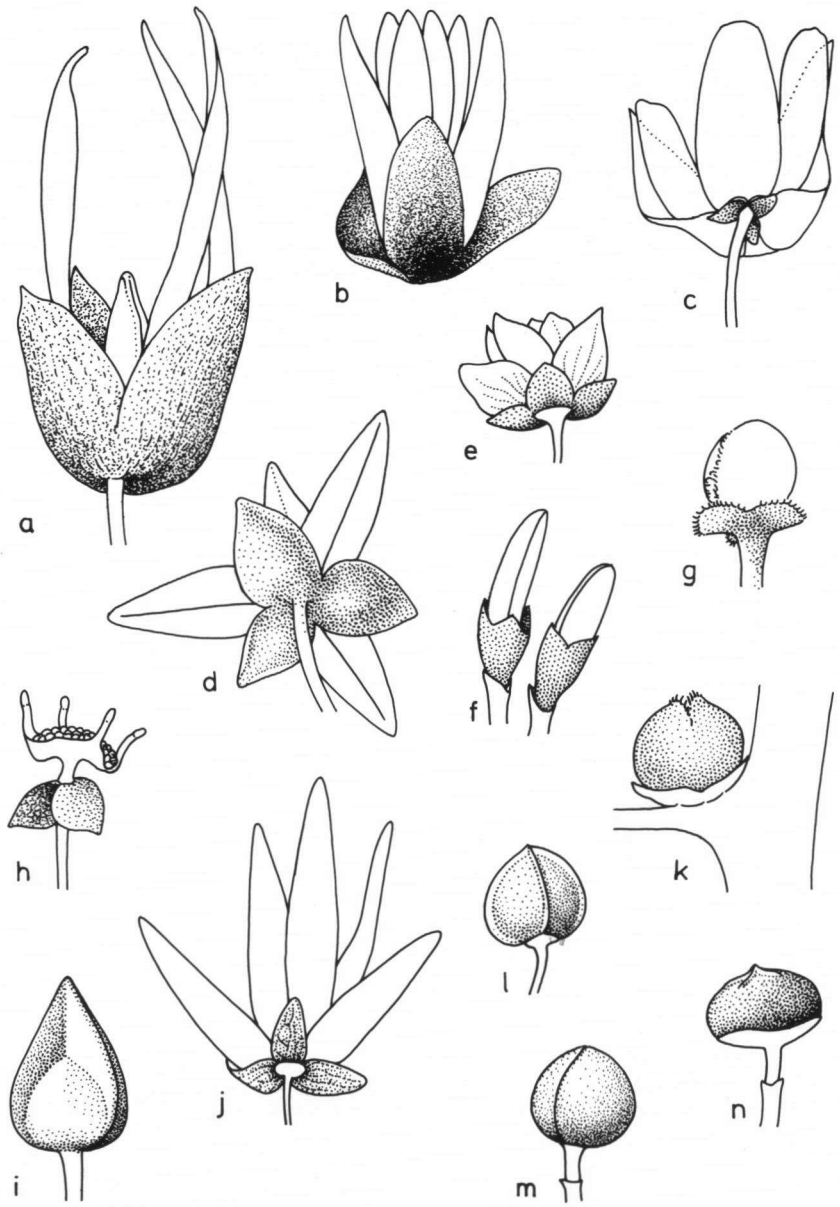


Fig. 1. Diversity in shape and relative size of the sepals — a. *Goniothalamus macrophyllus* (Anderson & Ilias bin Paie S28634); b. *Sphaerothalamus insignis* (= *Polyalthia insignis*) (Meijer 2232); c. *Porcelia sp.* (Heringer & Eiten 14988); d. *Uvariastrum pierreanum* (Touzet 65); e. *Ellipeiopsis ferruginea* (collector unknown (K)); f. *Xylopia nitida* (Reeder & Roberts LBB 12310); g. *Sageraea elliptica* (Mujin 33834); h. *Disepalum grandiflorum* (Hose 214); i. *Uvariastrum pierreanum* (Brenan & Richards 8827); j. *Polyalthia lamii* (Lam & Meeuse 6047); k. *Cleistochlamys kirkii* (Edwards & Vahrmeijer 4277); l. *Cardiopetalum calophyllum* (Daly et al. 1336); m. *Hexalobus bussei* (Zenker 3889); n. *Fusaea longifolia* (Cid et al. 2373).

3.3.4. Shape

The shape of (almost) free sepals ranges from depressed to narrowly ovate or to triangular. The latter situation is found in, e.g., *Miliusa, Phaeanthus,* and *Piptostigma.*

In genera with connate sepals two types are found: *Hornschuchia, Uvaria,* and *Xylopia* (fig. 1f) often have an entirely connate cup-shaped calyx. *Monocyclanthus, Pyramidanthe,* and several species of *Dennettia* and *Polyceratocarpus* have a circular calyx.

Gibbous to almost spur-like sepals are present in *Rollinia* sect. *Saccosepalum.*

3.3.5. Size

The length of the sepals ranges from 0.5 mm to 45 mm. Most genera have very small sepals. Large sepals (more than 25 mm) are only present in *Anonidium, Duguetia, Goniothalamus* (fig. 1a), *Sphaerothalamus* (fig. 1b), *Uvariastrum* (fig. 1d), and *Uvariodendron.*

The ratio length of petals/length of sepals differs within and between genera (compare figs. 1c and 1d). In most genera the (longest) petals are 3–5× as long as the sepals. In *Boutiquea, Piptostigma,* and *Polyalthia* the ratio is up to 30 and in *Neostenanthera* even up to 70. The ratio is low in, e.g., *Afroguatteria, Dielsiothamnus, Froesiodendron, Mischogyne, Ophrypetalum,* and *Uvariodendron.*

3.3.6. Texture

The sepals are usually more or less fleshy, sometimes they are thin. In part of the genera with thin sepals, the petals are rather thick, and vice versa. Sometimes both the sepals and petals are thin like in *Asimina, Monodora,* and *Sapranthus.*

In some species of *Enicosanthum* and *Goniothalamus,* and in *Sphaerothalamus* (synonym of *Polyalthia insignis*) the sepals enlarge excessively and become membranous during maturation (fig. 1a, b).

3.3.7. Venation

In the majority of the genera the veins of the sepals are not prominent. Veins are prominent throughout in, e.g., many *Polyalthia*-species from Madagascar (fig. 1j), and in *Asimina, Fenerivia,* and *Monodora.* Prominent longitudinal veins only are observed in, e.g., *Isolona, Pseudartabotrys, Sapranthus* p.p., and *Stenanona.*

3.3.8. Indument

The sepals are hairy throughout in most genera, but glabrous sepals and ciliate sepals (fig. 1g) are found in species of many genera as well.

Simple hairs are the predominant hair type, but in a number of genera the indument consists of stellate hairs or scales. Stellate hairs are present in, e.g., *Anomianthus, Dasoclema, Dielsiothamnus, Duguetia, Ellipeia, Ellipeiopsis, Pachypodanthium, Rauwenhoffia, Tetrameranthus, Tetrapetalum,* and *Uvaria.* In *Anaxagorea. Cyathocalyx* (few species), *Cyathostemma* (most species), and *Neo-uvaria* only part of the species have stellate hairs. Scales are only found in *Duguetia* and *Meiocarpidium.* In *Uvaria* the stellate hairs sometimes have a scale-like appearance.

Many genera are characterized by only one indument-type, but others are diverse in hair type and/or in distribution of indument, e.g., *Anaxagorea, Artabotrys, Cremastosperma, Cyathostemma, Hornschuchia, Isolona, Polyalthia,* and *Stelechocarpus.*

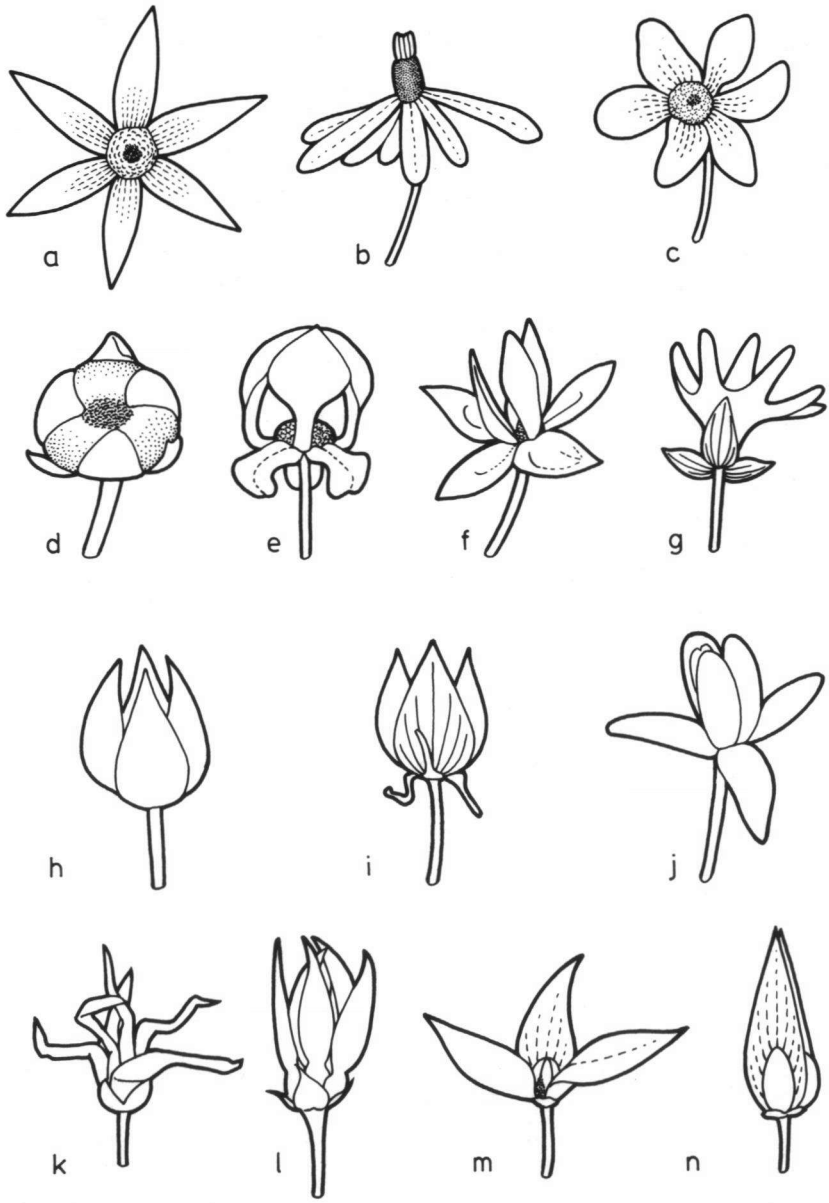


Fig. 2. Expansion of the petals in mature flowers — a. *Monocyclanthus vignei* (Leeuwenberg & Voorhoeve 4934); b. *Toussaintia hallei* (Hallé 4189); c. *Cremastosperma cauliflorum* (Prance et al. 23783); d. *Polyalthia crassa* (Kerr 11904); e. *Pseuduvaria sp.* (van Beusekom 2762); f. *Duguetia furfuracea* (Silva & Pinheiro 4136); g. *Isolona campanulata* (Versteegh & den Outer 22); h. *Tridimeris hahniana* (Schatz et al. 1198); i. *Phaeanthus ophthalmicus* (Whitmore FRI 12307); j. *Stelechocarpus burahol* (U-82, Cult. Hort. Bog. s.n.); k. *Hexalobus monopetalus* (Breteler 7288); l. *Artabotrys hexapetalus* (Cult. Hort. U., 76GR00015); m. *Boutiquea platypetala* (Letouzey 9436); n. *Dasymaschalon clusiflorum* (Cenabre et al. 28558).

3.3.9. Persistence

As a rule the sepals persist during and until shortly after anthesis. They are caducous before anthesis in some species of *Anaxagorea, Enantia,* and *Mischogyne.* Jessup (1988) reports that sepals and outer petals are caducous in one species of *Miliusa.*

3.4. Petals

3.4.1. Expansion

The petals in mature flowers may be reflexed, spreading, erect, or connivent (fig. 2). Genera may be quite uniform in this respect, or diverse. The latter situation is seen in *Diclinanona, Malmea, Toussaintia, Uvaria,* and, according to Vollesen (1980), also in *Asteranthe.* The expansion of the petals is used by Bentham (1862) to delimit the tribes Mitrephoreae, Unoneae, Uvarieae, and Xylopieae. Although many genera show a marked type of expansion, gradual transitions from one type to another are present.

Reflexed petals occur in a few genera, e.g., in some species of *Toussaintia* (fig. 2b) and *Uvaria.* In some species of *Friesodielsia* the outer petals are reflexed. In *Mezzettiopsis* (fig. 3d) the upper parts of the, much longer, inner petals are reflexed. In *Alphonsea* p.p. and *Miliusa* p.p. the apices of the inner petals are reflexed. In *Heteropetalum* (fig. 3h) the short outer petals and the sepals are apically reflexed.

Spreading petals are observed in, e.g., *Lettowianthus* (fig. 3j), *Malmea* p.p., *Monocyclanthus* (fig. 2a), *Neo-uvaria,* and *Uvaria* p.p.

Erect petals are present in, e.g., *Enantia, Greenwayodendron, Hornschuchia, Polyalthia* p.p., and *Xylopia.* Connivent petals in both whorls are found in, e.g., *Artabotrys* (fig. 21), *Cyathocalyx,* and *Pseudartabotrys.*

Both whorls of petals may be similar in expansion, or different. Examples of the latter are *Cleistopholis* (fig. 4d), *Friesodielsia* p.p., and *Sphaerocoryne.* Connivent inner petals are present in, e.g., *Boutiquea* (fig. 2m), *Goniothalamus, Mitrephora, Orophea, Neostenanthera, Pseuduvaria* (fig. 2e), and *Richella.* Also in some species of *Uvariodendron* the apices of the inner petals are adhering (Verdcourt, 1969b).

In this respect also the so-called 'Bestäubungskammer' (Gottsberger, 1970) or 'pollination chamber', famous to those who study the flower biology of Annonaceae, has to be mentioned. Some genera, indeed, have a dark, chamber-like room, formed by the petals, but a continuous transition from present to absent can be observed.

3.4.2. Aestivation

Five types of aestivation of the petals are observed: valvate, reduplicate-valvate, imbricate, transversely folded, and apert. In most genera only one aestivation type is found. The aestivation of the petals plays a major role in the delimitation of tribes in earlier classifications (e.g., Hooker & Thomson, 1855; Prantl, 1888; Fries, 1959). In a number of genera the exact aestivation is difficult to ascertain.

The valvate (fig. 3e) and the imbricate aestivation (fig. 3a) are most common. The imbricate aestivation may vary from slightly so in, e.g., *Ancana* and *Greenwayodendron* to strongly so in, e.g., *Pachypodanthium.*

Reduplicate-valvate petals (fig. 3i, p) are present in some species in several genera, e.g., *Annona, Dasymaschalon, Enantia, Mitrephora, Monanthotaxis, Orophea, Popowia, Raimondia,* and *Uvariopsis.*

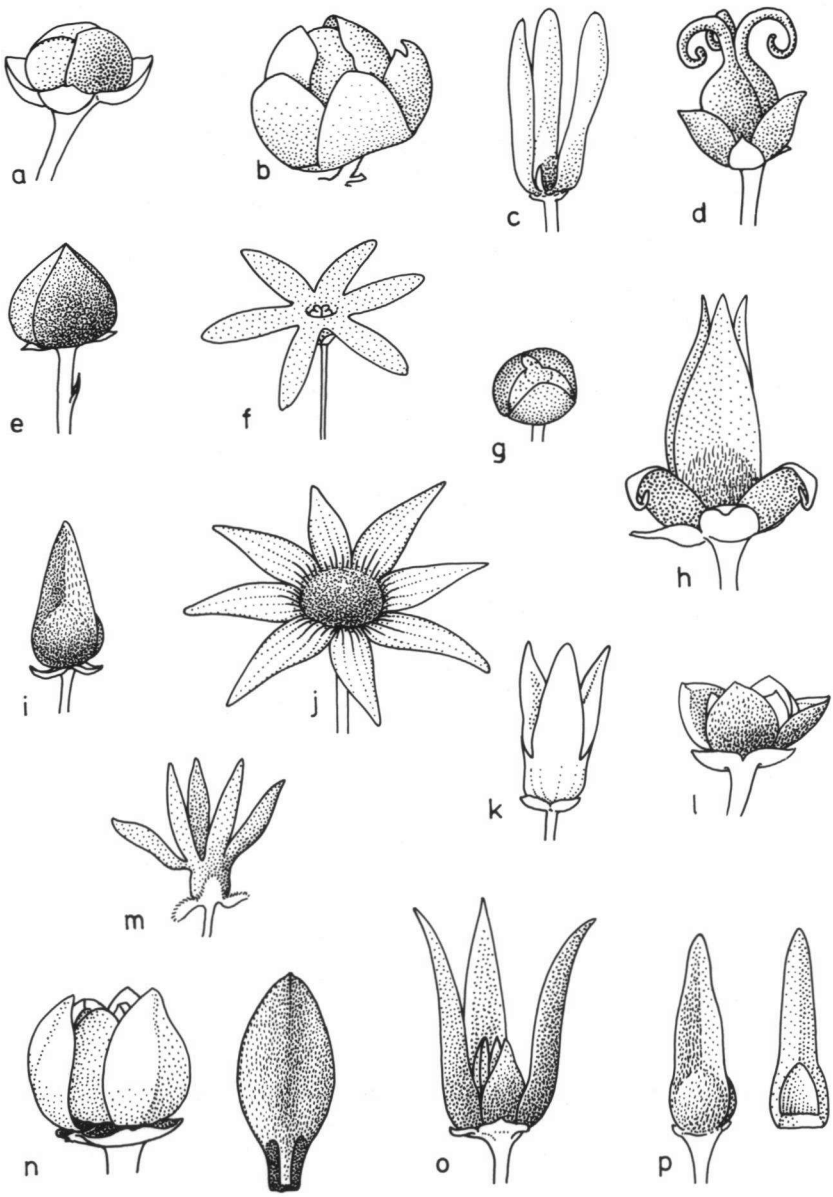


Fig. 3. Diversity in shape and relative size of the petals — a. *Stelechocarpus cauliflorus* (Henderson 23802); b. *Duguetia obovata* (Irwin et al. 47815); c. *Annona sp.* (Stevens 9710); d. *Mezzettiopsis creaghii* (Phusomsaeng 421); e. *Meiocarpidium lepidotum* (Zenker 2947); f. *Isolona cooperi* (Bernardi 8249); g. *Dennettia tripetala* (Geerling & Bokdam 2222); h. *Heteropetalum brasiliense* (Madison et al. 6142); i. *Raimondia cherimolioides* (Breteler 4469); j. *Lettowianthus stellatus* (Burtt 4994); k. *Annona haemathantha* (Mori & Boom 14754); l. *Monanthotaxis letestui* (Le Testu s.n.); m. *Isolona congolana* (Liben 3880); n. *Polyceratocarpus scheffleri* (Peter 18832); o. *Neostenanthera myristicifolia* (Breteler 1220); p. *Enantia chlorantha* (Brenan et al. 8610).

An apert aestivation is supposed to occur in, e.g., *Desmopsis, Desmos, Isolona,* and in most species of *Polyalthia.* Of these genera only opened flowers were found. In nearly all generic descriptions published, *Polyalthia* is reported to have valvate petals. Bailey (1899) mentions valvate petals in very young buds only. The present author did not observe such buds in *Polyalthia,* but observed the same phenomenon in *Sapranthus* which has imbricate petals in very young buds only. In one *Dicli-nanona*species and in *Stenanona* the petals seem to be open as soon as the sepals are open (probably valvate in closed buds).

In buds of *Hexalobus* the petals are transversely folded several times. Engler & Diels (1900) used this character state to delimit the tribe Hexalobeae.

In most genera the aestivation of the inner petals is similar to that of the outer petals. In a few genera the outer whorl is valvate and the inner whorl imbricate. This is seen in species of *Annona, Guatteriopsis, Monanthotaxis, Rollinia,* and *Uvariastrum.* In one species of *Cleistopholis* imbricate outer petals and valvate inner petals were seen.

3.4.3. Number of whorls

Most genera have two whorls of 3 petals each. In a few genera the two whorls cannot be recognized and all petals are placed on the same level: in *Dennettia, Diclinanona* (one species), *Disepalum* (fig. 1h), *Gilbertiella, Isolona* (figs. 2g, 3f), *Monanthotaxis* p.p., *Monocyclanthus* (fig. 2a), and *Uvariopsis.*

When only one whorl is present and the other one absent, such as in *Anaxagorea, Annona,* and *Dasymaschalon,* it is usually the outer one which is present, as can be deduced from the relation to the sepals. In *Enantia* only inner petals are present.

3.4.4. Number of petals

The number of petals varies from 2 to 12, most genera have 6 petals. A few genera have a different number or are rather inconstant in their number of petals.

Genera which often have 8 petals are *Disepalum, Lettowianthus* (fig. 3j), *Reed-rollinsia,* and *Tetrameranthus.* Nine petals are sometimes counted in *Asteranthe, Deeringothamnus, Fenerivia,* and *Toussaintia.* In *Lettowianthus* there are also specimens with 12 petals.

Less than 6 petals are found as well: 4 petals are present in some species of *Asimina* (one species), *Dennettia, Disepalum* (fig. 1h), *Tetrapetalum* (always), *Tridimeris* (fig. 2h; always), and *Uvariopsis.* Three petals are found in some species of *Anaxagorea, Annona, Dasymaschalon* (always), *Dennettia* (fig. 3g), *Enantia* (always), and *Uvariopsis.* In one species of *Anaxagorea* sometimes only 2 petals are found.

3.4.5. Fusion

The petals are usually free, sometimes connate. In several genera both species with free and with fused petals occur: e.g., *Annona* (fig. 3c, k), *Fusaea, Popowia,* and *Uvaria.* The petals are always connate in *Asteranthe, Cardiopetalum, Disepalum* (fig. 1h), *Haplostichanthus, Hexalobus, Isolona* (fig. 3f, m), *Papualthia, Raimondia, Rollinia,* and *Woodiellantha.* In some species of *Miliusa* only the inner petals are fused. In *Stenanona* the outer side of the inner petals is fused with the inner side of the outer petals, leaving the margins free.

3.4.6. Colour

Colours like white, yellow, and green prevail within the Annonaceae. Other colours found are red, pink, brown, purple, orange, grey, and even almost black. For most genera only a few colours have been reported, whereas other genera exhibit a wider spectrum of colours or they show two distinct colour types. Usually there is a difference in colour between juvenile and mature flowers.

A greenish or yellowish colour is reported for *Boutiquea, Cananga, Cleistopholis, Desmos, Malmea, Neostenanthera, Richella, Tetrameranthus,* and *Woodiellantha.*

White flowers are reported for, e.g., *Ambavia, Cleistochlamys, Mischogyne, Onychopetalum, Pseudephedranthus, Ruizodendron, Sageraea,* and *Toussaintia.* White flowers are prevailing in *Bocageopsis, Oxandra,* and *Unonopsis.*

Reddish to pinkish or purplish colours are reported for *Atopostema, Dennettia, Fitzalania, Haplostichanthus, Oncodostigma, Petalolophus, Reedrollinsia,* and *Stenanona.*

Genera which show a wide range of colours are, e.g., *Annona, Artabotrys, Duguetia, Friesodielsia, Goniothalamus, Guatteria, Mitrephora, Uvaria,* and *Xylopia.* In these genera one may find many of the following colours: whitish, yellowish, greenish, pinkish, reddish, purplish, orange, and brownish.

Two sets of colour types, often associated with a distinct morphology, are observed in a few genera. In *Uvaria* the species from eastern Asia and the Pacific have reddish to purplish flowers, whereas those from Africa and Sri Lanka have brownish, greenish, yellowish, or whitish flowers. *Sapranthus* is divided in two sections (Fries, 1959): the section *Sapranthus* with large reddish, purplish, or almost blackish flowers, and the section *Micro-Sapranthus* with much smaller, yellowish or greenish flowers. In *Asimina* species with greenish-white, pleasant-smelling flowers occur beside species with reddish- or purplish-brown, bad-smelling flowers.

In some genera the petals are tinged with a contrasting colour inside, usually reddish. This is found, for instance, in *Annona, Cymbopetalum, Isolona, Rollinia,* and *Uvariopsis.* In many genera the upper and the lower part at the inner side of the inner petals strongly differ in colour, e.g., in some species of *Duguetia, Guatteria, Mkilua, Monocyclanthus,* and *Xylopia.*

In several genera the inner and the outer petals or the inner and the outer side of the petals are different in colour, e.g., in *Exellia, Friesodielsia, Monanthotaxis, Monodora, Stelechocarpus, Uvariastrum, Uvariopsis,* and *Xylopia.*

Usually the petals are evenly coloured, but in *Monodora* and *Mitrephora* the petals are dotted with coloured spots.

3.4.7. Shape

Shape of the petals may vary from almost circular via ovate and obovate to linear (figs. 3, 4). Moreover, petals with special shapes or with appendages are found. Apex and base of the petals vary as well. Inner and outer petals may be similar or different in shape; usually the inner petals are somewhat narrower than the outer petals.

Linear to narrowly ovate petals are present in *Deeringothamnus, Fenerivia, Greenwayodendron, Hornschuchia, Isolona, Mezzettia, Polyalthia* p.p., *Reedrollinsia, Ruizodendron, Stenanona,* and *Xylopia* p.p. Broad petals are found in, e.g., *Cardiopetalum, Dennettia, Froesiodendron, Malmea, Monanthotaxis, Papualthia* (species from New Guinea), *Sageraea, Sphaerocoryne, Stelechocarpus,* and *Uvaria.*

The apex of the petals varies from acute in genera with valvate petals to roundish in genera with imbricate petals. In *Stenanona* the apices are elongate. The base of the petals varies from narrowly unguiculate to a broad base. In the latter situation the petals tend to fuse. Some taxonomists used the unguiculate base of some genera to define the tribe Mitrephoreae (Hooker & Thomson, 1855; Prantl, 1888). This character was found to be so diverse, and so difficult to observe in the closed flowers in herbarium specimens, that it is not used in the descriptions of the flowers in the present paper. The term 'mitriform' or 'mitre' is often used for genera which have marked unguiculate inner petals, the apices being connivent. This is found in *Boutiquea* (fig. 2m), *Goniothalamus, Mitrephora, Monodora, Neostenanthera, Orophea, Platymitra, Pseuduvaria* (fig. 2e), and *Richella.* In *Mitrephora, Monodora, Orophea,* and *Pseuduvaria* (fig. 2e) the unguiculate part is long and very narrow. A gradual transition from mitriform inner petals to closed (cleistopetalous) inner petals of a general shape is present.

In *Cymbopetalum* (fig. 4c) the inner petals are large, very thick, and boat-shaped, whereas the outer petals are smaller and rather thin.

Concave petals occur in a number of genera and this character is used in earlier classifications to delimit the tribe 'Xylopieae'. The whole petal may be concave, or only the basal part. Concave petals are found in, e.g., *Anaxagorea, Enantia* (fig. 3p), *Fissistigma, Meiogyne,* and *Unonopsis.* In *Artabotrys* (fig. 4b) and *Cyathocalyx* the petals are strongly concave with a rim enclosing the basal part, and a thread-like to blade-like, often flaring upper part. The same shape is found in the outer petals of *Boutiquea* and *Neostenanthera.*

In connate petals the tube may be narrowly cylindrical or widely cup-shaped. A narrowly cylindrical tube is found in *Isolona* (fig. 3m), *Papualthia* (species from the Philippines), and *Woodiellantha.* The tube is wide in the corolla of, e.g., *Asteranthe, Cardiopetalum, Disepalum* (fig. 1h), and *Hexalobus. Disepalum* differs from all other Annonaceae by its corolla shape. It has fused petals with a cylindrical tube narrowly enclosing the androgynophorous torus, then widening, and terminating in 4, 6, or 8 lobes with usually glandular tips.

Saccate petals are found in some genera: in *Asimina* all petals are saccate, in *Miliusa* only the inner petals.

Spirally twisting petals are observed in some species of *Dasymaschalon* with adhering petals.

Crisped margins are often found in the petals of *Hexalobus* and *Monodora,* and more or less in *Letestudoxa.*

Appendaged petals occur in a few genera. In *Rollinia* the outer petals have dorsal wings. In *Petalolophus* the inner petals are provided with large wings. In *Bocageopsis* p.p., *Gilbertiella,* and *Onychopetalum* the inner petals are provided with a hook-like tip which is curved inwards (downwards) (fig. 4g).

A fringe situated inside of the inner petals is present in *Mitrephora, Monodora,* and *Ophrypetalum.*

3.4.8. Size

The length of the petals varies considerably. The longest petals are measured in *Dasymaschalon* (up to 14.5 cm) and *Goniothalamus* (up to 16.5 cm). Also in *Asimina*

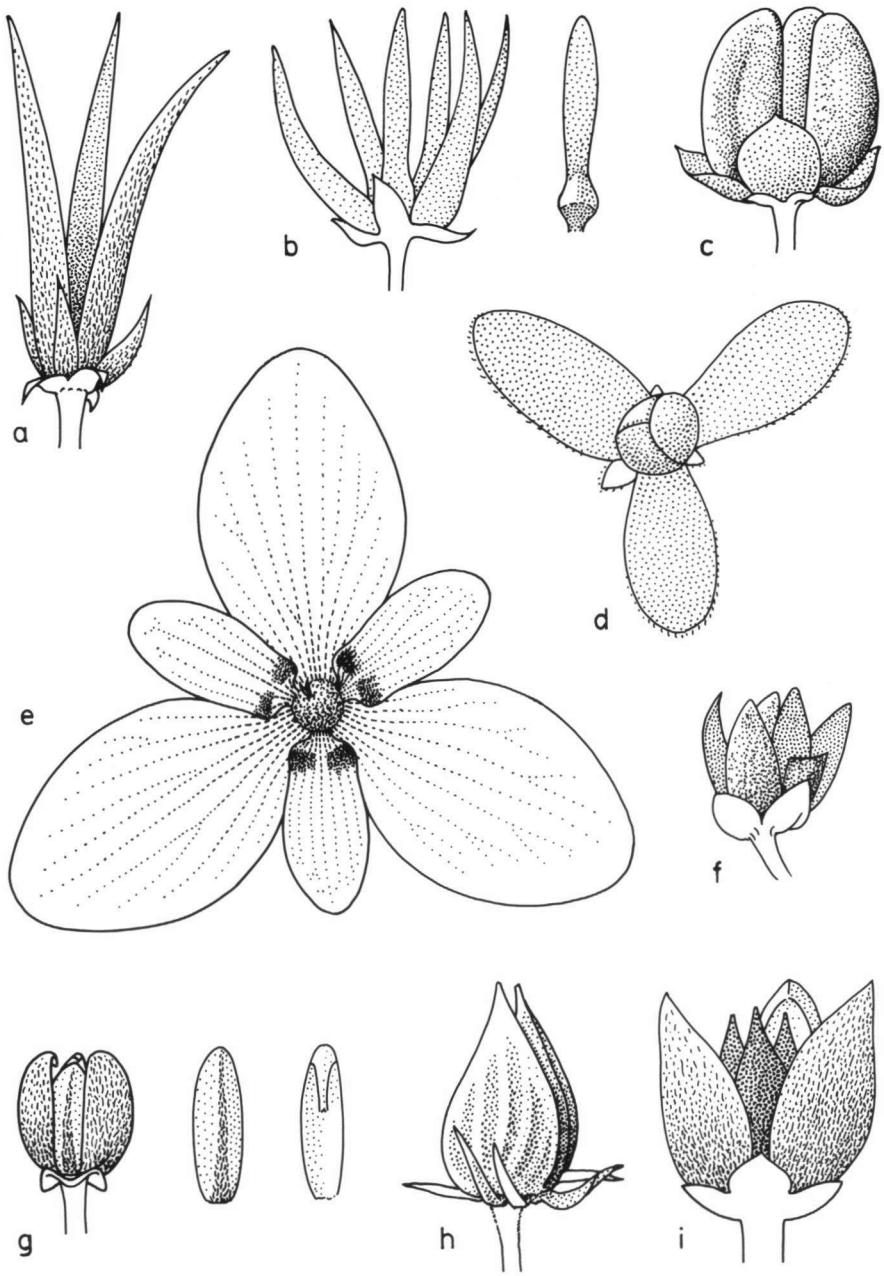


Fig. 4. Diversity in shape and relative size of the petals — a. *Piptostigma oyemense* (Hallé 2264); b. *Artabotrys thomsonii* (de Wit 12340); c. *Cymbopetalum stenophyllum* (Matuda 18588); d. *Cleistopholis glauca* (Lisowski 52356); e. *Asimina speciosa* (Cooley et al. 5937); f. *Duguetia stelechantha* (Prance et al. 215?); g. *Bocageopsis multiflora* (Prance et al. 5791); h. *Phaeanthus ophthalmicus* (Whitmore FRI 12307); i. *Fissistigma fulgens* (Ridley s.n.).

p.p., *Asteranthe, Reedrollinsia,* and *Sapranthus* the petals may be large. The shortest petals are less than 0.5 cm long: *Atopostema* (2–3 mm), *Bocagea* (2–4 mm), *Gilbertiella* (2–4 mm), *Monanthotaxis* (2–5 mm), and *Popowia* (outer ones 1–2 mm, inner ones 2–3 mm).

The outer and the inner petals may be equal (figs. 3j, m, 4b, f) or unequal in size. Either the inner or the outer petals can be smaller. Equal and subequal whorls are most common. It is, however, difficult to distinguish categories of relative sizes between inner and outer petals. A slight difference between outer and inner petals is found in, e.g., *Fissistigma* (fig. 4i), *Monanthotaxis,* and *Xylopia.*

A great difference is present in, e.g., *Annona* p.p., *Boutiquea, Cleistopholis* (fig. 4d), *Goniothalamus, Neostenanthera* (fig. 3o), *Richella,* and *Rollinia.* Rudimentary inner petals are present in some species of *Annona* (fig. 3c).

Very small and sepal-like outer petals (fig. 4a, h) are found in *Heteropetalum, Marsypopetalum, Mezzetiopsis, Miliusa, Phaeanthus, Piptostigma,* and *Pseuduvaria.*

The length/width ratio of the petals may be variable within a genus (e.g., 2–20 × in *Polyalthia,* 2–15 × in *Goniothalamus*) or only varying between small limits.

Growth of the petals during maturation of the flower may occur in the same rate as the sepals or it may be independent from the sepals. The latter situation is found in, e.g., *Diclinanona.*

3.4.9. Texture

As most specimens were examined as herbarium material, it was difficult to deduce the texture with certainty. Most flowers seem to have fleshy perianth parts. The thickness of the petals varies considerably between the genera. The thickest petals are found in *Anaxagorea, Cymbopetalum,* and *Enantia.* Thin petals are found in (most) species of *Asimina, Asteranthe, Isolona, Monodora, Piptostigma, Polyalthia, Ruizodendron, Sapranthus, Stenanona,* and *Uvaria.* In *Fitzalania* and *Pseuduvaria* only the outer petals are thin.

3.4.10. Floral glands

A number of genera possess a glandular, pulpous and corrugated tissue on the lower part of the inner surface of the inner petals. This is found in *Ancana, Asteranthe, Chieniodendron, Diclinanona* p.p., *Duguetia, Enicosanthum, Fitzalania, Meiogyne, Oncodostigma, Polyaulax, Pseuduvaria* p.p., *Sapranthus,* and *Tetrameranthus.* In many other genera the basal part is marked by a different colour or indument.

Sometimes there are two glands along the margins of the inner petals. This is occasionally found in *Anomianthus, Asimina* (fig. 4e), *Diclinanona, Ellipeiopsis, Porcelia,* and *Xylopia.*

In *Orophea* and *Pseuduvaria* sometimes two glands are present underneath the mitre. Keßler (1988) found quite a diversity of shapes and positions of these glands in *Orophea.*

3.4.11. Venation

In most genera the venation of the petals is not prominent. Venation is usually prominent in, e.g., *Asimina, Asteranthe, Cymbopetalum, Deeringothamnus, Des-*

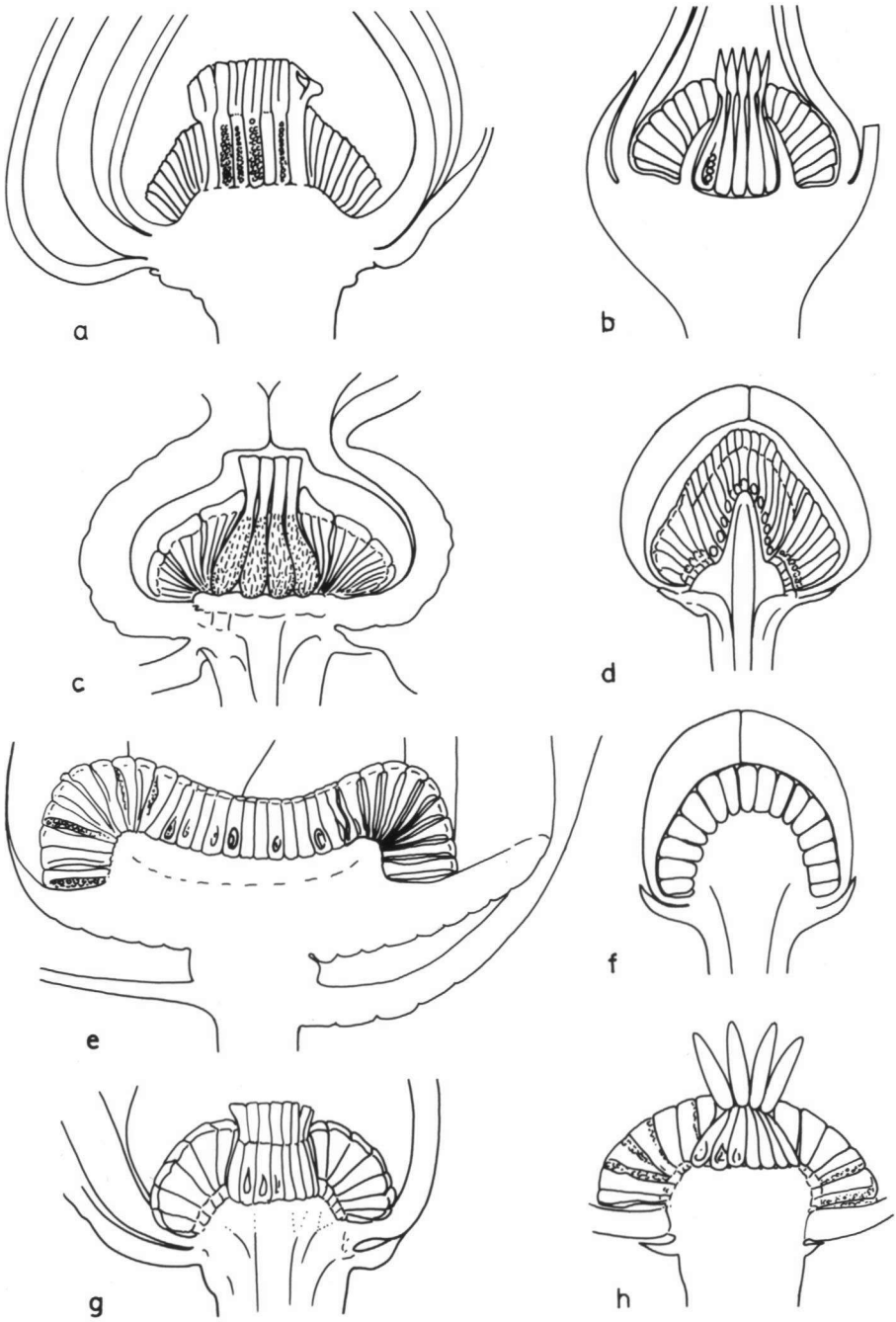


Fig. 5. Diversity in shape of the torus — a. *Uvaria elmeri* (Kartawinata 722); b. *Xylopia sp.* (Morawetz 11-22883); c. *Cyathocalyx biovulatus* (de Vogel 3425); d. *Annona* cf. *scandens* (Maas et al. 6194); e. *Disepalum anomalum* (Othman SAN 27317); f. *Uvariopsis dioica* (Winkler 909); g. *Guatteria dielsiana* (Maas et al. 6206); h. *Pseudoxandra sp.* (Morawetz 23-30883).

mopsis p.p., *Hexalobus, Monodora, Ophrypetalum, Reedrollinsia, Sapranthus,* and *Stenanona.* Only the longitudinal veins are prominent in *Cananga, Desmos, Ellipeiopsis* (fig. 1d), *Enicosanthellum, Fitzalania, Fusaea, Phaeanthus, Piptostigma,* and *Pseudartabotrys.*

3.4.12. Indument

Usually the petals possess an indument, sometimes they are glabrous or have a ciliate margin only. Similar to the sepals, simple hairs, stellate hairs, and scales may be found. Many genera show only one indument-type or distribution-type, whereas others are more diverse, e.g., *Anaxagorea, Cremastosperma, Isolona, Malmea, Mezzettiopsis,* and *Miliusa.*

Simple hairs are most common. Their distribution can be puberulent, pannose, tomentose, velutinous, villous, etc.

Stellate hairs are observed in, e.g., *Anomianthus, Cyathocalyx* p.p., *Cyathostemma, Dasoclema, Dielsiothamnus, Duguetia, Ellipeia, Ellipeiopsis, Neo-uvaria* p.p., *Pachypodanthium, Rauwenhoffia, Tetrameranthus, Tetrapetalum,* and *Uvaria.* In *Anaxagorea* only part of the neotropical species have stellate hairs. In *Annona* and *Rollinia,* both large genera, only few species have stellate hairs. In *Meiocarpidium* only the the inner petals have stellate hairs, whereas the outer petals have scales.

Scales are otherwise only found on the petals of part of the species of *Duguetia.* In *Uvaria,* the stellate hairs sometimes have a scale-like appearance.

In most genera the petals are hairy throughout. Ciliate petals occur in part of the species of many genera as well as in *Phoenicanthus* and *Sageraea.* An indument is lacking in part of the species of many genera as well as in *Cleistopholis* and *Fenerivia.* In many genera the inner side of all petals is glabrous. In a few genera only the inner petals are (almost) glabrous: *Boutiquea, Fissistigma,* the Asiatic species of *Friesodielsia, Schefferomitra,* and in some species of *Xylopia.* In *Bocageopsis, Onychopetalum,* and *Unonopsis* the inner petals often have an indument only along the faintly keeled primary vein. In *Oreomitra, Platymitra,* some species of *Polyceratocarpus* (fig. 3n), and *Tetrameranthus* the inner side of the inner petals is glabrous along the lower part of the margin.

3.5. Torus

Although diverse in shape, the torus is usually composed of a broad basal part on which the stamens are arranged and a central (apical) part bearing the carpels (fig. 5). The general outline of the torus varies from ovoid to depressed ovoid, from cylindrical to cushion-shaped, or it is shallowly conical, trapezoid, flat, or slightly concave. The apex of the torus may be slightly to deeply concave, flat, or it may be (depressed) ovoid. Within a genus the shape usually varies between certain limits, only in *Tetrameranthus* two very different shapes are found. The torus may be hairy or glabrous. Narrowly to depressed ovoid and cylindrical shapes are most common.

A flat torus is common in *Artabotrys* p.p., *Atopostema, Cyathocalyx* p.p. (fig. 5c), *Gilbertiella,* and *Monanthotaxis* p.p. A shallowly conical torus with a flat apex is commonly found in *Cyathostemma, Dasymaschalon, Mischogyne, Rauwenhoffia, Tetrapetalum, Uvaria* (fig. 5a), and *Uvariastrum.*

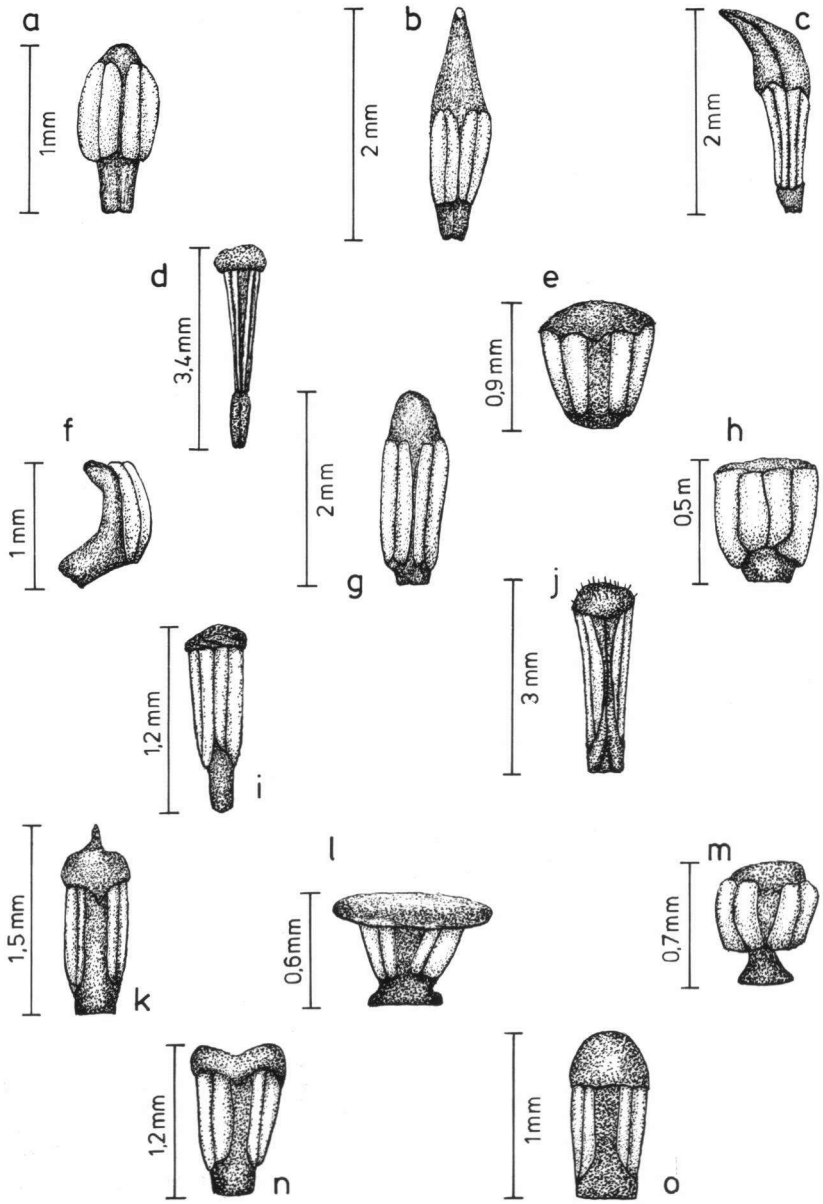


Fig. 6. Diversity in shape of the stamens and their apices — a. *Miliusa villosa* (Kerr 1078); b. *Bocageopsis canescens* (Prance et al. 5929); c. *Fissistigma fulgens* (Ridley s.n.); d. *Annona monticola* (Anderson 11804); e. *Artabotrys insignis* (Letouzey 12141); f. *Miliusa villosa*, lateral view (Kerr 1078); g. *Deeringothamnus rugelii* (Norman s.n.); h. *Pseuduvaria rugosa* (Lörzing 5597); i. *Rollinia parviflora* (Glaziou 2120); j. *Pseudartabotrys letestui* (Le Testu 1432); k. *Duguetia neglecta* (Maas & Tawjoeran, LBB 10791); l. *Cleistochlamys kirkii* (Vollesen 2957); m. *Monanthotaxis buchananii* (Harris 2594); n. *Polyalthia rumphii* (Jacobs 5273); o. *Desmos chinensis* (Maxwell 75-431).

An enlarged and variously shaped torus, which is sometimes constricted at the base is observed in *Asimina* p.p., *Dennettia, Monocarpia, Monocyclanthus, Polyceratocarpus, Uvariastrum, Uvariodendron,* and *Uvariopsis.*

A deeply concave torus is typical of *Fusaea, Ophrypetalum,* and *Xylopia* p.p. (fig. 5b). In *Xylopia* the torus is concave in the neotropical species and part of the African species. It is more or less flat in the Asiatic and the remaining African species.

A torus with a concave apex and an ovoid apicule is common in *Annona* (fig. 5d), *Duguetia, Rollinia,* and *Pachypodanthium.*

Disepalum (fig. 5e) and *Enicosanthellum* have a cushion-shaped torus. Also in *Duckeanthus* the torus is very broad. *Toussaintia* has a long cylindrical torus.

In genera with both unisexual and bisexual flowers (see below), the torus is narrowest in unisexual flowers.

3.6. Sex distribution

In general the flowers of Annonaceae are bisexual, but in a number of genera unisexual flowers are found. From the herbarium material it cannot be deduced whether these genera are monoecious or dioecious. In most of the genera with unisexual flowers, male flowers are found beside bisexual flowers but not in one herbarium specimen: these genera are probably androdioecious. In these genera the bisexual flowers have a large number of carpels and a small number of stamens.

Androdioecism in the given sense is observed in (species of) *Anonidium, Diclinanona, Ephedranthus, Greenwayodendron, Malmea, Oxandra, Polyceratocarpus, Pseudephedranthus, Pseuduvaria,* and *Raimondia.* In *Diclinanona* and *Pseuduvaria* (most species) also species with only unisexual flowers are found. This condition is also present in *Stelechocarpus* and *Uvariopsis.* In the latter genera male and female flowers are borne on different heights of the trunk.

3.7. Stamens

3.7.1. Number

The majority of the Annonaceae have a large number of stamens (> 12). In that case the exact number is not counted. The largest numbers of stamens occur in, e.g., *Afroguatteria, Annona, Asimina, Dennettia, Disepalum, Fusaea, Hexalobus, Monocyclanthus,* and *Toussaintia.* About 6–12 stamens are counted in: e.g., *Ambavia, Atopostema, Bocageopsis, Deeringothamnus* p.p., *Dendrokingstonia, Gilbertiella, Mezzettia, Mezzettiopsis, Miliusa* p.p., *Monanthotaxis* p.p., *Onychopetalum, Platymitra, Popowia,* and *Sageraea.* In *Bocagea* and *Hornschuchia* flowers with only 6 stamens are found. *Orophea* has flowers with 3 or 6 stamens.

3.7.2. Arrangement

In most genera the stamens are (more or less) spirally arranged and tightly packed, the latter due to the large number of stamens. In some genera with (relatively) few stamens different situations may be encountered.

In *Atopostema, Bocagea, Hornschuchia, Mezzettiopsis, Monanthotaxis* p.p., and *Orophea* the very few stamens are arranged in one whorl.

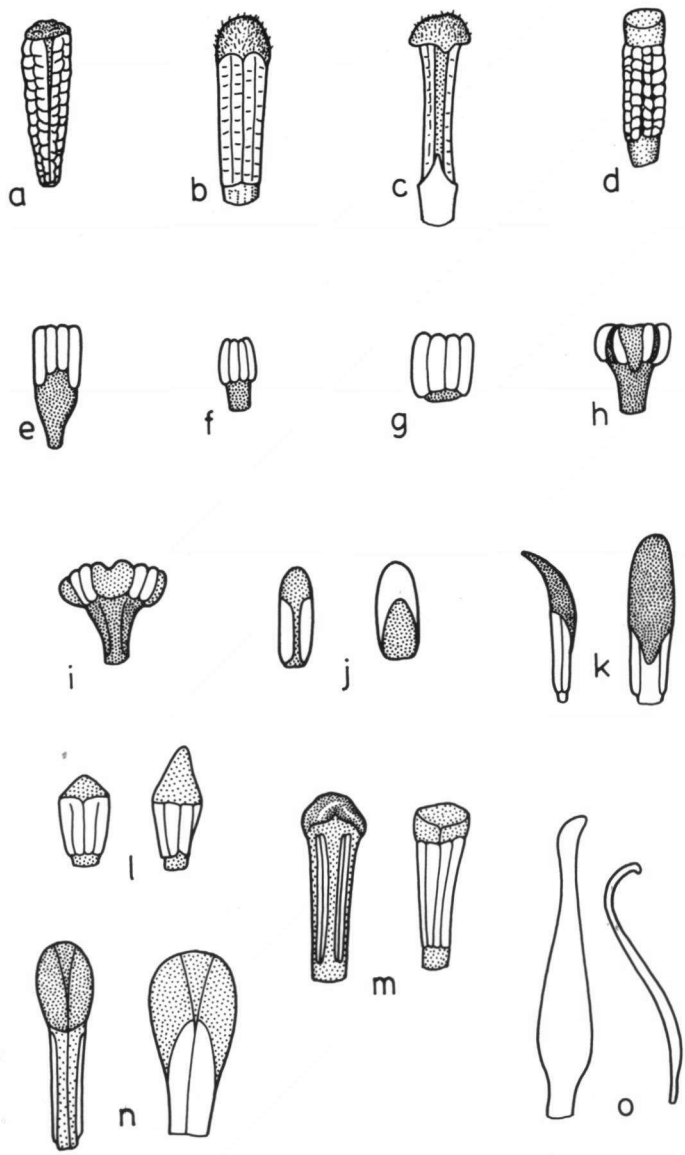


Fig. 7. Special stamen types — a. *Cardiopetalum calophyllum* (Maguire et al. 56954); b. *Neostenanthera hamata* (Versteegh & den Outer 673); c. *Xylopia grandiflora* (Lorence M23); d. *Xylopia aethiopica* (Bos 6296); e. *Annona tenuiflora* (de Granville B4878); f. *Platymitra macrocarpa* (Okada 3457); g. *Duguetia rhizantha* (Peckolt s.n.); h. *Monanthotaxis letestui* var. *hallei* (Hallé & Le Thomas 2); i. *Neo-uvaria acuminatissima* (Lörzing 5546); j. *Mezzettia leptopoda* (Muin Chai SAN 29839): left adaxial view, right lateral view; k. *Tetrameranthus pachycarpus* (Klug 1216): left lateral view, right abaxial view; l. *Ancana stenopetala* (Coveny 10627): left general shape, right inner stamen; m. *Pyramidanthe prismatica* (Maingay 74): left inner stamen, right general shape; n. *Uvaria latifolia* (Teijsmann s.n.): left fertile stamen, right staminodial stamen; o. *Anaxagorea javanica* var. *tripetala* (Kostermans 14010): staminodes, abaxial (left) and lateral (right) view.

In *Alphonsea* and *Miliusa* the stamens are imbricate [a term used by Hooker & Thomson (1855): tribe Saccopetaleae, and Bentham (1862): tribe Miliuseae], leaving part of the thecae free. These genera have relatively few stamens on a relatively long torus. In *Toussaintia* the numerous stamens are horizontally arranged on the long torus (fig. 2b).

The stamens are loosely packed in some genera with relatively few stamens per flower, e.g., in *Bocageopsis, Deeringothamnus, Greenwayodendron, Onychopetalum,* and *Oxandra.*

3.7.3. Shape

In general, the stamens of the Annonaceae are narrowly oblong to oblanceoloid, with a very short filament, two linear thecae, and a shield-like apical prolongation of the connective (fig. 6). Within this general concept a great variety in shapes and sizes is found. The stamens are often characteristic for genera.

More or less flattened stamens are found in, e.g., *Anaxagorea, Boutiquea, Enantia, Neostenanthera,* and *Uvaria* p.p. Very long and narrow stamens are typical of *Annona* (fig. 6d), *Uvariastrum,* and *Uvariodendron.* Very short and broad stamens occur in, e.g., *Artabotrys* (fig. 6e), *Cleistopholis, Dendrokingstonia, Monodora, Piptostigma,* and *Pseuduvaria* (fig. 6h). Such stamens, but with a distinct filament, are also found in *Monanthotaxis* (fig. 6m), *Neo-uvaria* (fig. 7i), and *Sageraea.*

In most genera the filament is (nearly) as broad as the anther, but in a few genera the basal part of the filament is sometimes narrowed. This is observed in *Anaxagorea, Annona,* and *Hexalobus.* In *Cleistochlamys* (fig. 6l) the base of the filament is broadened. In *Atopostema* the stamens are basally fused forming a ring on which the stamens are placed.

3.7.4. Length

The length of the stamens varies from 0.4 to 7 mm. In the majority of the genera the stamens are less than 2 mm long. The longest stamens are measured in *Mischogyne* and *Uvaria*: both up to 7 mm long. Stamens up to 5 mm occur in *Annona, Hornschuchia, Onychopetalum,* and *Uvariastrum.* In *Atopostema, Cleistochlamys, Cleistopholis, Monodora, Ophrypetalum, Polyaulax, Toussaintia,* and *Uvariopsis* stamens of more than 1 mm were never measured.

3.7.5. Texture and colour

The texture of the stamens is sometimes difficult to describe and may depend also on the age of the flower (sometimes fleshy in very young flowers). In most genera the texture of the stamens is more or less fleshy to herbaceous. The latter situation is, among others, found in *Cremastosperma* and *Pseudoxandra.* An indurate (more or less lignified) texture is found in *Cananga, Duckeanthus, Fusaea, Goniothalamus, Guatteria, Guatteriopsis, Heteropetalum, Letestudoxa, Mezzettia, Pseudartabotrys, Uvaria* (in 2 species), and *Xylopia.*

Glandular dots are sporadically observed on the stamens of *Greenwayodendron* and also of *Oxandra* (Maas et al., 1986), and on the apices only in *Sapranthus.*

The colour of the stamens is not often recorded on the labels. It can be, e.g., white, cream, (orange-)yellow, orange, red, (red-)brown, and purple. In many flowers the colour of the connectives is contrasting with that of the petals and the stigmas.

3.7.6. Thecae

The bisporangiate thecae dehisce longitudinally. In *Mezzettia* also monosporangiate thecae seem to occur (Van der Heijden & Keßler, 1990; fig. 7j). Extrorse thecae are most common. Latrorse thecae are present in many genera (fig. 7h, i, k, n). Introrse thecae are found in *Mezzettia* p.p. (fig. 7j). Intermediate forms are present too.

The thecae are hardly to deeply embedded in the tissue of the anther (compare figs. 6a and 6j). The latter situation is found in indurate stamens. The thecae are raised in, for instance, *Alphonsea, Bocageopsis, Miliusa, Onychopetalum, Orophea,* and *Oxandra.*

Usually, when the thecae dehisce, the margins of the thecae turn outwards. They are involute (turned inwards) in a few genera with indurate stamens: *Goniothalamus* p.p., *Guatteria, Guatteriopsis, Letestudoxa,* and *Pseudartabotrys.*

In several genera with pollen in tetrads or polyads, the thecae are transversely septate (fig. 7a–d). This was observed in *Cardiopetalum, Cymbopetalum, Froesiodendron, Goniothalamus* p.p., *Hornschuchia, Mkilua, Neostenanthera, Porcelia, Richella, Trigynaea,* and *Xylopia.*

3.7.7. Apex of the connective

Usually the anthers are shielded by a broadened apical prolongation of the connective; there is a lot of variation in shape and texture of the apex of the stamens (figs. 6 & 7). It usually varies from a slightly concave disc to a semi-globose structure. In several genera a tongue-shaped or umbonate apex is found. The apex is usually characteristic for a genus. In *Tetrameranthus* two distinct types are found.

In a number of genera the apical prolongation of the stamens is very small or absent (figs. 6a, 7e, f, g), e.g., in *Alphonsea, Annona* p.p., *Bocagea, Duguetia* (one species), *Hornschuchia, Mezzettiopsis, Miliusa, Ophrypetalum, Platymitra, Raimondia,* and *Trigynaea.* In *Annona, Duguetia* (one species), and *Uvariopsis* there are species with and without apical prolongation. The absence of an apical prolongation is used by Prantl (1888) to define the tribe Miliuseae. For this type of stamens often the term 'miliusoid stamens' is used, whereas the term 'uvarioid stamens' applies to genera with a dilated apical prologation. Genera with 'miliusoid' stamens (sensu Prantl, 1888), nevertheless show much differences in shape. The term 'miliusoid' is only correct when strictly applied to Asiatic genera with such stamens. The term 'uvarioid' covers even a much greater diversity of stamen types, whereas *Uvaria* itself has a quite distinctive stamen type. Therefore, the term 'uvarioid' is not very appropriate to indicate a general type of stamen.

In *Ancana* (fig. 7l), *Chieniodendron, Fitzalania, Isolona, Meiogyne, Oncodostigma,* and *Polyaulax* the apices of the inner stamens are elongate, covering the carpels.

The texture of the apices is generally fleshy. Apices with a rigid texture are found in a number of genera. In those genera apices are often hairy (figs. 6j, 7b, c), while also shiny and papillose surfaces can be found. Shiny apices are present in (some species of) *Dasymaschalon, Desmos, Fissistigma, Friesodielsia, Letestudoxa, Mitrella, Pachypodanthium, Polyalthia, Pyramidanthe,* and *Sphaerocoryne.* Papillose apices are observed in species of *Annona, Asimina, Cymbopetalum, Duguetia, Froesiodendron, Guatteria, Heteropetalum, Monodora,* and *Pachypodanthium.*

3.7.8. Staminodes

Staminodes are observed in a few genera only (fig. 7m, n, o). Either the inner stamens or the outer stamens are modified into staminodes. In *Xylopia* both situations may be encountered.

In *Fusaea* and *Uvaria* (Asiatic species; fig. 7n), both with a large number of stamens, the outer modified into staminodes. In *Fusaea* the staminodes are much longer than the fertile stamens, thus forming a conspicuous ring around the stamens.

In most species of *Anaxagorea* the inner stamens are sterile (fig. 7o) and exceed the stamens and carpels in length. Often the tips seem to be glandular. According to Endress (1984b) staminodes with secretory structures are otherwise only found in Eupomatiaceae, Himantandraceae, and probably Degeneriaceae.

In *Atopostema* and *Orophea* p.p. staminodes alternate with the few fertile stamens.

In *Pseuduvaria,* which usually has unisexual flowers, sometimes some sterile stamens are present in female flowers.

3.8. Carpels

3.8.1. Number

The number of carpels varies from one to numerous within and between genera. Most genera have c. 6–20 carpels. Numerous carpels (> 20) are found in some species of, e.g., *Annona* (fig. 5d), *Anonidium, Cremastosperma, Disepalum* (fig. 5e), *Duguetia, Enicosanthellum, Fusaea, Guatteria, Letestudoxa, Polyalthia, Rauwenhoffia,* and *Uvaria.*

Less than 6 carpels are often found in, e.g., *Alphonsea, Ancana, Asimina, Bocagea, Bocageopsis, Cyathocalyx, Deeringothamnus, Diclinanona, Haplostichanthus, Hexalobus, Hornschuchia, Monocarpia, Onychopetalum, Oxandra, Polyaulax,* and *Sageraea.* Only one carpel is present in, e.g., *Cyathocalyx* p.p., *Dasoclema, Dendrokingstonia, Dielsiothamnus, Isolona, Mezzettia, Monodora,* and *Tridimeris.*

3.8.2. Fusion

The majority of the Annonaceae is apocarpous, both in flower and in fruit. Syncarpous fruits occur in a minority of genera. In the flowering stage fused carpels are found in *Annona, Anonidium, Fusaea, Pseudartabotrys, Raimondia,* and *Rollinia.* In *Annona* and *Rollinia* also flowers with free carpels are found; the carpels coalesce during fructification. Only the basal part of the carpels is fused (semisyncarpy).

The carpel of *Isolona* and *Monodora* is considered to be composed of several carpels (see Chapter 1). Longitudinal sutures, however, which may indicate a composed origin of the carpel of these two genera as suggested by Deroin (1985), were not traced by the present author. On the other hand, a longitudinal suture on the carpel is sometimes perceived in other genera, e.g., *Ambavia* (SEM-photographs; Morawetz & Le Thomas, 1988) and *Mezzettia.* According to Sinclair (1955) a longitudinal groove adaxially from the stigma down to the ovary is present in the carpels of all Annonaceae.

The carpels are usually sessile in flower, whereas in many genera they are stipitate in fruit. The carpels are shortly stipitate in the flowers of *Disepalum* p.p., *Enantia, Lettowianthus,* and *Neostenanthera.*

3.8.3. Shape

The carpels are variously shaped (fig. 8). The shape of the ovary depends on the number of carpels per flower as well as the number of ovules per carpel and varies from narrowly cylindrical [e.g., in *Rauwenhoffia, Polyceratocarpus* (fig. 8g), *Tetrapetalum,* and *Uvaria* (fig. 5a)] to broadly ovoid [e.g., in *Cyathocalyx, Isolona, Monanthotaxis, Monocarpia, Monodora, Pseuduvaria, Sageraea, Stelechocarpus, Tridimeris* (fig. 8k), *Unonopsis,* and *Uvariopsis* (fig. 5f)].

3.8.4. Length

The length of the carpels during anthesis normally varies from 0.5 to 10 mm. In one species of *Mischogyne* a length of 20 mm was measured. Other genera with long carpels (7–10 mm) are *Annona, Duguetia, Polyceratocarpus,* and *Xylopia.* In *Cleistochlamys, Mezzettiopsis, Mitrephora, Popowia, Rollinia,* and *Ruizodendron* the length never exceeds 1 mm.

3.8.5. Indument

An indument may be present or absent. In many genera both conditions are found. Often the ovary and the stigma are different in this respect.

Usually the ovary is hairy and the stigma more or less glabrous (fig. 8j). Sometimes the reverse is found: a glabrous ovary and a hairy stigma. This is observed in *Ruizodendron,* and in species of *Anomianthus, Cananga, Duguetia, Ephedranthus, Malmea,* and *Polyalthia.*

Glabrous ovaries with glabrous stigmas occur in species of many genera. In a few genera only glabrous carpels are observed: *Ambavia, Cleistochlamys, Cleistopholis, Malmea, Pseudoxandra,* and *Sageraea.* Occasionally the carpels are glabrous with longitudinal rows of hairs only, as found in, e.g., *Onychopetalum* (fig. 8i).

If present, the indument usually consists of simple hairs. Stellate hairs are found in, e.g., *Ellipeiopsis, Rauwenhoffia, Tetrapetalum,* and *Uvaria.* Scales are found in *Meiocarpidium.* A papillose ovary was once found in *Tetrameranthus.*

3.8.6. Style and stigma

The shape of the stigma differs between and within genera and varies from ellipsoid (fig. 8a, h, j), spheroid, ovoid, cylindrical, obconical, discoid, bilobed (fig. 8l), to a flat, lobed stigma (fig. 8k). All types are widely distributed within the family.

A style may be present or absent. In most genera it is either absent or very short. Genera with a distinctive style are, e.g., *Duguetia, Enicosanthellum, Fusaea, Goniothalamus, Letestudoxa, Mezzettia, Ophrypetalum, Pachypodanthium, Pseudartabotrys,* and *Xylopia.*

In a number of genera it is difficult to indicate the boundary between style and stigma. This situation is found in genera with a cup-shaped to horseshoe-shaped style and/or stigma (fig. 8e, m). The inner side is probably stigmatic. In some genera with a cup-shaped stigma, the stigma is longitudinally grooved, e.g., in *Asteranthe, Cardiopetalum, Dennettia, Hexalobus, Uvaria* (fig. 5a), and *Uvariodendron.*

Sometimes the stigma is replaced by a ciliate rim, e.g., in specimens of *Duguetia, Goniothalamus, Letestudoxa, Pseudartabotrys,* and *Xylopia.*

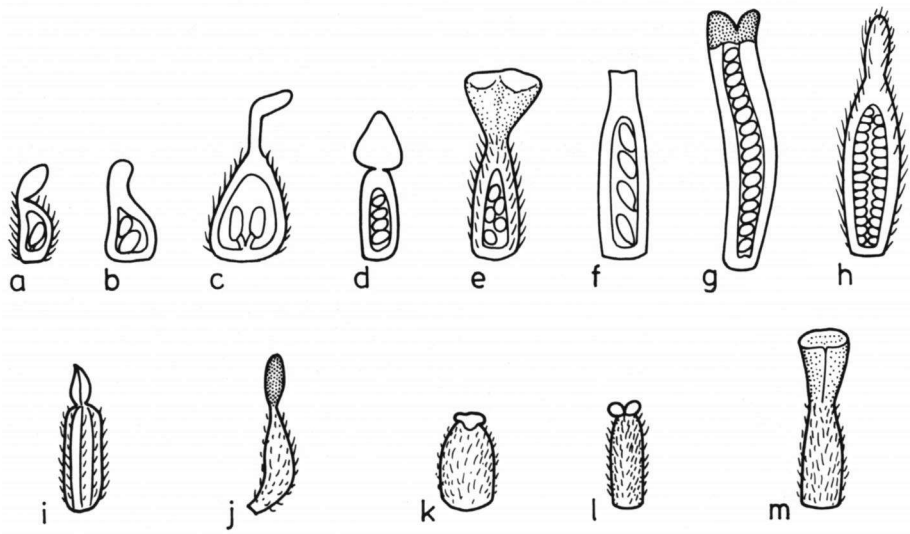


Fig. 8. Diversity in placentation types and shape of the carpels — a. *Trivalvaria nervosa* (Ridley s.n.); b. *Cleistopholis glauca* (Le Testu 8786); c. *Artabotrys scytophyllus* (Capuron 28510-SF); d. *Unonopsis mathewsii* (Plowman & Kennedy 5810); e. *Asteranthe asterias* (Reitsma & de Wilde 188); f. *Deeringothamnus pulchellus* (Moldenke 930); g. *Polyceratocarpus sp.* (J.J.F.E. de Wilde et al. 103); h. *Fissistigma sp.* (Jacobs 8290); i. *Onychopetalum lucidum* (Krukoff 8214); j. *Pachypodanthium staudtii* (Voorhoeve 1176); k. *Tridimeris hahniana* (Schatz et al. 1198); l. *Gilbertiella congolana* (Germain 4894); m. *Cardiopetalum calophyllum* (Maguire et al. 56954).

Observations on the shape of the stigma are often handicapped by the mucilaginous secretion which causes that the stigmas in ripe flowers to stick together in genera with densely aggregated carpels or by the fact that the stigmas are often released at the end of the female phase. The term compitum is used for such a sticky mass of stigmas (Carr & Carr, 1961; Endress, 1982). According to Carr & Carr (1961) pollen can germinate on one stigma and fertilize ovules in more than one carpel, when such a compitum is present. If this is also true for Annonaceae, this may explain why (nearly) all ovules develop well into seeds in fruits of genera such as *Annona* (fig. 5d), *Duguetia, Fusaea, Guatteria, Rollinia,* whereas in many other genera with less densely aggregated carpels part of the ovules and carpels are abortive.

3.9. Ovules

3.9.1. Number

The number of ovules per carpel ranges from one to numerous. In most genera less than 10 ovules are found. However, in several genera up to 20 ovules were counted. In some species of *Fissistigma* and *Uvaria* even up to c. 30 ovules are counted, whereas even a larger number is likely in *Isolona* and *Monodora.* In contrast, many genera are characterized by only 1 ovule per carpel. Also genera with

species with 1 ovule per carpel and with species with 2 or more ovules per carpel exist, e.g., *Disepalum, Friesodielsia, Goniothalamus, Monanthotaxis, Polyalthia, Popowia, Unonopsis,* and *Xylopia.*

3.9.2. Placentation

Placentation of the ovule may be lateral (= marginal) or basal (fig. 8a–h), rarely apical. In some genera both species with lateral and with basal placentation are found, e.g., *Cremastosperma, Disepalum, Friesodielsia, Monanthotaxis, Polyalthia, Popowia, Unonopsis,* and *Xylopia.*

Lateral placentation occurs in the majority of the genera. The ovules may be arranged in a single row or in two rows. A 2-seriate placentation is the common situation in genera with large numbers of ovules, e.g., *Asimina, Fissistigma* (fig. 8h), *Tetrapetalum, Trigynaea, Uvariastrum,* and *Uvaria.* In a 2-seriate placentation the ovules of the two rows may be in two parallel rows or alternating. The first situation is most common. The latter situation is found in *Asteranthe* (fig. 8e) and *Hexalobus,* and according to Verdcourt (1969b) also in some species of *Uvariodendron.*

A 1-seriate placentation is usually found in genera with few ovules per carpel, in, e.g., *Ancana, Bocageopsis, Cardiopetalum, Deeringothamnus, Monanthotaxis,* and *Unonopsis* (fig. 8d). A 1-seriate placentation of 20 ovules was once found in *Polyceratocarpus* (fig. 8g), but a similar situation may be found in *Uvariodendron* (Verdcourt, 1969b). In several genera (e.g., *Sapranthus*) both 1-seriate and 2-seriate placentations are found.

In most genera with a lateral placentation the ovules are inserted horizontally. They are upwards directed in, e.g., *Deeringothamnus* (fig. 8f), *Dasymaschalon, Desmos, Monanthotaxis* p.p., and *Xylopia.*

The ovules cover the surface of the whole ovary wall in *Isolona* and *Monodora.* As far as could be observed the ovules are evenly distributed over the ovary wall. Scattered ovules are also reported for *Exospermum* (Winteraceae). In this genus, however, the ovules are initiated in a single row on 2 separate placentas and become aligned in different directions in mature carpels (Sampson & Tucker, 1978).

A basal placentation is found in carpels with 1 or rarely 2 ovules per carpel. The first situation is present in, e.g., the genera *Annona, Anonidium, Cremastosperma* p.p., *Duguetia, Fusaea, Guatteria, Guatteriopsis, Heteropetalum, Oxandra, Pachypodanthium, Raimondia, Rollinia, Trivalvaria* (fig. 8a), and *Woodiellantha.* Two basal ovules are found in *Anaxagorea, Artabotrys* (fig. 8c), and *Polyalthia* p.p.

Subbasal ovules are often present in genera with two ovules, one being lateral, the other subbasal. This is present in, e.g., *Cleistopholis* (fig. 8b), *Mezzettia, Neouvaria,* and *Tetrameranthus.*

An apical placentation is found in some species of *Cremastosperma.* Fries (1959) reports a nearly apical placentation in *Pseudoxandra,* the ovule being pendulous, as well.

3.10. Smell

The smell of the flower is only rarely mentioned on the labels. Both pleasant and unpleasant smells are reported. Pleasant smells are most common; unpleasant smells are reported for *Sapranthus* and few *Duguetia*-species. For the latter genus there are

more reports about pleasant smells. For some genera several times the smell is mentioned, whereas for most genera records are lacking. More information on this subject can be found in studies on the flower biology (see for references Gottsberger, 1988).

Oil cells present in flowers of several genera may produce smell during flowering. When dissecting flowers, small cavities with fluid were sometimes noticed in the tissues of the flower parts. According to Diels (1912) the large-winged inner petals of *Petalolophus* are rich in oil cells.

4. DISTRIBUTION OF FLORAL FEATURES IN THE ANNONACEAE

4.1. Grouping of genera

It does not fit in the framework and purpose of this study to present a new classification of the family. The presentation and discussion of floral features in this paper is, however, facilitated by an informal classification of the genera into groups. The following groups are recognized.

The following considerations underly this informal classification:

- Groups are based on combinations of character states (table 3), in which the frequent presence or absence of certain features is decisive.
- Characters of the flowers, and especially those of stamens, carpels, and torus, are weighed most heavily.
- Discrepancies with non-floral features are avoided as much as possible, and as far as information goes.
- Groups are geographically coherent (table 4).

Elaboration and discussion of the floral characters of each of the groups is given in the present chapter, discussion of the distribution of character states is postponed to chapter 5.

4.2. Key to the groups

As a worldwide generic revision of the Annonaceae in the series The Families and Genera of Vascular Plants by P.J.A. Keßler is expected to be published within a short time, including keys to the genera, a key to the genera based on flowers only is not given here. For the time being one is referred to the generic keys made by Fries (1959), Hutchinson (1964), or those in local floras. The most recent generic key to neotropical Annonaceae is the synoptical key made by Maas et al. (1983). Those involved with African Annonaceae are advised to use: Flore du Congo Belge et du Ruanda-Urundi (Boutique, 1951), Flore du Gabon (Le Thomas, 1969), Flora of West Tropical Africa (Hutchinson & Dalziel, 1954), Flora Zambesiaca (Robson, 1960), Flora of tropical East Africa (Verdcourt, 1971a). Keys to the Asiatic genera are provided by the Flora of Ceylon (Huber, 1985) and Sinclair's revision of the Malayan Annonaceae (Sinclair, 1955).

Table 2. Informal groups in alphabetical order.

1. Annona-group: *Annona, Anonidium, Raimondia, Rollinia.*
2. Cremastosperma-group: *Cremastosperma, Ephedranthus, Malmea, Oxandra, Pseudephedranthus, Pseudoxandra, Ruizodendron.*
3. Cymbopetalum-group: *Bocagea, Cardiopetalum, Cymbopetalum, Froesiodendron, Hornschuchia, Mkilua, Porcelia, Trigynaea.*
4. Duguetia-group: *Duguetia, Pachypodanthium.*
5. Friesodielsia-group: *Artabotrys, Cyathocalyx, Dasoclema, Dasymaschalon, Desmos, Fissistigma, Friesodielsia, Mitrella, Monocarpia, Pyramidanthe, Schefferomitra, Sphaerocoryne.*
6. Fusaea-group: *Afroguatteria, Disepalum, Duckeanthus, Enicosanthellum, Fusaea, Letestudoxa, Pseudartabotrys.*
7. Guatteria-group: *Guatteria, Guatteriella, Guatteriopsis, Heteropetalum.*
8. Hexalobus-group: *Asimina, Asteranthe, Deeringothamnus, Diclinanona, Hexalobus, Isolona, Monodora, Ophrypetalum, Toussaintia.*
9. Meiogyne-group: *Ancana, Chieniodendron, Guamia, Meiogyne, Oncodostigma. Polyaulax.*
10. Miliusa-group: *Marsypopetalum, Miliusa, Phaeanthus.*
11. Mitrephora-group: *Fitzalania, Mezzettiopsis, Mitrephora, Oreomitra, Orophea, Petalolophus, Platymitra, Popowia, Pseuduvaria.*
12. Monanthotaxis-group: *Atopostema, Exellia, Gilbertiella, Monanthotaxis.*
13. Polyalthia-group: *Enicosanthum, Fenerivia, Haplostichanthus, Papualthia, Polyalthia, Sphaerothalamus, Trivalvaria, Woodiellantha.*
14. Sageraea-group: *Alphonsea, Phoenicanthus, Sageraea, Stelechocarpus, Tridimeris.*
15. Sapranthus-group: *Desmopsis, Reedrollinsia, Sapranthus, Stenanona.*
16. Unonopsis-group: *Bocageopsis, Onychopetalum, Unonopsis.*
17. Uvaria-group: *Anomianthus, Balonga, Cyathostemma, Ellipeia, Ellipeiopsis, Rauwenhoffia, Tetrapetalum, Uvaria.*
18. Uvariastrum-group: *Dennettia, Dielsiothamnus, Meiocarpidium, Mischogyne, Monocyclanthus, Polyceratocarpus, Uvariastrum, Uvariodendron, Uvariopsis.*
19. Xylopia-group: *Boutiquea, Cananga, Goniothalamus, Neostenanthera, Richella, Xylopia.*
20. A number of genera that cannot be accommodated in one of the groups: *Ambavia, Anaxagorea, Cleistochlamys, Cleistopholis, Dendrokingstonia, Enantia, Greenwayodendron, Lettowianthus, Mezzettia, Neo-uvaria, Piptostigma, Tetrameranthus.*

Table 3. The informal groups of genera with some important character states. The genera not accommodated in one of the groups, are listed separately (group 20).

1 = Buds consisting of: S = sepals, P = petals, A = open bud;
2 = Aestivation of the sepals: A = apert, I = imbricate, V = (reduplicate-)valvate;
3 = Aestivation of the petals: A = apert, I = imbricate, V = (reduplicate-)valvate;
4 = Hairs: Si = simple, St = stellate and/or lepidote;
5 = Petals (both whorls): A = one whorl absent, E = (sub)equal, U = unequal;
6 = Texture of the stamens: F = fleshy, I = indurate;
7 = Septation of the anthers: S = septate, N = not septate;
8 = Number of ovules per carpel: F = c. 2–8, M = >8;
9 = Placentation: B = basal, L = lateral (or laminal).
Two character states separated by , = both states occur, predominant one is mentioned first.
Two character states separated by - = both states occur as well as intermediates.

	1	2	3	4	5	6	7	8	9
1. Annona-group	P,S	V,A	V	Si,St	E,U,A	F	N	1	B
2. Cremastosperma-group	P	I	I	Si	E	F	N	1	B,L
3. Cymbopetalum-group	S,P	V,I	V,I	Si	E,U	F	S	M,F	L
4. Duguetia-group	S	V	I,V	St	E,U	F	N	1	B
5. Friesodielsia-group	P,A	V,A	V,A	Si,St	U,E,A	F	N	1-M	L,B
6. Fusaea-group	S	V	I,V	Si	E	I,F	N	1,2	B,L
7. Guatteria-group	S	V	I,V	Si	E,U	I	N	1	B
8. Hexalobus-group	S,A	V,A	I,V,A	Si	E,U	F	N	M,F	L
9. Meiogyne-group	P	V,A	V,I	Si	E	F	N	M,F	L
10. Miliusa-group	P	V,A	V	Si	U	F	N	1,2	B,L
11. Mitrephora-group	P	V,A	V,I	Si	U,E	F	N	1-M	L,B
12. Monanthotaxis-group	P	V,A	V	Si	E	F	N	1-M	L,B
13. Polyalthia-group	P,A	V,I,A	V,I,A	Si	E,U	F	N	1,F	B,L
14. Sageraea-group	P	A,V	I,V	Si	E	F	N	F,M	L
15. Sapranthus-group	A,S	V,A	I,A	Si	E	F	N	M,F	L
16. Unonopsis-group	P	V	V	Si	E	F	N	F,1	L,B
17. Uvaria-group	S,P	V,A	I,V	St	E,U	F	N	1-M	L
18. Uvariastrum-group	S,P	V,A	V	Si,St	E	F	N	M,F	L
19. Xylopia-group	S,P	V,A	V	Si	U,E	I	S,N	1,F	L,B
20. *Ambavia*	P	I	I	Si	E	F	N	2	L
20. *Anaxagorea*	S,P	V,I	V,I	Si,St	E,U,A	F	N	2	B
20. *Cleistochlamys*	S	V	I	Si	E	F	N	1	B
20. *Cleistopholis*	P	I	I		U	F	N	2	L
20. *Dendrokingstonia*	P	I	I	Si	E	F	N	F	L
20. *Enantia*	S	V	V	Si	A	F	N	1	B
20. *Greenwayodendron*	P	I	I	Si	E	F	N	2	L
20. *Lettowianthus*	S	I	I	Si	E	F	N	2	L
20. *Mezzettia*	P	I	I	Si	E	F-I	N	2	L
20. *Neo-uvaria*	P	V,A	V,I	Si,St	E	F	N	1	B
20. *Piptostigma*	S,P	V	V	Si	U	F	N	F,M	L
20. *Tetrameranthus*	S	V,I	I,V	St	E	F	N	1,2	L

Table 4. Geographic distribution of the informal groups of genera recognized.

'+' gives an indication of the number of representatives within one group in each continent: +++ = genera restricted to one continent; ++ = genera equally distributed in two or more continents, or genus endemic to that continent in case of genera which are not included in one of the groups; + = only one or few genera or species present. The genera of group 20 are listed separately.

	Neotropics	Africa	Asia/Australia	U.S.A.
1. Annona-group	++	+	·	·
2. Cremastosperma-group	+++	·	·	·
3. Cymbopetalum-group	++	+	·	·
4. Duguetia-group	++	+	·	·
5. Friesodielsia-group	·	+	++	·
6. Fusaea-group	++	++	++	·
7. Guatteria-group	+++	·	·	·
8. Hexalobus-group	+	++	·	+
9. Meiogyne-group	·	·	+++	·
10. Miliusa-group	·	·	+++	·
11. Mitrephora-group	·	·	+++	·
12. Monanthotaxis-group	·	+++	·	·
13. Polyalthia-group	·	+	++	·
14. Sageraea-group	+	·	++	·
15. Sapranthus-group	+++	·	·	·
16. Unonopsis-group	+++	·	·	·
17. Uvaria-group	·	+	++	·
18. Uvariastrum-group	·	+++	·	·
19. Xylopia-group	+	++	++	·
20. *Ambavia*	·	++	·	·
20. *Anaxagorea*	++	·	+	·
20. *Cleistochlamys*	·	++	·	·
20. *Cleistopholis*	·	++	·	·
20. *Dendrokingstonia*	·	·	++	·
20. *Enantia*	·	++	·	·
20. *Greenwayodendron*	·	++	·	·
20. *Lettowianthus*	·	++	·	·
20. *Mezzettia*	·	·	++	·
20. *Neo-uvaria*	·	·	++	·
20. *Piptostigma*	·	++	·	·
20. *Tetrameranthus*	++	·	·	·

A synoptical key to the groups is given below. The numbers mentioned are the group numbers, as given in table 2.

Buds fully enclosed by the sepals
present: 1, (2), 3, 4, 5, 6, 7, 8, 13, 15, 17, 18, 19, 20
absent: all groups but groups 4 and 6

Indument of the flowers (or at least of outer petals)
scales: 4, 18
stellate hairs: 1, 4, 5, 17, 18, 20
simple hairs: all groups but group 4 (rarely present in group 17)

Aestivation of the sepals
imbricate: (1), 2, 3, 13, 14, 17, 20
(reduplicate-)valvate: all groups but group 2

Number of sepals
= 2: 6, 8, 14, 17, 18, 20
= 4: 8, 15, 20
= 3: all groups

Sepals enlarging considerably at maturity
present: 13, 19
absent: all groups

Sepals in bud entirely connate, often apex apiculate
present: 4, 6, 17
absent: all groups

Aestivation of the petals
imbricate: 2, 3, 4, (5), 6, 7, 8, 9, (11), 13, 14, 15, (16), 17, 20
(reduplicate-)valvate: all groups but group 2

Number of petals
< 6: 1, 5, 6, (8), 14, 17, 18, 20
> 6: 6, 8, 13, 15, 20
= 6: all groups

Petals fused
present: 1, 3, 6, 8, 10, 11, 13, 15, 17
absent: all groups

Marked glandular base inside the inner petals
present: 4, 8, 9, 11, 13, 15, 20
absent: all groups (rarely so in group 9)

Two lateral glands on the inner petals
present: 3, 8, 11, 17, 19
absent: all groups

Margins of petals crisped
present: 6, 8
absent: all groups

Outer petals small and sepal-like
present: 7, 10, 11, (13), 20
absent: all groups but group 10

Inner petals connivent
present: (3), 5, (7), 8, 11, 13, (14?), (18), 19, 20
absent: all groups

Petals winged (inner or outer petals)
present: 1, 11
absent: all groups

Unisexual flowers
present: 1, 2, 8, 11, 12, 14, 18, 20
absent: all groups

Apex of (most) stamens (sometimes inner or outer whorl different)
(almost) without apical prolongation: 1, 3, (4), 8, 10, 11, 12, 14, 18
umbonate: 4, 7, 18, 19, 20
elongate to tongue-shaped: 2, 3, 5, 8, (15), 16, 17, 19, 20
shield-like: all groups

Staminodes
present: (5), 6, 11, 12, 17, 19, 20
absent: all groups

Unicarpellate
present: 5, 8, 14, 16, (17), 18, 20
absent: all groups

(Synoptical key continued)

Unicarpellate
present: 5, 8, 14, 16, (17), 18, 20
absent: all groups

Ovule number and placentation
one, basal: 1, 2, 4, 5, 6, 7, 10, 11, 12, 13, 16, 19, 20
two, basal: 5, 13, 20
one or more, lateral, 1-seriate: all groups but 1, 4, and 7
many, lateral, 2-seriate: 3, 5, 8, 9, (10?), 11, 12, 14, 15, 17, 18?, 19, 20
numerous, laminal, covering whole ovary wall: 8

Geographic distribution
Neotropics: 1, 2, 3, 4, 6, 7, 8, 14, 15, 16, 19, 20
Africa: 1, 3, 4, 5, 6, 8, 12, 13, 17, 18, 19, 20
Asia: 5, 6, 9, 10, 11, 13, 14, 17, 19, 20
North America: 1, 8
Cultivated (all over the world): 1, (5), 19

4.3. Family description (floral characters only)

Annonaceae A.L. Jussieu, Gen. Pl. 283 (1789) ('Anonae').

Buds formed by sepals or petals, occasionally flower opening before anthesis. *Perianth* more or less clearly differentiated into sepals and petals. *Sepals* valvate, reduplicate-valvate, imbricate, or apert, (2), 3, (4), free or connate, 1–50 mm long, more or less fleshy, veins prominent or not, indument present or absent, hairs simple or stellate, rarely scales, margins ciliate or not, sometimes caducous. *Petals* valvate, imbricate, reduplicate-valvate, apert, or rarely transversely folded, (2, 3, 4), 6, (8, 9, 12), free or connate, both whorls (sub)equal or (strongly) unequal, occasionally all petals in one whorl, 2–165 mm long, more or less fleshy, veins prominent or not, indument present or absent, hairs simple or stellate, or rarely scales, margins ciliate or not, rarely wings present; inner petals sometimes connivent, sometimes glandular at the base inside, or with 2 marginal glands, rarely fringe present. *Torus* variously shaped. *Stamens* 6 to numerous, 0.4–7 mm long, filament small to absent and scarcely or not differentiated from the connective, anthers extrorse, latrorse, or rarely introrse, sometimes septate, sometimes staminodes present; apex of connective prolonged and dilated above the anthers, discoid, tongue-shaped, or umbonate, sometimes apical prolongation reduced or absent. *Carpels* free or fused, closed, 1 to numerous, 0.5–10 mm long, hairy or glabrous, style present or absent, stigma variously shaped; ovules 1 to numerous, basal, lateral and 1- or 2-seriate, or laminal. *Flowers* bisexual or unisexual, plants then monoecious or androdioecious.

4.4. Descriptions of groups

1. Annona-group (figs. 9, 10; table 5)

Buds depressed ovoid (sepals), (triangular-)lanceoloid to (broadly depressed) triangular-ovoid, or more or less spheroid and winged (petals). *Sepals* valvate, rarely reduplicate-valvate or imbricate, 3, free or connate, 1–30 mm long, fleshy, veins usually not prominent, indument present, hairs simple, occasionally stellate. *Petals* greenish, brownish, reddish, yellowish, or whitish, valvate or reduplicate-valvate, sometimes inner whorl imbricate, 6 or 3, free or connate, both whorls equal in length or inner whorl (strongly) reduced in length, 4–65 mm long, 1–7 × as long as wide, 2–11 × length of sepals, fleshy, sometimes very thick, veins usually not prominent, indument present, hairs simple or sometimes stellate, outer petals sometimes winged, inner petals sometimes basally differently coloured inside. *Torus* depressed ovoid with concave apex and ovoid apicule, (broadly) ovoid, or broadly cylindrical, sometimes with an ovoid apicule, rarely depressed ovoid with slightly concave apex. *Stamens* numerous (rarely to few), 0.5–6.2 mm long, extrorse; apex discoid or sometimes apical prolongation absent, glabrous or hairy, often fleshy or papillose. *Carpels* free or fused, numerous (rarely to few), 0.7–7 mm long, hairy to glabrous, style present or absent, stigma (narrowly) cylindrical, ellipsoid, obconical, lanceoloid, or broadly (ob)ovoid; ovule 1, basal. *Flowers* bisexual or male and then plants androdioecious.

Distribution – 4 genera in tropical America and Africa, incl. Madagascar.

Notes – The Annona-group is characterized by fruits which, unlike most Annonaceae, consist of fused carpels. In the flowering stage, both specimens with fused and with free carpels are found. Furthermore, the genera of this group have one basal ovule per carpel (figs. 9e, i, 10a). The torus is usually composed of a broad base on which the stamens are placed, and an ovoid apical part bearing the carpels (fig. 9a, e, h). The sepals and petals are usually valvate (fig. 9a, b), whereas the inner petals are often (much) smaller or even lacking (figs. 9j, 10g, j).

The delimitation of the genera is problematic. Although as a rule the flowers of *Annona* and *Rollinia* are easy to distinguish, some species are more or less intermediate. In fruiting or sterile state, these two genera can hardly or not be distinguished. *Raimondia* differs from *Annona* by its androdioecious flowers.

The affinities of the Annona-group to other groups are uncertain. *Anonidium* (fig. 10e) shows much similarity with the genera of the Fusaea-group with which it shares the large sepals, the hairy apices of the stamens, and the single, basal ovule. The long and narrow stamens of many *Annona*-species (fig. 9f) remind of those often found in the Uvariastrum-group. The torus is comparable in shape to that of *Duguetia* though larger.

Annona Linnaeus, Sp. Pl. (1753) 536.

Buds triangular-lanceoloid to broadly depressed triangular-ovoid (petals). *Sepals* valvate, 3, connate or rarely free, 1.2–18 mm long, fleshy, veins not prominent, indument present, hairs simple or occasionally stellate. *Petals* white, cream, greenish-

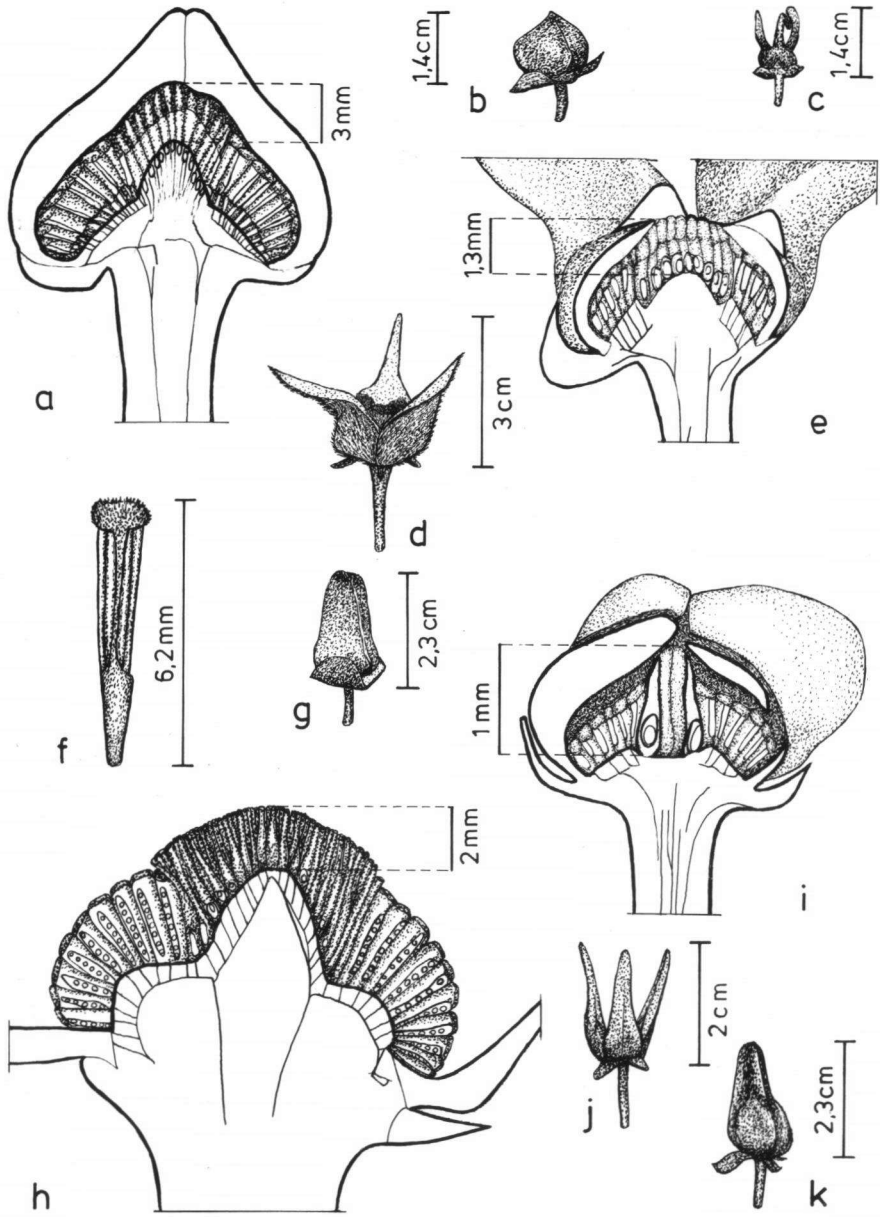


Fig. 9. Annona-group — a. *Annona scandens* (Maas et al. 6033): longitudinal section; b. *Annona amazonica* (Daly et al. 3954): bud; c. *Rollinia laurifolia* (Semir & Lima 4811): bud; d. *Raimondia cherimolioides* (Breteler 4469): flower; e. *Rollinia peruviana* (Maas et al. 5986): longitudinal section; f. *Annona purpurea* (van Rooden 821): stamen; g. *Annona giganthophylla* (Thomas 3177): bud; h. *Annona sericea* (Prance 25302): longitudinal section; i. *Rollinia cuspidata* (Maas et al. 6295): longitudinal section; j. *Annona reticulata* (Lewalle 2230): flower; k. *Raimondia cherimolioides* (Breteler 4469): bud.

yellow, (greenish-)brown, pale orange, or (purplish-)red, valvate or reduplicate-valvate, sometimes inner whorl imbricate, 6 or 3, free or connate, both whorls more or less equal in length, 6–65 mm long, or often inner whorl strongly reduced, outer ones 8–29 mm long, inner ones 1.5–11 mm long, 1–6 × as long as wide, 5–11 × length of sepals, fleshy, sometimes very thick, veins usually not prominent, indument present, hairs simple or occasionally stellate, inner petals sometimes basally differently coloured inside. *Torus* very broadly ovoid with a concave apex and a broadly ovoid apicule, or broadly cylindrical with an ovoid apex. *Stamens* numerous, 1.1–6.2 mm long, extrorse; apex discoid, or sometimes apical prolongation almost absent, glabrous, hairy, or papillose, sometimes fleshy. *Carpels* free or fused, numerous, 1.3–7 mm long, hairy to glabrous, style present or absent, stigma broadly ovoid, lanceoloid, ellipsoid, (narrowly) cylindrical; ovule 1, basal. *Flowers* bisexual.

Lectotype – *A. muricata* Linnaeus.

Distribution – About 125 species in tropical America, incl. the most southern part of Florida, U.S.A., and in Africa, incl. Madagascar. Cultivated all over the tropics.

Note – *Annona* (figs. 9b, g, j, 10d, h, i, j) shows diversity in floral shape. *Annona ambotay* (fig. 10h) and *A. tenuiflora* are different from other *Annona*-species in their stamens, carpels, and torus. The stamens of these two species lack a discoid apical prolongation.

Specimens examined:

AFRICA — *A. glabra:* Bels 99 (BR). — *A. senegalensis:* Gbile et al. 1165 (WAG); Geerling & Bokdam 2086 (BR); Lanjouw 1334 (U); Oldeman 903 (BR); Vollesen 3181 (WAG). — *A. stenophylla:* Teixeira & Andrade 531 (BR); de Granville B4878 (U).

NEOTROPICS — *A. acuminata:* Mori & Kallunki 3337 (U). — *A. acutiflora:* Mautone 248 (U); Sucre & Braga S4598 (U). — *A. amazonica:* Daly et al. 3954 (U). — *A. ambotay:* Meneces 668 (U); Mori et al. 14946 (U); Rosa & Santos 2077 (NY); Schunke V. 6558 (US). — *A. angustifolia:* Ducke RB 19635 (U). — *A. aurantiaca:* Hatschbach et al. 36071 (U). — *A. cacans* var. *glabriuscula:* Reitz 5815 (U). — *A. coriacea:* Plowman et al. 8266 (U); Prance et al. 19181 (U). — *A. crassiflora:* Prance 19059 (U). — *A. deminuta:* Davidson & Jones 9728C (U). — *A. densicoma:* Jangoux & Bahia 284, 420 (U). — *A. dioica:* Beck 3340 (U), 5380 (U); Pires & Furtado 17146 (U). — *A. dumetorum:* Ekman 12351 (U). — *A. echinata:* Wullschlaegel 2 (U). — *A. foetida:* Breteler 4760 (U); Cid et al. 1967 (U). — *A. gigantophylla:* Thomas 3177 (U). — *A. haematantha:* Mori & Boom 14754 (U). — *A. hypoglauca:* Berg & Akkermans 1061 (U); Davidson & Jones 9488 (U); Diaz & Osores 661 (U); Jangoux & Bahia 512 (U); Krukoff 8378 (U); Ramirez 2010 (U); Tunqui 115 (U). — *A. impressivenia:* Prance et al. 3186 (U). — *A. jahnii:* Aristeguieta 5051 (U). — *A. malmeana:* Prance et al. 18911 (U). — *A. membranacea:* Fróes 11607 (U). — *A. montana:* Daly et al. D294 (U), D607 (U); Lobo et al. 160 (U); Oldenburger et al. 501 (U); Schunke V. 4860 (U); Wagner 632 (U). — *A. monticola:* Anderson 11804 (U). — *A. muricata:* Plowman 5943 (U); von Türckheim 3678 (B). — *A. nutans:* de Michel 40 (U); Pires & Furtado 17327 (U). — *A. paludosa:* Austin et al. 7231 (U); Daly et al. 901 (U); Pires 51904 (U). — *A. purpurea:* van Rooden 821 (U). — *A. pygmaea:* Hatschbach & Kummrow 37282 (U). — *A. reticulata:* Lewalle 2230 (U); Proctor 27547 (U). — *A. salzmannii:* dos Santos 494 (U). — *A. scandens:* Maas et al. 6033, 6194 (U); Prance et al. 23870 (U). — *A. sericea:* Cid & Ramos 1052 (U); Jonker-Verhoef & Jonker 358 (U); Lindeman 6133 (U); Prance 25302 (U). — *A. tenuiflora:* de Granville B4878 (U?); Krukoff 8813 (K). — *A. tomentosa:* Prance et al. 24752 (U). — *A. sp.:* Maas et al. 5990 (U); Stevens 9710

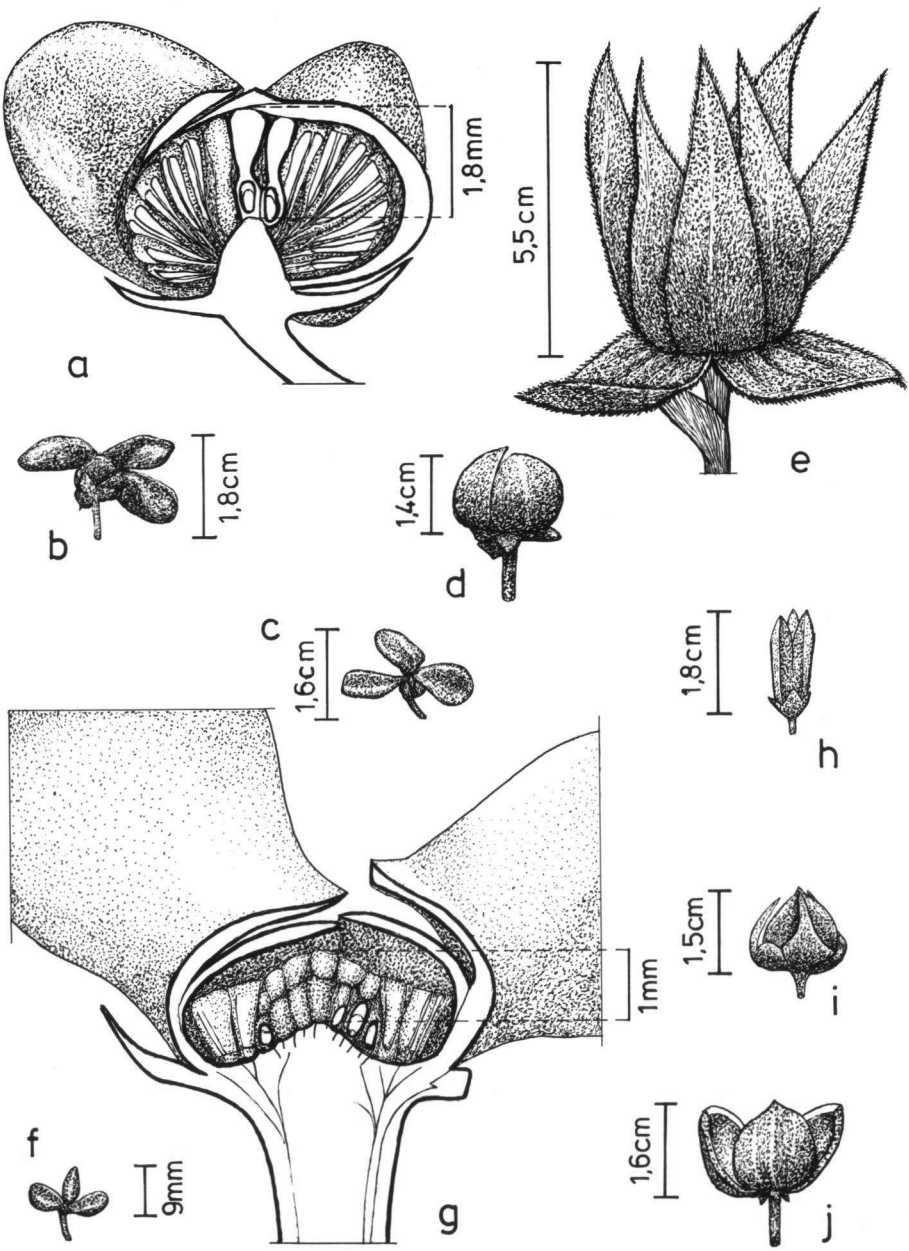


Fig. 10. Annona-group — a. *Rollinia parviflora* (Riedel s.n.): longitudinal section; b. *Rollinia exsucca* (BW 2665): flower; c. *Rollinia pittieri* (Burger & Matta 4703): flower (bud); d. *Annona densicoma* (Jangoux & Bahia 284): bud; e. *Anonidium mannii* (Aubréville G129): flower; f. & g. *Rollinia leptopetala* (Blanchet 3101): flower (bud) (f) and longitudinal section (g); h. *Annona ambotay* (Meneces 668): flower; i. *Annona sp.* (Maas et al. 5990): bud; j. *Annona hypoglauca* (Berg & Akkermans 1061): flower.

Anonidium Engler & Diels, Notizbl. Königl. Bot. Gart. Berlin 3 (1900) 56.

Buds depressed ovoid (sepals). *Sepals* valvate, reduplicate-valvate, or imbricate, 3, connate, 10–30 mm long, fleshy, rather thin, veins prominent, indument present, hairs simple. *Petals* green, valvate, 6, free, both whorls equal in length or outer ones slightly longer, 24–60 mm long, 2–7 × as long as wide, 2 × length of sepals, fleshy, veins prominent, indument present, hairs simple, inner petals basally differently coloured inside. *Torus* broadly cylindrical with a depressed ovoid apex, or depressed ovoid with an ovoid apex. *Stamens* numerous, 3–4 mm long in male flowers, 2.3 mm long in bisexual flowers, extrorse; apex discoid, hairy. *Carpels* fused, numerous, 2–3.5 mm long, glabrous, style present (long), stigma depressed obovoid; ovule 1, basal. *Flowers* androdioecious.

Lectotype – *A. mannii* (D. Oliver) Engler & Diels.

Distribution – 4 or 5 species in Africa, ranging from Nigeria to Tanzania.

Note – *Anonidium* (fig. 10e) in its perianth looks different from the other genera of the Annona-group, and rather resembles *Letestudoxa* and *Enicosanthellum*. The carpels and the torus of *Anonidium* resemble those of the members of the Annona-group.

Specimens examined:

A. floribundum: Le Testu 9149 (P). — *A. letestui:* Le Testu 9615 (BR). — *A. mannii:* Aubréville G129 (P); Christiaensen 1822 (WAG); Courtet s.n. (L); Devred 2153 (K, WAG); J.J.F.E. de Wilde 7930 (WAG).

Raimondia Safford, Contr. U.S. Natl. Herb. 16 (1913) 217.

Buds lanceoloid or (broadly) triangular-ovoid (petals). *Sepals* valvate, 3, free or connate, 2–3 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* cream, greenish, or yellow, valvate, 6, connate, inner whorl strongly reduced in size, outer ones 11–30 mm long, inner ones 4–6 mm long, 2 or 3 × as long as wide, 5–10 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner petals basally glabrous inside. *Torus* ovoid. *Stamens* numerous in male flowers, few in bisexual flowers, 1–1.3 mm long, extrorse; apical prolongation (almost) absent. *Carpels* fused, numerous, 1 mm long (indument and style/stigma not observed); ovule 1, basal. *Flowers* androdioecious.

Type – *R. cherimolioides* (Triana & Planchon) R.E. Fries.

Distribution – 2 species in South America: Colombia and Ecuador.

Note – Flowers of *Raimondia* (fig. 9d, k) resemble those of *Annona ambotay* and *A. haematantha*, which have narrow petals and small inner petals as well. *Annona ambotay* also lacks the apical prolongation of the stamens. *Raimondia tenuiflora*, later transferred to *Annona* by Fries (1959), differs from the other *Raimondia*-species, but does not fit in *Annona* very well, either. The status of *Raimondia* and of *Annona tenuiflora* need further examination.

Specimens examined:

R. cherimolioides: Breteler 4469 (U, WAG); Duque-Jaramillo 4682 (COL). — *R. quinduensis:* Augusto & Daniel 4560 (COL); de Rincón s.n. (COL); Santiago Diaz et al. 870 (COL), 985 (COL); Soejarto et al. 4015 (MO); Triana 4723 (COL), s.n. (BM).

Rollinia A.F.C.P. de Saint-Hilaire, Fl. Brasil. merid. 1 (1825) ed. qu. 28, t. 5.

Buds more or less spheroid, and gibbous to winged (petals). *Sepals* valvate, 3, free or connate, 1–4 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* (brownish- or yellowish-)green, (clear) yellow, cream, white, or red, valvate or sometimes inner whorl imbricate, 6, connate, inner whorl much smaller, outer ones 4–18 mm long, inner ones 2.5–7 mm long, 2–7 × length of sepals, fleshy, veins rarely prominent, indument present, hairs simple or sometimes stellate, inner side of petals usually differently coloured, outer petals dorsally winged. *Torus* depressed ovoid, sometimes with a slightly concave apex, or depressed ovoid with a concave apex and an ovoid apicule, or broadly cylindrical. *Stamens* numerous, 0.5–1.9 mm long, extrorse; apex discoid, fleshy. *Carpels* free or fused, numerous to few, 0.7–1.8 mm long, hairy or glabrous, style present (short) or absent, stigma ellipsoid, cylindrical, or obconical, glabrous; ovule 1, basal. *Flowers* bisexual.

Lectotype – *R. dolabripetala* (Raddi) R.E. Fries.

Distribution – About 45 species in Central and South America.

Note – *Rollinia* (figs. 9c, 10b, c, f) is easy to recognize by its 3-winged corolla. However, also a number of *Annona*-species have petals which are dorsally gibbous, making them look like some small-winged *Rollinia*-species. Except for the petals, *Rollinia* and *Annona* are highly alike, and may be one genus.

Specimens examined:

R. bahiensis: Bondar P3003 (F). — *R. cuspidata:* Croat 18727 (F, MO, NY), 19351 (GH, MO, NY); Killip & Smith 27650 (F); Krukoff 6017 (U), 6181 (A, NY, S, U); Maas et al. 6295 (U); Martius 2725 (M); McDaniel & Rimachi Y 20191 (US); Prance et al. 16689 (U); Rimachi 3235 (F); Schultes & Black 8564a (NY); Tessmann 4704 (B, G). — *R. danforthii:* Danforth 30 (F, GH). — *R. dolabripetala:* Duarte 4960, 4984 (MO); Ducke & Kuhlmann RB 16358 (S); Glaziou 15825 (C, S); Mosén 2396 (S), 3778 p.p. (S); Pereira et al. 4141 (MO); Porto 1792 (B). — *R. dolichopetala:* Asplund 18467 (NY, S). — *R. ecuadorensis:* Schultze-Rhonhof 2155 (S). — *R. edulis:* Barclay et al. 3629 (US); Idrobo 2547 (COL, F). — *R. emarginata:* Balansa 2296 (F, G); Glaziou 13507 (BR, C, G, LE); Hassler 3475 (A, B, G, MICH), 5202 (G, GH, UC); Kuntze s.n. (NY); Malme 2589 (S); Paretti & Rojas 10648 (MO); Prance et al. 19424 (U). — *R. exsucca:* BW 2665 (U), 5431 (BR, RB, U), 6507 (S, U); Irwin et al. 48207 (NY), 55108 (MICH, NY, U); Prévost 562 (U); Pulle 230 (S). — *R. ferruginea:* Kuhlmann RB 43586 (MO). — *R. herzogii:* Steinbach 5064 (F), 6454 (G), 6631 (F, G, S). — *R. insignis:* Krukoff 8239 (BR, F, MICH, NY, S, U); Ll. Williams 2685 (B). — *R. laurifolia:* Duarte 8583 (MO), 8605 (MO, NY); Irwin 2095 (F, MICH, NY, UC); Mexía 5311 (S); Semir & Lima 4811 (E, SP). — *R. leptopetala:* Blanchet 3101 (BR, F, G, GH, NY, OXF); Gardner 2033 (G, OXF); Glaziou 13508 (C, LE); Ule 7138 (B, L). — *R. membranacea:* P.H. Allen 6843 (F, NY); Calderón 1516 (NY); Skutch 4317 (NY); Standley 8365 (F), 21866 (GH, NY), 23022 (GH, NY). — *R. mucosa:* Dorantes 2997 (MO); Fuertes 1608 (F); Glaziou 2483 (BR); Killip & Smith 27231 (NY); Krukoff 1553 (NY); Ortiz & Martiniano 178 (F); Poiteau s.n. (G); Rimachi 1759 (NY); J.D. Smith 2058 (G, M, NY); R.F. Smith V3867 (VEN); Spruce 2403 (E, G, GOET); von Türckheim 4116 (BR); Ule 9371 (G); Ll. Williams 1965 (F). — *R. parviflora:* Glaziou 2120 (BR, C), 6077 (C); Kuhlmann RB 15325 (RB); Pereira 5139 (F, M); Riedel s.n. (M). — *R. peruviana:* Maas et al. 5986 (U); Torres 170 (U). — *R. pickelii:* Pickel 3004 (B, GH). — *R. pittieri:* Burger & Matta 4703 (MO, S); Huashikat 1080 (U); Jiménez 4042 (F); León 4355 (US). — *R. sylvatica:* Ducke s.n. (S); Mexía 5120 (S); Mosén 389 (S). — *R. ulei:* Ule 6425 (L). — *R. williamsii:* Fleischmann 319 (S), 437 (S), 590 (S); Rusby 766 (GH, NY); R.S. Williams 538 (NY). — *R. xylopifolia:* Duarte 2345 (GH); Gardner 307 (NY).

Table 5. List of character states found in the genera of the Annona-group.

	Annona	*Anonidium*	*Raimondia*	*Rollinia*
Flowers:				
perianth 3-merous	+	+	+	+
perianth 4-merous	(+)	–	–	–
hairs simple	+	+	+	+
hairs stellate	+	–	–	+
male	?	+	+	–
bisexual	+	+	+	+
Sepals:				
valvate	+	+	+	+
reduplicate-valvate	–	+	–	–
imbricate	–	+	–	–
connate	+	+	+,–	+,–
1–4 mm long	+	–	+	+
4–30 mm long	+	+	–	–
Petals:				
valvate	+	+	+	+
reduplicate-valvate	+	–	–	–
inner ones imbricate	+	–	–	+
3 in number	+	–	–	–
6 in number	+	+	+	+
inner ones much smaller	+	–	+	+
both whorls (sub)equal	+	+	–	–
4–20 mm long (outer ones)	+	–	+	+
20–65 mm long (outer ones)	+	+	+	–
winged to gibbous	–	–	–	+
Stamens:				
numerous	+	+	+,–	+
anthers extrorse	+	+	+	+
0.5–2 mm long	+	–	+	+
2–6.2 mm long	+	+	–	–
apex not prolonged	+	–	+	–
apex discoid	+	+	–	+
Carpels:				
connate	+,–	+	+	+,–
numerous	+	+	+	+,–
Ovules:				
1, basal	+	+	+	+

2. Cremastosperma-group (figs. 11, 12; table 6)

Buds lanceoloid, (very) (broadly) (depressed) ovoid, or ellipsoid (petals). *Sepals* imbricate (rarely more or less valvate), 3, free or connate, 1–4 mm long, fleshy, veins not prominent, indument present or absent, hairs simple, margins ciliate or not. *Petals* whitish, creamy, greenish, yellowish, or orange, imbricate, (3, 4, or) 6, free, both whorls equal in length or inner ones longer, 4–50 mm long, 1–6 × as long as wide, 3–10(–50) × length of sepals, fleshy, sometimes very thin, veins usually not prominent, indument present or absent, hairs simple, margins ciliate or not. *Torus* depressed ovoid, rarely with a slightly concave apex, flat, (broadly) cylindrical, rarely with a concave apex and an ovoid apicule, or rarely depressed obovoid. *Stamens* numerous to few, 0.7–3.7 mm long, extrorse; apex discoid to tongue-shaped, often fleshy, glabrous or sometimes hairy. *Carpels* free, 3 to numerous, 0.5–3 mm long, glabrous to hairy, style present or absent, stigma spheroid, (ob)lanceoloid, (ob)-ovoid, narrowly obconical, discoid, (broadly) cylindrical; ovule 1, basal or lateral. *Flowers* bisexual or androdioecious.

Distribution – 7 genera in tropical America.

Notes – This group is characterized by imbricate sepals and petals (fig. 12g), and one, basal or lateral ovule (fig. 11a, g). Sepals and petals are often ciliate (fig. 12a, g), whereas in several genera both species with androdioecious (fig. 12i) and with bisexual flowers occur. The sepals are small, up to 4 mm long. The flowers are usually whitish or greenish, sometimes yellowish.

The flowers of *Cremastosperma*, *Pseudoxandra*, *Ephedranthus*, and some *Malmea*-species are very similar in general appearance. These genera, however, show small differences in e.g. shape and texture of the apices of the stamens, presence or absence of male flowers, shape of the torus, or attachment of the ovules. *Ephedranthus* in its flowers is difficult to distinguish from some small-flowered *Malmea*-species.

The Cremastosperma-group seems to have most close affinities to the Sapranthus-group, the Sageraea-group, and the Unonopsis-group. It shares with the latter group the usually small flowers and the small sepals. The stamens of *Oxandra*, which have a long tongue-shaped apex, resemble those of *Bocageopsis* and *Onychopetalum* (both Unonopsis-group). *Ruizodendron* with its long petals (fig. 12d) reminds of the Sapranthus-group. In *Ephedranthus* and *Desmopsis* (Sapranthus-group) similar stamens are found. The stamens of *Ruizodendron* (fig. 12e) resemble those of, e.g., *Tridimeris* (Sageraea-group). *Sageraea* and *Stelechocarpus* (both Sageraea-group) in their perianth resemble the genera of the Cremastosperma-group, but have more ovules. Some *Cremastosperma*-flowers resemble those of *Guatteria* (Guatteria-group); *Guatteria*, however, has valvate sepals and indurate stamens. *Guatteria*, despite the overall similarity, is not related to *Cremastosperma*.

Cremastosperma R.E. Fries, Acta Horti Berg. 10 (1) (1930) 46, f. 6.

Buds ovoid or broadly depressed ovoid (petals). *Sepals* imbricate?, 3, free or connate, 2–4 mm long, fleshy, veins not prominent, indument present or absent, hairs simple, margins ciliate or not. *Petals* (violet-)green to (creamy-)yellow to

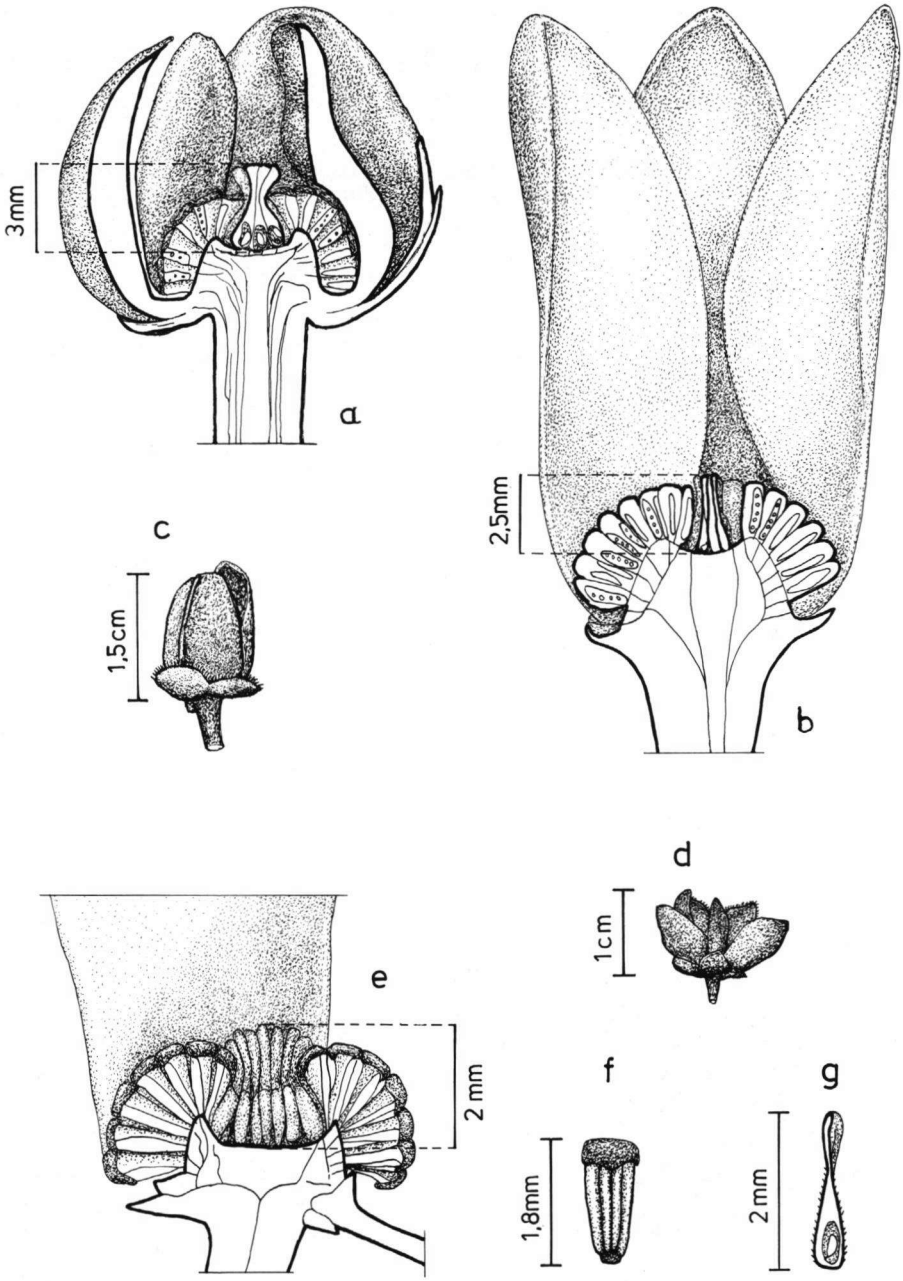


Fig. 11. Cremastosperma-group — a. *Cremastosperma cauliflorum* (Maas et al. 6281): longitudinal section; b. *Cremastosperma pendulum* (Maas et al. 4592): longitudinal section; c. *Cremastosperma pedunculatum* (Nelson 763): bud; d. *Cremastosperma pendulum* (Luteyn et al. 4890): flower; e. & f. *Cremastosperma cauliflorum* (Holm-Nielsen et al. 21501): longitudinal section (e) and stamen (f); g. *Cremastosperma cauliflorum* (Prance et al. 3527): carpel.

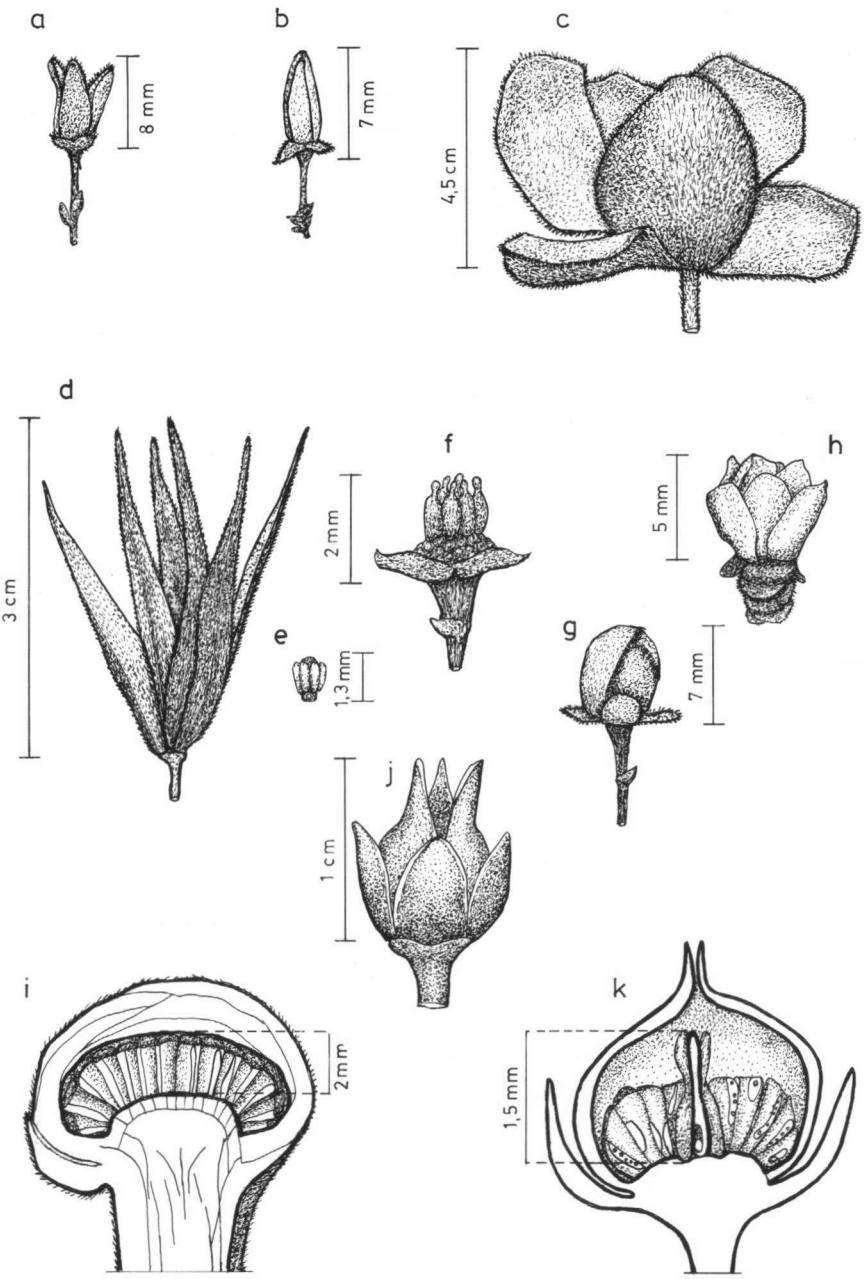


Fig. 12. Cremastosperma-group — a. & b. *Oxandra laurifolia* (Wright 4): flower (a) and bud (b); c. *Malmea xanthochlora* (Lugo 3413): flower; d. & e. *Ruizodendron ovale* (Schunke V. 4387): flower (d) and stamen (e); f. & g. *Oxandra polyantha* (Nelson et al. 515): flower after anthesis (f) and bud (g); h. *Oxandra sessiliflora* (Schatz et al. 941): flower; i. *Ephedranthus sp.* (Morawetz 21-13883); j. & k. *Pseudoxandra cuspidata* (Berg & Prance 757): flower (j) and longitudinal section (k).

orange, imbricate, 6, free, both whorls equal in length, 6–21 mm long, 1–2 × as long as wide, 3–6 × length of sepals, fleshy, often with thin margins, veins not prominent, indument present or absent, hairs simple, margins ciliate or not. *Torus* broadly ovoid or depressed ovoid with slightly concave apex. *Stamens* numerous, 1.2–1.8 mm long, extrorse; apex discoid, glabrous. *Carpels* free, numerous, 2–3 mm long, hairy or glabrous, style present, long to short, stigma oblanceoloid or spheroid and small; ovule 1, apical, lateral or basal. *Flowers* bisexual.

Type – *C. pedunculatum* (Diels) R.E. Fries.

Distribution – 17 species in tropical South America and adjacent Panama.

Note – *Cremastosperma* (fig. 11a–g) resembles *Ephedranthus*, *Malmea*, and *Pseudoxandra* in their flowers. The apices of the stamens of *Cremastosperma* are not fleshy like in the other three genera.

Specimens examined:

C. brevipes: Prance et al. 15079a (U). — *C. cauliflorum:* Cazalet & Pennington 7528 (US); Cuatrecasas 11125 (F); Holm-Nielsen et al. 21501 (AAU); Maas et al. 6281 (U); Prance et al. 3527, 23783 (U); Schunke V. 200 (A). — *C. megalophyllum:* Berlin 218 (U); Schunke V. 5645 (U). — *C. microcarpum:* Krukoff 6151 (U); Prance et al. 3527 (GH, U). — *C. pedunculatum:* Cid & Nelson 2724, 2868 (U); Lowrie et al. 463 (U); Nelson 680, 763 (U). — *C. pendulum:* Klug 3726 (A); Luteyn et al. 4890 (COL, U); Maas et al. 4592 (U); Schunke V. 7251 (U). — *C. sp.:* Barbour 4432 (U); Prance et al. 7885 (U); Schunke V. 7591, 8484 (U).

Ephedranthus S. Moore, Trans. Linn. Soc. London, Bot. ser. 2, 4 (1895) 296, pl. 21.

Buds depressed ovoid (petals). *Sepals* (aestivation not observed), 3, free, 2–2.5 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* cream to yellow, or green, imbricate, 6, free, both whorls equal in length, 8–12 mm long, 1.5 × as long as wide, 4–5 × length of sepals, fleshy, veins not prominent, indument present or absent, hairs simple, margins ciliate, inner petals sometimes basally glabrous, or with long hairs inside. *Torus* broadly cylindrical or depressed ovoid. *Stamens* numerous, 1–2 mm long, extrorse; apex discoid, fleshy, hairy. *Carpels* free, numerous, 2 mm long, hairy, style absent, stigma narrowly obconical, ciliate; ovule 1, basal. *Flowers* bisexual or androdioecious.

Type – *E. parviflorus* S. Moore.

Distribution – 4 or 5 species in the Guianas and Brazil.

Specimens examined:

E. amazonicus: Maas et al. 6955 (U); Prance et al. 11555 (U); Solomon 6484 (U). — *E. guianensis:* Irwin et al. 54720 (U); de Jong & Holthuijzen, LBB 15778 (U); Schulz 8568 (U). — *E. parviflorus:* Prance et al. 4987 (U). — *E. sp.:* Morawetz 21-13883 (U); dos Santos 1105 (U).

Malmea R.E. Fries, Ark. Bot. 5 (4) (1905) 3, t. 1, f. 7–12.

Buds broadly (depressed) ovoid (petals). *Sepals* imbricate, (2 or) 3, free or connate, 2–3 mm long, fleshy, veins not prominent, indument present or absent, hairs simple, margins ciliate. *Petals* greenish(-white), or (pale) yellow, imbricate, (4 or) 6, free, both whorls equal in length or inner ones longer, 7–40 mm long, 1–2 × as

long as wide, 3–10 × length of sepals, fleshy, veins not prominent, indument present or absent, hairs simple, margins ciliate or not. *Torus* cylindrical, sometimes with a concave apex and an ovoid apicule, or depressed obovoid. *Stamens* numerous, 1–3 mm long, extrorse; apex discoid, fleshy, sometimes hairy. *Carpels* free, numerous, 1.5–2 mm long, hairy or sometimes glabrous, style present and short, or absent, stigma obovoid, discoid, or cylindrical, glabrous or sometimes hairy; ovule 1, basal. *Flowers* bisexual or androdioecious.

Type – *M. obovata* R.E. Fries.

Distribution – About 15 species in Mexico, Central and South America.

Note – *Malmea*-flowers (fig. 12c) are usually larger than those of the other genera of this group. Some species, however, have smaller flowers which are difficult to distinguish from *Cremastosperma* and *Ephedranthus*. Buds of *M. diclina* resemble those of *Porcelia*.

Specimens examined:

M. costaricensis: Pittier 9990 (BR). — *M. depressa:* Reyes et al. 210 (U); Beaman & Alvarez del Castillo 6330 (U); Dorantes et al. 958, 1181 (U); Gandara & Dorantes 92 (U); Ortega Ortiz 291 (U); Tún Ortíz 2693 (U); Vasquez Torres 464 (U). — *M. diclina:* Krukoff 5632 (U). — *M. discolor:* Forest Departm. Brit. Guiana 4727 (U); Tutin 310 (U). — *M. lucida:* Prance et al. 7876 (U). — *M. obovata:* Daniëls & Jonker 859 (U). — *M. xanthochlora:* Lugo 3413 (U). — *M. sp.:* Croat 19130 (U).

Oxandra A. Richard in Sagra, Hist. fis. Cuba, Bot. (1845) 45.

Buds (very) (broadly) ovoid, lanceoloid, or ellipsoid (petals). *Sepals* imbricate, 3, free, 1.5–2.5 mm long, fleshy, veins not prominent, indument present or absent, hairs simple, margins ciliate. *Petals* white to cream, or green, imbricate, (3 or) 6, free, both whorls equal in length, 4–8 mm long, 3–5 × as long as wide, 3 × length of sepals, fleshy, veins not prominent, indument present or absent, hairs simple, margins ciliate, sometimes glandular dots on the petals. *Torus* depressed ovoid or cylindrical. *Stamens* numerous, 1.5–3.7 mm long, extrorse; apex long acute to tongue-shaped, fleshy. *Carpels* free, few (3 or more), 0.8–1.5 mm long, glabrous or hairy, style absent, stigma spheroid, hairy; ovule 1, basal. *Flowers* bisexual or androdioecious.

Lectotype – *O. lanceolata* (Swartz) Baillon.

Distribution – About 25 species in the Antilles and South America.

Note – *Oxandra* (fig. 12a, b, f, g, h) has stamens with long, acute apices, which hide the carpels.

Specimens examined:

O. acuminata: Krukoff 6096 (U). — *O. asbeckii:* Lindeman et al. 346 (U); Prévost 598 (U). — *O. euneura:* Prance et al. 16455 (U). — *O. krukoffii:* Oldenburger et al. 581 (U); Silva & Souza 2582 (U). — *O. lanceolata:* Fuertes 224 (U). — *O. laurifolia:* Fuertes 380 (U); Sintenis 4313 (U); Wright 4 (K). — *O. leucodermis:* Liesner & Clark 8949 (U). — *O. major:* Berg et al. P19834 (U); Krukoff 8497 (U). — *O. polyantha:* Krukoff 5628 (U); Nelson et al. 515 (U); Prance et al. 2316, 2538 (U). — *O. riedeliana:* Krukoff 5166 (U). — *O. sessiliflora:* Ducke RB 18347 (B); Schatz et al. 941 (U). — *O. surinamensis:* Lindeman, Görts-van Rijn et al. 34 (U). — *O. venezuelana:* Steyermark 99947 (U). — *O. xylopioides:* Huashikat 1519 (U); Krukoff 8447 (U); Prance et al. 22718 (U); Soejarto & Cardozo 709 (U).

Pseudephedranthus Aristeguieta, Mem. New York Bot. Gard. 18 (2) (1969) 43.

Buds broadly ovoid (petals). *Sepals* imbricate, 3, connate, 1.5 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* (cream-)white, imbricate, 6, free, both whorls equal in length, 9–15 mm long, 3 × as long as wide, 6–10 × length of sepals, fleshy, veins not prominent, indument present, hairs simple. *Torus* ovoid. *Stamens* numerous (in male flowers) to few (in female flowers), 1.6–2.5 mm long, extrorse; apex discoid to tongue-haped in male flowers, tongue-shaped in female flowers, fleshy. *Carpels* free, (number not observed) hairy, style absent, stigma spheroid, glabrous (ovules not observed). *Flowers* androdioecious.

Type – *P. fragrans* (R.E. Fries) Aristeguieta.

Distribution – 1 species in Northern Brazil and Venezuela.

Note – *Pseudephedranthus* closely resembles *Oxandra*, but it has longer petals and in bisexual flowers the stamens have discoid apices.

Specimens examined:

P. fragrans: Maguire & Wurdack 34954 (K); Maguire et al. 60189 (F, US), 60332 (US); Silva & Brazão 60683 (US).

Pseudoxandra R.E. Fries, Acta Horti Berg. 12 (2) (1937) 222, f. 1–3.

Buds (broadly) depressed ovoid (petals). *Sepals* imbricate, 3, free or connate, 1–2 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* white or (greyish-)green, imbricate, 6, free, both whorls equal in length, or inner ones longer, 7–9 mm long or outer ones 12 mm long, inner ones 15 mm long, 5–10 × length of sepals, fleshy, veins not prominent, indument present or absent, hairs simple. *Torus* depressed ovoid, sometimes with flat apex. *Stamens* numerous, 1.7–2 mm long, extrorse; apex discoid (sometimes elongate), fleshy. *Carpels* free, 6 to numerous, 1.2–3 mm long, glabrous, style present or absent, stigma (ob)lanceoloid or ovoid, glabrous; ovule 1, lateral? *Flowers* bisexual.

Lectotype – *P. leiophylla* (Diels) R.E. Fries.

Distribution – 6 species in tropical South America.

Note – *Pseudoxandra* (fig. 12j, k) resembles *Cremastosperma* in its flowers, but generally the flowers of *Pseudoxandra* are smaller.

Specimens examined:

P. cuspidata: Berg & Prance 757 (U). — *P. guianensis:* Lleras et al. P16938 (U). — *P. polyphleba:* Croat 18893 (U); Maas et al. 6338 (U); Revilla et al. 2552 (U); Vásquez & Jaramillo 284 (U). — *P. sp.:* Morawetz 23-30883 (U).

Ruizodendron R.E. Fries, Ark. Bot. 28B (4) (1936) 3.

Buds broadly ovoid (petals). *Sepals* (aestivation not observed), 3, connate, 1 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* white, imbricate, 6, free, both whorls equal in length, 4–50 mm long, 6 × as long as wide, 50 × length of sepals, fleshy to nearly membranous, veins prominent or not, indument present, sparse, hairs simple, inner side glabrous. *Torus* flat. *Stamens* numerous, 0.7–1.5 mm long, extrorse; apex discoid, fleshy. *Carpels* free, 9 to numerous, 0.5–

1.2 mm long, glabrous, style absent, stigma flat and lobed, ciliate, or spheroid, hairy; ovule 1, lateral. *Flowers* bisexual.

Type – *R. ovale* (Ruiz & Pavón) R.E. Fries.

Distribution – 1 species in Peru and Bolivia.

Note – *Ruizodendron* (fig. 12d) differs from the other genera of this group by its long, narrow petals.

Specimens examined:

R. ovale: Asplund 13193 (K); Begazo 99 (U); Krukoff 10669 (U); Reynel R. 832 (U); Schunke V. 4387 (F).

Table 6. List of character states found in the genera of the Cremastosperma-group.

Taxa: C = *Cremastosperma*, E = *Ephedranthus*, M = *Malmea*, O = *Oxandra*, P1 = *Pseudephedranthus*, P2 = *Pseudoxandra*, R = *Ruizodendron*.

	C	E	M	O	P1	P2	R
Flowers:							
perianth 3-merous	+	+	+	+	+	+	+
indument absent	+	–	+	–	–	+	–
ciliate margins only	+	+	+	+	–	–	–
indument of simple hairs	+	+	+	+	+	+	+
male	–	+	+	+	+	–	–
bisexual	+	+	+	+	+	+	+
Sepals:							
imbricate	+?	?	+	+	+	+	?
connate	–,+	–	–,+	–	+	–,+	+
1–4 mm long	+	+	+	+	+	+	+
Petals:							
imbricate	+	+	+	+	+	+	+
connate	–	–	–	–	–	–	–
4–15 mm long	+	+	+	+	+	+	+
15–50 mm long	+	–	+	–	–	–	+
Stamens:							
numerous	+	+	+	+,–	+,–	+	+
anthers extrorse	+	+	+	+	+	+	+
0.7–2.5 mm long	+	+	+	+	+	+	+
2.5–3.7 mm long	–	–	+	+	–	–	–
apex tongue-shaped to acute	–	–	–	+	+	–	–
apex discoid	+	+	+	–	+	+	+
Carpels:							
< 6 in number	–	–	–	+	?	(+)	–
> 6 in number	+	+	+	+	?	+	+
Ovules:							
1 in number	+	+	+	+	?	+	+
basal placentation	+	+	+	+	?	–	–
lateral placentation	+	–	–	–	?	+?	+
apical placentation	+	–	–	–	?	?	–

3. Cymbopetalum-group (figs. 13–15; table 7)

Buds (very) broadly or depressed ovoid (sepals), or lanceoloid, (very broadly or depressed) ovoid, or spheroid (petals). *Sepals* valvate, reduplicate-valvate, or imbricate, (2 or) 3, free or connate, 0.5–24 mm long, fleshy, veins not prominent, indument present or absent, hairs simple, margins ciliate or not. *Petals* whitish, creamy, yellowish, or greenish, valvate, reduplicate-valvate, or imbricate, (4 or) 6, free or connate, both whorls equal or unequal in length, 2–35 mm long, 1–6 × as long as wide, 1–7 × length of sepals, fleshy, sometimes very thick, veins prominent or not, indument present or absent, hairs simple, margins ciliate. *Torus* shallowly conical with a flat apex, depressed ovoid, or broadly cylindrical, rarely with a slightly concave apex and a constricted base. *Stamens* 6 or numerous, 1.4–5.2 mm long, extrorse, septate; apex discoid, or tongue-shaped to apical prolongation almost absent, glabrous, hairy, or papillose, sometimes fleshy. *Carpels* free, 1 to numerous, 1.5–5 mm long, hairy or rarely glabrous, style absent, sometimes present, stigma discoid to flat and lobed, obconical, ellipsoid, or bilobed; ovules 2–17, lateral, 1- or 2-seriate. *Flowers* bisexual.

Distribution – 8 genera in Mexico, Central and South America, and East Africa.

Notes – This predominantly neotropical group, with one representative in Africa, is characterized by septate stamens (which, however, are not indurate, like in the Xylopia-group), and many, lateral ovules (figs. 13h, 15e). Otherwise, this group shows a great diversity in its flower morphology.

This group is similar to the 'Trigynaea-gruppe' of Fries (1959), with exception of the African genus *Mkilua* (fig. 15a–c), which was published in 1970, and which has been added to this group because of the strong similarity with *Porcelia* (fig. 13b). These two genera only differ in the size of the inner petals and the ovule number. *Cardiopetalum* (fig. 13c) and *Froesiodendron* (fig. 15d) closely resemble each other in their flowers as well.

The Cymbopetalum-group is probably most related to the African genera *Asteranthe*, *Hexalobus*, and *Ophrypetalum* (all Hexalobus-group) as becomes evident when data on the morphology of flowers, fruits (Verdcourt, 1971a), and pollen (Walker, 1971a, 1972) are combined. Also these three African genera are very different in their flowers. The stamens of *Porcelia* resemble in shape and texture those found in *Asteranthe*, but the anthers in the latter genus are not septate. The stamens of *Hexalobus bussei* seem to be septate. The large, reduplicate-valvate sepals of *Cardiopetalum* (fig. 13d) and *Froesiodendron* remind of those of *Hexalobus, Mischogyne, Ophrypetalum, Toussaintia,* and *Uvariastrum* (all genera of either the Hexalobus-group or the Uvariastrum-group).

Bocagea A.F.C.P. de Saint-Hilaire, Fl. Brasil. merid. 1 (1825) 41.

Buds very broadly ovoid to spheroid (petals). *Sepals* valvate, 3, connate, 0.5–1 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* pale yellow, valvate or imbricate, 6, free, both whorls equal in length, 2–4 mm long, 1–2 × as long as wide, 4 × length of sepals, fleshy, veins not prominent, indument present or absent, hairs simple, margins ciliate. *Torus* flat. *Stamens* 6?, 1.4–1.6 mm long, extrorse (septation not observed); apical prolongation almost absent. *Carpels*

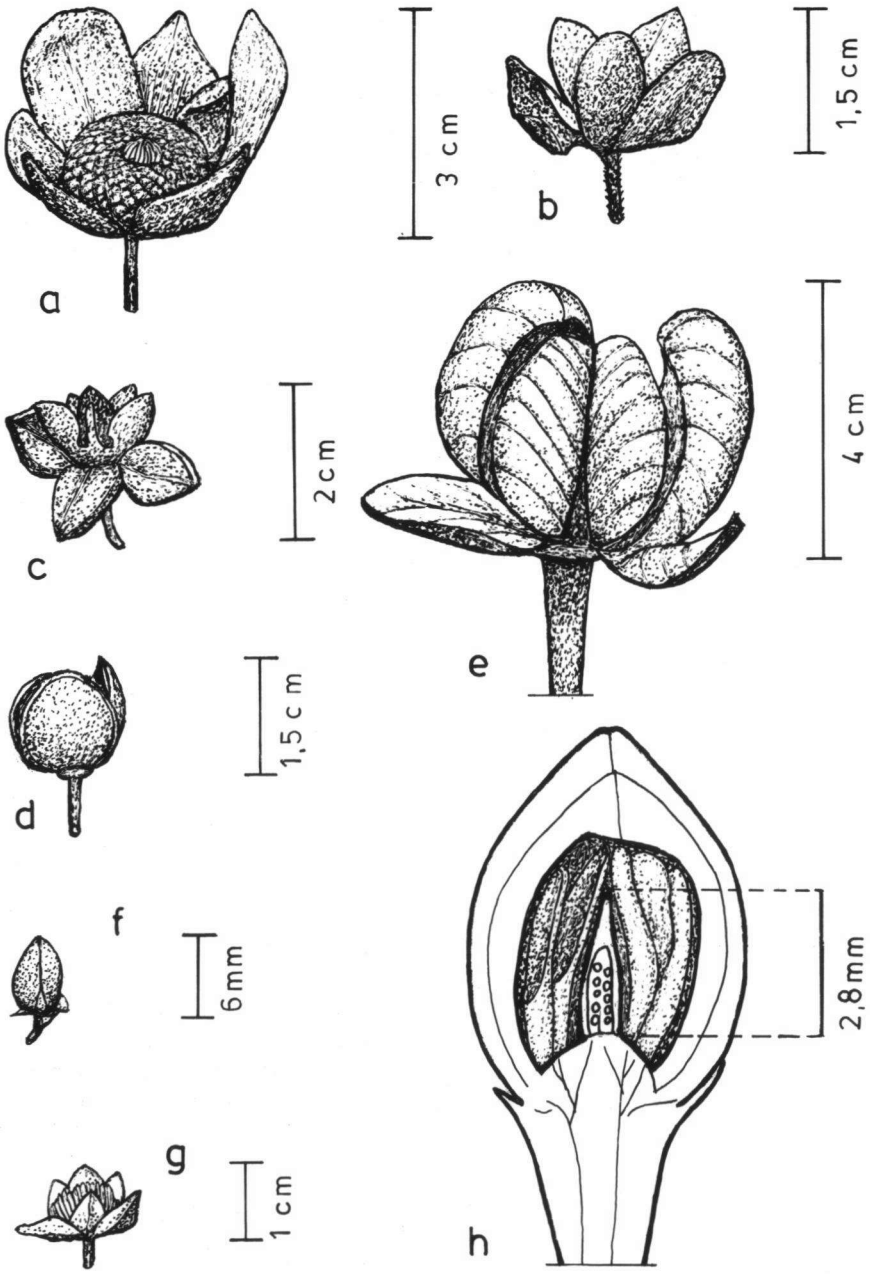


Fig. 13. Cymbopetalum-group — a. *Cymbopetalum brasiliense* (BW 3252): flower; b. *Porcelia nitidifolia* (Schunke V. 7832): flower; c. & d. *Cardiopetalum calophyllum* (Prance et al. 19359): flower (c) and bud (d); e. *Cymbopetalum baillonii* (van Rooden 800): flower; f. & g. *Trigynaea duckei* (Hartshorn 2428): bud (f) and flower (g); h. *Trigynaea duckei* (Maas et al. 6280): longitudinal section.

free, 2–3, 1.5 mm long, hairy, style absent or present (short), stigma discoid to flat; ovules 4–5, lateral, 2-seriate. *Flowers* bisexual.

Type – *B. viridis* A.F.C.P. de Saint-Hilaire.

Distribution – 2 species in Southeastern Brazil (Rio de Janeiro, Minas Gerais).

Note – *Bocagea* has tiny flowers. Due to the scarce material available, it could not be observed whether *Bocagea* has septate stamens.

Specimens examined:

B. longepedunculata: Magalhães 18868 (U). — *B. viridis:* Herb. A. de Jussieu s.n. (P); Sellow s.n. (B).

Cardiopetalum Schlechtendal, Linnaea 9 (1834) 328.

Buds (very) broadly ovoid (sepals). *Sepals* reduplicate-valvate, 3, connate, 9–17 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* yellow or white, imbricate, 6, connate, outer whorl slightly longer, 11 mm long, 1–2 × length of sepals, fleshy, veins not prominent, indument present, hairs simple. *Torus* shallowly conical with a flat apex. *Stamens* numerous, 2.5–3 mm long, extrorse, septate; apex discoid, fleshy. *Carpels* free, numerous, 3.5 mm long, hairy, style absent or present, stigma obconical and grooved (cup-shaped), bilobed, or discoid (lobed); ovules 3–8, lateral, 1-seriate. *Flowers* bisexual.

Type – *C. calophyllum* Schlechtendal.

Distribution – 1 species in Bolivia and Brazil.

Note – *Cardiopetalum* (fig. 13c) strongly resembles *Froesiodendron,* but differs from that genus by the more numerous and smaller flowers, and the texture of the apices of the stamens, fleshy and papillose, respectively.

Specimens examined:

C. calophyllum: Beck 6939 (U); Cid & Nelson 2776 (U); Daly et al. 1336, 1533 (U); Hatschbach & Koczicki 33353 (U); Maguire et al. 56954 (U); Prance et al. 19359 (U); Vilhena 183 (U).

Cymbopetalum Bentham, J. Proc. Linn. Soc., Bot. 5 (1860) 69.

Buds depressed ovoid (sepals). *Sepals* imbricate? or valvate?, 3, free or connate, 1.5–5 mm long, fleshy to herbaceous, veins not prominent, indument present or absent, hairs simple, margins ciliate. *Petals* cream, (pale or yellow-)green, sometimes tinged with maroon, valvate, 6, free, inner whorl longer, outer ones 8–20 mm long, inner ones 9–35 mm long, 1 × as long as wide, 2–6 × length of sepals, outer ones herbaceous to fleshy, inner ones fleshy, very thick, veins prominent, indument present or absent, hairs simple, margins ciliate; inner petals boat-shaped, sometimes inside basally differently coloured. *Torus* shallowly conical with a flat apex or broadly cylindrical. *Stamens* numerous, 2.2–4.5 mm long, extrorse, septate; apex discoid, glabrous and fleshy, hairy, or papillose. *Carpels* free, numerous, 2–5.3 mm long, glabrous, style absent, stigma obconical; ovules many (c. 17), lateral, 2-seriate. *Flowers* bisexual.

Type – *C. brasiliense* (Vellozo) Bentham ex Baillon.

Distribution – Mexico, Central and South America, 11–14 species.

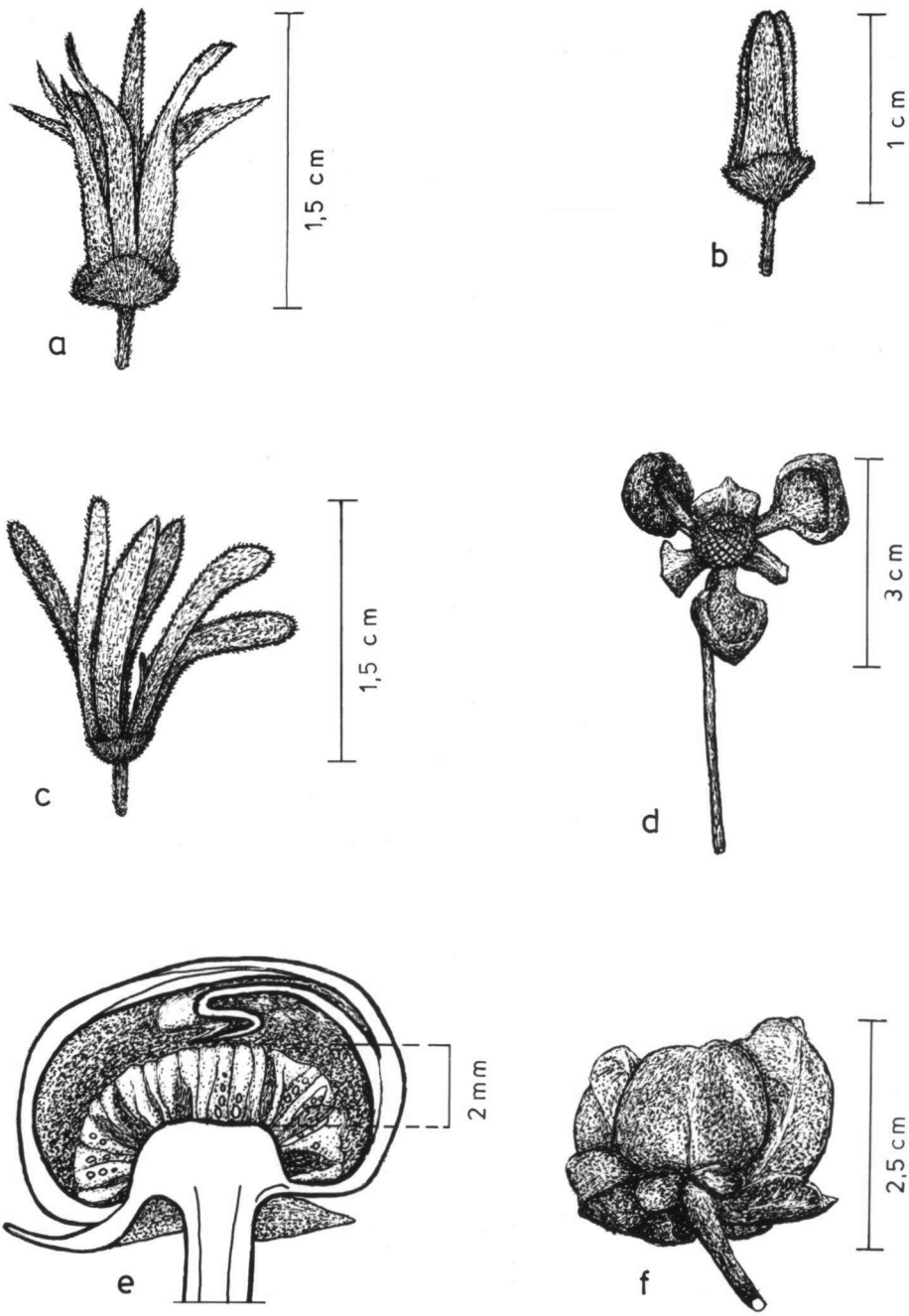


Fig. 14. Cymbopetalum-group — a. & b. *Hornschuchia sp.* (de Carvalho et al. 1172): flower (a) and bud (b); c. *Hornschuchia myrtillus* (Pinheiro 1824): flower; d. *Cymbopetalum costaricense* (Schatz & Grayum 1112): flower; e. *Porcelia macrocarpa* (Reitz 5891): longitudinal section; f. *Cymbopetalum longipes* (Prance et al. 12506): flower.

Note – *Cymbopetalum* (figs. 13a, e, 14d, f, 15e, f) is easy to recognize by the long-pedicellate and pendulous flowers with very thick and fleshy, boat-shaped, inner petals.

Specimens examined:

C. baillonii: Dorantes 2590 (U); Ponce C. 209 (U); van Rooden 800 (U). — *C. brasiliense:* BW 3252 (U); Strudwick et al. 3121 (U). — *C. costaricense:* Burger & Stolze 5847 (BM); Pittier 8104 (BR); Schatz & Grayum 1112 (U). — *C. lanugipetalum:* de Nevers & Herrera 5663 (U). — *C. longipes:* Prance et al. 12506 (U). — *C. mayanum:* Contreras 2363 (P); Gentle 5332 (P). — *C. odoratissimum:* Krukoff 4646 (U). — *C. penduliflorum:* Armstrong 9340 (U); Proctor 36081 (BM). — *C. stenophyllum:* Matuda 18588 (U). — *C. tessmannii:* Schunke V. 6977 (U). — *C. sp.:* Alencar 320 (U); Plowman 5981 (U); Prance et al. 12007 (U); Thomas et al. 3578 (U).

Froesiodendron R.E. Fries, Ark. Bot. new ser. 3 (13) (1956) 439.

Buds very broadly ovoid (sepals). *Sepals* reduplicate-valvate, 3, connate, 10–24 mm long, fleshy, veins not prominent, indument present or absent, hairs simple. *Petals* white, grey, or (pale) yellow, imbricate, 6, free or connate, both whorls equal in length or inner ones slightly longer, 16–20 mm long, 1 × as long as wide, as long as the sepals, fleshy, veins not prominent, indument present, hairs simple. *Torus* not observed. *Stamens* numerous, 2.5–3.5 mm long, extrorse, septate; apex discoid, papillose. *Carpels* free, numerous, hairy (incompletely observed). *Flowers* bisexual.

Type – *F. amazonicum* R.E. Fries.

Distribution – 2 species in tropical South America.

Note – *Froesiodendron* (fig. 15d) was separated from *Cardiopetalum* by Fries (1956) because of the venation of the leaves and the orientation of the seeds. In the flowers the differences between the two genera are very small.

Specimens examined:

F. amazonicum: Lleras et al. P17430 (U); Maas et al. P12734 (U); Ramirez 113 (U); Soejarto 550 (GH). — *F. surinamense:* Cid et al. 1925 (U); Lindeman et al. 331 (U). — *F. sp.:* Lleras et al. P17155 (U).

Hornschuchia C.G.D. Nees, Flora 4 (1821) 302.

Buds lanceoloid (petals). *Sepals* valvate, 3, connate (cup-shaped), 1–2.5 mm long, fleshy, veins not prominent, indument present or absent, hairs simple, margins ciliate or not. *Petals* whitish or cream, ± imbricate, 6, free, both whorls equal in length, 4–25 mm long, 4–6 × as long as wide, 4–10 × length of sepals, fleshy, veins prominent, indument present, hairs simple. *Torus* depressed ovoid. *Stamens* few (c. 6), 2.5–5.2 mm long, latrorse or extrorse, septate; apex acute and very small or apical prolongation absent. *Carpels* free, 1–3, 2.5–5 mm long, hairy, style absent, stigma ellipsoid, glabrous; ovules 5–8, lateral, 1- or 2-seriate. *Flowers* bisexual.

Lectotype – *H. bryotrophe* C.G.D. Nees.

Distribution – 2 species in the Brazilian states of Bahia and Rio de Janeiro.

Note – *Hornschuchia*-flowers (fig. 14a, b, c) look different from the flowers of the other genera of this group, because of the cup-shaped calyx and the narrow petals. Open flowers resemble those of *Greenwayodendron*; in bud *Hornschuchia* reminds of *Xylopia*.

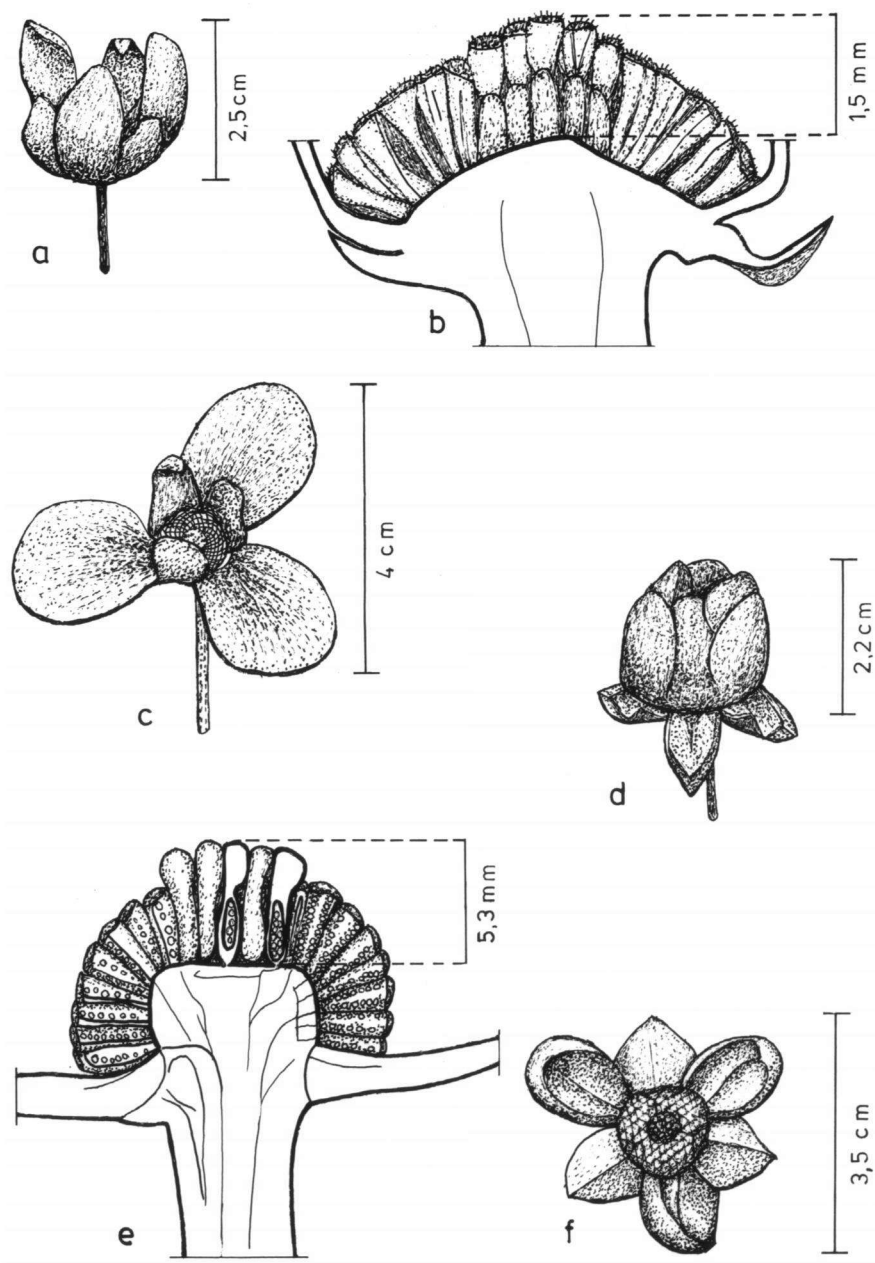


Fig. 15. Cymbopetalum-group — a. *Mkilua fragrans* (Greenway 8703): flower; b. *Mkilua fragrans* (Peter 21997): longitudinal section; c. *Mkilua fragrans* (Brenan & Greenway 8314): flower; d. *Froesiodendron surinamense* (Cid et al. 1925): flower; e. & f. *Cymbopetalum baillonii* (van Rooden 800): longitudinal section (e) and flower (f).

Specimens examined:

H. bryotrophe: Mori et al. 9292 (CEPEC), 9368 (CEPEC, U), 11348 (U); dos Santos 1168 (CEPEC), 3099 (U). — *H. myrtillus:* Pinheiro 1824 (CEPEC). — *H. sp.:* de Carvalho et al. 1172 (U); Hage & dos Santos 1447 (CEPEC); dos Santos 1690 (CEPEC, U), 1859 (U), 2091 (CEPEC), 2133 (CEPEC), 2157 (CEPEC).

Mkilua Verdcourt, Kew Bull. 24 (1970) 449, f. 1, 1–11.

Buds depressed ovoid (sepals). *Sepals* valvate? or imbricate?, 3, connate, 2.5–3.5 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* (greenish-)yellow, at the base dark purple or red-purple, imbricate, 6, free, outer whorl longer, outer ones 10–35 mm long, inner ones 7–15 mm long, 1–2 × as long as wide, 4–7 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner petals inside basally differently coloured. *Torus* depressed ovoid or shallowly conical. *Stamens* numerous, 2–2.3 mm long, extrorse, septate; apex discoid, hairy. *Carpels* free, numerous, 1.5–4 mm long, hairy, style absent, stigma obconical, hairy; ovules 2–5, lateral, 1- or 2?-seriate. *Flowers* bisexual.

Type – *M. fragrans* Verdcourt.

Distribution – 1 species in East Africa.

Note – *Mkilua* (fig. 15a, b, c) strongly resembles *Porcelia* in its flowers, only the inner petals are smaller than the outer petals in mature flowers, and it has fewer ovules. Remarkable is the geographical disjunction between this genus and the other genera of this group.

Specimens examined:

M. fragrans: Brenan & Greenway 8314 (BR); Drummond & Hemsley 3803 (BR); J.B. Gillett 21051 (B, BR); Graham 2212 (K); Greenway 8703 (BR); Peter 21997 (B, BR); Verdcourt 1892 (BR); R.O. Williams s.n. (K).

Porcelia Ruiz & Pavón, Fl. Peruv. Prodr. (1794) 84, t. 16.

Buds depressed ovoid (petals). *Sepals* imbricate, 3, free, 1–4 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* cream to vivid yellow to green, imbricate, 6, free, both whorls equal in length, 9–26 mm long, 1.5–3 × as long as wide, 5–6 × length of sepals, fleshy, veins prominent or not, indument present, hairs simple, or absent, margins ciliate, inner petals sometimes with 2 marginal glands. *Torus* broadly cylindrical, sometimes the apex slightly concave and constricted at the base. *Stamens* numerous, 1.6–3.5 mm long, extrorse, septate; apex discoid, fleshy, hairy. *Carpels* free, numerous, 2–4 mm long, hairy, style absent, stigma flat and lobed, hairy; ovules 5–17, lateral, 2-seriate. *Flowers* bisexual.

Type – *P. nitidifolia* Ruiz & Pavón.

Distribution – Tropical South America and Panama, 5–8 species.

Note – *Porcelia* (figs. 13b, 14e) differs from the other neotropical genera of this group by the imbricate aestivation of the sepals.

Specimens examined:

P. goyazensis: Glaziou 20636 (BR). — *P. macrocarpa:* Klein 1789 (B); Reitz 5891 (B). —

Table 7. List of character states found in the genera of the Cymbopetalum-group.

Taxa: B = *Bocagea*, C1 = *Cardiopetalum*, C2 = *Cymbopetalum*, F = *Froesiodendron*, H = *Hornschuchia*, M = *Mkilua*, P = *Porcelia*, T = *Trigynaea*.

	B	C1	C2	F	H	M	P	T
Flowers:								
perianth 3-merous	+	+	+	+	+	+	+	+(–)
hairs simple	+	+	+	+	+	+	+	+
ciliate margins	+	–	+	–	+,–	–	+	–
indument absent (sepals)	–	–	+,–	+,–	+,–	–	–	
bisexual	+	+	+	+	+	+	+	+
Sepals:								
valvate	+	–	+?	–	+	+?	–	+
reduplicate-valvate	–	+	–	+	–	–	–	–
imbricate	–	–	+?	–	–	+?	+	–
connate	+	+	+,–	+	+	+	–	+
0.5–5 mm long	+	–	+	–	+	+	+	+
9–24 mm long	–	+	–	+	–	–	–	–
Petals:								
valvate	+	–	+	–	(+)	–	–	+
reduplicate-valvate	–	–	–	–	–	–	–	+
imbricate	+	+	–	+	+?	+	+	–
connate	–	+	–	–,+	–	–	–	–
whorls unequal in size	–	–	+	–	–	+(–)	–	–
2–10 mm long	+	(+)	(+)	–	+	–	(+)	+
10–35 mm long	–	+	+	+	+	+	+	–
Stamens:								
6 in number	?	–	–	–	+	–	–	–
numerous	–	+	+	+	–	+	+	+
anthers extrorse	+	+	+	+	+,–	+	+	+
anthers septate	?	+	+	+	+	+	+	+
apex tongue-shaped	–	–	–	–	–	–	–	+
apex small tip	+	–	–	–	+	–	–	+
apex discoid	–	+	+	+	–	+	+	–
1.4–2.5 mm long	+	–	(+)	–	–	+	+	–
2.5–5.2 mm long	–	+	+	+	+	–	+	+
Carpels:								
1–3 in number	+	–	–	–	+	–	–	+
numerous	–	+	+	+	–	+	+	–
Ovules:								
2–8 in number	+	+	–	?	+	+	+	–
> 8 in number	–	–	+	?	–	–	+	+
1-seriate	–	+	–	?	+	+	–	–
2-seriate	+	–	+	?	+	+?	+	+

P. nitidifolia: Foster 6951 (F), 9223 (U); Maas et al. 6027, 6034 (U); Schunke V. 7832 (U). — *P. steinbachii:* Beck 7159 (U); Krukoff 5299, 5566 (U). — *P. venezuelensis:* Breteler 3900 (U); Liesner & González 9400 (U). — *P. sp.:* Croat 23763 (U); Heringer & Eiten 14988 (US).

Trigynaea Schlechtendal, Linnaea 9 (1835) 328.

Buds ovoid (petals). *Sepals* valvate, (2 or) 3, connate, 1–1.5 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* white, creamy, greyish, or brownish, (reduplicate-)valvate, (4 or) 6, free, both whorls equal in length, 5–8 mm long, 1 × as long as wide, 5 × length of sepals, fleshy, veins not prominent, indument present, hairs simple. *Torus* shallowly conical with a flat apex, or cylindrical. *Stamens* numerous, 3.5–4 mm long, extrorse, septate; apex tongue-shaped, fleshy. *Carpels* free, 2–3, 2–2.8 mm long, hairy, style absent, stigma discoid to lobed, glabrous; ovules 10, lateral, 2-seriate. *Flowers* bisexual.

Type – *T. oblongifolia* Schlechtendal.

Distribution – About 5 species in tropical South America.

Note – *Trigynaea* (fig. 13f, g, h) resembles *Unonopsis* and *Bocageopsis* in the flowers: all have valvate sepals and petals, which are of about the same size. Moreover, *Trigynaea* and *Bocageopsis* have stamens with tongue-shaped apices. *Trigynaea,* however, differs from both genera by the septate stamens and bractless pedicels.

Specimens examined:

T. caudata: Forest Dep. Brit. Guiana 7790 (U); Strudwick et al. 3072 (U). — *T. duckei:* Barbour 5127 (U); Hartshorn 2428 (U); Maas et al. 6280 (U). — *T. ecuadoriensis:* Gentry et al. 29632 (U). — *T. guianensis:* Silva & Souza 2532 (U). — *T. sp.:* Barbour 5048, 5780 (U); Steyermark et al. 126576 (U).

4. Duguetia-group (fig. 16; table 8)

Buds (very) broadly ovoid, spheroid, or ellipsoid (sepals); sepals rarely entirely connate in bud. *Sepals* valvate, reduplicate-valvate, 3, free or slightly to entirely connate, 4–35 mm long, fleshy, sometimes thin, veins usually not prominent, indument present, hairs stellate or lepidote. *Petals* whitish to yellowish to reddish, pinkish, purplish, greenish, or brownish, imbricate or sometimes valvate, 6, free, both whorls equal in length or inner whorl longer, 10–40 mm long, 2.5–3 × as long as wide, 1–5 × length of sepals, fleshy, veins usually not prominent, indument present, hairs stellate or lepidote, inner petals basally glandular or not inside. *Torus* depressed ovoid with a (slightly) concave apex and ovoid apicule, broadly cylindrical with a concave apex and ovoid apicule, or shallowly conical with a slightly concave apex. *Stamens* numerous, 0.7–5 mm long, extrorse; apex discoid, or sometimes umbonate or absent, glabrous, papillose, (densely) hairy, or sometimes shiny. *Carpels* free (or fused?), numerous, 1.5–10 mm long, (stellate) hairy or sometimes glabrous, style usually present, long, stigma lanceoloid, terete, obovoid, or discoid, glabrous or hairy, or replaced by a ciliate rim; ovule 1, basal. *Flowers* bisexual.

Distribution – 2 genera in South America, and in West & Central Africa.

Notes – This group is characterized by valvate sepals and imbricate petals, stellate

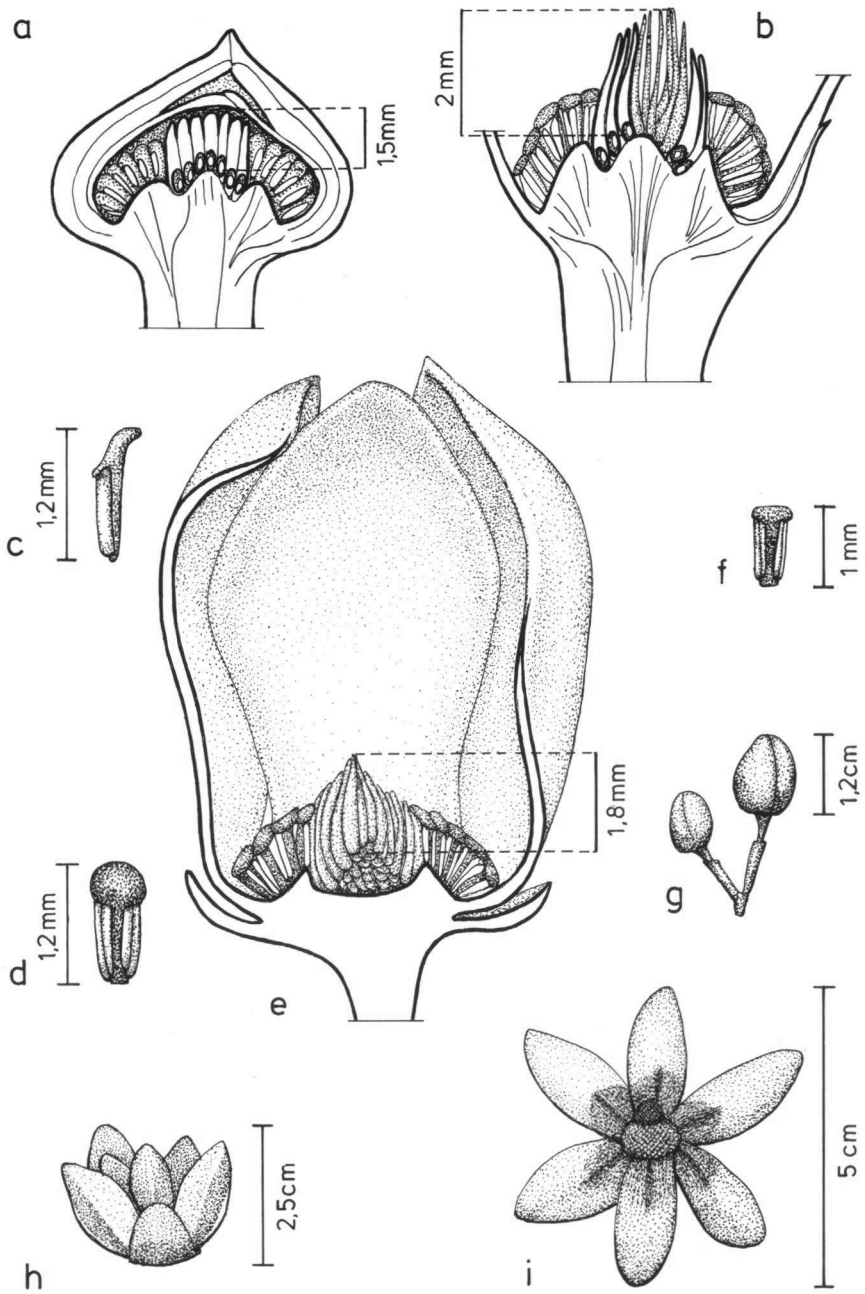


Fig. 16. Duguetia-group — a. *Duguetia sp.* (Schunke V. 14134): longitudinal section; b. *Duguetia* aff. *stelechantha* (Morawetz 36-19883): longitudinal section; c., d. & e. *Duguetia odorata* (Krukoff 4805): stamen (c & d) and longitudinal section (e); f. *Duguetia* aff. *stelechantha* (Morawetz 36-19883): stamen; g. *Pachypodanthium barteri* (Le Testu 9553): buds; h. *Duguetia dimorphopetala* (Huber & Tillett 3024): flower; i. *Duguetia furfuracea* (Brantjes 701607): flower.

or lepidote indument, a torus which is depressed ovoid with a slightly concave apex and ovoid apicule, and one basal ovule (fig. 16a, b).

The two genera are closely related. *Pachypodanthium* differs from most *Duguetia*-species in the indument on the flowers, the large bracts, and a different angle of the secondary veins of the leaves.

The Duguetia-group shares some features with the Uvaria-group (valvate sepals and imbricate petals, the same size and shape of the flower, and the stellate indument) and with the Fusaea-group (valvate sepals and imbricate petals, large sepals, and one basal ovule). The torus reminds of that found in the Annona-group, with which the Duguetia-group also shares the single, basal ovule. The stamens of *Pachypodanthium* resemble those of the African species of *Sphaerocoryne* (Friesodielsia-group).

Table 8. List of character states found in the genera of the Duguetia-group.

	Duguetia	*Pachypodanthium*
Flowers:		
perianth 3-merous	+	+
hairs stellate	+	+
hairs lepidote	+	–
bisexual	+	+
Sepals:		
valvate	+	+
reduplicate-valvate	+	–
connate	–,+	–
entirely connate in bud	–,+	–
4–35 mm long	+	+
Petals:		
imbricate	+	+
valvate	+	–
base glandular	+,–	+,–
10–40 mm long	+	+
Stamens:		
numerous	+	+
anthers extrorse	+	+
discoid apex absent	+	–
apex discoid	+	+
0.7–5 mm long	+	+
Carpels:		
numerous	+	+
fused	–	–,+?
Ovules:		
1, basal	+	+

Duguetia A.F.C.P. de Saint-Hilaire, Fl. Brasil. merid. 1 (1824) ('1825') ed. fol. 28; ed. qu. 35.

Buds (very) broadly ovoid, spheroid, or ellipsoid (sepals); rarely sepals entirely fused. *Sepals* valvate or reduplicate-valvate, 3, free or slightly to entirely connate, 4–35 mm long, fleshy, sometimes thin, veins usually not prominent, indument present, hairs stellate or lepidote. *Petals* white, cream, greenish(-brown) to yellow to (dark) red, dull purple, pinkish, or outer petals brownish and inner ones pale brown-rose, or petals outside rose-green, inside yellowish-green, sometimes basal part of inner petals maroon- or dark red, orange-yellow, dark pink, or white, imbricate or sometimes valvate, 6, free, both whorls equal in length, 10–40 mm long, or inner whorl longer, outer ones 13–14 mm long, inner ones 17–25 mm long, 2.5–3 × as long as wide, 1–5 × length of sepals, fleshy, veins usually not prominent, indument present, hairs stellate or lepidote, base of inner petals glandular inside. *Torus* depressed ovoid with a (slightly) concave apex and ovoid apicule. *Stamens* numerous, 1–5 mm long, extrorse; apex discoid, or sometimes umbonate, tongue-shaped, or apical prolongation absent, glabrous, papillose, or (densely) hairy. *Carpels* free, numerous, 1.5–10 mm long, (stellate) hairy or sometimes glabrous, style usually present, long, stigma lanceoloid, discoid, or terete, sometimes a ciliate rim only; ovule 1, basal. *Flowers* bisexual.

Type – *D. lanceolata* A.F.C.P. de Saint-Hilaire.

Distribution – About 70 species in tropical South America.

Note – *Duguetia* (fig. 16, except 16g) is diverse in floral shape. The species of sect. *Geanthemum* (Fries, 1959) differ from the other *Duguetia*-species in their stamens.

Specimens examined:

D. argentea: Liesner & Clark 8939 (U). — *D. asterotricha:* L. Coêlho INPA3803 (U). — *D bracteosa:* Martius s.n. (BR); Santos 2149 (U). — *D. cadaverica:* Daniëls & Jonker 935, 1159 (U); Florschütz & Maas 2702, 2897 (U); Geijskes 1030 (U); Schulz, LBB 10335 (U); Wessels Boer 867 (U). — *D. calycina:* BW 2477, 2584, 2876, 3130, 3425, 3955, 6009 (U); de Granville 473, 3972 (U); Irwin et al. 47788, 47815 (U); Lindeman 6414 (U); Maguire et al. 22868a (U); Silva & Pinheiro 4279 (U); A.C. Smith 2532 (U). — *D. caudata:* Krukoff 6258 (U). — *D. cauliflora:* BW 3426 (U); Cid et al. 2340 (U). — *D. dimorphopetala:* Huber & Tillett 3024 (U); Liesner 7097 (U). — *D. echinophora:* Pires et al. 50732 (U); Prance & Silva 58684, 58931 (U). — *D. eximia:* Mori et al. 8739 (U). — *D. flagellaris:* Berg & Steward, P19895 (U); Ducke RB 19626, RB 19627 (U). — *D. furfuracea:* Anderson et al. 9031, 36831 (U); Brantjes 701607 (U); Irwin et al. 25488 (U); Silva & Pinheiro 4136 (U). — *D. glabriuscula:* Pires & Furtado 17164 (U). — *D. inconspicua:* Lindeman & Stoffers et al. 239 (U). — *D. insculpta:* Bahia 69 (U). — *D. lanceolata:* Hoehne s.n. (U); Kuhlmann 3951 (U); Reitz 3585 (U). — *D. latifolia:* Krukoff 6068 (U). — *D. lepidota:* Kappler 1686 (U); Prance et al. 4327; Rosa 3058 (U). — *D. longicuspis:* Morawetz 14-18883 (U). — *D. lucida:* Krukoff 5390 (U); Steyermark et al. 101865 (U). — *D. macrocalyx:* Wilson-Browne 475 (U). — *D. marcgraviana:* Prance et al. 19087 (U); Prance & Silva 59305, 59551 (U). — *D. megalophylla:* Fanshawe, Forest Dep. Brit. Guiana 4826 (U). — *D. neglecta:* Forest Dep. Brit. Guiana 2348 (U); Maas & Tawjoeran, LBB 10791 (U). — *D. odorata:* Krukoff 4805 (U). — *D. pycnastera:* Lindeman & Stoffers et al. 110, 712 (U). — *D. quitarensis:* Krukoff 8260 (U); R.H. Schomburgk s.n. (U); A.C. Smith 2483 (U). — *D. rhizantha:* Frazão RB7140 (U); Peckolt s.n. (B). — *D. rigida:* Steyermark & Dunsterville 104241 (U). — *D. schulzii:* Elburg, LBB 9858 (U); Kramer & Hekking 2442 (U). — *D. spixiana:* Hartshorn 2436 (U); Krukoff 5738 (U); Lleras et al., P16673 (U); Prance et al. 10216 (U). — *D. spruceana:* Krukoff 8436 (U). — *D. stelechantha:* Berg

et al., P18809 (U); Cid et al. 1957 (U); Morawetz 36-19883 (U); Prance et al. 2151, 17747, 22826, 22848 (U). — *D. stenantha:* Krukoff 8582 (U). — *D. surinamensis:* BW 6883 (U). — *D. tenuis:* Fanshawe, Forest Dep. Brit. Guiana 6007 (U). — *D. tessmannii:* Krukoff 5556 (U). — *D. ulei:* Krukoff 8938 (U). — *D. uniflora:* D. Coêlho & Mello INPA3924 (U); Prance et al. 17865 (U); Prance & Lleras 23735 (U). — *D. sp.:* Schunke V. 14134 (U).

Pachypodanthium Engler & Diels, Notizbl. Königl. Bot. Gart. Berlin 3 (1900) 55.

Buds (very) broadly ovoid (sepals). *Sepals* valvate, 3, free, 11–20 mm long, fleshy, veins not prominent, indument present, hairs stellate. *Petals* white-yellowish or creamy with purple spots, imbricate, 6, free, both whorls equal in length?, 19–22 mm long, 2 × as long as wide, 1–2 × length of sepals, fleshy, veins not prominent, indument present, hairs stellate, inner petals basally glandular or not inside. *Torus* broadly cylindrical with a narrowly triangular-ovoid apex or with a depressed ovoid apex on flat-topped base, or shallowly conical and slightly concave apex. *Stamens* numerous, 0.7–1.7 mm long, extrorse; apex discoid, glabrous, often shiny or papillose. *Carpels* free (or fused?), numerous, 2 mm long, hairy, style present, stigma obovoid or ellipsoid, glabrous; ovule 1, basal. *Flowers* bisexual.

Lectotype – *P. staudtii* (Engler & Diels) Engler & Diels.

Distribution – 3 species in West & Central Africa.

Note – When using the key to the sections of *Duguetia* (Fries 1959), *Pachypodanthium* (fig. 16g) keys out to section 8, with among others *Duguetia uniflora,* which resembles *Pachypodanthium* most. The two genera seem to differ in their flower biology (observations from herbarium specimens): in *Pachypodanthium* the sepals remain closed, whereas in *Duguetia* the sepals open before anthesis. Voorhoeve (1965), however, gives an illustration of open flowers.

Specimens examined:

P. barteri: Le Testu 9553 (BR, P). — *P. confine:* Le Testu 1774 (BR); Zenker 3195 (L). — *P. staudtii:* Bernardi 8401 (WAG); van Dillewijn 53 (WAG); Leeuwenberg 2579 (WAG); Le Testu 8368, 9424 (BR); Sargos 201 (BR); Voorhoeve 1176 (WAG).

5. Friesodielsia-group (figs. 17–20; table 9)

Buds (broadly depressed) (triangular-)ovoid (sepals), or broadly (depressed) ovoid, or lanceoloid to triangular-ovoid, or apert? (petals). *Sepals* valvate, or sometimes reduplicate-valvate or apert?, 3, free or connate, 1–20 mm long, fleshy, sometimes thin, veins prominent or not, indument present, hairs simple or sometimes stellate, or absent, margins ciliate or not. *Petals* whitish, creamy, yellowish, greenish, brownish, orange, reddish, or pinkish, valvate or sometimes apert?, (3 or) 6, free, both whorls equal in length or outer whorl longer, 3.5–145 mm long, 1–11 × as long as wide, 2–12 × length of sepals, fleshy or sometimes very thin, veins prominent or not, indument present, hairs simple or rarely stellate; inner petals sometimes connivent, sometimes basally glabrous inside. *Torus* shallowly conical, broadly cylindrical to cushion-shaped, with a flat, slightly concave, or shallowly conical apex, depressed ovoid, sometimes with a concave apex, flat, or depressed obovoid, sometimes with a slightly concave apex. *Stamens* numerous or rarely few, 0.5–4

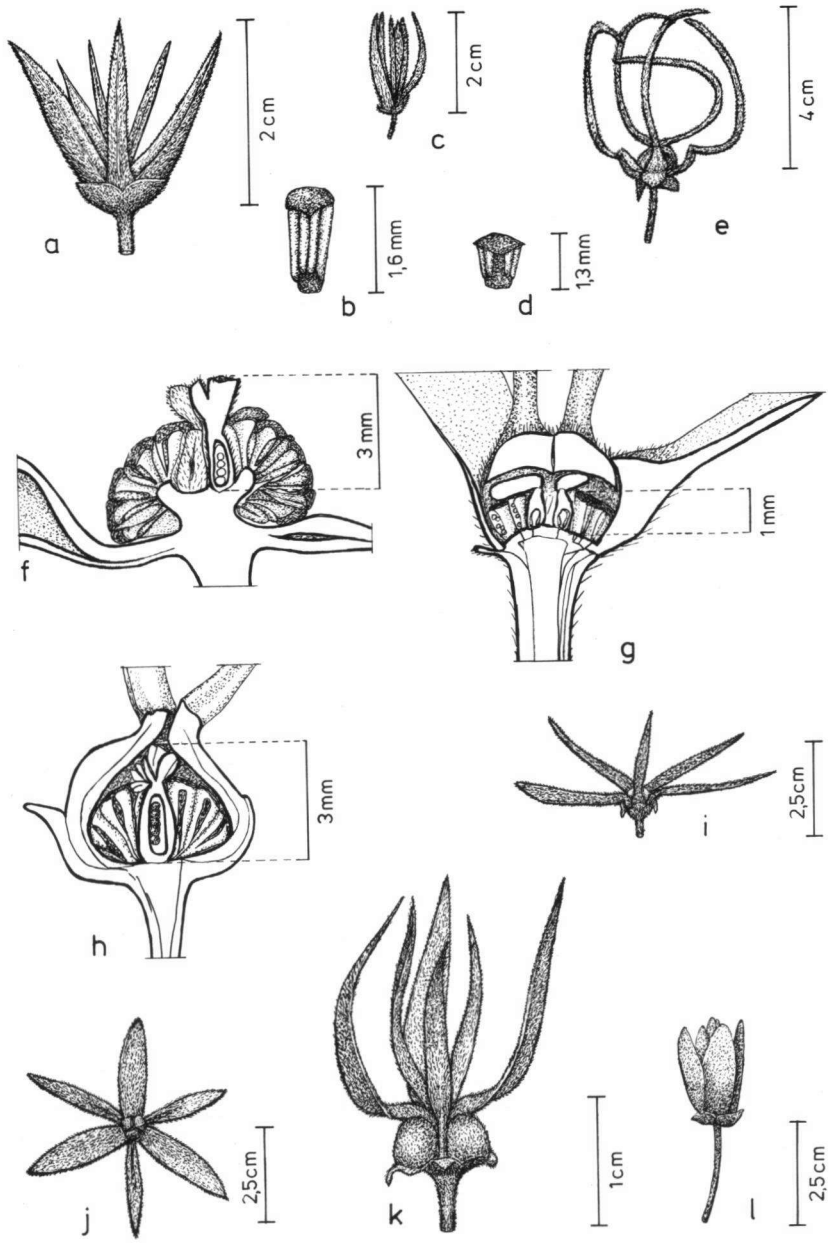


Fig. 17. Friesodielsia-group — a. *Artabotrys zeylanicus* (Kostermans s.n.): flower (bud); b. *Monocarpia euneura* (Selvaraj 11196): stamen; c. & d. *Artabotrys stenopetalus* (Leeuwenberg 3796): flower (bud) (c) and stamen (d); e. *Cyathocalyx acuminatus* (Lam 5365): flower (bud); f. *Monocarpia euneura* (Selvaraj 11155): longitudinal section; g. *Artabotrys stenopetalus* (Leeuwenberg 3796): longitudinal section; h. *Cyathocalyx martabanicus* (Okada 3252): longitudinal section; i. & j. *Artabotrys aurantiacus* (Cult. Arb. Wag. 96): flowers (buds); k. *Cyathocalyx novoguineensis* (Henty & Foreman NGF 42684): flower (bud); l. *Dasoclema siamensis* (Kerr 6087): flower.

mm long, extrorse; apex discoid or tongue-shaped, glabrous, sometimes fleshy, often shiny. *Carpels* free, 1 to numerous, 1–4.5 mm long, hairy or glabrous, style present or absent, stigma discoid, bilobed, (ob)lanceoloid, ellipsoid, (ob)ovoid, cylindrical, or very shallowly obconical; ovules 1–20, lateral or rarely basal, 1- or 2-seriate. *Flowers* bisexual.

Distribution – 12 genera in tropical Asia, Taiwan included, in New Caledonia, Fiji, New Guinea, Australia, and in tropical Africa.

Notes – This group is predominantly Asiatic, with 3 genera extending into Africa (*Artabotrys*, *Friesodielsia*, and *Sphaerocoryne*). The genera of this group usually have valvate or apert sepals, valvate petals (figs. 17j, 19a, m, 20b, g), both whorls of petals being equal in length (fig. 17j, k) or the inner whorl smaller (figs. 19d, m, 20b), and usually lateral ovules (figs. 17f, h, 19j, 20a). The apices of the stamens are often shiny.

Although this group is not very uniform, it is not possible to divide it into smaller, more homogeneous groups. The inclusion of *Artabotrys, Cyathocalyx, Dasoclema,* and *Monocarpia* in this group is uncertain.

Some genera of this group have links to other groups. Some African species of *Friesodielsia* closely resemble some large-flowered species of *Monanthotaxis*. Although the Friesodielsia-group and the Monanthotaxis-group are closely related, as appears from non-floral characters, in the floral characters these two groups only share the valvate perianth and the frequent presence of a bilobed stigma (fig. 19j, 20e). In contrast to the Monanthotaxis-group, the genera of this group have a general type of stamens (figs. 17b, d, 18a, 19b, i). In general appearance the flowers of the Friesodielsia-group resemble those of the Xylopia-group. The Friesodielsia-group, however, lacks the indurate and septate stamens found in the Xylopia-group.

Artabotrys R. Brown ex Ker-Gawler, Bot. Reg. 5 (1820) 423.

Buds broadly depressed ovoid (sepals) or broadly ovoid (petals). *Sepals* valvate or reduplicate-valvate, 3, free or connate, 1–16 mm long, fleshy, veins not prominent, indument present or absent, hairs simple, margins ciliate or not. *Petals* whitish to yellow, sometimes reddish or beige at the base, greenish-yellow, pale pink, orange, or reddish-buff, valvate, 6, rarely inner ones imbricate, free (or connate), both whorls equal in length or outer ones slightly longer, 3.5–48 mm long, or outer ones 5–18 mm long, inner ones 4–14 mm long, 2–11 × as long as wide, 2–8 × length of sepals, basally constricted, fleshy, veins prominent, indument present, hairs simple, inner petals sometimes basally glabrous inside. *Torus* flat, broadly cylindrical, depressed (ob)ovoid, or shallowly conical with flat apex. *Stamens* (few to) numerous, 0.7–4 mm long, extrorse; apex discoid or sometimes tongue-shaped or umbonate, glabrous. *Carpels* free, 3 to numerous, 1–6 mm long, glabrous or hairy, style absent or present, stigma (ob)ovoid or shallowly obconical (cup-shaped); ovules 1 or 2, basal. *Flowers* bisexual.

Type – *A. hexapetalus* (L.f.) Bhandari.

Distribution – Tropical Africa incl. Madagascar, tropical Asia, New Guinea, and Australia, 80–85 species. One species occasionally cultivated elsewhere in the tropics.

Note – *Artabotrys* (fig. 17a, c, d, g, i, j) is easy to recognize because the petals are basally constricted and the inflorescences are shaped like hooks. In *A. brachypetalus* the petals are not constricted and remind of those of *Uvariastrum*. *Artabotrys dielsiana* has a very large number of carpels.

Specimens examined:

AFRICA (MADAGASCAR INCLUDED) — *A. aurantiacus:* Cult. Arb. Wag. 96 (= Breteler 2097) (WAG). — *A. brachypetalus:* Davies D2619 (L); Schlieben 5609 (M). — *A. coccineus:* Onochie 40296 (WAG). — *A. dielsiana:* Zenker 510 (U). — *A. hildebrandtii:* Bernardii 11879, 11937 (L). — *A. insignis:* Letouzey 12141 (WAG); Zenker 2801 (L). — *A. likimensis:* Stam 111 (L). — *A. luxurians:* Herb. d'Alleizette s.n. (L). — *A. monteiroae:* Herb. d'Alleizette s.n. (L); Edwards 3304 (WAG); W.J.J.O. de Wilde & de Wilde-Duijfjes 6986 (WAG). — *A. scytophyllus:* Capuron 28510-SF (P). — *A. stenopetalus:* Leeuwenberg 3796, 3856 (WAG); J.J.F.E. de Wilde & Voorhoeve 3747 (WAG). — *A. stolzii:* Pawek 5054 (WAG). — *A. thomsonii:* Breteler 1429, 2799; de Wit 12340 (WAG). — *A. velutinus:* Morton 1008, 3664 (WAG). — *A. sp.:* Schlieben 8226 (B).

ASIA — *A. desmidantha:* Docters van Leeuwen 11388 (L, U). — *A. gracilis:* Anderson S25409 (L); Purseglove 5402 (L). — *A. havilandii:* Haviland 1629 (L). — *A. hexapetalus:* Cult. Hort. U, 76 GR00015; Dransfield 3013 (L). — *A. intermedius:* Herb. d'Alleizette s.n. (L). — *A. polygyna:* Korthals s.n. (U). — *A. rolfei:* Elmer 17363 (U). — *A. siamensis:* Teijsmann 5973 (U). — *A. stolonifera:* Elmer 14610 (U). — *A. suaveolens:* Anderson 9114 (L); Teijsmann s.n. (U). — *A. sumatranus:* Korthals s.n. (L). — *A. trichopetalus:* Elmer 20118, 20489 (U). — *A. trigyna:* Ramos 1178 (L). — *A. wrayi:* Morawetz 15-28285 (U). — *A. zeylanicus:* Hepper & da Silva 4773 (L); Kostermans s.n. (L).

Cyathocalyx Champion ex J.D. Hooker & T. Thomson, Fl. Ind. 1 (1855) 126.

Buds ovoid (sepals). *Sepals* valvate or reduplicate-valvate, 3, free or connate, 3–10 mm long, fleshy, veins not prominent, indument present, hairs simple or stellate. *Petals* cream to yellow to green, or light brown, valvate, 6, free, whorls equal in length, basally constricted, 6–70 mm long, 2–7 × as long as wide, 2–6 × length of sepals, fleshy, veins prominent or not, indument present, hairs simple or sometimes stellate. *Torus* very shallowly conical with a flat or concave apex, cushion-shaped, sometimes with a concave apex, or flat. *Stamens* numerous, 1–1.5 mm long, extrorse; apex discoid, glabrous, often fleshy. *Carpels* free, 1 to numerous, 1.5–3.5 mm long, sometimes slightly stipitate, hairy, style present or absent, stigma obovoid, oblanceoloid, cylindrical, or very shallowly obconical (cup-shaped), glabrous; ovules 2–7, lateral, 1- or 2?-seriate. *Flowers* bisexual.

Type – *C. zeylanicus* Champion ex J.D. Hooker & T. Thomson.

Distribution – About 35 species in tropical Asia, New Guinea, New Britain, and Fiji.

Notes – *Cyathocalyx* (fig. 17e, k) resembles *Artabotrys* in the flowers because the petals are constricted above the reproductive organs. The flowers of *Artabotrys*, however, are placed on hooks. Also the ovule number differs: *Artabotrys* has 2 basal ovules whereas *Cyathocalyx* has 2 or more lateral ovules.

Cyathocalyx martabanicus and *C. zeylanicus* have only one carpel with a large, cup-shaped stigma (fig. 17h). Their carpel resembles that of *Isolona* and *Monodora* in general shape.

Specimens examined:

C. acuminatus: Lam 2738, 5365 (L). — *C. apoensis:* Edaño 41683 (L); Ramos 1662 (L). — *C. apornis.* Elmer 13625 (U). — *C. bancana:* Kostermans & Anta 49 (L). — *C. biovulatus:* Bujang

13138 (L); Sanusi & Tahir 12322 (L); de Vogel 3425 (L). — *C. carinatus:* Cockburn FRI 7815 (L); Okada 3380 (U). — *C. insularis:* A.C. Smith 9176, 9424 (L). — *C. kingii:* Koorders 16016b (L). — *C. magnificus:* Anderson S31627 (L). — *C. martabanicus:* van Beusekom & Phengkhlai 1051 (L); Okada 3252 (U). — *C. minahassae:* Koorders 16039b (L). — *C. novoguineensis:* Henty & Foreman NGF 42684 (L); Kalkman BW 6488 (L); White NGF 10483 (L). — *C. olivaceus:* King's collector 6653 (L). — *C. osmanthus:* Hyndman 11 (L); Vink 12060 (L). — *C. papuanus:* Gjellerup 376, 977 (U); Kostermans & Soegeng 482 (L); Schodde (& Craven) 4230 (L). — *C. petiolatus:* Henty & Frodin NGF 27317 (L). — *C. ridleyi:* Soepadmo & Mahmud 1182 (L). — *C. sumatranus:* Ampuria 35295 (L). — *C. zeylanicus:* Cult. Hort. Bog. IV H49 (L), IV H49a (U); Kostermans 24762 (L); Ridsdale 322 (L). — *C. sp.:* Streimann & Katik NGF 28997 (L).

Dasoclema J. Sinclair, Gard. Bull. Straits Settlem. ser. 3, 14 (1955) 273.

Buds not observed. *Sepals* (aestivation not observed), 3, connate?, 4–5 mm long, fleshy, veins not prominent, indument present, hairs stellate. *Petals* (aestivation not observed), 6, free, whorls equal in length, 16–28 mm long, 4 × as long as wide, 4 × length of sepals, fleshy, veins not prominent, indument present, hairs stellate. *Torus* and *stamens* not observed. *Carpel* 1, hairy (incompletely observed).

Type – *D. siamensis* (Craib) J. Sinclair.

Distribution – 1 species in Thailand.

Note – *Dasoclema* (fig. 17l) is a poorly known genus of which only one collection seems to exist. Because of the incomplete material, *Dasoclema* is only tentatively placed in this group. According to Sinclair (1955), *Dasoclema* has c. 8 ovules. The stellate indument and the single carpel remind of the flowers of *Dielsiothamnus* (Uvariastrum-group). *Dasoclema* seems to be intermediate between the Friesodielsia-group, the Uvaria-group, and the Uvariastrum-group.

Specimen examined:
D. siamensis: Kerr 6087 (K).

Dasymaschalon (J.D. Hooker & T. Thomson) Dalla Torre & Harms, Gen. siphon. (1901) 174.

Buds triangular-lanceoloid (petals). *Sepals* (aestivation not observed), 3, free or connate, 2–20 mm long, fleshy, sometimes thin, veins prominent or not, indument present, hairs simple. *Petals* yellow to pale orange, pink, or red, valvate, 3, free, inner whorl absent, outer whorl 15–145 mm long, 2.5–3 × as long as wide, 7 × length of sepals, fleshy, veins prominent or not, indument present, hairs simple. *Torus* shallowly conical with a flat apex. *Stamens* numerous, 2–3 mm long, extrorse; apex discoid, glabrous, often shiny. *Carpels* free, numerous, 4.5 mm long, hairy, style present or absent, stigma discoid or bilobed, glabrous; ovules 5, lateral, (number of series not observed). *Flowers* bisexual.

Lectotype – *D. blumei* Finet et Gagnepain.

Distribution – 11 species in tropical Asia.

Notes – *Dasymaschalon* (figs. 18b, c, d, 19e) is often included in *Desmos*, though as a separate section, e.g., Hooker & Thomson (1872), Ridley (1922), Sinclair (1955), because they have the same type of fruits (moniliform). There are, however, several differences between *Desmos* and *Dasymaschalon*: *Desmos* has 6

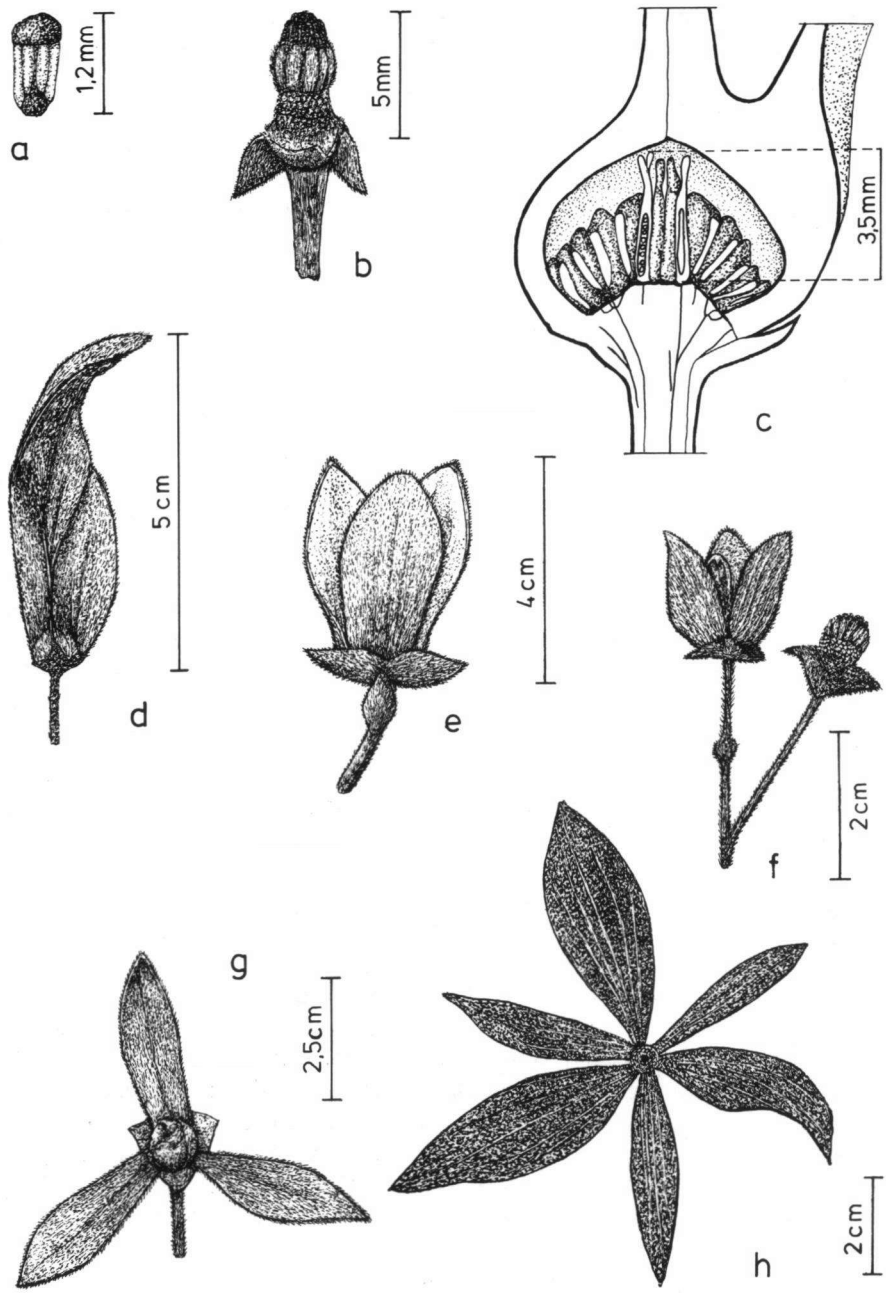


Fig. 18. Friesodielsia-group — a. *Desmos sp.* (Cult. Hort. Bog. s.n.): stamen; b. *Dasymaschalon clusiflorum* (Lagrimas 39382): flower after anthesis; c. & d. *Dasymaschalon sp.* (Burck s.n./5971): longitudinal section (c) and flower (bud) (d); e. *Friesodielsia hirsuta* (Jaeger 8237): flower; f. *Friesodielsia enghiana* (Le Testu s.n.): flower and one flower after anthesis; g. *Friesodielsia desmoides* (Ridley 14725): flower (bud); h. *Desmos dumosus* (Bon 5367): flower.

petals, whereas *Dasymaschalon* has 3 petals because the inner whorl is lacking. The flowers of *Desmos* are greenish to yellowish, whereas those of *Dasymaschalon* are reddish, pinkish, orange or yellowish. The torus of both genera differs in shape: shallowly conical in *Dasymaschalon* (fig. 18c), in *Desmos* usually flat. The species of *Desmos* are mostly climbers, whereas the species of *Dasymaschalon* are usually trees or shrubs.

Dasymaschalon macrocalyx differs from the other species by the large sepals.

Specimens examined:

D. blumei: van Balgooy 2546 (L); Suppiah FRI 14878 (L). — *D. clusiflorum:* Cenabre et al. 28558 (L); Conklin & Buwaya I-1376 (L); Lagrimas 39382 (L). — *D. longiflorum:* Thakur Rup Chand 5567A (L), 8348 (W). — *D. macrocalyx:* How 70714 (B); Liang 61659 (B); Tsang 379 (B). — *D. sp.:* Burck s.n. 5971 (L).

Desmos Loureiro, Fl. Cochinch. (1790) 352.

Buds not observed, apert? *Sepals* apert?, 3, free, 4–13 mm long, fleshy, sometimes thin, veins prominent or not, indument present, hairs simple. *Petals* yellow to (pale) green, sometimes base inside dark red, apert?, 6, free, outer whorl longer, outer ones 18–65 mm long, inner ones 12–35 mm long, 2–6 × as long as wide, 4–12 × length of sepals, fleshy, sometimes thin, veins prominent, indument present, hairs simple, inner petals basally glabrous inside. *Torus* flat, sometimes with slightly concave apex, or depressed ovoid with a slightly concave apex. *Stamens* numerous, 1–1.2 mm long, extrorse; apex discoid, shiny. *Carpels* free, numerous, 1.5–2 mm long, hairy or glabrous, style present or absent, stigma discoid, obovoid, or cylindrical, glabrous; ovules 2–7, lateral, 1-seriate. *Flowers* bisexual.

Lectotype – *D. cochinchinensis* Loureiro.

Distribution – About 20 species in tropical Asia and Australia.

Note – *Desmos* (figs. 18h, 19c) seems to be related to *Friesodielsia*: some large-flowered species of the heterogeneous (in floral shape) genus *Friesodielsia* closely resemble *Desmos*. The flowers resemble those of *Sapranthus* and *Desmopsis* (both Sapranthus-group) as well. Only the texture of the apices of the stamens is different. In non-floral features *Desmos* is different from the genera of the Sapranthus-group.

Specimens examined:

D. chinensis: Herb. d'Alleizette s.n. (L); Griffith s.n. (L); Gwynne Vaughan 602 (L); Kerr 1827 (L); Maxwell 75-431 (L); Schmid s.n. (P); Scott s.n. (L); Sillet 6423 (L); Teo & P. 405 (L); Woo 147 (P). — *D. cochinchinensis:* Bunchuay 72 (L); Chew & Kiah SFN 40994 (L); Kasin 161 (P); Teo & P. 346 (L). — *D. dumosus:* Bon 5367 (P); Burkill 1812 (L); Brand 24589 (L); Kerr 8871 (L); King 8617 (L); Korthals s.n. (L); Masters s.n. (L). — *D. elegans:* Kostermans 25649 (L). — *D. goezeanus:* v. Mueller s.n. (K). — *D. sp.:* Cult. Hort. Bog. s.n. (L).

Fissistigma W. Griffith, Not. Pl. Asiat. 4 (1854) 706.

Buds (broadly) ovoid (petals). *Sepals* valvate, 3, connate or rarely free, 1–10 mm long, fleshy, sometimes thin, veins not prominent, indument present, hairs simple. *Petals* light yellow, purplish-pink, or light brown, sometimes inside white tinged with pink, or inner petals pink, valvate or slightly imbricate, 6, free, outer whorl longer, outer ones 8–28 mm long, inner ones 7–14 mm long, 2 × as long as wide,

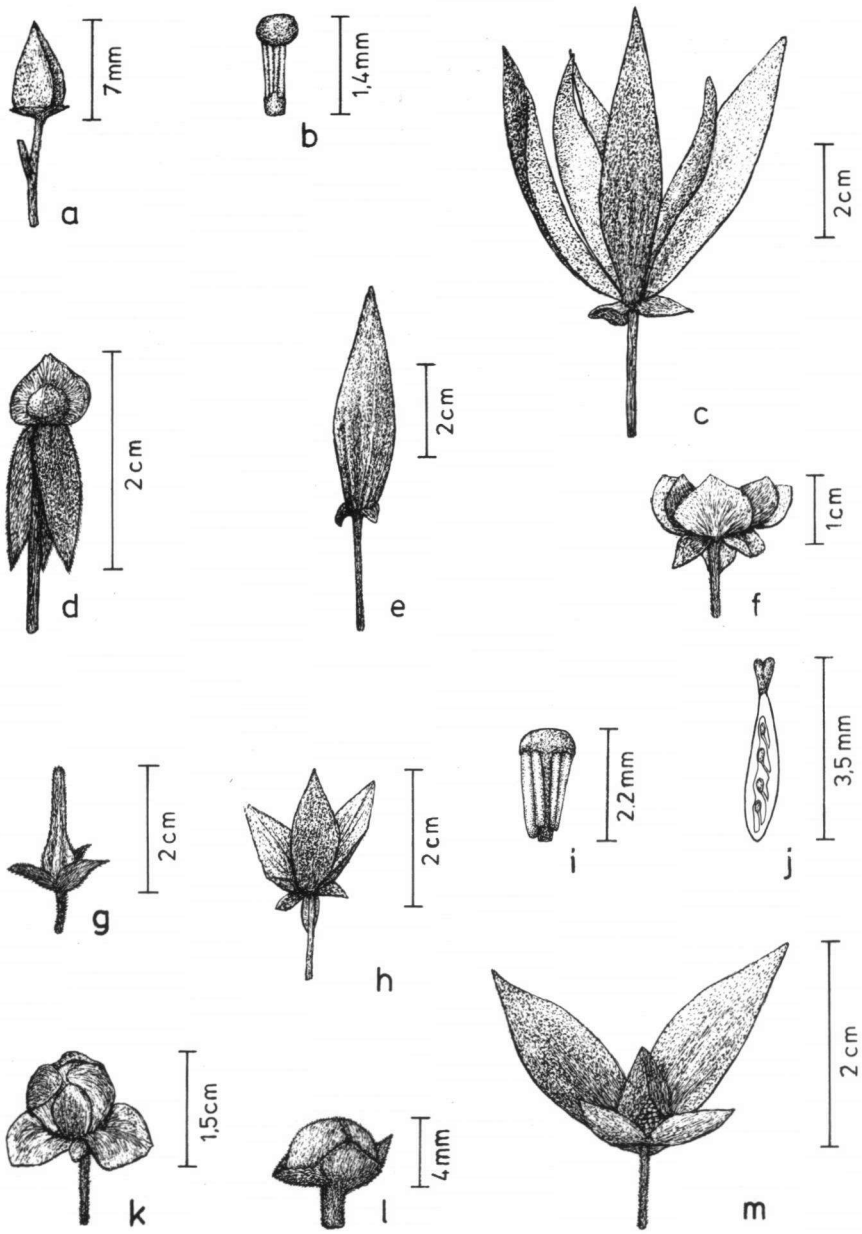


Fig. 19. Friesodielsia-group — a. *Friesodielsia discostigma* (Zenker 516): bud; b. *Friesodielsia gracilipes* (Bos 3077): stamen; c. *Desmos chinensis* (Schmid s.n.): flower; d. *Friesodielsia montana* (Louis 3828): flower bud; e. *Dasymaschalon blumei* (van Balgooy 2546): flower bud; f. *Friesodielsia obovata* (Richards 13409): flower; g. *Friesodielsia biglandulosa* (Cult. Hort. Bog. 7697): bud; h. *Friesodielsia gracilis* (Meikle 956): flower (bud); i. & j. *Dasymaschalon sp.* (Burck s.n./ 5957): stamen (i) and carpel (j); k. *Friesodielsia obovata* (Richards 13409): bud; l. *Schefferomitra subaequalis* (Hoogland & Craven 10431): bud; m. *Friesodielsia gracilipes* (Ahmed & Chizea FHI 19780): flower (bud).

3–5 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner petals basally glabrous inside. *Torus* cylindrical or broadly ovoid. *Stamens* (few to) numerous, 0.9–2 mm long, extrorse; apex tongue-shaped, glabrous, often shiny. *Carpels* free, numerous, 1.8–3 mm long, hairy, style absent, stigma ellipsoid, glabrous or hairy; ovules 4–20, lateral, 2-seriate. *Flowers* bisexual.

Type – *F. scandens* W. Griffith.

Distribution – About 60 species in tropical Asia, incl. Taiwan, in New Caledonia?, and New Guinea.

Notes – *Fissistigma* (fig. 20a, c, g) is easy to recognize by its conical buds, the densely hairy outer petals, the glabrous inner petals, and the tongue-shaped and shiny apices of the stamens. The flowers are often clustered in cymes or panicles.

A few specimens differ from the other species: *Fissistigma sp.* (Moll BW 9772, L), from New Guinea: inner petals connivent, apparently cleistogamous, thus intermediate between *Fissistigma* and *Mitrella. Fissistigma sp.* (Jacobs 8290, L) from Sumatra with different shaped stamens and 26 ovules per carpel. *Fissistigma pallens* and *F. petelotii,* apparently conspecific, have flowers which look like large *Sphaerocoryne*-flowers. Finet & Gagnepain (1906) mention 30 ovules per carpel for *F. pallens.*

Specimens examined:

F. bicolor: Sillet 6466 or 1139 (L); Wallich 6466 (L). — *F. borneense:* Korthals s.n. (L). — *F. elmeri:* Elmer 20881 (L). — *F. fulgens:* Ahamad s.n. (L); Ridley s.n. (L). — *F. glaucescens:* Tsang 26762 (P). — *F. kingii:* J. & M.S. Clemens 27439 (L); King 4070 (L); Teijsmann s.n. (L). — *F. lanuginosum:* Maingay 71 (L); Rahmat si Toroes 4460 (L). — *F. latifolium:* Burkill 2608 (L). — *F. litseaefolium:* King 4063 (L). — *F. longipes:* Rahmat si Boeea 8449 (L). — *F. pallens:* Eberhardt 4748 (P). — *F. petelotii:* Pételot 4862 (P). — *F. rufum:* Cuming 2340 (W). — *F. sp.:* Jacobs 8290 (L); Moll BW 9772 (L).

Friesodielsia van Steenis, Bull. Jard. Bot. Buitenzorg ser. 3, 17 (1948) 458.

Buds lanceoloid to broadly depressed ovoid (sepals or petals). *Sepals* valvate, 3, free or connate, 2–12 mm long, fleshy, sometimes thin, veins prominent or not, indument present or absent, hairs simple. *Petals* red, pinkish, cream, (pale) (greenish-)yellow, or outer ones violet, brownish, greenish to yellowish to creamy-white, inner ones yellowish, cream or white with violet base, or wine-red, or outside yellow, inside red, valvate, 6, free, outer whorl longer, outer ones 6–36 mm long, inner ones 5–8 mm long, 1–4 × as long as wide, 2–7 × length of sepals, fleshy, sometimes thin, veins prominent or not, indument present, hairs simple; inner petals sometimes connivent, sometimes basally glabrous inside. *Torus* broadly cylindrical and apex depressed ovoid, sometimes with broad margin, or depressed ovoid, sometimes with a slightly concave apex. *Stamens* numerous, 0.5–1.4 mm long, extrorse; apex discoid, shiny or fleshy. *Carpels* free, (few to) numerous, 1.5–1.7 mm long, hairy or glabrous, style absent, stigma ellipsoid, glabrous; ovules 1–3, basal or lateral, 1-seriate. *Flowers* bisexual.

Type – *F. cuneiformis* (Blume) van Steenis.

Distribution – About 40 species in tropical Asia and tropical Africa.

Notes – *Friesodielsia* is diverse in its flowers. Verdcourt (1971b) proposed 3 subgenera for the African species: subgenus *Ambrymitra* for *F. obovata* (fig. 19f, k),

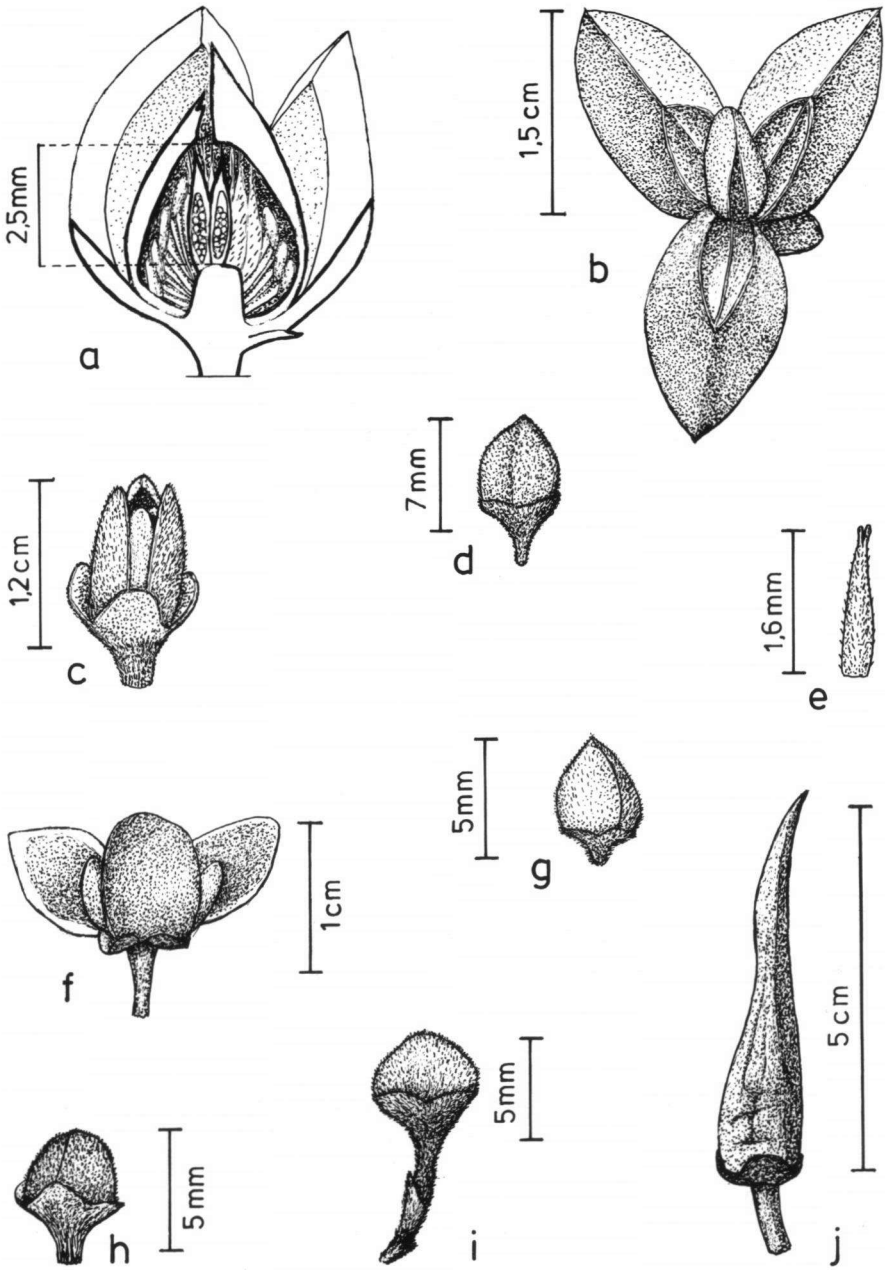


Fig. 20. Friesodielsia-group — a. *Fissistigma fulgens* (Ridley s.n.): longitudinal section; b. *Mitrella kentii* (Lobb s.n.): flower, front petals reflexed; c. *Fissistigma bicolor* (Wallich 6466): young flower; d. *Mitrella kentii* (Sinclair s.n.): bud; e. *Sphaerocoryne aberrans* (Pierre 1317bis): carpel; f. *Sphaerocoryne gracilis* (Holmes 1185): flower; g. *Fissistigma glaucescens* (Tsang 26762): bud; h. *Sphaerocoryne gracilis* (Holmes 1185): bud; i. *'Popowia' humbertii* (Humbert & Capuron 24174): bud; j. *Pyramidanthe prismatica* (Cult. Hort. Bog. XI-A-59): bud.

subgenus *Oxymitropsis* for *F. enghiana* (fig. 18f) and *F. hirsuta* (fig. 18e), and subgenus *Friesodielsia* for the remaining species (fig. 19a, d, h, m). The Asiatic species (figs. 18g, 19g) usually differ considerably from the African species, but intermediate forms are present. The flowers of the African species have reddish, pinkish, and purplish colours, the Asiatic species do not.

Part of the species of *Friesodielsia* seem to be closely related to *Desmos*, especially *F. fornicata* and *F. hirsuta*, whereas some of the African species closely resemble some large-flowered species of *Monanthotaxis*.

The two African species *F. discostigma* (fig. 19a) and *F. gracilipes* (fig. 19b, m) look rather different from the remaining *Friesodielsia*-species. The pollen of *F. discostigma* and *F. gracilipes* was examined by Walker (1971a), and appeared to be different from the Asiatic species of *Friesodielsia*. The leaves of *F. discostigma* closely resemble those of *Afroguatteria*. Le Thomas (1981) examined the pollen of *F. enghiana*, which she subsequently placed in the Monanthotaxis-group.

Specimens examined:

AFRICA — *F. dielsiana:* Zenker 2473 (BR). — *F. discostigma:* Zenker 516 (U). — *F. enghiana:* Leonard 2768, 3848 (BR); Le Testu s.n. (BR). — *F. gracilipes:* Ahmed & Chizea FHI 19780 (K); Bos 3077, 4180 (BR); Zenker 360 (U). — *F. gracilis:* Akpabla 1106 (P); Meikle 956 (K, P). — *F. hirsuta:* Bamps 1381 (BR); Jaeger 8237 (K). — *F. montana:* Dewulf 987 (BR); Louis 3644, 3828 (BR). — *F. obovata:* Burtt 3453, 5089 (BR); Davies 1688 (BR); Milne-Redhead & P. Taylor 8548 (BR); Phipps 2355 (BR); Richards 13409 (K); G. Taylor 3332 (BR).

ASIA — *F. acuminata:* Kadir & Enggoh 10348 (K, L). — *F. affinis:* Sinclair 10303 (L). — *F. biglandulosa:* Cult. Hort. Bog. 7697, XI-A-23 (L). — *F. cuneiformis:* Okada 3253 (U). — *F. desmoides:* Maung Law Tek 1385 (K); Ridley 14725 (K); Sinclair 38851 (L). — *F. excisa:* Haviland 2216 (L); Korthals s.n. (L). — *F. fornicata:* Masters s.n. (L); Wallich 6423A (BR, L). — *F. glauca:* Beccari 3742 (K).

Mitrella Miquel, Ann. Mus. Bot. Lugduno-Batavum 2 (1865) 38.

Buds triangular-ovoid (petals). *Sepals* (aestivation not observed), 3, connate, 1.5–3 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* (brownish-)yellow or yellowish- or light green, valvate, 6, free, outer whorl longer, outer ones 6–22 mm long, inner ones 4–9 mm long, 1.5 × as long as wide, 5 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner petals connivent. *Torus* broadly cylindrical, sometimes with a slightly concave apex. *Stamens* numerous, 1.2–2.5 mm long, extrorse; apex tongue-shaped or discoid, fleshy or shiny. *Carpels* free, few to numerous, 1–2.5 mm long, glabrous, style present, stigma discoid, glabrous; ovules 4, lateral, 1?- or 2-seriate. *Flowers* bisexual.

Type – *M. kentii* Miquel.

Distribution – 5? species in Asia (Malaysia, Borneo, Sumatra), and New Guinea.

Note – *Mitrella* (fig. 20b, d) is kept apart from *Fissistigma* by some authors, e.g., by Sinclair (1955), while others include it in *Fissistigma*, e.g., Fries (1959). *Mitrella* differs from *Fissistigma* in the much smaller and mitriform inner petals (fig. 20b), and the fleshy apices of the stamens. *Mitrella* seems to have affinities to both *Fissistigma* and *Sphaerocoryne*.

Specimens examined:

M. dielsii: Beccari 3899 (B). — *M. kentii:* Chai S36712 (K); Ilias et al. S32176 (K); Lobb s.n.

(K); Mohd Kasim Zainudin 1061 (L); Sinclair s.n. (K); Yeo & Jugah S38404 (K). — *M. ledermannii:* Ledermann 6672 (K); Schram BW 9393 (L). — *M. sp.:* Elmer 20338 (L); Ramos 1474 (L).

Monocarpia Miquel, Ann. Mus. Bot. Lugduno-Batavum 2 (1865) 12.

Buds broadly triangular-ovoid (sepals). *Sepals* valvate, 3, free or connate, 9–12 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* yellowish(-white) to orange-green, valvate? or imbricate?, 6, free, both whorls equal in length, 10–45 mm long, 2 × as long as wide, 2–4 × length of sepals, fleshy, veins prominent, indument present, hairs simple, inner petals basally with long hairs inside. *Torus* depressed obovoid with a flat or slightly concave apex. *Stamens* numerous, 1.3–1.6 mm long, extrorse; apex discoid, fleshy. *Carpels* free, 3, 2.5–3 mm long, hairy, style short or absent, stigma shallowly obconical (cup-shaped), hairy, enlarging considerably when receptive; ovules 6, lateral, 2-seriate. *Flowers* bisexual.

Type – *M. euneura* Miquel.

Distribution – 1 species in Asia, ranging from Thailand to Indonesia.

Note – *Monocarpia* (fig. 17f) has flowers of similar size as *Desmos,* but differs from that genus by the possession of only 3 carpels and a stigma which enlarges considerably when it becomes receptive. The latter phenomenon is also observed in *Dendrokingstonia.* The shape of the torus resembles that of some genera of the Uvariastrum-group, although it is smaller in *Monocarpia.*

Specimens examined:

M. euneura: Burkill 1796 (L); David 87 (P); Korthals s.n. (BR, U); Ng FRI 20995 (L); Selvaraj FRI 11155, FRI 11183, FRI 11196 (L); Whitmore FRI 12315 (L).

Pyramidanthe Miquel, Ann. Mus. Bot. Lugduno-Batavum 2 (1865) 39.

Buds (ovoid-)lanceoloid (petals). *Sepals* (aestivation not observed), 3, connate, 4–5 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* valvate, 6, free, outer whorl longer, outer ones 35–50 mm long, inner ones 7 mm long, 6 × as long as wide, 7–9 × length of sepals, fleshy, veins not prominent, indument present, hairs simple. *Torus* depressed ovoid with a flat or concave apex. *Stamens* numerous, 1.2–2.8 mm long, extrorse; apex discoid, shiny. *Carpels* few, 2.5 mm long, hairy, style absent, stigma discoid (incompletely observed). *Flowers* bisexual.

Type – *P. rufa* Miquel [= *P. prismatica* (J.D. Hooker & T. Thomson) Merrill].

Distribution – 1 species in Asia (Thailand, Malaysia, Borneo, and Sumatra).

Notes – *Pyramidanthe* (fig. 20j) is kept apart by Sinclair (1955), while Fries (1959) included *Pyramidanthe* in *Fissistigma. Pyramidanthe* differs from *Fissistigma* by the greater difference in size of the inner and the outer petals, and the stamens which have a discoid apex.

Pyramidanthe seems related to both *Sphaerocoryne* and *Fissistigma.* In one specimen the inner stamens tend to become staminodial such as found in the Xylopia-group.

Specimens examined:

P. prismatica: Kerr 7492 (K); Maingay 74 (K); Cult. Hort. Bog. XI-A-59 152 (K).

Schefferomitra Diels, Bot. Jahrb. Syst. 49 (1912) 152.

Buds spheroid (petals). *Sepals* (aestivation not observed), 3, connate, 2–3 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* green, valvate, 6, free, outer whorl slightly longer, 5–6 mm long, 1 × as long as wide, 2 × length of sepals, fleshy, veins not prominent, indument present, hairs simple. *Torus* not observed. *Stamens* numerous, 1.7–2.3 mm long, extrorse; apex tongue-shaped, fleshy. *Carpels* free, numerous, (length not measured), hairy, style absent, stigma lanceoloid; (ovules not observed). *Flowers* bisexual.

Type – *S. subaequalis* (R.H.C.C. Scheffer) Diels.

Distribution – 1 species in New Guinea.

Note – *Schefferomitra* (fig. 191) has very small, globose flowers, which resemble more or less the flowers of, e.g., *Popowia* and *Papualthia* (the species from New Guinea). The glabrous inner petals and the tongue-shaped apices of the stamens, however, remind of *Fissistigma.* According to the illustration in Diels (1912), *Schefferomitra* has one lateral ovule.

Specimens examined:
S. subaequalis: Beccari 523 (B); Hoogland & Craven 10431 (L); Ledermann 9831 (L).

Sphaerocoryne (Boerlage) Ridley, J. Straits Branch Roy. Asiat. Soc. 75 (1917) 8.

Buds broadly depressed ovoid to spheroid (petals). *Sepals* (aestivation not observed), 3, connate, 1.5–3 mm long, fleshy, veins not prominent, indument present or absent, hairs simple. *Petals* creamy, or green to yellow, valvate, 6, free, outer whorl longer, outer ones 5–13 mm long, inner ones 3–4.5 mm long, 1–2 × as long as wide, 3–4 × length of sepals, fleshy, veins not prominent, indument present, hairs simple. *Torus* broadly cylindrical, sometimes with a very shallowly conical apex, or shallowly conical with a flat apex. *Stamens* numerous, 1–2 mm long, extrorse; apex discoid, glabrous, often fleshy or shiny. *Carpels* free, numerous, 1–2 mm long, hairy or glabrous, style absent, stigma bilobed, glabrous; ovules 2, lateral, 1-seriate. *Flowers* bisexual.

Lectotype – *S. siamensis* (Boerlage) Ridley.

Distribution – Asia (Indochina, Thailand, Malaysia, Borneo), and in eastern and southern tropical Africa and Madagascar, 3–4 species.

Notes – *Sphaerocoryne* (fig. 20e, f, h, i) seems to have affinities to *Mitrella, Pyramidanthe, Fissistigma,* and also resembles *Rauwenhoffia. Sphaerocoryne* differs from these genera in having fewer ovules. Ban (1974) included *Sphaerocoryne* in *Mitrella.*

Some of the *Popowia*-species of Madagascar, which were not transferred to *Monanthotaxis* by Verdcourt (1971b), should be referred to *Sphaerocoryne.* That would imply that *Sphaerocoryne* has a much wider, but disjunct, distribution in Asia (Indochina, Thailand, and Malaya), East Africa, and Madagascar.

Specimens examined:
AFRICA — *S. gracilis:* Abberley & Harris 1517 (K); Angus 433 (K); Holmes 1185 (K); Mgaza 741 (K); Schlieben 5339 (B). — *'Popowia' greveana:* Decary s.n. (L). — *'Popowia' humbertii:* Humbert & Capuron 24174 (P).

ASIA — *S. siamensis:* Chaloenphol 88 (K); Kerr 3525 (BM); Phengkhlai BKF 54515/1954 (K); Pierre 1615 (K); Poilane 193, 11967 (B); Vidal 1287 (L). — *S. aberrans:* Pierre 1317bis (L). — *S. sp.:* Phengnaren 631 (K).

Table 9. List of character states found in the genera of the Friesodielsia-group.

Taxa: A = *Artabotrys*, C = *Cyathocalyx*, D1 = *Dasoclema*, D2 = *Dasymaschalon*, D3 = *Desmos*, F1 = *Fissistigma*, F2 = *Friesodielsia*, M1 = *Mitrella*, M2 = *Monocarpia*, P = *Pyramidanthe*, S1 = *Schefferomitra*, S2 = *Sphaerocoryne*.

	A	C	D1	D2	D3	F1	F2	M1	M2	P	S1	S2
Flowers:												
3-merous	+	+	+	+	+	+	+	+	+	+	+	+
hairs simple	+	+	–	+	+	+	+	+	+	+	+	+
hairs stellate	–	(+)	+	–	–	–	–	–	–	–	–	–
bisexual	+	+	?	+	+	+	+	+	+	+	+	+
Sepals:												
valvate	+	+	?	?	?	+	+	?	+	?	?	?
reduplicate-valvate	+	+	?	?	?	–	–	?	–	?	?	?
connate	–,+	–,+	+?	–,+	–	+(–)	–,+	+	–,+	+	+	+
indument absent	–,+	–	–	–	–	–	–,+	–	–	–	–	–,+
1–5 mm long	+	+	+	+	+	+	+	+	–	+	+	+
5–20 mm long	+	+	–	+	+	+	+	–	+	–	–	–
Petals:												
valvate	+	+	?	+	?	+	+	+	?	+	+	+
one whorl absent	–	–	–	+	–	–	–	–	–	–	–	–
inner whorl smaller	–,+	–	–	–	+	+	+	+	–	+	(+)	(+)
3.5–30 mm long	+	+	+	+	+	+	+	+	+	–	+	+
30–145 mm long	+	+	–	+	+	–	+	–	+	+	–	–
Stamens:												
numerous	+,–	+	?	+	+	+,–	+	+	+	+	+	+
anthers extrorse	+	+	?	+	+	+	+	+	+	+	+	+
apex tongue-shaped	+	–	?	–	–	+	–	+	–	–	+	–
apex discoid	+	+	?	+	+	–	+	+	+	+	–	+
apex shiny	–	–	?	+,–	+	+,–	+,–	–,+	–	+	–	+,–
0.5–4 mm long	+	+	?	+	+	+	+	+	+	+	+	+
Carpels:												
1 in number	–	+	+	–	–	–	–	–	–	–	–	–
few	+	?	–	–	–	+	+	+	+	?	–	–
numerous	+	+	–	+	+	+	+	+	–	?	+	+
stigma enlarging	–	–	–	–	–	–	–	–	+	–	–	–
Ovules:												
1, basal	+	–	?	–	–	–	+	–	–	?	?	–
2, basal	+	–	?	–	–	–	–	–	–	?	?	–
1–7, lateral	–	+	?	+	+	+	+	+	+	?	?	+
> 7, lateral	–	–	?	–	–	+	–	–	–	?	?	–

6. Fusaea-group (figs. 21, 22; table 10)

Buds triangular- to depressed-ovoid (sepals); sometimes sepals entirely fused. *Sepals* valvate or reduplicate-valvate, 2 or 3, free or connate, 5–25 mm long, fleshy, sometimes rather thin, veins prominent or not, indument present or absent, hairs simple. *Petals* whitish to yellowish to reddish, pink, brownish, or greenish, imbricate or rarely valvate, 4, 6, or 8, free or sometimes connate, both whorls equal in length or inner or outer ones longer, 5–70 mm long, 0.8–5 × as long as wide, 1–5 × length of sepals, fleshy, veins prominent or not, indument present, hairs simple, inner petals sometimes basally glabrous, shiny, or with fewer hairs inside. *Torus* depressed ovoid with a slightly to deeply concave apex, sometimes with an ovoid apicule, or cushion-shaped with slightly concave apex. *Stamens* very numerous, 0.7–4 mm long, usually indurate, extrorse or rarely latrorse, sometimes margins of slit inflexed, staminodes sometimes present; apex discoid or rarely depressed ovoid, usually hairy, sometimes shiny, rarely fleshy. *Carpels* free or sometimes fused, numerous, 1–5 mm long, rarely stipitate, hairy, style present or rarely absent, stigma discoid, flat and lobed, or replaced by a ciliate rim; ovule 1 or rarely 2, basal or sometimes lateral. *Flowers* bisexual.

Distribution – 7 genera in the Neotropics, in Central Africa, and in Southeast Asia.

Notes – This group is characterized by large, valvate sepals, usually imbricate petals, numerous stamens with a (more or less) indurate texture, and numerous carpels with usually one basal ovule (fig. 21a). The apices of the stamens are usually hairy (fig. 22c) and the torus is shallowly to deeply concave (fig. 21a).

In *Afroguatteria, Disepalum* and *Enicosanthellum* the texture of the stamens is not indurate, but these genera share so many features with the other 4 genera, that it is preferred to place them in this group. *Disepalum*, despite its aberrant morphology, is closely related to *Enicosanthellum*. *Pseudartabotrys* differs in the shape of its petals (fig. 21e) from the other genera of this group, but the torus, the stamens, and the carpels point to a close relationship with *Letestudoxa*. *Afroguatteria* (fig. 21d) seems to have a midway position between the Friesodielsia-group (e.g., *Sphaerocoryne* and *Desmos*) and the Fusaea-group (e.g., *Duckeanthus* and *Enicosanthellum*). Because of the imbricate petals and the large torus *Afroguatteria* is included in the Fusaea-group, although in non-floral features it is rather a member of the Friesodielsia-group.

The Fusaea-group may have affinities to the Friesodielsia-group (via *Afroguatteria*, see above) and the Xylopia-group. With the latter group it has the indurate texture of the stamens and the presence of a style in common. Like *Xylopia, Fusaea* has staminodes and a deeply concave torus.

Afroguatteria Boutique, Bull. Jard. Bot. État Brux. 21 (1951) 104, t. 2.

Buds very broadly ovoid (sepals). *Sepals* reduplicate-valvate, 3, free, 5–7 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* (yellow-) orange or green-yellowish, imbricate, 6, free, both whorls equal in length or inner ones slightly longer, outer ones 20–35 mm long, inner ones 25–35 mm long, 1.7 × as long as wide, 5 × length of sepals, fleshy, veins not prominent, indument present, hairs simple. *Torus* not observed. *Stamens* numerous, 0.7–1 mm long, more or less

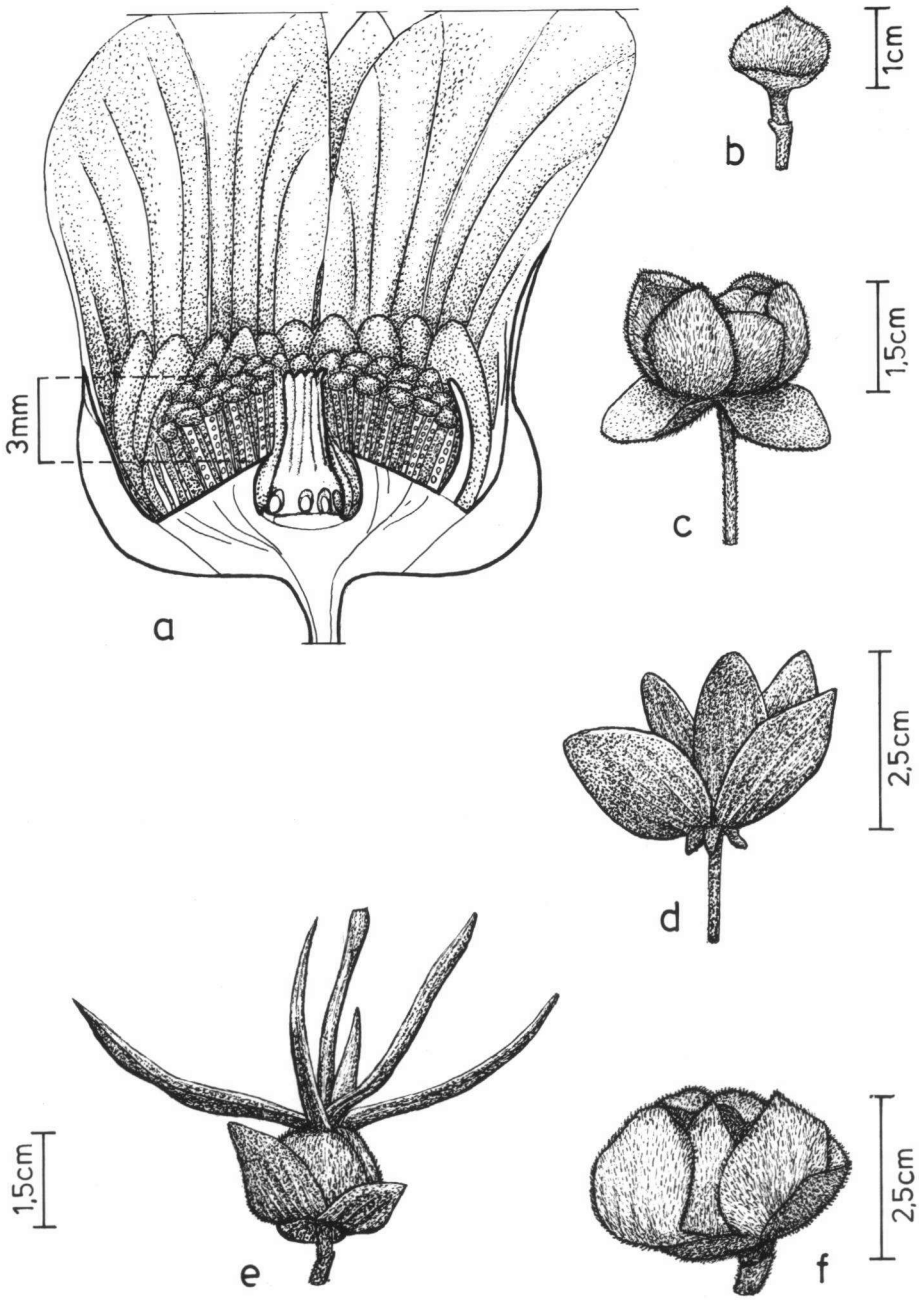


Fig. 21. Fusaea-group — a. *Fusaea longifolia* (van Hall 9i): longitudinal section; b. *Fusaea longifolia* (Cid et al. 2373): bud; c. *Enicosanthellum plagioneura* (How 70331): flower; d. *Afroguatteria bequaertii* (Louis 14142): flower; e. *Pseudartabotrys letestui* (Le Testu 1432): flower bud; f. *Letestudoxa bella* (Le Testu 8362): young flower.

latrorse; apex discoid to depressed ovoid, shiny or sometimes fleshy. *Carpels* free, numerous, hairy (incompletely observed). *Flowers* bisexual.

Type – *A. bequaertii* (De Wildeman) Boutique.

Distribution – 1 (or 2?) species in Africa (Zaire).

Notes – *Afroguatteria* (fig. 21d) seems to have affinities to *Desmos, Disepalum, Duckeanthus, Enicosanthellum, Friesodielsia,* and *Sphaerocoryne* (genera of either the Friesodielsia-group or the Fusaea-group). With *Duckeanthus* it shares a similar texture of sepals and petals, and sometimes similar leaves. *Enicosanthellum* and *Disepalum* have similar stamens and carpels as *Afroguatteria.* In *Friesodielsia discostigma* exactly the same leaves are found as in *Afroguatteria.* With *Sphaerocoryne* it has similar leaves and pedicel in common. Some species of *Desmos* have petals with a similar texture as *Afroguatteria.*

The stamens of *Afroguatteria* have an unusual small diameter.

Specimens examined:

A. bequaertii: Bequaert 6663 (BR); Evrard 4146 (BR); Lejoly 4865 (BR); Louis 13271, 14142 (BR). — *A. sp.:* Evrard 5343 (BR).

Disepalum J.D. Hooker, Trans. Linn. Soc. London 23 (1862) 156, t. 20.

Buds triangular-ovoid (sepals). *Sepals* valvate or reduplicate-valvate, 2, free, 5–10 mm long, fleshy, thin, veins prominent or not, indument present, hairs simple. *Petals* greenish-white or green with red lobes, imbricate?, 4, 6, or 8, connate, all petals in one whorl, 5–18 mm long, 1–5 × as long as wide, 1–2 × length of sepals, fleshy, veins not prominent, indument present or absent, hairs simple. *Torus* cushion-shaped, apex slightly concave. *Stamens* numerous, 1.2–1.8 mm long, extrorse; apex discoid, hairy. *Carpels* free, numerous, 1–2 mm long, sometimes stipitate, hairy, style present or absent, stigma discoid or flat and lobed; ovules 1 or 2, basal or lateral. *Flowers* bisexual.

Type – *D. anomalum* J.D. Hooker.

Distribution – 6 species in tropical Asia (Sumatra, Borneo, and Malaya).

Note – *Disepalum* (fig. 22g) has the most aberrant flowers within the Annonaceae. The wide, cup-shaped petals, the sepals placed distinctly below the torus, the very broad but short torus, and the very large number of carpels are unique within the family. *Disepalum* is closely related to *Enicosanthellum.*

Specimens examined:

D. aciculare: Haviland 1652 (L). — *D. anomalum:* Ashton S7899 (L); Hose 214; Lajanah SAN 33604 (L); Nicholson 39763 (L); van Niel 4102 (L); Othman SAN 27317 (L); Pitty 63184 (L); Pitty & Ogata SAN 63300 (L); Sundaling 83862 (L). — *D. coronatum:* Jumatin 72519 (L); Mondi 237 (L). — *D. grandiflorum:* Hose 142 (L). — *D. longipes:* Boschbouwproefstation 7658 (L); Bünnemeijer 3210 (U); Cockburn FRI 7847 (L); Everett FRI 14013 (L). — *D. platypetalum:* van Steenis 9843 (L).

Duckeanthus R.E. Fries, Acta Horti Berg. 12 (1) (1934) 106, t. 5.

Buds depressed (triangular-)ovoid (sepals). *Sepals* valvate, 3, free, 9–20 mm long, fleshy, thin, veins not prominent, indument absent. *Petals* white or green,

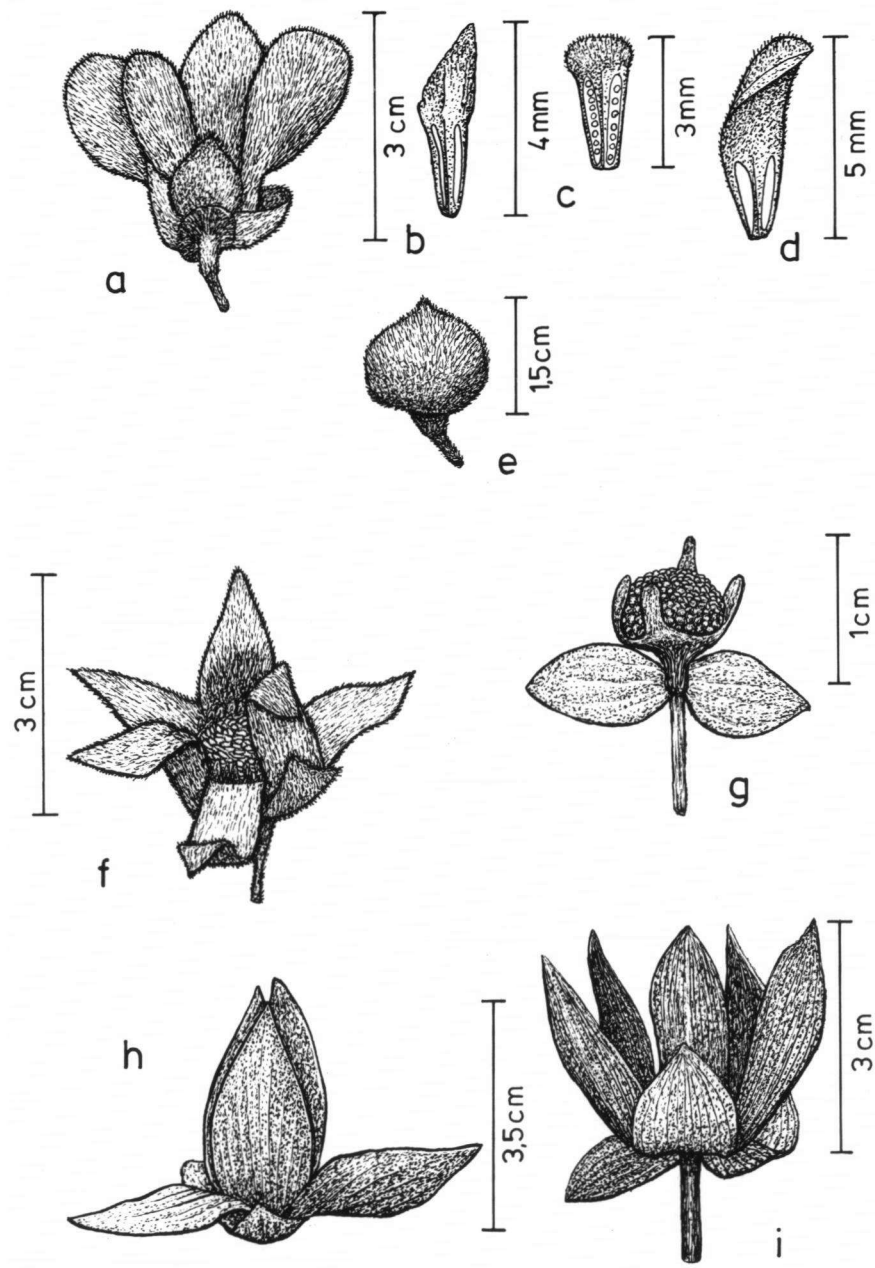


Fig. 22. Fusaea-group — a. *Fusaea peruviana* (Begazo 92): flower; b., c. & d. *Fusaea peruviana* (Berlin 637): fertile stamen (c) and staminodia (b and d); e. *Letestudoxa bella* (Le Testu 8383): bud; f. *Fusaea longifolia* (Hekking 1198): flower; g. *Disepalum anomalum* (van Niel 4102): flower; h. *Duckeanthus grandiflorus* (Pran e et al. 15696): flower; i. *Enicosanthellum pulchrum* (van Balgooy 2645): flower.

imbricate, 6, free, inner whorl longer, outer ones 27–55 mm long, inner ones 35–70 mm long, 2 × as long as wide, 3.5–5 × length of sepals, fleshy, sometimes thin, veins prominent, indument present, hairs simple. *Torus* depressed ovoid, apex slightly concave. *Stamens* numerous, 3 mm long, indurate, extrorse to latrorse; apex discoid, hairy. *Carpels* free, numerous, 8 mm long, glabrous, style present, stigma obconical?, hairy; ovule 1, basal. *Flowers* bisexual.

Type – *D. grandiflorus* R.E. Fries.

Distribution – 1 species in the Rio Negro-area of Brazil.

Note – *Duckeanthus* (fig. 22h) closely resembles *Fusaea,* but differs from that genus in the glabrous sepals, the absence of staminodes, the free carpels, and the torus which is not deeply concave.

Specimens examined:

D. grandiflorus: Ducke RB 23904 (B, K); Maas et al. 6772 (U); Prance et al. 15696 (K, U); Rodrigues 931 (S).

Enicosanthellum N.T. Ban, Bot. Zurn. (Moscow & Leningrad) 60 (1975) 808.

Buds triangular-ovoid (sepals). *Sepals* reduplicate-valvate, (2 or) 3, free (or connate), 10–15 mm long, fleshy, thin, veins prominent or not, indument present, hairs simple. *Petals* yellow, ochraceous-red, or pale green, imbricate, 6 (or 7), free, both whorls equal in length or outer longer, 12–35 mm long, or outer ones 25–32 mm long, inner ones 25 mm long, 2–3 × as long as wide, 2–3 × length of sepals, fleshy, veins prominent or not, indument present, hairs simple. *Torus* depressed ovoid, apex slightly concave. *Stamens* numerous, 1.3–3.2 mm long, extrorse; apex discoid, hairy. *Carpels* free, numerous, 1.3–3 mm long, hairy, style present (long), stigma replaced by a ciliate rim, or discoid, glabrous; ovule 1 (place of attachment not observed). *Flowers* bisexual.

Type – *E. petelotii* (Merrill) N.T. Ban.

Distribution – 3 species in Asia, ranging from southern China to Malaya.

Note – The flowers of *Enicosanthellum* (figs. 21c, 22i) resemble those of *Letestudoxa* because of the large, valvate sepals, the imbricate petals, the numerous stamens and carpels, and the single ovule. The stamens and carpels resemble those of *Disepalum.* Johnson (1989) includes *Enicosanthellum* in *Disepalum.*

Specimens examined:

E. petelotii: Pételot 1780, 6362 (P). — *E. plagioneura:* Eberhardt 4964 (K, P), 4970 (P); How 70331 (K); Pételot 3954 (BM); Poilane 32356 (P). — *E. pulchrum:* van Balgooy 2645 (L); Burkill H.M.B. 813 (K); S. & W.L. Chew s.n. (L); Durant 28734 (L); Kochummen FRI 16735 (L); Robinson s.n. (K).

Fusaea (Baillon) Safford, Contr. U.S. Natl. Herb. 18 (1914) 64.

Buds depressed ovoid (sepals); sepals entirely fused, calyx rupturing irregularly. *Sepals* valvate, 3, connate, 10–20 mm long, fleshy, veins prominent or not, indument present, hairs simple. *Petals* greenish to yellowish, cream (with brown base), silver with purple base, pale greyish- or silvery brown, imbricate, 6, free or connate, inner whorl longer, outer ones 10–40 mm long, inner ones 20–50 mm long, 2–2.5 ×

length of sepals, fleshy, veins prominent or not, indument present, hairs simple, inner petals basally glabrous or with fewer hairs inside. *Torus* (shallowly) depressed ovoid, apex deeply concave. *Stamens* numerous, 3 mm long, indurate, extrorse, staminodes present; apex discoid, hairy. *Carpels* fused, numerous, 2.8–5 mm long, hairy, style present, stigma discoid, with long hairs; ovule 1, basal. *Flowers* bisexual.

Type – *F. longifolia* (Aublet) Safford.

Distribution – 3 species in the Neotropics, ranging from Peru to the Guianas.

Note – *Fusaea* (fig. 22a, f) is easily distinguished by its conspicuous ring of staminodes (formed by the outer stamens and unique within the Annonaceae, fig. 22b, c, d, f), and an entirely fused calyx (fig. 21b).

Specimens examined:

F. longifolia: Cid et al. 1435, 1895, 2179, 2373; van Hall 9i; Hekking 1198; Nascimento 350; Plowman et al. 9426; Prance et al. 8441, 25392; Silva & Rosário 3993; Silva & Santos 4622; Steward et al. 47 (all U). — *F. peruviana:* Berlin 637 (U); Begazo 92 (U).

Letestudoxa Pellegrin, Bull. Mus. Hist. Nat. Paris 26 (1920) 654.

Buds depressed ovoid (sepals); sepals entirely fused, with apiculate apex, calyx rupturing irregularly. *Sepals* 3, connate, 21–25 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* yellow- to reddish- to old-rose, imbricate, 6, free, outer whorl slightly longer, outer ones 30–40 mm long, inner ones 20–30 mm long, 0.8–1.3 × as long as wide, 1.5–2 × length of sepals, fleshy, veins prominent, indument present, hairs simple, margins sometimes slightly crisped, inner petals basally glabrous and shiny inside. *Torus* depressed ovoid, apex concave, sometimes with an ovoid apicule. *Stamens* numerous, 2.8–4 mm long, indurate, extrorse, margins of slit inflexed; apex discoid, shiny. *Carpels* free, numerous, (length not measured), hairy, style very long, stigma replaced by a ciliate rim; ovules not observed. *Flowers* bisexual.

Type – *L. bella* Pellegrin.

Distribution – 2 species in Africa (Gabon and Angola).

Note – *Letestudoxa* (figs. 21f, 22e) resembles *Fusaea* in many features, but lacks the staminodes present in *Fusaea*. In some specimens, however, the outer stamens are somewhat deformed and tend to resemble the staminodes of *Fusaea*.

Specimens examined:

L. bella: Le Testu 5509, 6336 (P), 8362 (BM, BR), 8383 (BR, P), 9364 (BM, BR). — *L. lanuginosa:* Le Testu 9570 (BM, P).

Pseudartabotrys Pellegrin, Bull. Mus. Hist. Nat. Paris 26 (1920) 656.

Buds broadly triangular-ovoid (sepals). *Sepals* reduplicate-valvate, 3, free, 14–21 mm long, fleshy, thin, veins prominent, indument present, hairs simple. *Petals* yellowish, valvate, 6, free, both whorls equal in length, 35–65 mm long, 3 × as long as wide, 2–3 × length of sepals, fleshy, longitudinal veins prominent, indument present, hairs simple, inner petals basally glabrous inside. *Torus* depressed ovoid with a slightly concave apex and a depressed ovoid apicule. *Stamens* numerous,

Table 10. List of character states found in the genera of the Fusaea-group.

Taxa: A = *Afroguatteria*, D1 = *Disepalum*, D2 = *Duckeanthus*, E = *Enicosanthellum*, F = *Fusaea*, L = *Letestudoxa*, P = *Pseudartabotrys*.

	A	D1	D2	E	F	L	P
Flowers:							
hairs simple	+	+	+	+	+	+	+
bisexual	+	+	+	+	+	+	+
Sepals:							
valvate	–	+	+	–	+	(+)	–
reduplicate-valvate	+	+	–	+	–	–	+
entirely connate in bud	–	–	–	–	+	+	–
2 in number	–	+	–	(+)	–	–	–
3 in number	+	–	+	+	+	+	+
indument absent	–	–	+	–	–	–	–
5–25 mm long	+	+	+	+	+	+	+
Petals:							
imbricate	+	+?	+	+	+	+	–
valvate	–	–	–	–	–	–	+
4 or 8 in number	–	+	–	–	–	–	–
6 in number	+	+	+	+	+	+	+
connate	–	+	–	–	–,+	–	–
5–20 mm long	–	+	–	+	+	–	–
20–70 mm long	+	–	+	+	+	+	+
Torus:							
deeply concave	?	–	–	–	+	(+)	–
Stamens:							
numerous	+	+	+	+	+	+	+
indurate	–	–	+	–	+	+	+
anthers extrorse	–	+	+	+	+	+	+
anthers latrorse	+	–	(+)	–	–	–	–
apex discoid, hairy	–	+	+	+	+	–	+
apex discoid, shiny	+	–	–	–	–	+	–
0.7–2 mm long	+	+	–	+	–	–	–
2–4 mm long	–	–	+	+	+	+	+
staminodes present	–	–	–	–	+	–	–
Carpels:							
connate	–	–	–	–	+	–	+
numerous	+	+	+	+	+	+	+
Ovules:							
1, basal	?	+	+	+	+	?	+
2, lateral	?	+	–	–	–	?	–

2.7–3 mm long, indurate, extrorse, margin of slit inflexed; apex discoid, hairy. *Carpels* fused, numerous, 1.5–5 mm long, hairy, style very long, stigma replaced by a ciliate rim; ovule 1, basal. *Flowers* bisexual.

Type – *P. letestui* Pellegrin.

Distribution – 1 species in Africa (Congo).

Note – *Pseudartabotrys* (fig. 21e) differs from the other genera of this group in the shape of its petals which are constricted above the stamens and carpels, and which have long and narrow apices.

Specimen examined:
P. letestui: Le Testu 1432 (BM, P).

7. Guatteria-group (fig. 23; table 11)

Buds broadly (depressed) (triangular-)ovoid, rarely broadly or shallowly deltoid, or spheroid (sepals). *Sepals* valvate or reduplicate-valvate, 3, free or connate, 2–12 mm long, fleshy, veins not or rarely prominent, indument present, hairs simple. *Petals* whitish to yellowish, brownish, orange, reddish, pinkish, or greenish, imbricate to/or valvate, free or rarely connate, both whorls equal in length or inner ones much longer, rarely outer ones longer, 7–45 mm long, or outer ones 7–8 mm long, inner ones 13–32 mm long, 1–3 × as long as wide, 2–5 × length of sepals, fleshy, veins prominent or not, indument present, hairs simple, inner petals basally glabrous, glandular, papillose, differently coloured, or with different indument inside. *Torus* depressed ovoid with a slightly concave apex, cylindrical with a slightly concave apex and sometimes with a broad margin, or rarely shallowly conical with a flat apex. *Stamens* numerous, 0.8–2 mm long, indurate, extrorse, often margins of slit inflexed; apex discoid, usually hairy, sometimes papillose. *Carpels* free, numerous, 1.3–4 mm long, hairy, style present or absent, stigma obovoid, discoid, or obconical, sometimes cup-shaped and grooved; ovule 1, basal. *Flowers* bisexual.

Distribution – 4 genera in the Neotropics.

Notes – This group is characterized by valvate sepals, imbricate to valvate petals, one basal ovule per carpel (fig. 23d, g, h, i), and numerous carpels and stamens. The stamens are indurate and the margins of the slit of the thecae are usually inflexed. Also in non-floral features this is a coherent group (e.g., Morawetz & Waha, 1985). *Guatteriella* and *Guatteriopsis* in their flowers are very close to *Guatteria,* and probably should be included in that genus. *Heteropetalum* differs from the other 3 genera by the difference in size between inner and outer petals, the slightly different stamens (less indurate in texture and the margins of the slit of the thecae not inflexed when dehiscing), and the different shape of the stigma (fig. 23i).

The Guatteria-group shows most similarities with the Fusaea-group: both have the same aestivation of the sepals and petals, indurate stamens, and one basal ovule in common. They differ in the diameter of the torus which is much smaller in the Guatteria-group, and in the more numerous stamens in the Fusaea-group. *Guatteria* also resembles *Cremastosperma* (Cremastosperma-group): the size of the flowers is similar, both have one basal ovule per carpel, and about the same number of stamens and carpels. *Cremastosperma,* however, has imbricate sepals and its stamens are not

indurate. In its flower morphology *Guatteria* is intermediate between *Cremastosperma* and the Fusaea-group. The same is found in seed morphology (Van Setten, 1990), but not in pollen morphology (Walker, 1971a).

Guatteria Ruiz & Pavón, Fl. Peruv. Prodr. (1794) 85, t. 17 (nom. cons.).

Buds broadly (depressed) (triangular-)ovoid, rarely shallowly deltoid or spheroid (sepals); rarely sepals entirely fused. *Sepals* valvate or reduplicate-valvate, 3, free or connate, 2–12 mm long, fleshy, veins prominent or not, indument present, hairs simple. *Petals* cream, (pale) green (with yellowish center) to yellow, greenish-, reddish-, yellow-, or dull brown, orange, or outside brown, inside green, imbricate or ± valvate, 6 (or 8), free (or connate), both whorls equal in length or inner whorl slightly longer, rarely outer whorl longer, 7–45 mm long, 2–3 × as long as wide, 3 × length of sepals, fleshy, veins prominent or not, indument present, hairs simple, inner petals basally glabrous, papillose, with different indument, or rarely glandular inside. *Torus* broadly ovoid with a slightly concave apex, cylindrical with a slightly concave apex and a broad margin, or cushion-shaped with a slightly concave apex. *Stamens* numerous, 0.8–2 mm long, indurate, extrorse, margins of slit inflexed; apex discoid, hairy or papillose. *Carpels* free, many, 1.3–4 mm long, hairy, style present, stigma discoid to obovoid, or obconical, glabrous or hairy; ovule 1, basal. *Flowers* bisexual.

Type – *G. glauca* Ruiz & Pavón.

Distribution – About 250 species in the Neotropics.

Note – *Guatteria* (fig. 23a–g), despite the large number of species, is very uniform in its flowers. *Guatteria nigrescens* has an entirely connate calyx in bud.

Specimens examined:

G. aeruginosa: Hartshorn 1537, 1542 (U). — *G. amplifolia:* Maas 1127 (U); Mori et al. 4555 (U). — *G. calva:* Farinas et al. 336 (U); Liesner 8733, 8748 (U). — *G. conspicua:* Fanshawe, Forest Dep. Brit. Guiana 5542 (U); Jonker-Verhoef & Jonker 494 (U). — *G. dielsiana:* Maas et al. 6206 (U). — *G. discolor:* Grenand 554 (U); Prance et al. 3925, 8495 (U). — *G. dusenii:* Lindeman & de Haas 5764 (U). — *G. ferruginea:* Wurdack & Monachino 41177 (U). — *G. foliosa:* Breteler 4752 (U); D. Coêlho 3872 (U); Prance et al. 17959 (U). — *G. glauca:* Ruiz s.n. (B). — *G. gracilipes:* Lindeman, Stoffers, et al. 429 (U); Maguire 24589 (U). — *G. latisepala:* Cuatrecasas & Llano 24070 (U). — *G.* aff. *laurina:* Luteyn et al. 4774 (U). — *G. macropus:* Eupunino 100 (U). — *G. maypurensis:* Berg & Steward P19926 (U); O. Huber 606, 1898 (U); Prance et al. 3504 (U); A.C. Smith 3055 (U). — *G. megalophylla:* Cid et al. 1829 (U); Prance et al. 8335, 8934, 22853 (U). — *G. melosma:* Jones & Davidson 9595 (U). — *G. mexiae:* Mexía 4249 (U). — *G. nigrescens:* Maas & Martinelli 3222 (U); Regnell III 252 (U). — *G. olivacea:* Krukoff 6853 (U); Prance et al. 23035 (U). — *G. oliviformis:* Hartshorn 1462 (U). — *G. ovalifolia:* Fróes 11787 (U). — *G. paraensis:* Fróes 1753 (U); Pires 51684 (U). — *G. poeppigiana:* Fróes 11590 (U); Marcano Berti 422 (U). — *G. pteropus:* Pennington et al. P22756 (U). — *G. punctata:* BW 2364 (U); de Granville B4554 (U); Kramer & Hekking 2438 (U); Mori & Bolten 8383 (U); Pires & Cavalcante 52186, 52336 (U); dos Santos 489 (U); Schulz et al. LBB 10235 (U); Schulz LBB 10306 (U); Vreden LBB 13711 (U). — *G. sandwithii:* Sandwith 1578 (U). — *G. scandens:* BW 1827 (U); J. & P.A. Florschütz 2214 (U); Hekking 788 (U); Stahel s.n. (U); Wurdack & Adderley 43438 (U). — *G. schomburgkiana:* BW 6409 (U); Elburg LBB 9817 (U); Pulle 365 (U); A.C. Smith 2445, 3058 (U). — *G. sellowiana:* Hatschbach 29943 (U); Duarte 8797 (U); Mexía 5245 (U). — *G. sessilis:* Liesner 8546, 8738 (U); Steyermark & Bunting 102893 (U). — *G. trichoclonia:* Plowman & Schunke V. 7517 (U); Schunke V. 5777 (U). — *G. umbonata:* Maguire & Fanshawe 23121 (U). — *G. villosissima:* Anderson et al. 36315 (U); Meneces 607 (U); Mexía 4620 (U). — *G. sp.:* Maas et al. 5106, 5619 (U).

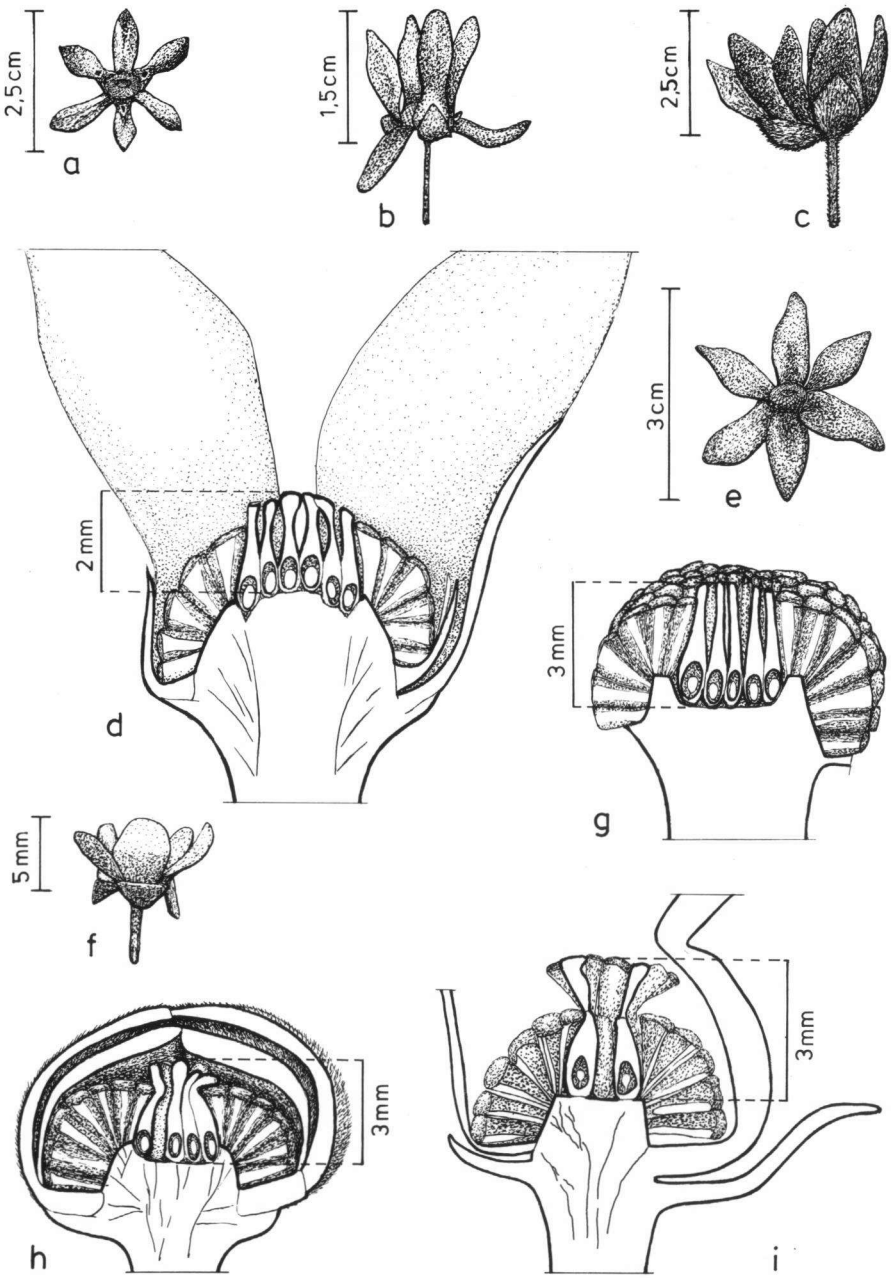


Fig. 23. Guatteria-group — a. *Guatteria foliosa* (Breteler 4752): flower; b. *Guatteria* aff. *laurina* (Luteyn et al. 4774): flower; c. *Guatteria latisepala* (Cuatrecasas & Llano 24070): flower; d. *Guatteria sp.* (Maas et al. 5106): longitudinal section; e. *Guatteria scandens* (Wurdack & Adderley 43438): flower; f. *Guatteria foliosa* (Breteler 4752): flower; g. *Guatteria sp.* (Maas et al. 5619): longitudinal section; h. *Guatteriopsis blepharophylla* (Morawetz & D. Coêlho 19-10883): longitudinal section; i. *Heteropetalum brasiliense* (Maguire et al. 36371): longitudinal section.

Guatteriella R.E. Fries, Acta Horti Berg. 12 (3) (1939) 540, f. 39.

Buds broadly triangular-ovoid (sepals). *Sepals* valvate, 3, connate to free?, 7–9 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* greenish or brown, imbricate, 6, free?, both whorls equal in length, 15–16 mm long, 1.5 × as long as wide, 2 × length of sepals, fleshy, veins not prominent, indument present, hairs simple. *Torus*, *stamens*, and *carpels* not observed.

Type – *G. tomentosa* R.E. Fries.

Distribution – 2 species in Amazonas, Brazil.

Note – *Guatteriella* was established by Fries (1939), because the fruits differ from those of *Guatteria*. Collections with flowers are scarce, but as far as could be observed, *Guatteriella* is not distinct from *Guatteria*.

Specimens examined:

G. tomentosa: Daly et al. 4494 (U); Krukoff 8765 (A, U). — *G. sp.:* Rabelo et al. 3132 (U).

Guatteriopsis R.E. Fries, Acta Horti Berg. 12 (1) (1934) 108, t. 6–8.

Buds broadly depressed ovoid (sepals). *Sepals* valvate, 3, free, 5–10 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* white to (golden) yellow to green, or orange, valvate, 6, free, both whorls equal in length, 12–40 mm long, 1–2 × as long as wide, 2–4 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inside glabrous. *Torus* cylindrical with a slightly concave apex and a broad margin. *Stamens* numerous, 1.5–2 mm long, indurate, extrorse, margins of slit inflexed; apex discoid, hairy. *Carpels* free, numerous, 3–4 mm long, hairy, style present, stigma obovoid; ovule 1, basal. *Flowers* bisexual.

Type – *G. sessiliflora* (Bentham) R.E. Fries.

Distribution – Amazonas, Brazil, 4–6 species.

Note – *Guatteriopsis* is said to be distinct from *Guatteria* because the petals are valvate (fig. 23h). In *Guatteria* sect. *Megalophylla*, however, specimens intermediate between *Guatteria* and *Guatteriopsis* are found.

Specimens examined:

G. blepharophylla: Daly et al. 783 (U); G. & L. Eiten 8902 (U); Fróes 22108 (U); Morawetz & D. Coêlho 19-10883 (U); Prance et al. 3889, 11415 (U); Prance & Silva 59392 (U); Rodrigues 534 (U); N.T. Silva & Rosário 5090 (U); Ule 8843 (L); Vieira 745, 939, 1025 (U). — *G. sessiliflora:* Ducke RB 23892 (B); Ule 5012 (L). — *G. sp.:* Plowman et al. 9413 (U).

Heteropetalum Bentham, J. Proc. Linn. Soc., Bot. 5 (1860) 69.

Buds broadly deltoid (sepals). *Sepals* valvate, 3, free, 6 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* (rose-red-)greenish, or yellow, flushed orange outside, valvate, 6, free, inner whorl longer, outer ones 7–8 mm long, inner ones 13–32 mm long, 2–3 × as long as wide, 2–5 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner petals basally glabrous or with different indument inside. *Torus* shallowly conical with a flat apex. *Stamens* numerous, 1.3–1.5 mm long, more or less indurate, extrorse; apex discoid, hairy or papillose. *Carpels* free, numerous, 3.3–4 mm long, hairy,

style absent, stigma obconical, sometimes cup-shaped and grooved, hairy; ovule 1, basal. *Flowers* bisexual.

Type — *H. brasiliense* Bentham.

Distribution – 2 species in Amazonas, Brazil.

Note – *Heteropetalum* (fig. 23i) is the only neotropical genus with outer petals which are as small as the sepals. This feature is more common in the Asiatic genera.

Specimens examined:

H. brasiliense: Madison et al. 6142 (U); Maguire et al. 36371 (U); Nascimento 591 (U). — *H. spruceanum:* O. Huber & Medina 5818 (U). — *H. sp.:* Stevenson 1115 (U).

Table 11. List of character states found in the genera of the Guatteria-group.

	Guattaria	*Guatteriella*	*Guatteriopsis*	*Heteropetalum*
Flowers:				
perianth 3-merous	+	+	+	+
hairs simple	+	+	+	+
bisexual	+	?	+	+
Sepals:				
valvate	+	+	+	+
reduplicate-valvate	+	–	–	–
connate	–,+	+,–?	–	–
< 5 mm long	+	–	–	–
5–12 mm long	+	+	+	+
Petals:				
imbricate	+	+	–	–
valvate	(+)	–	+	+
whorls equal in size	+	+	+	–
outer whorl smaller	(+)	–	–	+
7–45 mm long	+	+	+	+
Stamens:				
numerous	+	?	+	+
indurate	+	?	+	(+)
anthers extrorse	+	?	+	+
0.8–2 mm long	+	?	+	+
apex discoid	+	?	+	+
Carpels:				
numerous	+	?	+	+
Ovules:				
1, basal	+	?	+	+

8. Hexalobus-group (figs. 24, 25; table 12)

Buds spheroid, triangular-ovoid, (very) (broadly) ovoid, or ellipsoid (sepals) or apert? (petals). *Sepals* valvate or reduplicate-valvate, sometimes apert?, (2,) 3 or 4 , free or connate, 1–23 mm long, fleshy to almost membranous, veins prominent or not, indument present or sometimes absent, hairs simple, margins ciliate or not. *Petals* purplish, reddish, brownish, greenish, yellowish, or whitish, imbricate or valvate, sometimes apert?, 4, 5, 6, or 9, free or connate, sometimes petals in one whorl, both whorls of equal or of different length, 4–75 mm long, 1–10 × as long as wide, 1–12 × length of sepals, fleshy to almost membranous, veins prominent or rarely not, indument present or absent, hairs simple, margins rarely ciliate, sometimes crisped; inner petals sometimes connivent, sometimes glandular or differently coloured inside, sometimes fringe present, sometimes 2 marginal glands present. *Torus* cylindrical, shallowly conical with a flat apex, or depressed ovoid to cylindrical to cushion-shaped with a slightly to deeply concave apex. *Stamens* numerous, or rarely few, 0.5–3.5 mm long, extrorse or rarely latrorse; apex discoid or tongue-shaped, or apical prolongation absent, fleshy or not, glabrous, hairy, or papillose. Carpels free, 1 to numerous, 1.5–4.5 mm long, hairy or glabrous, style present or absent, stigma obconical and grooved, cylindrical, (narrowly) ellipsoid, (ob)lanceoloid, (very) shallowly obconical and sometimes many-lobed (cup-shaped), or bilobed; ovules 3–16, lateral, 1- or 2-seriate or covering the whole ovary wall. *Flowers* bisexual, or occasionally unisexual, plants occasionally androdioecious.

Distribution – 9 genera in the U.S.A., South America, and tropical Africa, Madagascar included.

Notes – This group is somewhat heterogeneous in its flower morphology. The genera of this group often show several of the following features: large, valvate sepals and valvate to imbricate petals, rather thin petals with a prominent venation (fig. 24b, d, j), short stamens, one or few carpels, and many, lateral, 2-seriate ovules, or ovules which cover the whole ovary wall (fig. 25f).

Monodora and *Isolona* were placed in a subfamily Monodoroideae, because their carpel is considered as a unilocular, syncarpous gynoecium with a parietal placentation. No evidence, however, is found supporting the idea that the gynoecium of *Monodora* and *Isolona* is indeed syncarpous. Therefore, the two genera are not kept separate from the remaining Annonaceae in the present study. *Asimina, Deeringothamnus,* and *Diclinanona* are placed in this group with doubt. Consequently, this group is geographically not coherent, but good distinguishing character states are not present in the flowers.

The Hexalobus-group is closely related to the Uvariastrum-group, but differs from it by the less enlarged torus, the short stamens, the less numerous carpels, and because some genera have imbricate petals. These differences, however, are only gradual.

Asimina Adanson, Fam. Pl. 2 (1763) 365.

Buds spheroid (sepals). *Sepals* valvate, (2 or) 3, free, 7–14 mm long, fleshy to almost membranous, veins prominent, indument present, hairs simple. *Petals* (greenish-)white, pink, reddish-brown, or brownish-purple, imbricate, (4 or) 6, free, both

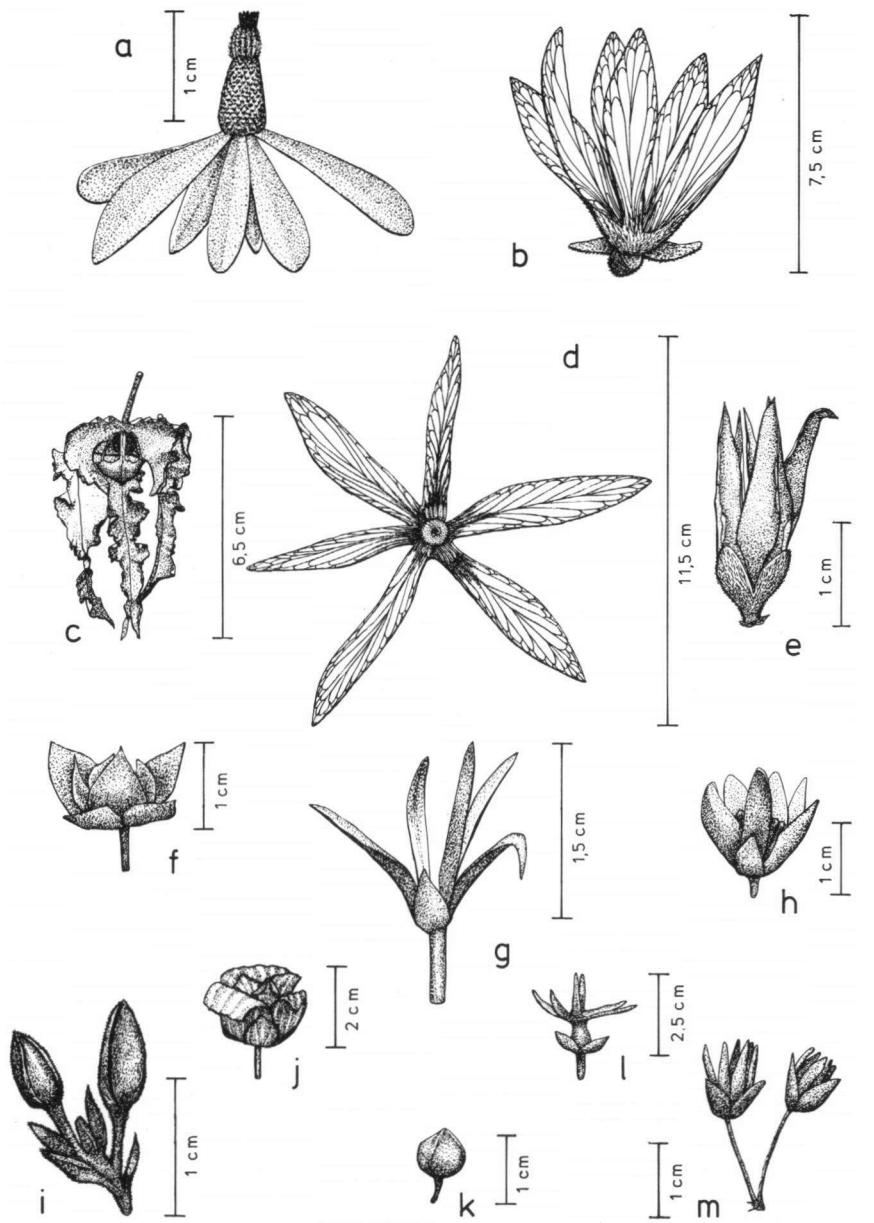


Fig. 24. Hexalobus-group — a. *Toussaintia hallei* (Hallé 4189): flower; b. *Asteranthe asterias* (Verdcourt 5287): flower; c. *Monodora crispata* (J.J.F.E. de Wilde 867): flower; d. *Asteranthe asterias* (Verdcourt 5287): flower; e. *Hexalobus monopetalus* (J.J.F.E. de Wilde 950): flower; f. *Asimina tetramera* (Kral 2517): flower; g. *Deeringothamnus pulchellus* (Small et al. 10925): flower; h. *Deeringothamnus sp.* (Small s.n.): flower; i. *Toussaintia orientalis* (Shabani 472): buds; j. *Asimina triloba* (Cult. Vienna/Morawetz): flower; k. *Ophrypetalum odoratum* (Verdcourt 1075): bud; l. *Isolona campanulata* (de Koning 6748): flower; m. *Diclinanona tessmannii* (Lleras et al. P17323): flowers.

whorls equal in length or outer petals longer, 8–30 mm long or outer ones 15–60 mm long and inner ones 9–35 mm long, 1–1.5 × as long as wide, 1–4 × length of sepals, fleshy to almost membranous, veins prominent, indument present, hairs simple, petals more or less saccate; inner petals sometimes glandular at the base inside, often with two marginal glands. *Torus* (broadly) cylindrical. *Stamens* numerous, 1–2 mm long, extrorse; apex discoid, fleshy, glabrous or papillose. *Carpels* free, 1–7, 3–5 mm long, hairy, style present or absent, stigma ellipsoid (to obovoid); ovules 5–16, lateral, 2-seriate. *Flowers* bisexual.

Type – *A. triloba* (Linnaeus) Dunal.

Distribution – About 8 species in eastern U.S.A. and most southern part of Ontario, Canada.

Note – *Asimina* (figs. 24f, j, 25a, b, c) is the only genus within the Annonaceae extending outside the tropics. As a result, in part of the species the flowers are borne on leafless branches, and appear before the leaves.

Specimens examined:

A. longifolia: Genelle & Fleming 2052 (U); Kral 4712 (BM). — *A. pygmaea:* Lakela 29761 (L); Nash 359 (B). — *A. reticulata:* Eaton 1257 (L); Hekking 1617 (U); Schallert 15195 (U); Wunderlin 5932 (L). — *A. speciosa:* Cooley et al. 5937 (GH); Curtiss 4588 (L); van Heerdt 113 (U); Schallert 6111 (U). — *A. tetramera:* Kral 2517 (BM). — *A. triloba:* Bartholomew 1244 (U); Buysman 1687 (U); Chase 8684 (U); Cult. Gimborn Arb. s.n. (U); Cult. Vienna/Morawetz s.n. (U); Gradstein 1645 (U); Kramer 458, 521 (U); Radford 44739 (U); Rickson 181 (U).

Asteranthe Engler & Diels, in Engler, Monogr. afrik. Pflanzen-Fam. 6 (1901) 30.

Buds triangular-ovoid (or pyriform) (sepals). *Sepals* valvate, 3, free or connate, 4–8 mm long, fleshy, thin, veins not prominent, indument present, hairs simple. *Petals* yellow, cream, or white, basal part at inner side dark red, dark rose, or (dark) yellow, imbricate to valvate, 6 (or 9), connate, both whorls equal in length, 10–70 mm long, 4–10 × as long as wide, 3–9 × length of sepals, fleshy to almost membranous, veins prominent, indument present, hairs simple, inner petals glandular at the base inside. *Torus* depressed ovoid with a slightly concave apex. *Stamens* numerous, 1.5–2 mm long, extrorse; apex discoid, hairy. *Carpels* free, numerous to few, 3.5 mm long, hairy, style absent, stigma obconical (cup-shaped), grooved and folded inwards, hairy; ovules 5, lateral, 2-seriate. *Flowers* bisexual.

Type – *A. asterias* (S. Moore) Engler & Diels.

Distribution – 2 species in East Africa.

Note – *Asteranthe* has large, showy flowers (fig. 24b, d). According to the illustration of Vollesen (1980) *A. lutea* has erect and more or less connivent petals. *Asteranthe asterias* has 'open' flowers.

Specimens examined:

A. asterias: Faulkner 1772, 3683 (BR), 3900 (P); Gillett & Kibuwa 19882 (WAG); Hildebrandt 1987 (B); Reitsma & de Wilde 188 (WAG); Verdcourt 5287 (BR). — *A. lutea:* Vollesen 4838 (WAG).

Deeringothamnus J.K. Small, Bull. Torrey Bot. Club 51 (1924) 389.

Buds not observed. *Sepals* (aestivation not observed), 3 or 4, free or connate, 2–6 mm long, fleshy, veins prominent, indument present or absent, hairs simple, mar-

gins ciliate. *Petals* (greenish-)white or pale to deep yellow, imbricate, 5–9, free, both whorls equal in length, 7–17 mm long, 5–6 × as long as wide, 2–3 × length of sepals, fleshy, veins prominent, indument present or absent, hairs simple. *Torus* shallowly conical with a flat apex. *Stamens* 10–17, 2 mm long, extrorse or latrorse; apex tongue-shaped, fleshy. *Carpels* free, 1–3, 3 mm long, hairy, style present, short, stigma cylindrical, glabrous; ovules 4, lateral, 1-seriate. *Flowers* bisexual.

Type – *D. pulchellus* J.K. Small.

Distribution – 2 species in Florida, U.S.A.

Note – *Deeringothamnus* (fig. 24g, h) is closely related to *Asimina*, but differs from that genus by the tongue-shaped apices of the stamens and the more fleshy petals. Wilbur (1970) includes *Deeringothamnus* in *Asimina*.

Specimens examined:

D. pulchellus: Kral 2129 (BM); Moldenke 930 (US), 981 (B); Small et al. 10925 (K, U), s.n. (BM). — *D. rugelii:* Kral 2509 (BM); Norman s.n. (U); Rugel 108 (BM). — *D. sp.:* Small s.n. (BM).

Diclinanona Diels, Notizbl. Bot. Gart. Berlin-Dahlem 10 (1927) 174.

Buds broadly deltoid (sepals). *Sepals* valvate, 3, free or connate, 4–6 mm long, fleshy, veins prominent or not, indument present, hairs simple. *Petals* greenish (-white), yellow, creamy, rose-red, or orange, valvate or apert?, 6, free, in one whorl with equal petals or in 2 whorls with inner ones longer, both 8–15 mm long or outer ones 5–18 mm long and inner ones 7–23 mm long, 7 × as long as wide, 2.5–3 × length of sepals, fleshy, sometimes thick, veins not prominent, indument present, hairs simple, inner petals rarely connivent, sometimes glandular at the base inside, 2 marginal glands present. *Torus* broadly or depressed ovoid, or more or less flat. *Stamens* numerous, 0.8–1.1 mm long, extrorse; apex discoid or elongate (inner stamens), glabrous or papillose. *Carpels* free, few?, c. 2–2.5 mm long, hairy, style absent, stigma spheroid; ovules 3, lateral 1-seriate? *Flowers* unisexual or bisexual in androdioecious plants.

Type – *D. tessmannii* Diels.

Distribution – 2 species in the Amazone-area, South America.

Notes – *Diclinanona* (fig. 24m) differs from the other genera of this group because of its androdioecism. As the other genera of this group are found in Africa and North America, its position in this group is uncertain. The flowers show similarities with *Dielsiothamnus* and *Isolona*. The torus and stamens of male flowers resemble those of *Stelechocarpus*, while the inner petals are sometimes glandular at the base like in the Meiogyne-group.

In *Diclinanona tessmannii* the petals are arranged in one whorl, whereas a 2-whorled arrangement is present in *D. calycina*. The top-stamens in the specimen Thomas et al. 5280 are fused over a considerable length. Probably *Diclinanona* consists of 3 species.

Specimens examined:

D. calycina: Liesner 8470 (U); Prance et al. 17801 (U); Vásquez & Jaramillo 3236 (U). — *D. tessmannii:* Lleras et al. P17323 (U); Revilla 929, 1171 (U); Spichiger et al. 1762 (U); Vásquez & Jaramillo 6794 (U). — *D. sp.:* Silva & Souza 2552 (U); Thomas et al. 5268, 5280 (U).

Hexalobus Alph. de Candolle, Mém. Soc. Phys. Genève 5 (1832) 212.

Buds spheroid to very broadly ovoid or ovoid to ellipsoid (sepals). *Sepals* valvate or reduplicate-valvate, 3, free or connate, 4–17 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* (pale) yellow or (greenish-)creamy, sometimes with pale red base and dark red inside, transversely folded in bud, 6, connate, both whorls equal in length, 13–60 mm long, 4–5 × as long as wide, 3–4 × length of sepals, fleshy, veins prominent, indument present, hairs simple, margins crisped. *Torus* cylindrical, often apex slightly or deeply concave. *Stamens* numerous, 1.5–3.5 mm long, extrorse or latrorse, rarely septate; apex discoid, tongue-shaped, or apical prolongation almost absent, glabrous. *Carpels* free, 4–10, 1.8–4 mm long, hairy, style present or absent, stigma obconical (cup-shaped) and grooved, or lanceoloid, glabrous; ovules 10–12, lateral, 2-seriate. *Flowers* bisexual.

Lectotype – *H. senegalensis* Alph. de Candolle, nom. illeg. = *H. monopetalus* (A. Rich.) Engler & Diels.

Distribution – 5 species in tropical Africa.

Note – *Hexalobus* (fig. 24e) is easy to recognize because of the large sepals together with petals with crisped margins. The petals are folded in bud. Several specimens, apparently from drier areas, are flowering on leafless branches. The stamens of the specimen Delvaux 599 resemble those of *Mischogyne*. One specimen of *H. bussei* (Bos 5370) seems to have septate stamens.

Specimens examined:

H. bussei: Bos 5370 (WAG); Zenker 2889 (BR), 3550 (BR), 3889 (BR), 4831 (BM). — *H. crispiflorus:* Deistel 99 (U); Delvaux 599 (BR); Gerard 2132 (WAG); Le Testu 1987, 8838 (BR); Liben 2390 (WAG); Morton & Gledhill SL 989 (WAG); Versuchsanstalt Kamerun 240 (U); J.J.F.E. de Wilde & Leeuwenberg 3605 (WAG). — *H. monopetalus:* Angus 197 (BR); Brenan & Greenway 7856 (BR); Breteler 7288 (WAG); Fanshawe 1559 (BR); Geerling & Bosch 5455 (WAG); Ledermann 5178 (U); Teixeira & Andrade 335 (WAG); White 2872 (BR); J.J.F.E. de Wilde 950 (WAG); de Witte 6882 (BR, WAG).

Isolona Engler, in Engler & Prantl, Nat. Pflanzenfam. Nachtr. 1 (1897) 161.

Buds spheroid (tiny) (sepals) or apert. *Sepals* apert? or rarely valvate, 3, free or connate, 1–10 mm long, fleshy, thin, veins prominent or not, indument present or absent, hairs simple, margins ciliate or not. *Petals* (pale) yellow, reddish, or green, sometimes inside reddish or dark yellow, apert?, rarely valvate or more or less imbricate?, 6, connate, all petals in one whorl of equal length, 7–75 mm long, 2.5–7 × as long as wide, 3–12 × length of sepals, fleshy, sometimes thin, veins prominent or not, indument present or absent, hairs simple, margins ciliate or not. *Torus* shallowly conical with flat apex or cushion-shaped with slightly concave apex. *Stamens* numerous, 1–1.3 mm long, extrorse; apex discoid, sometimes elongate in the inner stamens, glabrous, fleshy. *Carpel* 1, 3 mm long, indument and style absent, stigma shallowly obconical (cup-shaped) and many-lobed, glabrous; ovules many, lateral, all over the ovary-wall. *Flowers* bisexual.

Lectotype – *I. madagascariensis* (Baillon) Engler.

Distribution – About 15 species in tropical Africa, incl. Madagascar.

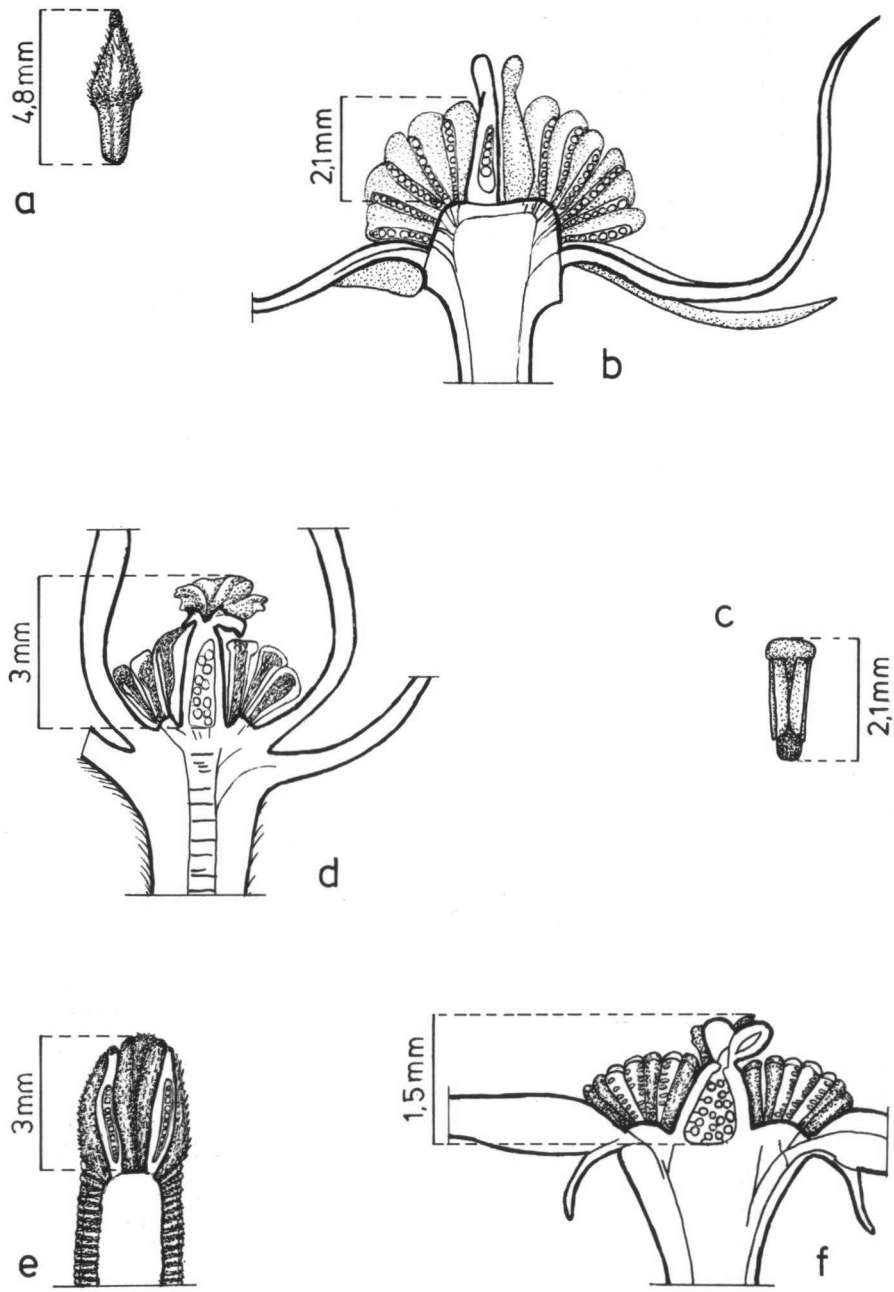


Fig. 25. Hexalobus-group — a., b. & c. *Asimina triloba* (Cult Gimborn Arb. s.n.): carpel (a), longitudinal section (b), and stamen (c); d. *Isolona pilosa* (Le Testu 8740): longitudinal section; e. *Toussaintia orientalis* (Shabani 472): longitudinal section; f. *Monodora crispata* (J.J.F.E. de Wilde 867): longitudinal section.

Note – *Isolona* (figs. 241, 25d) is easy to recognize by the basally connate petals of which the lobes are arranged in one whorl and the single carpel with a large stigma. Except for the carpel, *Isolona* resembles *Diclinanona* more than *Monodora.*

Specimens examined:

I. campanulata: de Koning 6748 (WAG); Versteegh & den Outer 22 (U). — *I. congolana:* Liben 3880 (BR). — *I. cooperi:* Bernardi 8249 (WAG); Cult. Arb. Wag. s.n. (WAG); W.J.J.O. de Wilde 249 (WAG). — *I. dewevrei:* Toussaint 2028 (WAG). — *I. hexaloba:* Donis 2824 (BR); Le Testu 8563 (BM); Zenker 267 (U). — *I. letestui:* Le Testu 1252 (BM). — *I. madagascariensis:* Perrier de la Bathie 1511 (B). — *I. perrierii:* Perrier de la Bathie 4951 (B). — *I. pilosa:* Gossweiler 6112 (BM); Le Testu 8602, 8740 (BR). — *I. thonneri:* Binuyo FHI 41274 (WAG). — *I. zenkeri:* Bos 4947 (WAG).

Monodora Dunal, Monogr. Anonac. (1817) 79.

Buds not observed. *Sepals* (aestivation not observed), 3 (or 4), free, 6–18 mm long, almost membranous, veins prominent, indument present or absent, hairs simple. *Petals* white, yellow(-violet), or outer ones pale green or reddish, inner ones whitish, both often with deep red, red-brown, or dark-brown spots, valvate, 6 (or 8), free or connate, outer whorl longer, outer ones 30–70 mm long, inner ones 12–45 mm long, 1.2–7.5 × as long as wide, 1.5–4 × length of sepals, almost membranous, veins prominent, indument present or absent, hairs simple, margins usually crisped; inner petals connivent, with fringe, sometimes with 2 auriculate appendages. *Torus* cushion-shaped with a slightly concave apex, depressed ovoid with a slightly concave apex, or cylindrical. *Stamens* numerous, 0.5–1 mm long, extrorse (in one specimen opening apically); apex discoid, fleshy, glabrous or papillose. *Carpel* 1, 1.5–2.5 mm long, indument absent, style absent, stigma very shallowly obconical (cup-shaped) and many-lobed, or shallowly obconical, glabrous; ovules numerous, lateral, all over the ovary-wall. *Flowers* bisexual.

Lectotype – *M. myristica* (J. Gaertner) Dunal.

Distribution – About 12 species in tropical Africa.

Note – *Monodora* (fig. 24c) is exceptional within the Annonaceae because of its showy flowers: large, conspicuously coloured with many coloured dots, and petals with crisped margins, which give the flowers an 'orchid-like' look.

Specimens examined:

M. brevipes: Bos 2306 (WAG). — *M. congolensis:* Ghesquière 2845 (U); Lebrun 939 (U). — *M. crispata:* Cult. Bot. Utrecht 64-66 (U); Versteegh & den Outer 100 (U); J.J.F.E. de Wilde 867 (WAG). — *M. grandidieri:* Archbold 2182 (BR); Burtt 5044 (BR); Faulkner 2755 (BR); Wallace 497 (BR). — *M. junodii:* Gomes & Sousa 3879 (BR); Mendonça 3216 (BR). — *M. myristica:* Hedberg 4567 (K); Versteegh & den Outer 410 (U). — *M. tenuifolia:* Leeuwenberg 2884 (U); Zenker 64 (U). — *M. zenkeri:* Zenker 776 (B).

Ophrypetalum Diels, Notizbl. Bot. Gart. Berlin-Dahlem 13 (1936) 269, t. 9, 1.

Buds very broadly ovoid (sepals). *Sepals* reduplicate-valvate, 3, connate, 5–7 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* (light) yellow or brownish, imbricate, 6, free, inner whorl longer, outer ones 4–7 mm long,

inner ones 6–7 mm long, 1 × as long as wide, 1 × length of sepals, fleshy, veins prominent, indument present, hairs simple, inner petals with fringe. *Torus* depressed ovoid, apex deeply concave. *Stamens* numerous, 0.6–0.7 mm long, extrorse; apical prolongation absent. *Carpels* free, few to numerous, 2.3 mm long, hairy, style cylindrical, stigma narrowly ellipsoid or oblanceoloid, glabrous; ovules 4–5, lateral, 1?-seriate. *Flowers* bisexual.

Type – *O. odoratum* Diels.

Distribution – 1 species in East Africa.

Note – *Ophrypetalum* has an unusual combination of character states. It has a deeply concave torus which is, beside in *Ophrypetalum*, only found in *Fusaea* (Fusaea-group) and *Xylopia* (Xylopia-group). The carpels are long-styled (also in *Fusaea* and *Xylopia*), but the conspicuous sepals (fig. 24k), the short stamens without an apical prolongation, and the petals with a fringe on the inner side are very different from those of *Fusaea* and *Xylopia*. Similar sepals are found in *Cardiopetalum, Froesiodendron, Hexalobus, Mischogyne, Toussaintia,* and *Uvariastrum* (genera of the Cymbopetalum-group, the Hexalobus-group, and the Uvariastrum-group).

Specimens examined:

O. odoratum: Greenway 9634 (B); Kokwato 3918 (MO); Schlieben 5670 (B); Verdcourt 1075 (K).

Toussaintia Boutique, Bull. Jard. Bot. État Brux. 21 (1951) 97.

Buds (narrowly) ovoid (sepals). *Sepals* reduplicate-valvate, 3, free, 8–23 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* white, imbricate, 6 (or 9), free, both whorls equal in length or outer ones longer, outer ones 11–22 mm long, inner ones 11–18 mm long, 3–5 × as long as wide, 1.5–2 × length of sepals, fleshy, veins prominent, indument present, hairs simple. *Torus* cylindrical. *Stamens* numerous, 0.5–0.8 mm long, latrorse, rarely septate?; apex discoid, fleshy. *Carpels* free, numerous, 2.5–4.5 mm long, hairy, style absent, stigma bilobed, glabrous; ovules c. 13, lateral, 2-seriate. *Flowers* bisexual.

Type – *T. congolensis* Boutique.

Distribution – 3 species in Central Africa.

Note – *Toussaintia* (fig. 24a, i) is characterized by a very long torus (fig. 25e), as in *Mischogyne* (Uvariastrum-group), but unlike in *Mischogyne*, the stamens are very small and resemble those of *Monodora*. *Toussaintia* also resembles *Mischogyne* in its sepals. Verdcourt (1986) described *Uvariopsis bisexualis* (Uvariastrum-group) with bisexual flowers, which resembles *Toussaintia*. The species *T. orientalis* seems cleistogamous: the sepals are never found open (in the herbarium-specimens), until, after anthesis, all sepals, petals, and stamens are shed off. When there are more than 6 petals, they are arranged in 2–3 irregular whorls (Le Thomas, 1969; Verdcourt, 1971a).

Specimens examined:

T. congolensis: Wagemans 260 (BR). — *T. hallei:* Hallé 4189 (P). — *T. orientalis:* Haerdi 410/0 (BR); Shabani 189 (K), 472 (BR).

Table 12. List of character states found in the genera of the Hexalobus-group.

Taxa: A1 = *Asimina*, A2 = *Asteranthe*, D1 = *Deeringothamnus*, D2 = *Diclinanona*, H = *Hexalobus*, I = *Isolona*, M = *Monodora*, O = *Ophrypetalum*, T = *Toussaintia*.

	A1	A2	D1	D2	H	I	M	O	T
Flowers:									
hairs simple	+	+	+	+	+	+	+	+	+
bisexual	+	+	+	+	+	+	+	+	+
unisexual	–	–	–	+	–	–	–	–	–
Sepals:									
valvate	+	+	?	+	+	+	?	–	–
reduplicate-valvate	-	–	?	–	+	–	?	+	+
3 in number	+	+	+	+	+	+	+	+	+
4 in number	–	–	+	–	–	–	(+)	–	–
connate	–	+,–	+,–	+,–	+,–	+,–	–	+	–
1–23 mm long	+	+	+	+	+	+	+	+	+
Petals:									
imbricate	+	+	+	–	(+)	–	–	+	+
valvate	–	+	–	+	–	(+)	+	–	–
6 in number	+	+	+	+	+	+	+	+	+
not 6 in number	(+)	(+)	+	–	–	–	–	–	+
connate	–	+	–	–	+	+	+,–	–	–
in one whorl	–	–	–	–,+	–	+	–	–	–
veins prominent	+	+	+	–	+	–,+	+	+	+
with 2 marginal glands	+,–	–	–	+	–	–	(+)	–	–
base glandular	+,–	+	–	+,–	–	–	–	–	–
fringe present	-	–	–	–	–	–	+	+	–
4–25 mm long	+	+	+	+	+	+	–	+	+
25–75 mm long	+	+	–	–	+	+	+	–	–
Stamens:									
numerous	+	+	–	+	+	+	+	+	+
anthers extrorse	+	+	+	+	+	+	+	+	–
anthers latrorse	–	–	+	–	+	–	–	–	+
apex not prolonged	–	–	–	–	(+)	–	–	+	–
apex tongue-shaped	–	–	+	–	+	–	–	–	–
apex discoid	+	+	–	+	+	+	+	–	+
0.5–2 mm long	+	+	+	+	+	+	+	+	+
2–3.5 mm long	-	–	–	–	+	–	–	–	–
Carpels:									
1 in number	+	–	+	–?	–	+	+	–	–
> 1 in number	+	+	+	+?	+	–	–	+	+
Ovules:									
3–9 in number	+	+	+	+	–	–	–	+	–
> 9 in number	+	–	–	–	+	+	+	–	+
lateral, 1-seriate	–	–	+	+?	–	–	–	+?	–
lateral, 2-seriate	+	+	–	–?	+	–	–	–?	+
laminal	–	–	–	–	–	+	+	–	–

9. Meiogyne-group (figs. 26, 27; table 13)

Buds lanceoloid to (very) (broadly) ovoid to ellipsoid (petals). *Sepals* valvate or apert?, 3, free or sometimes connate, 1–8 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* whitish, yellowish, greenish, reddish, or brownish, imbricate to valvate, 6, free, both whorls equal in length or outer whorl longer, 5–30 mm long, 1.5–7 × as long as wide, 2–8 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner petals often glandular at the base inside. *Torus* shallowly conical with a flat apex, or broadly cylindrical, sometimes with a depressed ovoid apex. *Stamens* 12 to numerous, 0.7–2 mm long, extrorse; apex discoid to depressed ovoid, often tongue-shaped in inner stamens, fleshy, glabrous. *Carpels* free, 1 to numerous, 1.6–4 mm long, hairy or sometimes glabrous, style absent, stigma ellipsoid, conical, or obconical and cup-shaped; ovules 4–12, lateral, 1- or 2-seriate. *Flowers* bisexual.

Distribution – 6 genera in tropical Asia and the Pacific (New Guinea, Australia, New Hebrides, New Caledonia, Guam, and Marianas Islands).

Notes – This group is characterized by inner petals which are often very glandular at the inner side, an often tongue-shaped apex in the inner stamens (fig. 27e), and several to many, lateral ovules (fig. 26d). The aestivation of the sepals could often not be observed, petals range from valvate to imbricate.

The delimitation of the genera within this group is not clear. All genera of this group seem to form one genus or a genus-complex. The differences between the genera in this group may be due to the isolated distribution over various remote islands and areas: Australia, New Guinea, New Hebrides, Guam, Philippines, Hainan, Borneo, and the Asiatic continent. The status of *Chieniodendron* is in discussion, as it seems intermediate between several genera, especially between *Meiogyne* and *Oncodostigma*. Although it has been included in *Fissistigma*, *Chieniodendron* is not related to the latter genus (Friesodielsia-group). *Ancana* has been included in *Fissistigma* as well, by Fries (1955), but it certainly does not belong in that genus.

The Meiogyne-group seems to have affinities to several other genera or groups, e.g., *Fitzalania* (Mitrephora-group), *Unonopsis* (Unonopsis-group), and to the Polyalthia-group, and via *Ancana* to the Sapranthus-group. Morawetz (1988) found the same pollen type within *Ancana*, *Fitzalania*, *Haplostichanthus* (Polyalthia-group), and *Sapranthus*.

Ancana F. von Mueller, Fragm. 5 (1865) 27, t. 35.

Buds lanceoloid (petals). *Sepals* (aestivation not observed), 3, connate (or free), 4–5 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* cream to light orange, or reddish towards the base, slightly imbricate, 6, free, both whorls equal in length, 14–27 mm long, 7 × as long as wide, 4 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner petals basally glandular inside. *Torus* shallowly conical with a flat apex. *Stamens* c. 21, 1–2 mm long, extrorse; apex discoid, those of the inner stamens tongue-shaped, fleshy. *Carpels* free, few, c. 3.5 mm long, hairy, style absent, stigma ellipsoid, glabrous; ovules 5, lateral, 1-seriate. *Flowers* bisexual.

Type – *A. stenopetala* F. von Mueller.

Distribution – 1 species in Australia.

Note – The petals of *Ancana* (fig. 26c, d) are (relatively) longer and narrower than those of the other genera of the Meiogyne-group.

Specimens examined:

A. stenopetala: Blake 15822 (K); Coveny 10627 (K); Moore 5767 (K); Morawetz 31-14285 (U).

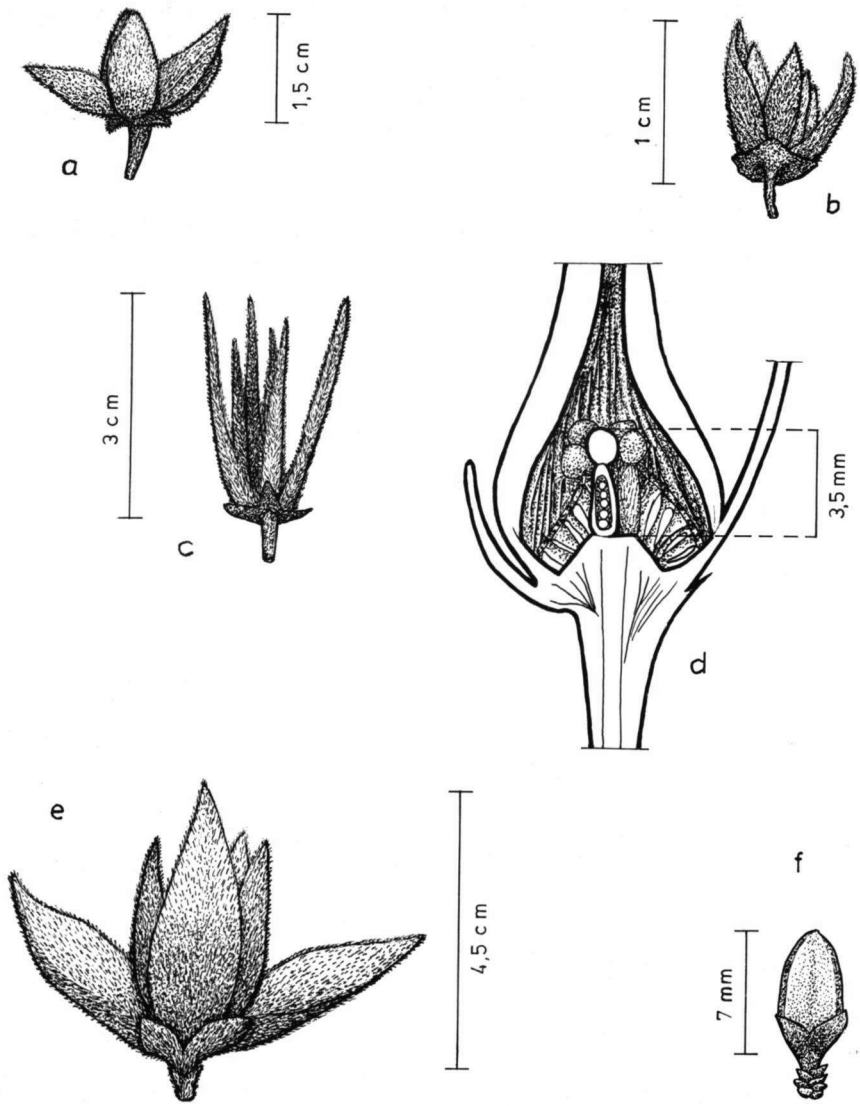


Fig. 26. Meiogyne-group — a. *Oncodostigma monosperma* (Sangkachan 1261): (young) flower; b. *Oncodostigma mindorense* (Elmer 15399): flower; c. *Ancana stenopetala* (Moore 5767): flower; d. *Ancana stenopetala* (Morawetz 31-14285): longitudinal section; e. *Meiogyne pannosa* (Wight s.n.): flower; f. *Oncodostigma leptoneura* (Schlechter 17657): bud.

Chieniodendron Tsiang & Li, Acta Phytotax. Sin. 9 (1964) 374.

Buds very broadly to broadly depressed ovoid (petals). *Sepals* (aestivation not observed), 3, free, 4–6 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* (dark) brown, valvate or imbricate, 6, both whorls equal in length, 14 mm long, 2 × as long as wide, 2 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner petals glandular inside. *Torus* shallowly conical with a flat apex. *Stamens* numerous, 1.5 mm long, extrorse; apex discoid, tongue-shaped in the inner stamens, fleshy, glabrous. *Carpels* free, numerous, 2 mm long, hairy, style absent, stigma ellipsoid; ovules 6, lateral, 1-seriate? *Flowers* bisexual.

Type – *C. hainanense* (Merrill) Tsiang & Li.

Distribution – 1 species in Vietnam and Hainan (South China).

Note – *Chieniodendron* (figs. 27c, d) was created by Tsiang & Li (1964), but its status remains a matter of discussion. Since, it has been included in *Meiogyne* (Ban, 1973), in *Oncodostigma* (Anonymous, 1982), and again recognized as *Chieniodendron* (Anonymous, 1983). In the past it was a species of *Fissistigma,* which it resembles in general appearance. It is, however, not related to that genus. *Chieniodendron* seems intermediate between *Meiogyne* and *Oncodostigma.*

Specimens examined:
C. hainanense: B.C.A. 39 (K); Chun & Tso 44583 (K); Ko 52227 (K, P).

Guamia Merrill, Philipp. J. Sci., Bot. 10 (1915) 243.

Buds (broadly) ovoid (petals). *Sepals* (aestivation not observed), 3, free, 2–3 mm long, fleshy, veins not prominent, indument present, hairs simple (rarely absent with ciliate margins). *Petals* yellowish-brown, imbricate?, 6, free, outer whorl slightly longer than the inner one, outer ones 9–13 mm long, inner ones 8–11 mm long, 2 × as long as wide, 4–5 × length of sepals, fleshy, veins not prominent, indument present, hairs simple (inner side of inner petals not observed). *Torus* not observed. *Stamens* 1.5 mm long; apex discoid, glabrous. (stamens incompletely observed). *Carpels* free, numerous, hairy (incompletely observed). *Flowers* bisexual.

Type – *G. mariannae* (Safford) Merrill.

Distribution – 1 species in the Pacific: Guam and Marianas.

Note – *Guamia* (fig. 27g) strongly resembles *Oncodostigma* and is probably congeneric.

Specimens examined:
G. mariannae: Kanehira 14 (P); Palomo 1203 (US); Stone 5169 (K).

Meiogyne Miquel, Ann. Mus. Bot. Lugduno-Batavum 2 (1865) 12.

Buds ovoid (petals). *Sepals* valvate, 3, free, 2–8 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* cream or yellow(-green), valvate, 6, free, both whorls equal in length or outer whorl longer, outer ones 11–30 mm long, inner ones 10–25 mm long, 1.5–6 × as long as wide, 4–8 × length of sepals,

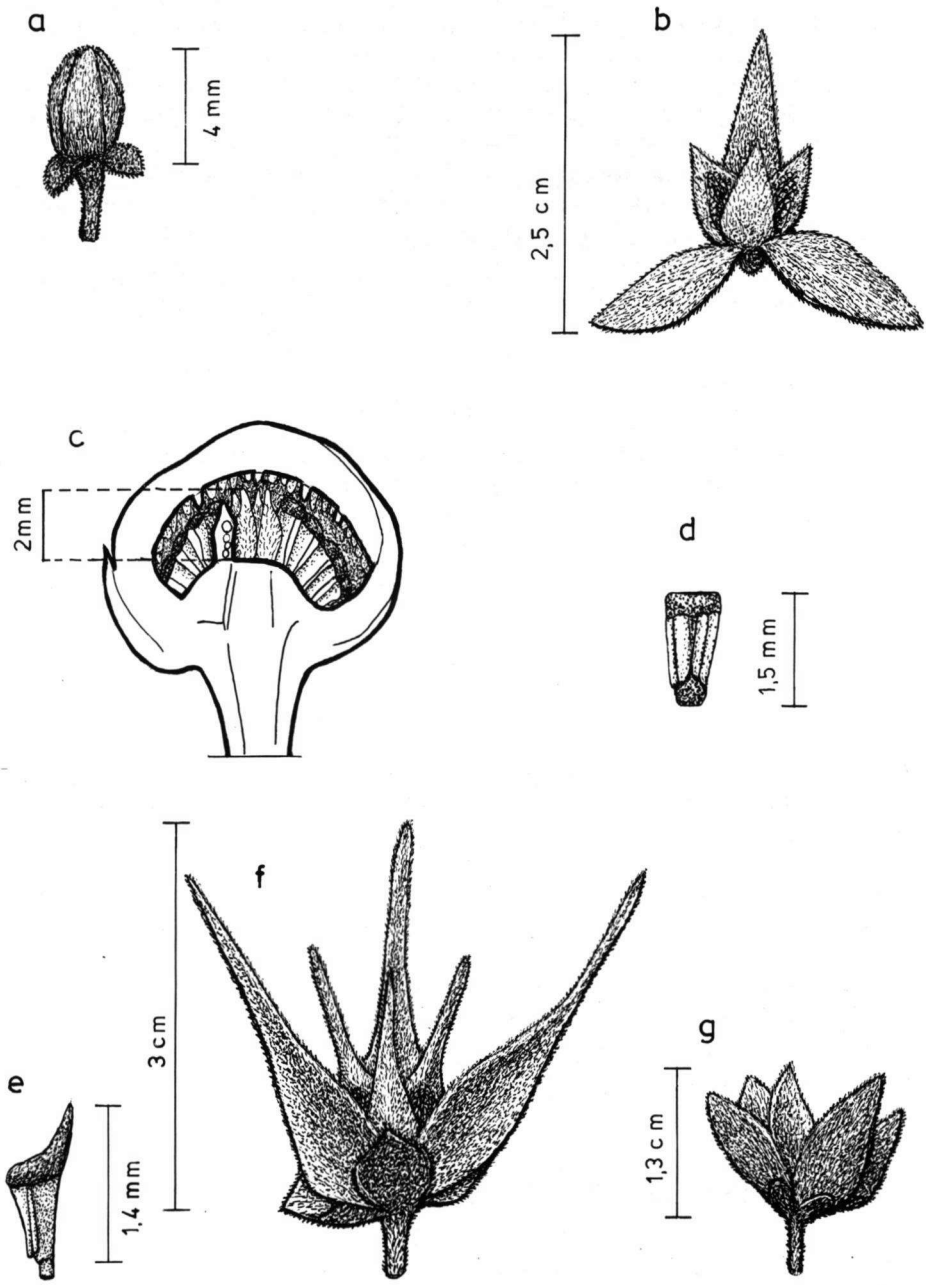


Fig. 27. Meiogyne-group — a. & b. *Polyaulax cylindrocarpa* (Lee S38066): bud (a) and flower (b); c. & d. *Chieniodendron hainanense* (Ko 52227): longitudinal section (c) and stamen (d); e. *Meiogyne eriantha* (Martin & Ismawi S36910): stamen; f. *Meiogyne virgata* (Cult. Hort. Bog. s.n.): flower; g. *Guamia mariannae* (Kanehira 14): flower.

fleshy, veins not prominent, indument present, hairs simple, inner petals glandular at the base inside. *Torus* shallowly conical with a flat apex or cylindrical. *Stamens* 12–numerous, 0.8–1.4 mm long, extrorse; apex discoid to depressed ovoid, those of inner stamens tongue-shaped, fleshy. *Carpels* free, 1 to numerous, 1.6–4 mm long, hairy, style absent, stigma conical, or obconical and cup-shaped; ovules 4–12, lateral, 2-seriate. *Flowers* bisexual.

Type – *M. virgata* (Blume) Miquel.

Distribution – About 7 species in tropical Asia.

Note – *Meiogyne* (fig. 27f) has flowers with generally larger and thicker petals than the other genera of this group. *Meiogyne pannosa* (fig. 26e) strongly resembles *Oncodostigma*; possibly it should be transferred to that genus.

Specimens examined:

M. eriantha: Haviland 410 (L); Martin & Ismawi S36910 (K, L). — *M. lucida:* Elmer 13984 (L, U). — *M. montana:* Wiriadinata 270 (L). — *M. pannosa:* Sundara Raghavan 97065 (K); Wight s.n. (K). — *M. paucinervia:* Ramos 15381 (BM). — *M. virgata:* J. & M.S. Clemens 28279 (BM); Cult. Hort. Bog. s.n. (U); Elmer 21379 (U); Haviland 2041 (BM); Mail 2968 (K); Montri Rameli 2462 (U); Sinclair 39472 (L).

Oncodostigma Diels, Bot. Jahrb. Syst. 49 (1912) 143, f. 2.

Buds ovoid (petals). *Sepals* (aestivation not observed), 3, connate, 1.5–3 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* red, brown-yellow, light brown, or white with a yellow center, more or less imbricate to valvate?, 6, free, both whorls equal in length, 7–26 mm long, 2–3 × as long as wide, 3–6 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner petals basally glabrous or glandular inside. *Torus* broadly cylindrical, apex depressed ovoid. *Stamens* numerous, 1.4–1.7 mm long, extrorse; apex discoid, those of inner stamens tongue-shaped, glabrous. *Carpels* free, numerous, (length not measured), hairy, (style and stigma not observed); ovules c. 8, lateral, 2-seriate. *Flowers* bisexual.

Type – *O. leptoneura* Diels.

Distribution – 4 species in tropical Asia (Malaysia, Indonesia, and Philippines), New Guinea, New Hebrides, and New Caledonia.

Note – *Oncodostigma* (fig. 26a, b, f) is not clearly distinct from *Chieniodendron*, *Guamia*, and *Meiogyne*.

Specimens examined:

O. leptoneura: Barker LAE 66506 (L); Schlechter 17657 (B, BR). — *O. mindorense:* Conklin 19197 (L); Elmer 15399 (L). — *O. monosperma:* Haviland 1779 (K); Sangkachan 1261 (L); Shah MS169 (K). — *O. wilsonii:* Wilson 986 (K). — *O. sp.:* McPherson 5220 (U).

Polyaulax Backer, Blumea 5 (1945) 492.

Buds ovoid to ellipsoid (petals). *Sepals* (aestivation not observed), 3, free?, 1 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* yellow-white or outer ones reddish-yellow, inner ones dark red, valvate, 6, free, both whorls equal in length, 5–6 mm long, or outer ones slightly longer, or outer

ones 11–12 mm long, inner ones 9 mm long, 2 × as long as wide, 5 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner petals glandular at the base inside. *Torus* shallowly conical with a flat apex to cylindrical. *Stamens* (number not observed), 0.7–0.8 mm long, extrorse; apex discoid, those of inner stamens tongue-shaped, glabrous. *Carpels* free, 5–6, 2 mm long, hairy (incompletely observed). *Flowers* bisexual.

Type – *P. cylindrocarpa* (Burck) Backer.

Distribution – 1 species in Java, Borneo, New Guinea, and northern Australia.

Note – *Polyaulax* (fig. 27a, b) has the smallest flowers within this group.

Specimens examined:
P. cylindrocarpa: Lee S 38066 (L, U); Main 2064 (K, L).

Table 13. List of character states found in the genera of the Meiogyne-group.

Taxa: A = *Ancana*, C = *Meiogyne*, G = *Guamia*, M = *Meiogyne*, O = *Oncodostigma*, P = *Polyaulax*.

	A	C	G	M	O	P
Flowers:						
perianth 3-merous	+	+	+	+	+	+
hairs simple	+	+	+	+	+	+
bisexual	+	+	+	+	+	+
Sepals:						
valvate	?	?	?	+	?	?
connate	+(–)	–	–	–	+	–?
1–3 mm long	–	–	+	+	+	+
3–8 mm long	+	+	–	+	–	–
Petals:						
valvate	–	+	–	+	+?	+
imbricate	+	+	+?	–	+	–
base glandular	+	+	?	+	+,–	+
5–15 mm long	(+)	+	+	+	+	+
15–30 mm long	+	–	–	+	+	–
Stamens:						
(12–)numerous	+	+	?	+	+	?
anthers extrorse	+	+	?	+	+	+
apex discoid	+	+	+	+	+	+
apex inner ones elongate	+	+	?	+	+	+
0.7–2 mm long	+	+	+	+	+	+
Carpels:						
1–6 in number	+	–	–	+	–	+
numerous	–	+	+	+	+	–
Ovules:						
4–12 in number	+	+	?	+	+	?
1-seriate	+	+?	?	–	–	?
2-seriate	–	?	?	+	+	?

10. Miliusa-group (fig. 28; table 14)

Buds ovoid to broadly depressed ovoid, or triangular-ovoid to -lanceoloid (petals). *Sepals* valvate or aestivation not observed, 3, free or connate, 0.5–10 mm long, fleshy, veins not prominent, indument present or sometimes absent, hairs simple, margins ciliate. *Petals* creamy, yellowish, greenish, pinkish, purplish, or brownish, valvate, 6, free or rarely inner ones connate, outer whorl very small and sepal-like, 0.5–8 mm long, inner whorl 3.5–26 mm long, 1.5–4 × as long as wide, 5–15 × length of sepals, fleshy, veins prominent or not, indument present or absent, hairs simple, margins ciliate or not. *Torus* (broadly) cylindrical, depressed ovoid, sometimes with flat apex, or ovoid. *Stamens* numerous to few, sometimes imbricate, 0.7–3 mm long, extrorse; apical prolongation discoid to almost absent, fleshy. *Carpels* free, numerous, 1–3 mm long, hairy, style absent, stigma narrowly ellipsoid, obovoid, cylindrical to spheroid, glabrous; ovules 1–2, basal or lateral, 1-seriate. *Flowers* bisexual.

Distribution – 3 genera in tropical Asia, New Guinea, and Australia.

Notes – This group is characterized by small, sepal-like, outer petals (fig. 28c, d, g, h), and much larger, valvate, inner petals. This group may be heterogeneous. There was not enough material of *Marsypopetalum* to enable good examination of the inner structures of the flowers.

The Miliusa-group only gradually differs from the Mitrephora-group. In that group several genera have very small outer petals, too, e.g. *Fitzalania, Mezzettiopsis, Orophea, Popowia,* and *Pseuduvaria.* It is difficult to decide in which group these genera should be placed. Some *Miliusa*-species show transitional features to *Pseuduvaria.* Incorporation of the Miliusa-group in the Mitrephora-group would result in a very heterogeneous group. In *Alphonsea* (Sageraea-group) similar stamens are found as in *Miliusa. Marsypopetalum* (according to the literature) and *Phaeanthus* have one basal ovule, which is shared with some genera of the Polyalthia-group, and with *Neo-uvaria* (not included in a group) and *Popowia* (Mitrephora-group).

Marsypopetalum R.H.C.C. Scheffer, Natuurk. Tijdschr. Ned.-Indië 31 (1870) 342.

Buds ovoid (petals). *Sepals* (aestivation not observed), 3, free, 2.5 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* (aestivation not observed), 6, free, outer whorl very small, 3 mm long, inner ones 15–26 mm long, 5–7 × length of sepals, fleshy, veins not prominent, indument present, hairs simple. *Torus* not observed. *Stamens* numerous, 3 mm long, extrorse; apex discoid, fleshy, small. *Carpels* numerous (incompletely observed). *Flowers* bisexual.

Type – *M. pallidum* (Blume) Kurz.

Distribution – 1 species in tropical Asia (Malaysia, Borneo, and Java).

Notes – *Marsypopetalum* has been poorly collected with regard to the flowers.

Probably *Polyalthia crassa* (Parker, 1929) from Burma and Thailand belongs to *Marsypopetalum* as well. The fruits and leaves are (almost) similar to those of *Marsypopetalum.* The stamens of *P. crassa* are unusual for *Polyalthia,* and similar to

those of *Marsypopetalum*. The fruits of *Marsypopetalum* are rather diverse, but the same diversity is found in the fruits of *P. crassa*. Only the petals are somewhat different: the difference in size between outer and inner petals is less in *P. crassa* than in *Marsypopetalum*, and the inner petals are shorter than those of *Marsypopetalum*. The stamens and the texture of the perianth, however, are the same.

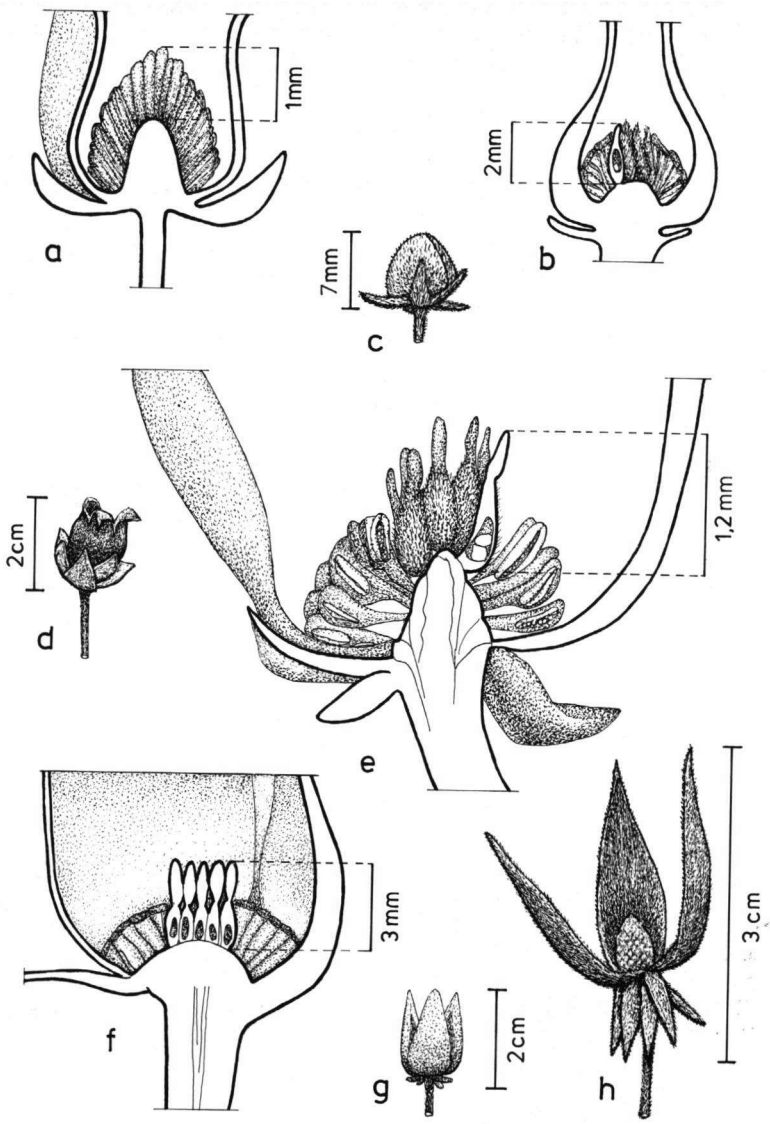


Fig. 28. Miliusa-group — a. *Miliusa longiflora* (Cult. Hort. Calcutta s.n.): section; b. *Phaeanthus macropodus* (Schramm 5993): longitudinal section; c. *Miliusa villosa* (Dickason 8625): bud; d. *Miliusa macrocarpa* (Bar 2719): flower; e. *Miliusa eriocarpa* (Vajravelu 38635): longitudinal section; f. *Phaeanthus sp.* (Morawetz 17-28285): longitudinal section; g. *Phaeanthus crassipetalus* (Madani SAN 76023): flower; h. *Miliusa sp.* (Kalkman 3723): flower.

Another problem is that Blume (1830) based his description of *Guatteria pallida* on a specimen with fruits, while Scheffer (1870) bases *Marsypopetalum ceratosanthus* on a specimen with flowers. Kurz (1874) and Backer (1911) brought *M. ceratosanthus* into synonymy with *M. pallidum*.

As defined by Sinclair, *Marsypopetalum* should have one, basal ovule (Sinclair, 1955). According to Backer & Bakhuizen van den Brink (1963) the flowers develop slowly, the buds remaining dormant for a long time.

Specimen examined:
M. pallidum: Cult. Hort. Bog. 7706 (K, L).

Miliusa Leschenault ex Alph. de Candolle, Mém. Soc. Phys. Genève 5 (1832) 213, t. 3.

Buds ovoid to broadly depressed ovoid (petals). *Sepals* valvate, 3, free or connate, 0.5–10 mm long, fleshy, thin, veins not prominent, indument present or absent, hairs simple, margins ciliate. *Petals* (pale) yellow, pink, light brown, dark brown with purple streaks inside, or reddish-brown with yellowish-green margins, valvate, 6, outer ones free, inner ones free or connate, inner whorl longer, outer ones 1–5 mm long, inner ones 3.5–22 mm long, 2–3 × as long as wide, 5–7 × length of sepals, fleshy, sometimes thin, veins prominent or not, indument present or absent, hairs simple, margins ciliate or not. *Torus* ovoid. *Stamens* few to numerous, imbricate, 1.5 mm long, extrorse; apex tongue-shaped to small discoid or apical prolongation absent, fleshy. *Carpels* free, numerous (12–17), 1–1.2 mm long, (sparsely to densely) hairy, style (almost) absent, stigma obovoid or cylindrical to spheroid; ovules 2, lateral, 1-seriate. *Flowers* bisexual.

Type – *M. indica* Leschenault ex Alph. de Candolle.

Distribution – Tropical Asia, New Guinea, and Australia, 36–40 species.

Note – *Miliusa* (fig. 28a, c, d, e, h) resembles *Alphonsea* (Sageraea-group) in the stamens, but in *Alphonsea* the outer and inner petals are equal in size. The number of ovules in *Alphonsea* is also much higher. In literature also higher ovule numbers are mentioned for *Miliusa*, e.g., 6–8 in *M. horsfieldii* (Jessup, 1988).

Specimens examined:
M. balansae: Hansen et al. 10928 (L); Tsang 28960 (L). — *M. banghoiensis:* Poilane 2948 (L). — *M. eriocarpa:* Vajravelu 38635 (L). — *M. globosa:* Simons s.n. (L). — *M. horsfieldii:* Koorders 28847b (L). — *M. indica:* Wirawan 731 (K). — *M. koolsii:* Schram BW 7847 (BR). — *M. longiflora:* Cult. Hort. Calcutta s.n. (L). — *M. macrocarpa:* Bar 2719 (K). — *M. macropoda:* King s.n. (L); Korthals s.n. (L). — *M. tomentosum:* without collector and number (BR). — *M. vidalii:* Ramos 42172 (BR); Sulit 6871 (BR). — *M. villosa:* Dickason 8625 (L); Kerr 1078 (K); Wallich 6441 (BR); without collector 99 (BR). — *M. sp.:* Kalkman 3723 (L).

Phaeanthus J.D. Hooker & T. Thomson, Fl. Ind. 1 (1855) 146.

Buds triangular-ovoid to -lanceoloid (petals). *Sepals* (aestivation not observed), 3, free, 0.5–8 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* white or yellow(-cream), valvate, 6, free, inner whorl much longer, outer ones 0.5–8 mm long, inner ones 8–25 mm long, 1.5–4 × as long as wide,

15 × length of sepals, fleshy, veins prominent or not, indument present, hairs simple. *Torus* depressed ovoid, sometimes with a flat apex. *Stamens* numerous, 0.7–1.8 mm long, extrorse; apex discoid or tongue-shaped, fleshy. *Carpels* free, numerous, 2–3 mm long, hairy, style absent, stigma narrowly ellipsoid, glabrous; ovule 1, basal. *Flowers* bisexual.

Type – *P. nutans* J.D. Hooker & T. Thomson [= *P. ophthalmicus* (Roxburgh ex G. Don) J. Sinclair].

Distribution – Tropical Asia and New Guinea, 12–16 species.

Note – *Phaeanthus* (fig. 28b, f, g) differs from *Miliusa* in the shape of the stamens.

Specimens examined:

P. crassipetalus: Anderson et al. 15364 (L); Kostermans 9243 (L); Madani SAN 76023 (L). — *P. ebracteolatus:* Alvarez 13375 (BR); Sulit 35772 (BR). — *P. lucidus:* Krukoff 4206 (BR). — *P. macropodus:* Schram BW 5993 (L); Wada et al. 1 (U). — *P. ophthalmicus:* Maingay 67 (L); Sinclair s.n. (L); Whitmore FRI 12307 (L). — *P. pubescens:* Ramos & Edaño 47238 (BR). — *P. sp.:* Morawetz 17-28285 (U).

Table 14. List of character states found in the genera of the Miliusa-group.

	Marsypopetalum	*Miliusa*	*Phaeanthus*
Flowers:			
3-merous	+	+	+
hairs simple	+	+	+
bisexual	+	+	+
Sepals:			
valvate	?	+	?
connate	–	–,+	–
0.5–10 mm long	+	+	+
Petals:			
valvate	?	+	+
inner whorl connate	–	–,+	–
outer whorl sepal-like	+	+	+
outer whorl 0.5–8 mm long	+	+	+
inner whorl 3.5–26 mm long	+	+	+
Stamens:			
numerous	+	+,–	+
anthers extrorse	+	+	+
apex prolonged, discoid	+	(+)	+
apex not prolonged	(+)	+	–
0.7–3 mm long	+	+	+
Carpels:			
numerous	+	+	+
Ovules:			
1, basal	?	–	+
2 (or >2), lateral	?	+	–

11. Mitrephora-group (table 15; fig. 29)

Buds broadly (depressed) ovoid (petals). *Sepals* valvate (or reduplicate-valvate), 3, free or connate, 1–5(–9) mm long, fleshy, sometimes thin, veins not or rarely prominent, indument present or rarely absent, hairs simple, margins ciliate. *Petals* whitish to yellowish to reddish, pinkish, purplish, brown, or greenish, valvate or reduplicate-valvate, rarely inner ones imbricate, 6, free or connate, both whorls equal or unequal in length, outer whorl 1–34 mm long, inner whorl 2–50 mm long, 0.6–3 × as long as wide, 1–10 × length of sepals, fleshy, sometimes thin, or outer ones thin, inner ones fleshy, veins prominent or not, indument present or sometimes absent, hairs simple, margins ciliate or not; inner petals often connivent, sometimes 2 glands present, rarely basally glandular inside, rarely fringe present, rarely with large wings. *Torus* very shallowly conical, (broadly) cylindrical, depressed ovoid, sometimes with flat apex, ovoid with a concave apex, or flat. *Stamens* 3 to numerous, 0.4–1.8 mm long, extrorse, sometimes staminodes present; apex discoid, sometimes elongate in inner stamens, or apical prolongation (almost) absent, fleshy, glabrous. *Carpels* free, 1 to numerous, 0.7–2.5 mm long, hairy, style absent, stigma cylindrical, discoid, ellipsoid, flat and lobed, spheroid, or narrowly obconical, glabrous; ovules 1–15, lateral or sometimes basal, 1- or 2-seriate. *Flowers* bisexual or sometimes unisexual.

Distribution – 9 genera in tropical Asia, New Guinea, and Australia.

Notes – This group is characterized by valvate sepals, valvate or reduplicate-valvate petals, usually connivent and different-sized and -shaped inner petals (fig. 29d, e), and mostly several lateral ovules (fig. 29a, c, i, k). The flowers are mostly small.

The delimitation of some genera within this group is not very clear. *Platymitra* and *Mezzettiopsis* are not clearly delimited from *Orophea* on the base of their flowers. The differences between *Platymitra* and *Orophea* only seem quantitative. *Mezzettiopsis* only gradually differs from *Orophea* section *Sphaerocarpon* (Keßler, 1988). Some species of *Pseuduvaria* from New Guinea are difficult to distinguish from *Mitrephora*. *Petalolophus* may be an abnormal (in the shape of the petals, which have large wings) relative of *Pseuduvaria*. It resembles in leaves and inflorescence some *Pseuduvaria*-species from New Guinea. *Fitzalania* (fig. 29b), the relationship of which to other genera was a puzzle for a long time, in the indument and texture of the flowers, as well as in the glandular base at the inner side of the inner petals, bears most resemblance to some New Guinean species of *Pseuduvaria*.

The Mitrephora-group exhibits affinities to some other groups. *Fitzalania* p.p., *Mezzettiopsis* and *Pseuduvaria* have very small, sepal-like outer petals, which is typical of the Miliusa-group. The small flowers of *Popowia* remind of those of *Papualthia* and *Trivalvaria* (Polyalthia-group). *Fitzalania* has a midway position between *Pseuduvaria*, the Meiogyne-group, and the Miliusa-group.

Fitzalania F. von Mueller, Fragm. 4 (1863) 33.

Buds broadly ovoid (petals). *Sepals* (aestivation not observed), 3, free, 1.5–3.5 mm long, fleshy, thin, veins not prominent, indument present, hairs simple. *Petals*

very dark purple, imbricate (inner ones), 6, free, inner whorl longer or both whorls (becoming) equal in length, outer ones 5–12 mm long, inner ones 10–35 mm long or both 13 mm long, 2 × as long as wide, 6–10 × length of sepals, outer ones almost membranous, inner ones fleshy, thin, veins prominent, indument present, hairs simple, inner petals basally glandular inside. *Torus* (broadly) cylindrical. *Stamens* numerous, 1.1–1.8 mm long, extrorse; apex discoid, apices of inner ones elongate and covering the carpels, fleshy. *Carpels* free, 6 to numerous, 2.3–2.5 mm long, hairy, style absent, stigma ellipsoid, small, glabrous; ovules 3–5, lateral, 1-seriate?. *Flowers* bisexual.

Type – *F. heteropetala* (F. von Mueller) F. von Mueller.

Distribution – 1 species in Australia.

Note – *Fitzalania* (fig. 29a, b) differs from the other genera of this group by the imbricate inner petals. It shares with the Meiogyne-group the glandular base of the inner petals and the elongate apices of the inner stamens.

Specimens examined:
F. heteropetala: Fitzalan s.n. (K); Jessup 586 (U); Michael 1156 (BM).

Mezzettiopsis Ridley, Bull. Misc. Inform. (1912) 389.

Buds broadly ovoid with reflexed apices (petals). *Sepals* (aestivation not observed), 3, connate, 1 mm long, almost membranous, veins not prominent, indument present, hairs simple. *Petals* red or yellowish, valvate, 6, free, inner whorl longer, outer ones 2–2.5 mm long, inner ones 6–8 mm long, 3 × as long as wide, 6–8 × length of sepals, outer ones almost membranous, inner ones fleshy, veins not prominent, indument present or absent, hairs simple, margins ciliate or not, apices of inner petals reflexed and glandular at the inner side. *Torus* depressed ovoid with a flat apex. *Stamens* 12, 0.7 mm long, extrorse; apical prolongation (almost) absent to tongue-shaped. *Carpels* free, numerous, 0.8 mm long, hairy to almost glabrous, style absent, stigma spheroid or flat and lobed; ovules 3, lateral, 1-seriate? *Flowers* bisexual.

Type – *M. creaghii* Ridley.

Distribution – 1 species in tropical Asia (North Borneo and Thailand).

Note – *Mezzettiopsis* (fig. 29h, k) seems intermediate between *Orophea* and *Pseuduvaria*. Keßler (1988) counted 15–30 stamens in *Mezzetiopsis*.

Specimens examined:
M. creaghii: van Balgooy 5657 (U); Elmer 20948 (BR); Nordin 46137 (K); Phusomsaeng 421 (L).

Mitrephora J.D. Hooker & T. Thomson, Fl. Ind. 1 (1855) 112.

Buds broadly depressed ovoid (petals). *Sepals* valvate or reduplicate-valvate, 3, free or connate, 1–5 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* white, cream, purple, (yellow-)green, often with reddish or purplish stripes or spots or tinged violet, or outer ones light yellow or greenish-white, inner ones red-pinkish, orange- or dark yellow, reduplicate-valvate, 6, free, outer whorl longer, outer ones 10–34 mm long, inner ones 10–24 mm long, 1–3 × as long as wide, 3–7 × length of sepals, fleshy, veins prominent or not, indument present, hairs simple; inner petals connivent, with a long and narrow claw, and often with

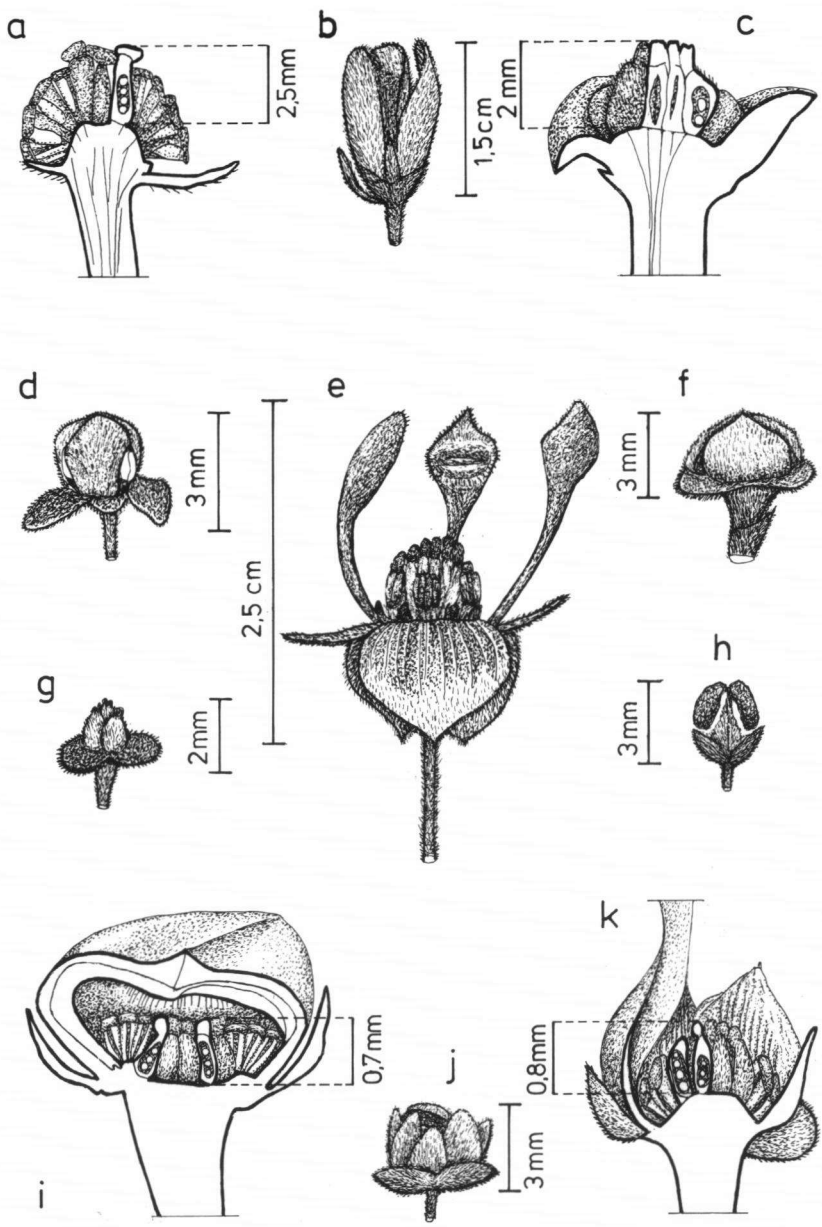


Fig. 29. Mitrephora-group — a. & b. *Fitzalania heteropetala* (Jessup 586): longitudinal section (a) and flower (b); c. *Pseuduvaria rugosa* (Burck s.n./Cult. Hort. Bog. s.n.): longitudinal section; d. *Platymitra macrocarpa* (Bejaud s.n.): flower; e. *Orophea brandisii* (van Beusekom & Phlengkhlai 257): flower; f. *Platymitra macrocarpa* (Bejaud s.n.): bud; g. *Platymitra macrocarpa* (Koorders 15679b): flower after anthesis; h. *Mezzettiopsis creaghii* (Nordin 46137): bud; i. *Mitrephora celebica* (Jacobs/Cult. Hort. Bog. IV-H-51a): longitudinal section; j. *Popowia* cf. *odoardii* (Ilias bin Paie S25289): flower; k. *Mezzettiopsis creaghii* (Elmer 20948): longitudinal section.

fringe. *Torus* cushion-shaped. *Stamens* numerous, 1–1.3 mm long, extrorse; apex discoid, glabrous. *Carpels* free, (few to) numerous, 0.7–1.5 mm long, hairy, style absent, stigma narrowly obconical; ovules 4–6, lateral, 2-seriate. *Flowers* bisexual.

Lectotype – *M. obtusa* (Blume) J.D. Hooker et T. Thomson.

Distribution – About 40 species in tropical Asia.

Note – *Mitrephora* (fig. 29i) has conspicuous, mitriform inner petals. It differs from *Pseuduvaria* by the large outer petals and small inner petals, and it differs from *Orophea* and *Platymitra* by the discoid apices of the stamens, which are (almost) lacking in the latter two genera.

Specimens examined:

M. celebica: Jacobs, Cult. Hort. Bog. IV-H-51a (L). — *M. glabra:* Tinggi S 29566 (L). — *M. heyneana:* Jayasuriya 1261, 1284 (L). — *M. javanica:* Kostermans 19190 (L); Soepadmo 302 (L); Teo 203 (L); de Vogel 3022 (L). — *M. korthalsiana:* Kostermans 10422 (L). — *M. longipetala:* Korthals s.n. (L). — *M. maingayi:* King's collector 6508 (L, U); Maxwell 76-113 (L); Sinclair 40116 (L). — *M. obtusa:* Teijsmann s.n. (L). — *M. polypyrena:* Cult. Hort. Bog. 7698 (I); Versteegh BW 741 (L). — *M. reflexa:* Ramos 41545 (L); Sulit 6469 (L).

Oreomitra Diels, Bot. Jahrb. Syst. 49 (1912) 151, f. 3.

Buds not observed. *Sepals* (aestivation not observed), 3, connate, 1.5 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* (aestivation and number not observed), connate, both whorls equal in length, 4–5 mm long, 1 × as long as wide, 3 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner ones glabrous along the margin outside. *Torus* cylindrical to shallowly conical with a flat apex. *Stamens* numerous, 1–1.5 mm long, extrorse; apex discoid, fleshy. *Carpels* free (incompletely observed); ovule 1, lateral. *Flowers* bisexual.

Type – *O. bullata* Diels.

Distribution – 1 species in New Guinea.

Note – *Oreomitra* has been collected only once, and this specimen has scarcely flowers. *Oreomitra* is only tentatively placed in the Mitrephora-group, also based on the illustrations of Diels (1912).

Specimen examined:

O. bullata: Schlechter 17655 (B, BR).

Orophea Blume, Bijdr. (1825) 18.

Buds broadly ovoid (petals). *Sepals* valvate, 3, free or connate, 1–2.5 mm long, fleshy, thin, veins prominent or not, indument present or absent, hairs simple, margins ciliate. *Petals* cream-white to yellow, sometimes reddish-tinged, pale green, or pale greenish-yellow with light brown lines at the base, valvate or reduplicate-valvate, 6, free, inner whorl longer, outer ones 2–7 mm long, inner ones 4–11 mm long, 0.7–3 × as long as wide, 4 × length of sepals, fleshy, thin, sometimes inner ones fleshy, veins prominent or not, indument present or absent, hairs simple, margins ciliate; inner petals connivent, often with 2 glands underneath the mitre. *Torus* very broadly ovoid with a concave apex. *Stamens* 3 or 6, 1–1.5 mm long, extrorse, staminodes present or absent; apical prolongation (almost) absent. *Carpels* free, 3 or 5,

1–1.8 mm long, hairy or glabrous, style absent, stigma cylindrical, glabrous; ovules 2–5?, lateral, 2-seriate? *Flowers* bisexual.

Lectotype – *O. hexandra* Blume.

Distribution – About 43 species in tropical Asia.

Notes – *Orophea* (fig. 29e) differs from the other genera with conspicuous mitres in the few (3 or 6) stamens without an apical prolongation and the longer inner petals. Like *Pseuduvaria, Orophea* has 2 glands underneath its mitre. *Orophea* is often considered as intermediate between the Miliuseae and the Mitrephoreae (e.g., Sinclair 1955), as *Orophea* has mitriform, inner petals (Mitrephoreae), and stamens without apical prolonged connective (Miliuseae).

Keßler (1988) recognizes two sections in *Orophea*, of which subg. *Sphaerocarpon*, according to his illustrations, has more or less similar petals as *Mezzettiopsis*.

Specimens examined:

O. brandisii: van Beusekom & Phengkhlai 257 (L). — *O. cumingiana:* Elmer 13985 (U); Ramos & Edaño 49072 (BR); Whitford 1456 (BR). — *O. enneandra:* Koorders 20477b (WAG). — *O. enterocarpa:* van Balgooy 2427 (L). — *O. hexandra:* Koorders 14332b, 32476b (WAG). — *O. merrillii:* Edaño 3399 (BR). — *O. myriantha:* Elmer 20912, 20999, 21133 (BR); Puasa 1709 (K). — *O. polycarpa:* Lau 326 (K); Squires 895 (BR); Thwaites 2406 (BR). — *O. sericea:* Wenzel 3378 (BR). — *O. trigyna:* Korthals s.n. (BR); de Vogel 986 (K). — *O. wenzelii:* Wenzel 3358 (BR).

Petalolophus K. Schumann, in K. Schumann et Lauterbach, Nachtr. Fl. Schutzgeb. Südsee (1905) 265.

Buds not observed. *Sepals* valvate, 3, (fusion?), 3 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* old rose-red-purple, valvate, 6, (fusion?), inner petals with very large wings, outer ones 4 mm long, inner ones (wings included) 50 mm long, 1.5 × as long as wide, 15 × length of sepals, fleshy, veins prominent, indument present, hairs simple. *Torus* not observed. *Stamens* numerous, extrorse (incompletely observed); apex discoid, fleshy. *Carpels* free, numerous, hairy (incompletely observed). *Flowers* bisexual.

Type – *P. megalopus* K. Schumann.

Distribution – 1 species in New Guinea.

Note – *Petalolophus* is easy to recognize because of the large wings on the inner petals. According to the illustration in Diels (1912) the stamens resemble those of *Fitzalania*, while it should have 8–9 ovules.

Specimen examined:

P. megalopus: J. & M.S. Clemens 860 (B).

Platymitra Boerlage, Icon. Bogor. 1 (1899) 179, t. 62.

Buds broadly depressed ovoid (petals). *Sepals* valvate, 3, connate, 1–1.3 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* valvate, 6, free, outer whorl longer, outer ones 2–4 mm long, inner ones 2 mm long, 4 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner petals connivent. *Torus* flat. *Stamens* few, 1–1.8 mm long, extrorse; apical prolongation (almost) absent to small discoid, fleshy. *Carpels* free, 1–3, 1.3–1.5 mm long, hairy, style absent, stigma flat and lobed; ovules 6–15, lateral, 2-seriate. *Flowers* bisexual.

Type – *P. macrocarpa* Boerlage.

Distribution – 2 species in the southeastern part of Asia.

Note – The flowers of *Platymitra* (fig. 29d, f, g) have a distinct mitre and, like *Orophea*, have stamens of which the apical prolongation is (almost) lacking. *Platymitra*, however, has smaller flowers, more ovules, and generally fewer carpels than *Orophea*.

Specimens examined:

P. arborea: Rozenbluth 12729 (L) — *P. macrocarpa:* Bejaud s.n. (P); Koorders 15679b (B, P); Merrill s.n. (US); Okada 3457 (U)..

Popowia Endlicher, Gen. Pl. (1839) 831.

Buds depressed ovoid (petals). *Sepals* (aestivation not observed), 3, free or connate, 1.5–5 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* white to yellowish, (reduplicate-)valvate, 6, free or connate, inner whorl longer, outer ones 1–2 mm long, inner ones 2–5 mm long, 1.3–2× as long as wide, 1–2× length of sepals, fleshy, veins prominent or not, indument present, hairs simple. *Torus* flat or shallowly conical. *Stamens* few, 0.8–1.4 mm long, extrorse; apex discoid, fleshy. *Carpels* free, 5–8, 0.7–1.5 mm long, hairy or glabrous, style absent, stigma discoid to flat and lobed; ovules 1 or 2, basal or lateral, 1-seriate. *Flowers* bisexual.

Type – *P. pisocarpa* (Blume) Endlicher.

Distribution – About 30 species in tropical Asia and New Guinea.

Note – *Popowia* (fig. 29j) resembles *Trivalvaria* (Polyalthia-group) in its flowers, but inner and outer petals of *Popowia* are unequal in size, which was a reason to place *Popowia* in the Mitrephora-group.

Specimens examined:

P. affinis: Korthals s.n. (U). — *P. fusca:* Kochummen FRI 16340 (L). — *P.* cf. *odoardii:* Ilias bin Paie S 25289 (L). — *P. pachypetala:* Schlechter 18352 (BR). — *P. perakensis:* King's collector 2922 (L). — *P. pisocarpa:* Edaño 76438 (U); Rahim Ismail 104257 (L); King's collector 7995 (L); Kochummen 99506 (L); Othman Haron S 29352 (K). — *P. ramosissima:* Maingay 52 (K); Scortechini 137a (U). — *P. tomentosa:* Kostermans 7181 (L).

Pseuduvaria Miquel, Fl. Ned. Ind. 1 (2) (1858) 32.

Buds broadly depressed ovoid (petals). *Sepals* (aestivation not observed), 3, free, 1–3(–9) mm long, fleshy, thin, veins not prominent, indument present, hairs simple. *Petals* white, yellowish to yellow- or dark brown, deep purple-red, (dull or pinkish-) purple, or cream with maroon edges, valvate, 6, free, inner whorl much longer, outer ones 1–7 mm long, inner ones 4–15 mm long, 1–3 × as long as wide, 4–7 × length of sepals, outer ones thin, inner ones fleshy, veins not prominent, indument present, hairs simple; inner petals connivent, sometimes 2 glands present on the lower side of the mitre, or sometimes the inner petals glandular inside. *Torus* very shallowly conical, depressed ovoid, or cushion-shaped. *Stamens* numerous, 0.4–1.4 mm long, extrorse, staminodes present or not; apex discoid, glabrous, more or less fleshy. *Carpels* free, few to numerous, 1–2 mm long, hairy, style absent, stigma cylindrical, glabrous; ovules 2–4, lateral, 1- or 2?-seriate. *Flowers* unisexual or sometimes bisexual.

Type – *P. reticulata* (Blume) Miquel.

Table 15. List of character states found in the genera of the Mitrephora-group.

Taxa: F = *Fitzalania*, M1 = *Mezzettiopsis*, M2 = *Mitrephora*, O1 = *Oreomitra*, O2 = *Orophea*, P1 = *Petalolophus*, P2 = *Platymitra*, P3 = *Popowia*, P4 = *Pseuduvaria*.

	F	M1	M2	O1	O2	P1	P2	P3	P4
Flowers:									
3-merous	+	+	+	+	+	+	+	+	+
hairs simple	+	+	+	+	+	+	+	+	+
bisexual	+	+	+	+	+	+	+	+	+
unisexual	–	–	–	–	–	–	–	–	+
Sepals:									
valvate	?	?	+	?	+	+	+	?	?
reduplicate-valvate	?	?	+	?	–	–	–	?	?
connate	–	+	–,+	+	–,+	?	+	–,+	–
1–5 mm long	+	+	+	+	+	+	+	+	+
5–9 mm long	–	–	–	–	–	–	–	–	+
Petals:									
valvate	–	+	–	?	+	+	+	+	+
reduplicate-valvate	–	–	+	?	+	–	–	+	–
imbricate (inner ones)	+	–	–	–	–	–	–	–	–
connate	–	–	–	+	–	?	–	–,+	–
whorls equal in size	+	–	–	+	–	–	–	–	(+)
outer whorl longer	–	–	+	–	–	–	+	–	–
inner whorl longer	+	+	–	–	+	+	–	+	+
inner whorl connivent	–	–	+	–	+	+?	+	–	+
two glands present	–	–	–	–	+	–	–	–	+
base glandular	+	–	–	–	–	–	–	–	–,+
apex glandular (inner)	–	+	–	–	–	–	–	–	–
fringe present	–	–	+	–	–	–	–	–	–
large wings present	–	–	–	–	–	+	–	–	–
outer whorl 1–7 mm long	+	+	–	+	+	+	+	+	+
outer whorl 7–34 mm long	+	–	+	–	–	–	–	–	–
inner whorl 2–15 mm long	+	+	+	+	+	–	+	+	+
inner whorl 15–50 mm long	+	–	+	–	–	+	–	–	–
Stamens:									
numerous	+	–(+)	+	+	–	+	–	–	+
anthers extrorse	+	+	+	+	+	+	+	+	+
apex discoid	+	–	+	+	–	+	–	+	+
apical prolongation absent	–	+(–)	–	–	+	–	+	–	–
staminodes present	–	–	–	–	–,+	?	–	–	–,+
0.4--1.8 mm long	+	+	+	+	+	?	+	+	+
Carpels:									
1--5 in number	–	–	–?	?	+	–	+	(+)	(+)
> 5 in number	+	+	+	?	–	+	–	+	+
Ovules:									
1, basal	–	–	–	–	–	?	–	+	–
1--5, lateral, 1-seriate	+	+	–	+	+?	?	–	+	+
4--15, lateral, 2-seriate	–	–	+	–	+	?	+	–	+?

Distribution – About 20 species in tropical Asia, ranging from the Andamans to the Philippines, in New Guinea, and Australia.

Notes – *Pseuduvaria* (fig. 29c) differs from the other genera with distinct mitres in the unisexual flowers and the small outer petals. In New Guinea, however, *Pseuduvaria* is more diverse in its flower morphology, and the differences between *Pseuduvaria* and *Mitrephora* or other related genera are less marked. These species are usually bisexual and have longer outer petals. Bentham (1862) included *Pseuduvaria* in *Mitrephora*, in later classifications the two genera were separated.

In *Pseuduvaria filipes* (New Guinea) the inner and outer petals are equal in length, thus tending to *Mitrephora*. Also in two Australian species the inner and outer petals are about the same length (Jessup, 1987). In *P. grandifolia* the inner petals are basally glandular like in *Fitzalania* and the genera of the Meiogyne-group. *Pseuduvaria nova-guineensis* resembles *Fitzalania* in the inner petals which are basally glandular at the inner side as well. It resembles *Miliusa* in the long torus. According to Sinclair (1956) this species is bisexual.

Specimens examined:

P. diepenhorstii: Cult. Hort. Bog. s.n. (U). — *P. filipes:* Clemens 8049 (B). — *P. grandiflora:* R.S. Williams 510 (K). — *P. grandifolia:* Floyd & Hoogland 3709 (L). — *P. mulgraveana:* Gray 268 (L); Hyland 5787 (L). — *P. nova-guineensis:* Carr 16186 (B); Hoogland 4032 (L). — *P. philippinensis:* Ramos 24449 (L). — *P. reticulata:* Lörzing 5585, 15243 (L). — *P. rugosa:* Lörzing 5597 (L, U); Burck s.n./Cult. Hort. Bog. s.n. (L). — *P. silvestris:* Brass 29283 (L, US). — *P. sp.:* van Beusekom 2762 (L); Katik NGF 43953 (L); Katik & Womersley NGF 43953 (L); Morawetz 11-22185 (W); Phusomsaeng 455 (L).

12. Monanthotaxis-group (figs. 30, 31; table 16)

Buds (very) broadly (triangular-)ovoid to spheroid (petals). *Sepals* valvate or reduplicate-valvate, 3, free or connate, 0.5–5 mm long, fleshy, rarely thin, veins not or rarely prominent, indument present, hairs simple. *Petals* greyish, whitish, creamy, yellowish, greenish, brownish, or reddish, valvate or reduplicate-valvate, sometimes inner whorl imbricate, 6, free or connate, in 2 whorls of 3 or one whorl of 6 petals, both whorls equal in length or outer whorl longer, 2–13 mm long, 1–4 × as long as wide, 2–7 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner petals rarely glandular at the base inside. *Torus* flat, sometimes broadly ovoid, shallowly conical, depressed obovoid, or cushion-shaped, sometimes with a slightly concave apex. *Stamens* 6 to numerous, 0.4–2.5 mm long, extrorse to latrorse to more or less introrse, rarely staminodes present; apex discoid or truncate, rarely more or less tongue-shaped, glabrous or rarely hairy, sometimes fleshy. *Carpels* free, 3 to numerous, 0.7–2 mm long, hairy, style absent, stigma bilobed, ellipsoid, spheroid, lanceoloid, narrowly or shallowly obconical, shallowly conical, or broadly obovoid; ovules 1–19, lateral or basal, 1- or 2-seriate. *Flowers* bisexual or sometimes unisexual.

Distribution – 4 genera in tropical Africa, incl. Madagascar.

Notes – This group is characterized by small flowers, with valvate sepals and petals (fig. 30f, g), often a flat torus, usually few stamens (fig. 31c) with a distinctive shape, usually few carpels and 1-seriate ovules (fig. 31d). Also in other respects this group is coherent: they are all climbers, the fruits are more or less constricted (except

in *Exellia*), the venation of the leaves is similar, and according to Walker (1971a, b), they have the same distinctive pollen type.

The Monanthotaxis-group is closely related to *Friesodielsia*: some *Monanthotaxis*-species with large flowers are difficult to distinguish from certain *Friesodielsia*-species. In the Monanthotaxis-group and the Friesodielsia-group carpels with a bilobed stigma are common, whereas this type of carpel is rare in other groups. In the stamens and the perianth these two groups are very different.

Atopostema Boutique, Bull. Jard. Bot. État Brux. 21 (1951) 121, pl. 4.

Buds spheroid (petals). *Sepals* (aestivation not observed), 3, connate, 1 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* reddish, valvate, 6, free, both whorls equal in length, 2–3 mm long, 1–2 × as long as wide, 3 × length of sepals, fleshy, veins not prominent, indument present, hairs simple. *Torus* flat. *Stamens* 9, in one whorl and alternating with small staminodes, basally connate, 1 mm long, latrorse; apex truncate, hairy. *Carpels* free, numerous, 1.8 mm long, hairy, style absent or short, stigma broadly obovoid or shallowly obconical; ovules 2, lateral, 1-seriate. *Flowers* bisexual.

Type – *A. klainii* (Engler) Boutique.

Distribution – 2 species in Central Africa (Zaire and Gabon).

Note – *Atopostema* is generally included in *Monanthotaxis* (Verdcourt, 1971b; Le Thomas, 1969: in *Popowia*). It differs from the other species of *Monanthotaxis* by its connate stamens (unique within the Annonaceae) which alternate with small staminodes, and by the reddish flowers, whereas the other genera have whitish, yellowish, greenish, or brownish flowers. Also the leaves look rather different.

Specimen examined:

A. klainii var. *lastoursvillensis:* Le Testu 8674 (P).

Exellia Boutique, Bull. Jard. Bot. État Brux. 21 (1951) 117, pl. 3.

Buds very broadly ovoid (petals). *Sepals* (aestivation not observed), 3, free, 1 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* greenish, or brown outside, white or cream inside, valvate, 6, free, both whorls equal in length, 7 mm long, 1 × as long as wide, 7 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inside glabrous, sometimes glandular. *Torus* shallowly conical. *Stamens* few, 1.8–1.9 mm long, extrorse; apex discoid (dilatated), fleshy. *Carpels* free, 3, 3 mm long, hairy, style absent, stigma spheroid to ellipsoid, glabrous; ovules 9–19, lateral, 2-seriate. *Flowers* bisexual.

Type – *E. scamnopetala* (Exell) Boutique.

Distribution – 1 species in Central Africa and Angola.

Note – *Exellia* (fig. 30b) has many 2-seriate ovules, and differs in this respect from the other genera of this group, of which the ovules are 1-seriate. The stamens remind of those of *Cleistochlamys*.

Specimens examined:

E. scamnopetala: Gossweiler 6105 (BM), 6884 (K); Hallé & Le Thomas 163 (P); Toussaint 205 (BR).

Gilbertiella Boutique, Bull. Jard. Bot. État Brux. 21 (1951) 124.

Buds spheroid (petals). *Sepals* (aestivation not observed), 3, connate, 0.5–1 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* yellowish, valvate, 6, free, all petals in 1 whorl, equal in length or 'outer' ones longer, 2–4 mm long, or 'outer' ones 2.5–3 mm long, 'inner' ones 2 mm long, 1.3 × as long as wide, 4 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, apex of inner petals cuspidate inwards. *Torus* flat. *Stamens* c. 12, 1–1.4 mm long, extrorse, (septation not observed); apex triangular-tongue-shaped, fleshy, hairy. *Carpels* free, 6–9, 1.2–1.3 mm long, hairy, style absent, stigma shallowly conical or bilobed; ovules 6, lateral, 1-seriate. *Flowers* bisexual.

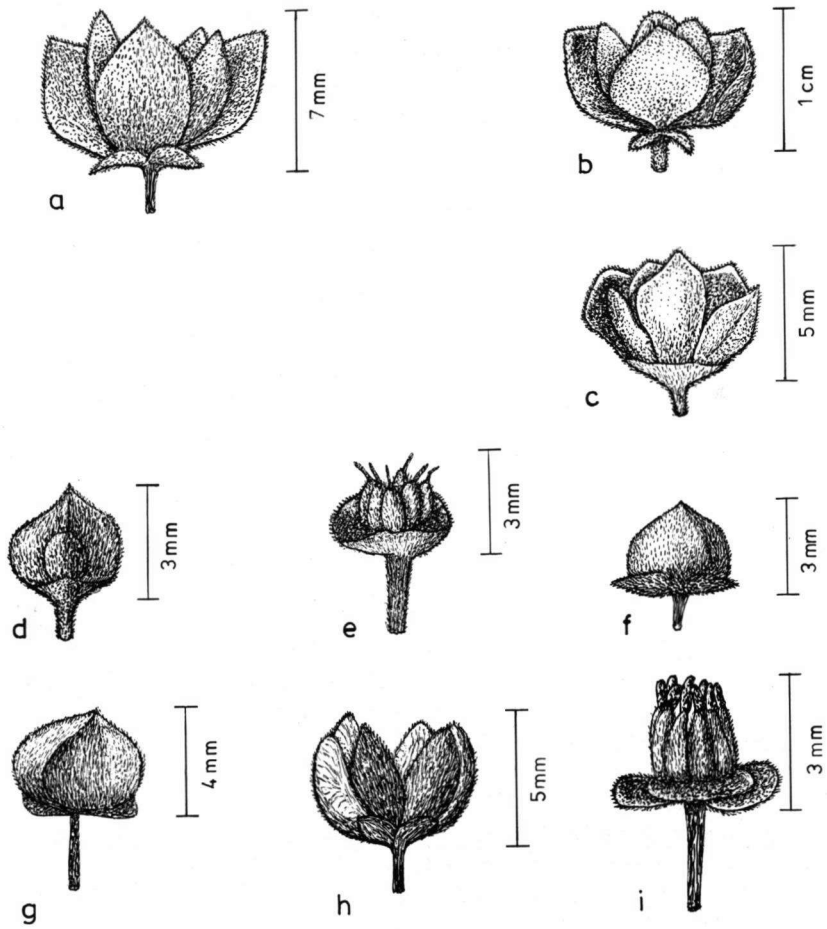


Fig. 30. Monanthotaxis-group — a. *Monanthotaxis buchananii* (Milne-Redhead & Taylor 7505): flower; b. *Exellia scamnopetala* (Hallé & Le Thomas 163): flower; c., d. & e. *Monanthotaxis schweinfurthii* var. *seretii* (Louis 15072): flower (c), bud (d), and flower after anthesis (e); f. *Monanthotaxis buchananii* (Milne-Redhead & Taylor 7505): bud; g. *Monanthotaxis orophila* (Reekmans 8908): bud; h. *Monanthotaxis letestui* var. *hallei* (Hallé & Le Thomas 2): flower; i. *Monanthotaxis orophila* (Reekmans 8908): flower after anthesis.

Type – *G. congolana* Boutique.

Distribution – 1 species in Central Africa (Zaire).

Note – *Gilbertiella* (fig. 31e) differs from the other genera of this group in the type of stamens, but in the other characters it agrees with the Monanthotaxis-group. The petals are cuspidate with an inwardly curved tip, which is otherwise only found in *Onychopetalum* and some *Bocageopsis*-specimens.

Specimens examined:
G. congolana: Germain 4894 (BR); Louis 11414 (BR).

Monanthotaxis Baillon, Bull. Mens. Soc. Linn. Paris 1 (1890) 878.

Buds broadly ovoid to spheroid (petals). *Sepals* valvate or reduplicate-valvate, 3, free or connate, 0.5–5 mm long, fleshy, sometimes thin, veins rarely prominent, indument present, hairs simple. *Petals* white, greenish to yellowish, creamy(-brown), or outside greenish, inside often creamy, valvate or reduplicate-valvate, sometimes inner whorl imbricate, 6, free or connate, all petals in 1 whorl or in 2 whorls, equal in length or outer whorl longer, 2–13 mm long, 1–4 × as long as wide, 2–5 × length of sepals, fleshy, veins not prominent, indument present, hairs simple. *Torus* flat, broadly ovoid, cushion-shaped, sometimes with a slightly concave apex, or depressed obovoid. *Stamens* 6–12 (to numerous), 0.4–2.5 mm long, extrorse to latrorse to introrse; apex discoid or truncate, fleshy. *Carpels* free, 3 to numerous, 0.7–2 mm long, hairy or sometimes ciliate, style absent (to present), stigma bilobed, ellipsoid, lanceoloid, sphaeroid, narrowly obconical, shallowly conical, or flat (lobed); ovules 1–7, lateral or basal, 1-seriate. *Flowers* bisexual or sometimes unisexual (only female flowers observed).

Type – *M. congoensis* Baillon.

Distribution – Tropical Africa, incl.Madagascar, 70–75 species.

Note – *Monanthotaxis* has a distinctive stamen type: a relatively broad connective, narrow filaments, and usually more or less latrorse anthers. *Monanthotaxis* includes the former genera *Monanthotaxis* s.s. (figs. 30h, 31b, c), *Enneastemon* (fig. 30c, d, e), and the African species of *Popowia* (figs. 30a, f, i, 31a, d) (Verdcourt, 1971b). These genera only differ in the arrangement of the petals: petals in one whorl (*Monanthotaxis* s.s.), in one whorl at the base and in two whorls at the apex of the petals (*Enneastemon*), or in two whorls (the African species of *Popowia*). There is no relationship with the Asiatic genus *Popowia*.

Specimens examined:
M. ambrensis: Perrier de la Bathie 18826 (P). — *M. barteri:* Berhaut 6319 (BR); Espirito Santo 2037 (WAG); Le Testu 2549, 3853 (BR). — *M. bokoli:* Le Testu 8626 (BR); Louis 10970 (K). — *M. brachytricha:* Perrier de la Bathie 16989 (B, P). — *M. buchananii:* Harris 2594 (WAG); Milne-Redhead & Taylor 7505 (BR, K). — *M. caesia:* Perrier de la Bathie 1192, 1192bis (B). — *M. caffra:* de Koning 7766 (BR). — *M. cauliflora:* Bos 6037 (BR), 6293 (BR, WAG). — *M. congoensis:* Thollon 813 (P). — *M. diclina:* Lebrun 1870 (BR). — *M. filamentosa:* Zenker 357 (U). — *M. foliosa:* Brenan & Richards 8826 (BR). — *M. fornicata:* Faulkner 532, 1652 (BR). — *M. heteranthа:* Herb. d'Alleizette s.n. (L). — *M. laurentii:* Le Testu 4512 (BR). — *M. letestui:* Hallé & Le Thomas 2 (BR, P); Le Testu s.n. (?). — *M. mannii:* Zenker 356 (U), 3495 (L). — *M. orophila:* Bamps 3213 (BR); Bouxin 665, 1088 (BR); Lewalle 4604 (L); Reekmans 1332, 5037, 7970, 8908 (BR). — *M. parviflora* var. *kenyensis:* Verdcourt 2620 (BR). — *M. pilosa:* Perrier de la Bathie 91

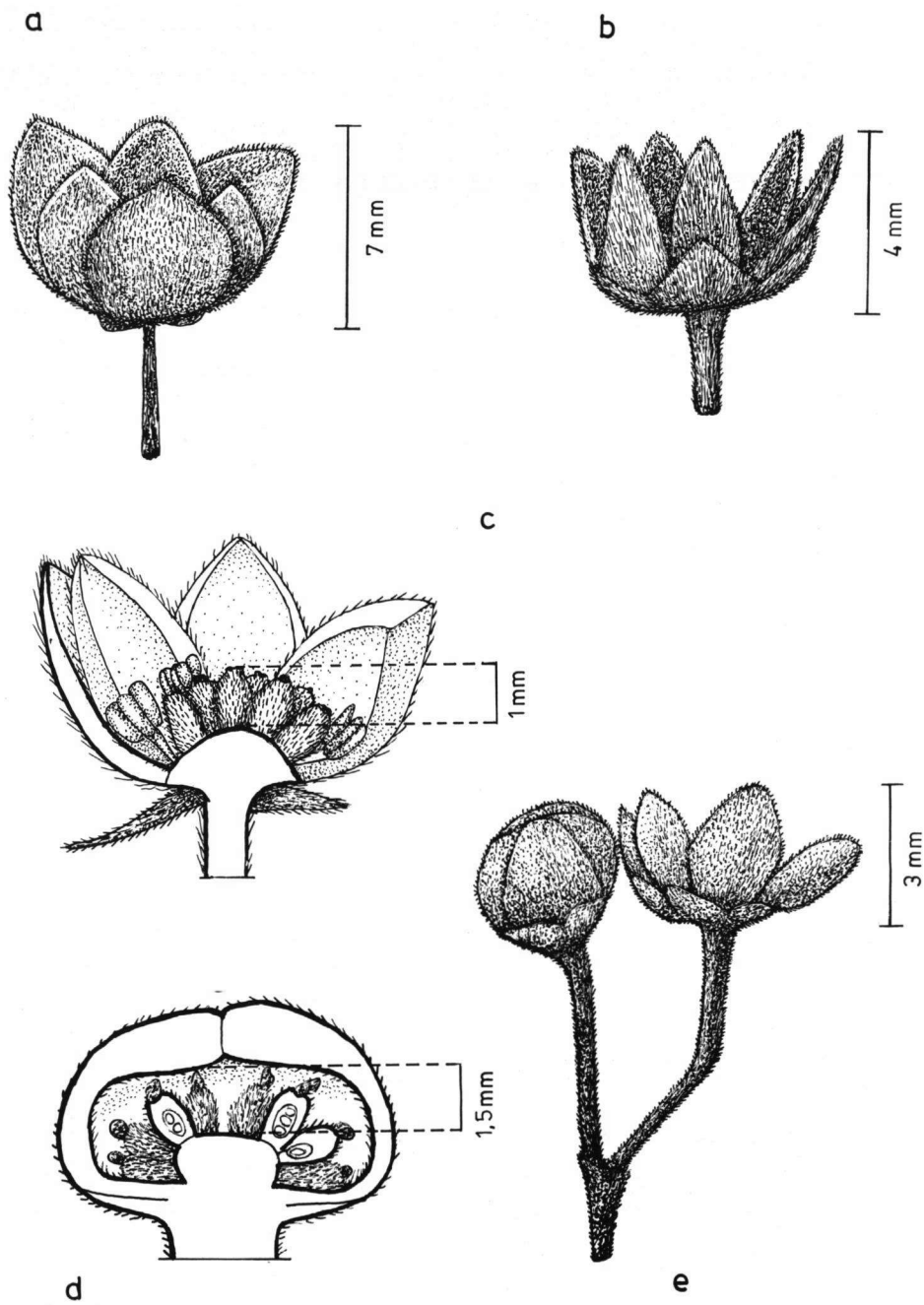


Fig. 31. Monanthotaxis-group — a. *Monanthotaxis orophila* (Reekmans 8908): flower; b. *Monanthotaxis poggei* (Herman 2192): flower; c. *Monanthotaxis poggei* (Liben 3916): longitudinal section; d. *Monanthotaxis cauliflora* (Bos 6293): longitudinal section: e. *Gilbertiella congolana* (Germain 4894): bud and flower.

(L). — *M. poggei:* Herman 2192 (BR); Liben 3916 (BR); Mullenders 1243, 1673 (BR); Pirozynski 77 (BR); Schlechter 12801 (B, WAG); Verdcourt 3365 (BR). — *M. schweinfurthii* (incl. var. *seretii*): Fanshawe 2818 (BR); Gerard 2898 (WAG); Germain 1 (BR); Leonard 3888 (WAG); Louis 14318 (BR), 15072 (BR, K); Milne-Redhead 3044 (BR); Quarré 2708 (BR); Stolz 170 (L); Tisserant 1710 (BR); Troupin 4755 (BR, WAG). — *M. soraria:* Perrier de la Bathie 914bis (B). — *M. trichocarpa:* Breteler 7553 (WAG); Polhill 4813 (BR). — *M. vogelii:* Espirito Santo 2476 (WAG); Morton & Gledhill SL 1160 (WAG). — *M. whytei:* Cult. Hort. Wag. s.n. (WAG).

Table 16. List of character states found in the genera of the Monanthotaxis-group.

	Atopostema	*Exellia*	*Gilbertiella*	*Monanthotaxis*
Flowers:				
3-merous	+	+	+	+
hairs simple	+	+	+	+
bisexual	+	+	+	+
female	–	–	–	+
male	–	–	–	?
Sepals:				
valvate	?	?	?	+
reduplicate-valvate	?	?	?	+
connate	+	–	+	+,–
0.5–5 mm long	+	+	+	+
Petals:				
valvate	+	+	+	+
reduplicate-valvate	–	–	–	+
inner ones imbricate	–	–	–	–,+
connate	–	–	–	–,+
in one whorl	–	–	+	+,–
2–5 mm long	+	–	+	+
5–13 mm long	–	+	–	+
Stamens:				
6–15 in number	+	+	+	+
numerous	–	–	–	+
connate basally	+	–	–	–
anthers extrorse	–	+	+	+
anthers latrorse	+	–	–	+
anthers introrse	–	–	–	+
staminodes present	+	–	–	–
0.4–2.5 mm long	+	+	+	+
Carpels:				
3 in number	–	+	–	+
> 3 in number	+	–	+	+
Ovules:				
1, basal	–	–	–	+
> 1, lateral, 1-seriate	+	–	+	+
> 1, lateral, 2-seriate	–	+	–	–

13. Polyalthia-group (figs. 32, 33; table 17)

Buds very broadly or broadly depressed ovoid, spheroid, ellipsoid, or apert? (petals). *Sepals* valvate, imbricate, or apert?, 3 (or 4), free or connate, 0.5–50 mm long, fleshy to almost membranous, veins prominent or not, indument present or absent, hairs simple, margins ciliate or not. *Petals* whitish, yellowish, greenish, brown, (pale) orange, red, pink, or purple, valvate, imbricate, or apert?, 6, (8), or 9, free or connate, both whorls equal in length or sometimes unequal, 2.5–95 mm long, 1–20 × as long as wide, 1–30 × length of sepals, fleshy to almost membranous, veins prominent or not, indument present or absent, hairs simple, inner petals sometimes basally glandular, glabrous, or differently coloured inside. *Torus* depressed ovoid, sometimes with a slightly concave apex, shallowly conical, or broadly cylindrical. *Stamens* numerous (rarely few), 0.7–4 mm long, extrorse; apex discoid, often fleshy, glabrous, sometimes hairy or shiny. *Carpels* free, numerous (sometimes few), 1–3 mm long, hairy or glabrous, style absent or rarely present, stigma ellipsoid, spheroid, cylindrical, or obconical, glabrous or hairy; ovules 1–5, basal or lateral. *Flowers* bisexual.

Distribution – 7 genera in tropical Asia, New Guinea, Australia, Pacific, in Madagascar, and East Africa.

Notes – This group is characterized by usually a valvate or imbricate aestivation of both petals and sepals, usually equal-sized petals, usually many stamens and carpels, and few, basal or lateral ovules (figs. 32b, e, 33b, f).

The differences between some genera are small, and seem mostly quantitative. *Enicosanthum* (fig. 32c) differs from *Polyalthia* (fig. 32d, f) in the larger size of the flowers. The same applies to the former genus *Sphaerothalamus* (fig. 32g), included in *Polyalthia* by Airy Shaw (1939), and of which the sepals enlarge to a length of 50 mm. Also *Trivalvaria* (fig. 32h) seems very close to *Polyalthia*, differing from that genus in the smaller size of the flowers and the dense indument on the petals and sepals. *Papualthia*, especially the species from the Philippines, differ from *Polyalthia* because of their basally connate petals. *Woodiellantha* (fig. 33h) seems close to *Enicosanthum*, and differs from that genus by the connate petals as well. In the classification of Prantl (1888) *Trivalvaria* was a section of *Polyalthia*, beside the sections *Polyalthia* and *Monoon*. Since Engler & Diels (1900) *Trivalvaria* is considered as a distinct genus, and in classifications it is placed far from *Polyalthia* (Sinclair, 1955; Fries, 1959; Hutchinson, 1964). Judged from the flowers, *Enicosanthum, Papualthia, Polyalthia* (with the sections *Polyalthia* and *Monoon*, and including the former genus *Sphaerothalamus*), *Trivalvaria*, and *Woodiellantha* seem to form one genus rather than well-delimited, distinct genera.

The Polyalthia-group seems to have links with the Cremastosperma-, Miliusa-, and Mitrephora-group (via *Popowia*), the Sageraea-group, to *Neo-uvaria*, and via *Haplostichanthus* to the Sapranthus-group and perhaps to the Unonopsis-group.

Enicosanthum Beccari, Nuovo Giorn. Bot. Ital. 3 (1871) 183, t. 5.

Buds very broadly ovoid or ellipsoid (petals). *Sepals* imbricate?, 3, free or connate, 4.5–10 mm long, fleshy or very thin, veins prominent or not, indument pres-

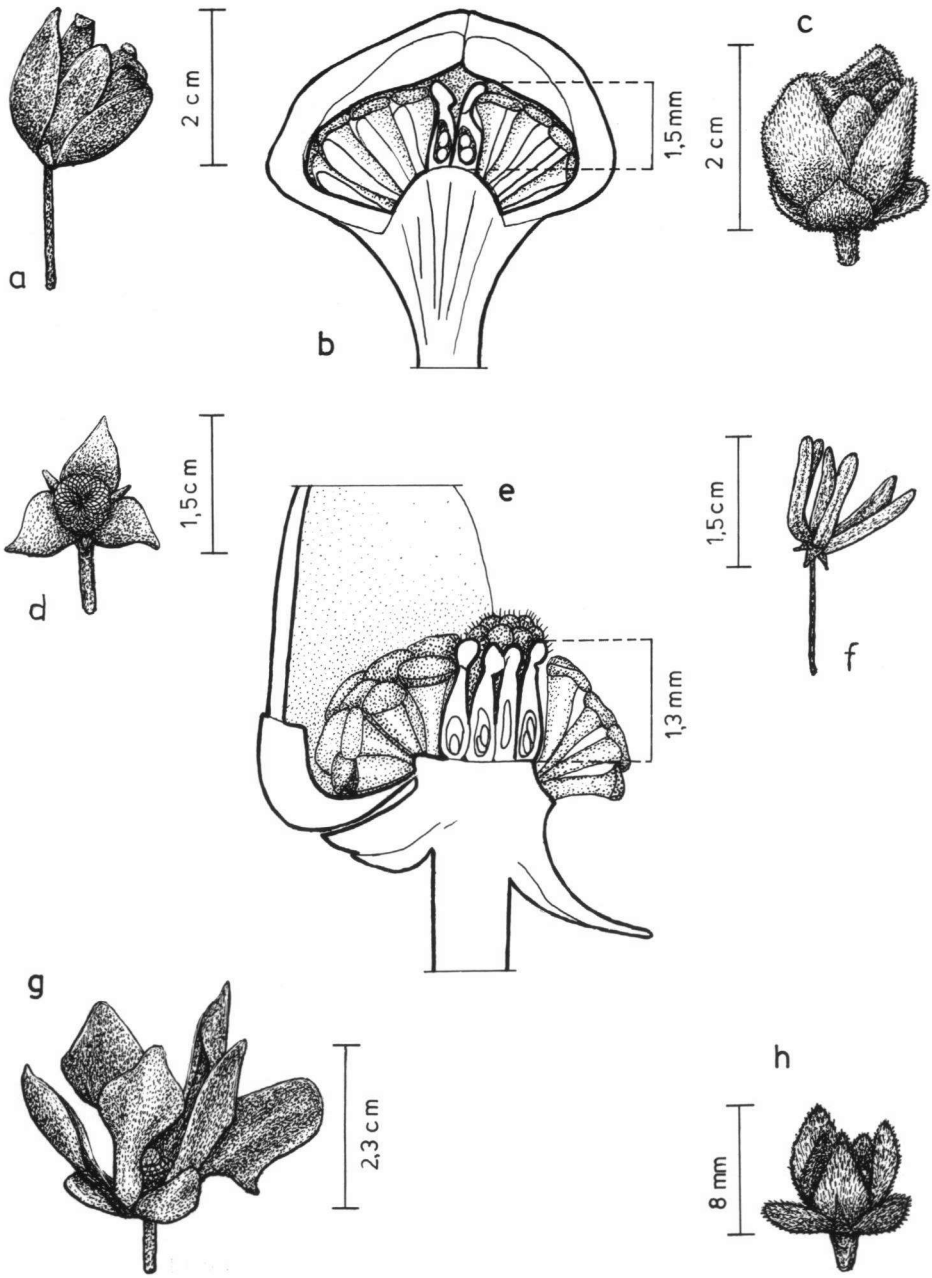


Fig. 32. Polyalthia-group — a. *Papualthia sp.* (Edaño 37135): flower; b. *Haplostichanthus sp.* (Morawetz 36-2185): longitudinal section; c. *Enicosanthum fuscum* (Sinclair 9904): flower; d. *Polyalthia evecta* (Koelz 22755): flower; e. *Polyalthia nitidissima* (Gray 235): longitudinal section; f. *Polyalthia evecta* (Maxwell 76-360): flower; g. *Sphaerothalamus insignis* (Kokawa & Hotta 1581): flower; h. *Trivalvaria macrophylla* (Sinclair & Kadim 10366): flower.

ent, hairs simple. *Petals* (greenish-)white to (greenish-)yellow, imbricate, 6, free, both whorls equal in length, 14–28(–60) mm long, 1.5–3 × as long as wide, 3 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner petals basally glandular inside. *Torus* shallowly conical with a flat apex. *Stamens* numerous, 1.2–3 mm long, extrorse; apex discoid, fleshy. *Carpels* free, numerous, hairy (incompletely observed); ovule 1, basal. *Flowers* bisexual.

Type – *E. paradoxum* Beccari.

Distribution – About 15 species in tropical Asia.

Note – *Enicosanthum* (fig. 32c) seems closely related to *Polyalthia*, especially to the species with one ovule, but differs from that genus because of the larger flowers. In this respect it reminds of *Polyalthia insignis*, formerly referred to the genus *Sphaerothalamus*.

Specimens examined:

E. acuminatum: Nooteboom 3222 (L). — *E. congregatum:* King 7613 (L). — *E. coriaceum:* Nahar 12660 (L). — *E. erianthoides:* Sundaling 78120 (L). — *E. fuscum:* Chan FRI 13245 (K); Kostermans 707 (K); Loh FRI 13440 (K); Sinclair 9904 (L); Suppiah FRI 11400 (L). — *E. magnoliiflorum:* Kadim & Noor 531 (L). — *E. paradoxum:* Wood & Wyatt-Smith A4334 (L). — *E. sp.:* Sangkhachand 464 (L).

Fenerivia Diels, Notizbl. Bot. Gart. Berlin-Dahlem 9 (1925) 355.

Buds not observed. *Sepals* (aestivation not observed), 3, free, 20–21 mm long, fleshy, veins prominent, indument absent. *Petals* green, (aestivation not observed), 9, free, the worls unequal in length, 25–33 mm long, 9–10 × as long as wide, 1.5 × length of sepals, fleshy, thick, veins not prominent, indument absent. *Torus* broadly cylindrical. *Stamens* numerous, 2.7–3 mm long, extrorse; apex discoid, glabrous. *Carpels* free, numerous, (length not measured), glabrous, (style and stigma not observed); ovule 1, basal. *Flowers* bisexual.

Type – *F. heteropetala* Diels.

Distribution – 1 species in Madagascar.

Notes – *Fenerivia heteropetala* has been collected only once; the investigated specimen consists of flower fragments only. There is confusion about the correct number of petals in the genus *Fenerivia*. Many authors regard the flower of *Fenerivia* as having 12 petals: 3 ovate outer petals and 9 linear inner petals (Cavaco & Keraudren, 1958; Diels, 1925; Fries, 1959). However, the flower resembles the flowers of *Polyalthia*-species of Madagascar, which have linear petals, and triangular-ovate sepals with a prominent venation. Thus it seems more probable that the flower of *Fenerivia* has 9 linear petals and 3 ovate sepals, as was already suggested by Perrier de la Bathie on the label of the herbarium-sheet and by Ghesquière (1939). The pedicel is widened at the apex; the widened part was considered as a connate, circular sepal by the taxonomists favouring the concept of the flower with 12 heterogeneous petals.

The stamens resemble those of the Asiatic genus *Woodiellantha*. Most present-day taxonomists include *Fenerivia* in *Polyalthia*.

Specimen examined:

F. heteropetala: Perrier de la Bathie 4942 (B).

Haplostichanthus F. von Mueller, Victoria Naturalist 7 (1891) 180.

Buds spheroid (petals). *Sepals* valvate, 3, free or connate, 1.5–3.5 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* orange, inner ones reddish inside, or cream, valvate, 6, connate, both whorls equal in length or inner ones longer, 2.5–4 mm long or outer ones 3–4 mm long, inner ones 5–7 mm long, 2 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner petals connivent. *Torus* depressed ovoid, sometimes with flat apex, or shallowly conical with a flat apex. *Stamens* numerous, 1.3 mm long, extrorse; apex discoid, glabrous. *Carpels* free, few (c. 2?–8), c. 1.5 mm long, hairy, style absent, stigma ellipsoid, small, glabrous; ovules 2, lateral, 1-seriate. *Flowers* bisexual.

Type – *H. johnsonii* F. von Mueller.

Distribution – 1(?) species in Queensland, Australia.

Note – *Haplostichanthus* (fig. 32b) may be congeneric with *Papualthia*. The specimen Frodin NGF 26547 from New Britain resembles so strongly the Australian specimen Hyland 3016 R.F.K. that they possibly belong to the same species. *Haplostichanthus*, thusfar, is considered to occur in Australia only. The genus may consist of more than one species.

Specimens examined:

H. johnsonii: Hyland 3016 R.F.K. (L), 7142 (L); Jessup 537 (U); F. von Mueller s.n. (K). — *H. sp.:* Frodin NGF 26547 (L); Morawetz 36-2185 (U).

Papualthia Diels, Bot. Jahrb. Syst. 49 (1912) 138, f. 1.

Buds spheroid (petals; New Guinea), no (young) buds observed in the Philippine species. *Sepals* valvate, 3, connate, 1.5–6 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* purplish-yellow, dull pinkish, cream, or white, sometimes tinged with pink or with a yellow center, valvate or imbricate, 6, connate or free, both whorls equal in length or sometimes unequal, 5–36 mm long, 1–3 × as long as wide, 2–5 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, sometimes inside glabrous. *Torus* shallowly conical with a flat apex. *Stamens* numerous, 0.8–2.5 mm long, extrorse; apex discoid, fleshy or glabrous. *Carpels* free, numerous to few, 1.3–1.6 mm long, hairy, style absent, stigma ellipsoid or spheroid, small, glabrous; ovules 2?–5, lateral, 1-seriate? *Flowers* bisexual.

Lectotype – *P. pilosa* Diels.

Distribution – 20 species in New Guinea, Solomon Islands, and the Philippines.

Note – *Papualthia* is found in New Guinea and the Philippines only. In their flowers the specimens from the Philippines look different from those from New Guinea. In the Philippines the flowers are usually middle-sized, with long and narrow petals (figs. 32a, 33a, c). In New Guinea the flowers are small with short and broad petals (fig. 33g). The Philippine species have long pedicels, whereas the flowers from New Guinea are usually subsessile. However, too little material is present to decide whether the Philippine species should be separated from *Papualthia* or not. The New Guinean species of *Papualthia* seem congeneric with the Australian genus *Haplostichanthus*. Two of the examined specimens possess flowers with free petals, thus tending to *Polyalthia*.

Specimens examined:

NEW GUINEA AND SOLOMON ISLANDS — *P. auriculata:* Gillison NGF 22126 (L); Mauriasi et al. BSIP 8635 (L); Pullen 6731 (L); Streimann & Kairo NGF 17484 (L); Dept. of Forests Staff s.n. (L). — *P. pilosa:* Schlechter 17911 (P). — *P. sp.:* Foreman & Stevens LAE 58066 (L); Frodin NGF 26547 (L); Gillison NGF 25002 (L); Hoogland 3641 (L).

PHILIPPINES — *P. bakeri:* Elmer 17775 (K, P, U), 18327 (P). — *P. boholensis:* Ramos 43095 (BM, K). — *P. heteropetala:* Ramos 32853 (K). — *P. lanceolata:* Conklin 740 (L); Cuming 450 (K). — *P. loheri:* Ramos & Edaño 47012 (K, P). — *P. reticulata:* Ramos 24398, 76965 (K); Ramos & Edaño 49460 (P). — *P. samarensis:* Ramos 24180 (K). — *P. sympetala:* Ramos 20515 (BM, K). — *P. urdanetensis:* Elmer 13931 (K). — *P. sp.:* Edaño 37135 (K).

Polyalthia Blume, Fl. Javae Anonac. 28–29 (1830) 68, t. 33–34, 36B, C.

Buds apert?, sometimes spheroid to broadly depressed ovoid (petals). *Sepals* apert?, valvate, or imbricate, 3 (or 4), free or connate, 0.5–8 mm long, fleshy to almost membranous, veins prominent or not, indument present or absent, hairs simple, margins ciliate or not. *Petals* white to green to yellow, dark red, or reddish-brown, apert?, sometimes valvate or imbricate, 6 (or 8), free, both whorls equal in length or sometimes outer longer, 4–95 mm long, 2–20 × as long as wide, 1–30 × length of sepals, fleshy to almost membranous, veins prominent or not, indument present or absent, hairs simple, inner petals sometimes basally differently coloured inside. *Torus* depressed ovoid, sometimes with a slightly concave apex, cylindrical to cushion-shaped, or shallowly conical with a flat apex. *Stamens* numerous, 0.7–1.8 mm long, extrorse, apex discoid, glabrous, fleshy, sometimes shiny. *Carpels* free, 3 to numerous, 1–3 mm long, hairy or glabrous, style absent or rarely present, stigma spheroid, cylindrical, or obconical, glabrous or hairy; ovules 1 or 2, basal or lateral. *Flowers* bisexual.

Lectotype – *P. subcordata* (Blume) Blume.

Distribution – Tropical Asia, New Guinea, Australia, Solomon Islands, Fiji, Madagascar, and East Africa, 155–160 species.

Notes – *Polyalthia* (fig. 32d, f) is the largest annonaceous genus of Asia; the flowers in general appearance resemble the flowers of the large neotropical genus *Guatteria.* Remarkable is that the flowers of the species from Madagascar and East Africa (fig. 33d) and Australia and New Guinea (fig. 33e) resemble each other most, whereas in Asia there is much more diversity. Nevertheless, the genus is rather uniform in its flowers.

Polyalthia consists of two sections: section *Polyalthia,* with 2 lateral ovules (fig. 33b), and section *Monoon,* with one basal ovule (fig. 33f). The species of section *Monoon* are very close to *Enicosanthum.* The main difference is the slender flowers in *Polyalthia* versus robust flowers in *Enicosanthum.* The flowers of the section *Polyalthia* are closer to those of *Papualthia.* Also *Trivalvaria,* which has been considered as a third section of *Polyalthia* by the earliest taxonomists, seems close to the section *Monoon*; the flowers of *Trivalvaria* are smaller than most *Polyalthia*-flowers.

Polyalthia celebica differs from the other species in the small number of carpels (c. 3), which are unlike those of the other *Polyalthia*-species, but resemble more those of, e.g., *Ancana.* Probably it is a *Papualthia*-species. *Polyalthia glauca* (Hoogland 3529, wrongly identified?) has imbricate sepals and petals, and ciliate sepals,

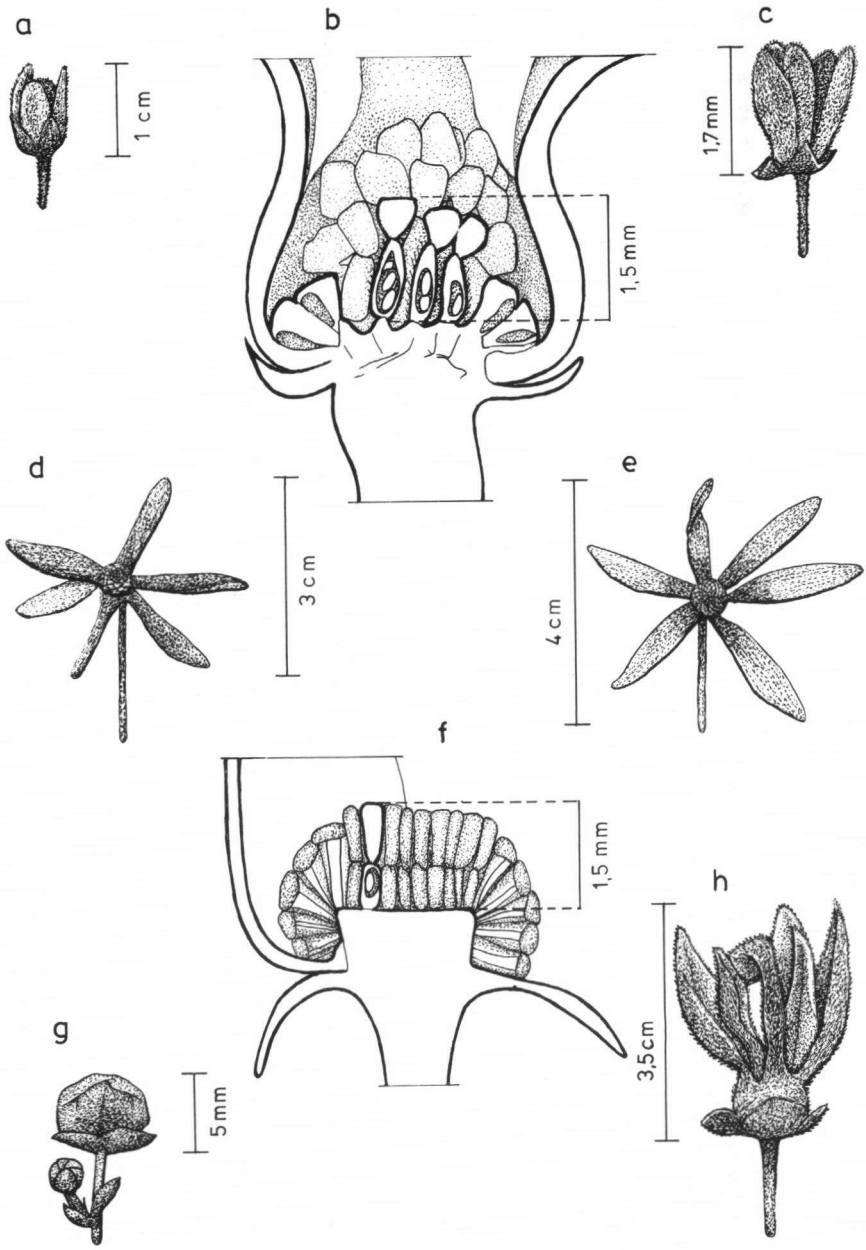


Fig. 33. Polyalthia-group — a. *Papualthia reticulata* (Ramos 76965): bud; b. *Polyalthia glauca* (Okada 3389): longitudinal section; c. *Papualthia reticulata* (Ramos 76965): flower; d. *Polyalthia stuhlmannii* (Faden & Evans 71/697): flower; e. *Polyalthia forbesii* (Streimann & Kairo NGF 26147): flower; f. *Polyalthia forbesii* (Docters van Leeuwen 11052): longitudinal section; g. *Papualthia auriculata* (Pullen 6731): buds; h. *Woodiellantha sympetala* (Wood & Wyatt-Smith SAN A4544): flower.

and reminds in its buds of *Oncodostigma* and related genera. In *Polyalthia jucunda* the torus resembles that of *Disepalum*. *Polyalthia crassa* has stamens which are unlike those of the other *Polyalthia*-species, but resembling those of *Alphonsea* and *Miliusa*. Possibly this species belongs to *Marsypopetalum* (see there, Miliusa-group). *Polyalthia rumphii* and *P. forbesii* may be conspecific: they both have a yellow mouldiness on their leaves, and also their flowers closely resemble each other. In a specimen of *P. sumatrana* (Morawetz 16-26285) the sepals are absent.

According to Bailey (1899) the petals of *Polyalthia* are valvate in very young buds only.

Specimens examined:

AFRICA, MADAGASCAR INCLUDED — *P. angusti-elliptica:* Service Forestier (Capuron) 18237 (B). — *P. capuronii:* Service Forestier (Capuron) 22349 (BR, P). — *P. decora:* Perrier de la Bathie 4974 (B). — *P. emarginata:* Perrier de la Bathie 14910 (B). — *P. ghesquiereana:* Réserves Naturelles 8843 (B). — *P. henrici:* Service Forestier (Capuron) 23116 (B); Perrier de la Bathie 4960 (B). — *P.* aff. *humbertii:* Service Forestier (Capuron) 20977 (BR). — *P. lamii:* Lam & Meeuse 6047 (BR, L); Ursch s.n. (L). — *P. oligosperma:* Perrier de la Bathie 4938 (B). — *P. stuhlmannii:* Faden & Evans 71/697 (BR); J.B. Gillett 19842 (BR); Mgaza 717 (K); Rawlins 262 (K).

ASIA — *P. cauliflora* var. *cauliflora:* Cockburn FRI 7458 (L); Wood SAN A4129 (L). — *P. cauliflora* var. *beccarii:* Elmer 20988 (U); King 4522 (U). — *P. celebica:* Koorders 16018b (L); Warburg 15364 (B). — *P. cerasoides:* Ellis 16730 (L); Maxwell 75-161, 76-154 (L). — *P. congesta:* Kostermans 9926 (L); Wood SAN 16076 (L). — *P. crassa:* Kerr 9743, 11572, 11904, 18307 (BM). — *P. crassipetala:* Geesink et al. 5595 (L); Lei 640 (L). — *P. curtisii:* Nedi 763 (L). — *P. evecta:* Bunkhrong 47/BKF 25826 (L); Koelz 22755 (L); Maxwell 76-360 (L). — *P. flagellaris:* Chew W.L. 345 (L). — *P. forbesii:* Docters van Leeuwen 9924, 10619, 11052 (U); Gafui et al. BSIP 8972 (L); Koster BW 4380 (L); Streimann & Kairo NGF 26147 (L). — *P. fragrans:* Raghavan 67929 (L). — *P. glauca:* Hoogland 3529 (L); Okada 3389 (U). — *P. hypogaea:* Jacobs 5288 (L). — *P. hypoleuca:* Zainuddin Sohadi FRI 14631 (L). — *P. jenkensii:* Kochummen FRI 16408 (L); Ramos 24233 (L). — *P. jucunda:* Maxwell 76-152 (L). — *P. korinti;* Jayasuriya 1269 (L). — *P. lateriflora:* Bakhuizen van den Brink 5774 (U); Maxwell 75-154 (L). — *P. loriformis:* Tothill 7536 (K). — *P. michaelii:* Sanderson 40 (L). — *P. micrantha:* Backer s.n. (U). — *P. microtus:* Korthals s.n. (U). — *P. nitidissima:* Gray 235 (L); von Mueller s.n. (L). — *P. rumphii:* Bakhuizen van den Brink 2669, 6258 (U); Jacobs 5273 (L?). — *P. sclerophylla:* Morawetz 12-25285 (U). — *P. subcordata:* Bakhuizen van den Brink 2044 (U); Jeswiet 1391 (WAG). — *P. sumatrana:* Morawetz 16-26285 (U). — *P. tenuipes:* Awang Morshidi S24092 (U).

Sphaerothalamus J.D. Hooker, Trans Linn. Soc. London 23 (1860) 156.

Buds not observed. *Sepals* (aestivation not observed), 3, free, 10–50 mm long, fleshy, thin, veins prominent, indument present or absent, hairs simple, margins ciliate. *Petals* orange or red, (aestivation not observed), 6, free, both whorls equal in length, 23–80 mm long, 2–6 × as long as wide, 1.5–2 × length of sepals, fleshy, veins prominent or not, indument present, hairs simple, inner petals sometimes glandular or differently coloured at the base inside. *Torus* depressed ovoid. *Stamens* numerous, 2.3–4 mm long, extrorse; apex discoid, fleshy. *Carpels* free, numerous, (length not measured), hairy, (style and stigma not observed); ovules 2, lateral. *Flowers* bisexual.

Type – *S. insignis* J.D. Hooker.

Distribution – 1 species in tropical Asia (Borneo).

Note – *Sphaerothalamus* (fig. 32g), usually referred to *Polyalthia*, has larger flowers than the other species of *Polyalthia* and sepals which enlarge considerably, so it was decided to treat this species separately from *Polyalthia*. If *Sphaerothalamus* is included in *Polyalthia*, also *Enicosanthum* should be included in *Polyalthia*.

Specimens examined:

S. insignis: Andjah 602 (K); Haviland s.n. (K); Lobb s.n. (K); Kokawa & Hotta 1581 (L); Maidin 1690 (K); Meijer 2232 (L); de Vogel 852 (K, L).

Trivalvaria (Miquel) Miquel, Ann. Mus. Lugduno-Batavum 2 (1865) 19.

Buds very broadly ovoid (petals). *Sepals* (aestivation not observed), 3, free, 3 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* white or (yellow-)cream, valvate or imbricate, 6, free, both whorls equal in length or inner ones longer, outer ones 3–7 mm long, inner ones 5–9 mm long, or both 7–12 mm long, 1 × as long as wide, 2–4 × length of sepals, fleshy, thin or thick, veins not prominent, indument present, hairs simple, inner petals basally glabrous inside. *Torus* broadly ovoid with flat apex. *Stamens* few to numerous, 1.2–1.5 mm long, extrorse; apex discoid, glabrous or hairy. *Carpels* free, numerous, 2 mm long, hairy, style absent, stigma ellipsoid, glabrous; ovule 1, basal. *Flowers* bisexual.

Type – *T. macrophylla* (Blume) Miquel.

Distribution – Tropical Asia, 4–6 species

Note – *Trivalvaria* (fig. 32h) has two types of flowers: *T. macrophylla* has thick, fleshy, erect, valvate petals, and resembles *Popowia* and *Papualthia* (species from New Guinea), whereas *T. pumila* and *T. nervosa* have thinner, spreading, imbricate petals which resemble those of *Polyalthia* and more or less those of *Sageraea*.

Specimens examined:

T. macrophylla: Chan FRI 19990 (L); Korthals s.n. (U); Sinclair & Kadim 10366 (K, L); H.B. 497 (U). — *T. nervosa:* Ridley s.n. (K); Shah MS1622 (K); Whitmore FRI 15739 (K). — *T. pumila:* Ridley s.n. (K); Robinson s.n. (P).

Woodiellantha Rauschert, Taxon 31 (1982) 555 (= *Woodiella* Merrill).

Buds not observed. *Sepals* (aestivation not observed), 3, connate, 4–8 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* green-yellow, (aestivation not observed), 6, connate, both whorls equal in length, 26–37 mm long, 2 × as long as wide, 5 × length of sepals, fleshy, veins not prominent, indument present, hairs simple. *Torus* depressed ovoid. *Stamens* numerous, 2.3 mm long, extrorse; apex discoid, fleshy. *Carpels* free, numerous, 2 mm long, hairy, style absent, stigma obconical, hairy on the apex; ovule 1, basal. *Flowers* bisexual.

Type – *W. sympetala* (Merrill) Rauschert.

Distribution – 1 species in tropical Asia (North Borneo).

Notes – *Woodiellantha* (fig. 33h) is easy to recognize by its large flowers with fused petals. In this respect it closely resembles some Philippine species of *Papualthia*. *Papualthia* has several lateral ovules, whereas *Woodiellantha* has one basal ovule. *Woodiellantha* seems most related to *Enicosanthum*.

The petals in the specimen Purseglove P5316 look free; however, the inner side of the outer petals seems connate with the outer side of the inner petals (as in *Stenanona*).

Specimens examined:
W. sympetala: Fabia A 4008 (K); Purseglove P5316 (L); Ramos 1562 (B, P); Wood & Wyath-Smith A 4544 (L).

Table 17. List of character states found in the genera of the Polyalthia-group.

Taxa: E = *Enicosanthum*, F = *Fenerivia*, H = *Haplostichanthus*, P1 = *Papualthia*, P2 = *Polyalthia*, S = *Sphaerothalamus*, T = *Trivalvaria*, W = *Woodiellantha*.

	E	F	H	P1	P2	S	T	W
Flowers:								
3-merous	+	+	+	+	+	+	+	+
hairs simple	+	–	+	+	+	+	+	+
indument absent	–	+	–	–	+	–	–	–
bisexual	+	+	+	+	+	+	+	+
Sepals:								
valvate	–	?	+	+	+	?	?	?
imbricate	+?	?	–	–	+	?	?	?
connate	–,+	–	–,+	+	–,+	–	–	+
0.5–10 mm long	+	–	+	+	+	–	+	+
10–50 mm long	+	+	–	–	–	+	–	–
Petals:								
valvate	–	?	+	+	+	?	+	?
imbricate	+	?	–	+	+	?	+	?
9 in number	–	+	–	–	–	–	–	–
6 in number	+	–	+	+	+	+	+	+
connate	–	–	+	+,–	–	–	–	+
base glandular	+	–	–	–	–	–,+	–	–
2.5–12 mm long	–	–	+	+	+	–	+	–
12–95 mm long	+	+	–	+	+	+	–	+
Stamens:								
numerous	+	+	+	+	+	+	+,–	+
anthers extrorse	+	+	+	+	+	+	+	+
apex discoid	+	+	+	+	+	+	+	+
apex shiny	–	–	–	–	+,–	–	–	–
0.7–4 mm long	+	+	+	+	+	+	+	+
Carpels:								
numerous	+	+	–	+,–	+,–	+	+	+
Ovules:								
1, basal	+	+	–	–	+	–	+	+
2, basal	–	–	–	–	+	–	–	–
2–5, lateral	–	–	+	+	+	+	–	–

14. Sageraea-group (fig. 34; table 18)

Buds (broadly) (depressed) ovoid or sometimes spheroid (petals). *Sepals* valvate or not observed, (2 or) 3, free or connate, 1–6 mm long, fleshy, veins not prominent, indument present or absent, hairs simple, margins ciliate or not. *Petals* white, yellow, green, pink, red, or brown, imbricate or valvate, (4 or) 6, free, both whorls equal in length or outer whorl longer, 3.5–18 mm long, 1–2× as long as wide, 2–6 × length of sepals, fleshy, veins not or rarely prominent, indument present or absent, hairs simple, margins ciliate or not. *Torus* flat, (depressed) ovoid, or (broadly) cylindrical. *Stamens* few to numerous, sometimes imbricate, 1–1.7 mm long, extrorse or latrorse; apical prolongation almost absent or sometimes discoid, fleshy. *Carpels* free, 1 to numerous, 1–2 mm long, hairy or glabrous, style very short or absent, stigma spheroid or cylindrical; ovules 2–19, lateral, 1- or 2-seriate. *Flowers* bi- or unisexual.

Distribution – 5 genera in tropical Asia and Mexico.

Notes – This group is characterized by valvate or presumably imbricate sepals (the latter situation was not observed, but could be deduced from the shape of the sepals and the aestivation of the petals), valvate or imbricate petals (fig. 34h), and stamens with a broad truncate apex, or without or with a very small apical prolongation. The number of carpels and stamens is low (fig. 34a, b, f, i), except in the unisexual flowers of *Stelechocarpus* (fig. 34e). The carpels have few to many, lateral ovules (fig. 34b, e, f, i, j). This group is perhaps rather ill-defined, but the genera of this group do not agree with other groups, whereas they share a number of character states. So it was decided to recognize them as a group of their own.

The Sageraea-group may have affinities to *Miliusa* (Miliusa-group), which has similar stamens and carpels as *Alphonsea*. Contrary to *Miliusa*, the petals of *Alphonsea* are (sub)equal. *Tridimeris* resembles *Fitzalania* (Mitrephora-group) and *Ruizodendron* (Cremastosperma-group) in the stamens. The stamens of *Sageraea* resemble those of *Monanthotaxis* (Monanthotaxis-group) and *Neo-uvaria* (not included in a group).

Alphonsea J.D. Hooker & T. Thomson, Fl. Ind. 1 (1855) 152.

Buds (broadly) ovoid (petals). *Sepals* valvate, 3, connate, 1–3 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* cream, or yellow to green, valvate, 6, free, both whorls equal in length or outer ones slightly longer, 5–18 mm long or outer ones 11 mm long, inner ones 8 mm long, 1–2 × as long as wide, 6 × length of sepals, fleshy, veins prominent or usually not, indument present, hairs simple, often saccate at the base, inner petals basally glabrous inside. *Torus* cylindrical. *Stamens* numerous, imbricate, 1.1 mm long, extrorse; apical prolongation tongue-shaped to almost absent. *Carpels* free, 1–c. 7, 2 mm long, hairy, style absent or very short, stigma cylindrical or spheroid, small, glabrous or hairy; ovules 10–19, lateral, 2-seriate. *Flowers* bisexual.

Lectotype – *A. ventricosa* (Roxburgh) J.D. Hooker & T. Thomson.

Distribution – About 30 species in tropical Asia.

Note – The carpels of *Alphonsea* (fig. 34g) are placed on a long torus and exceed the short 'miliusoid' stamens (fig. 34f, i). *Alphonsea* in this respect, resembles *Toussaintia* and *Fissistigma*.

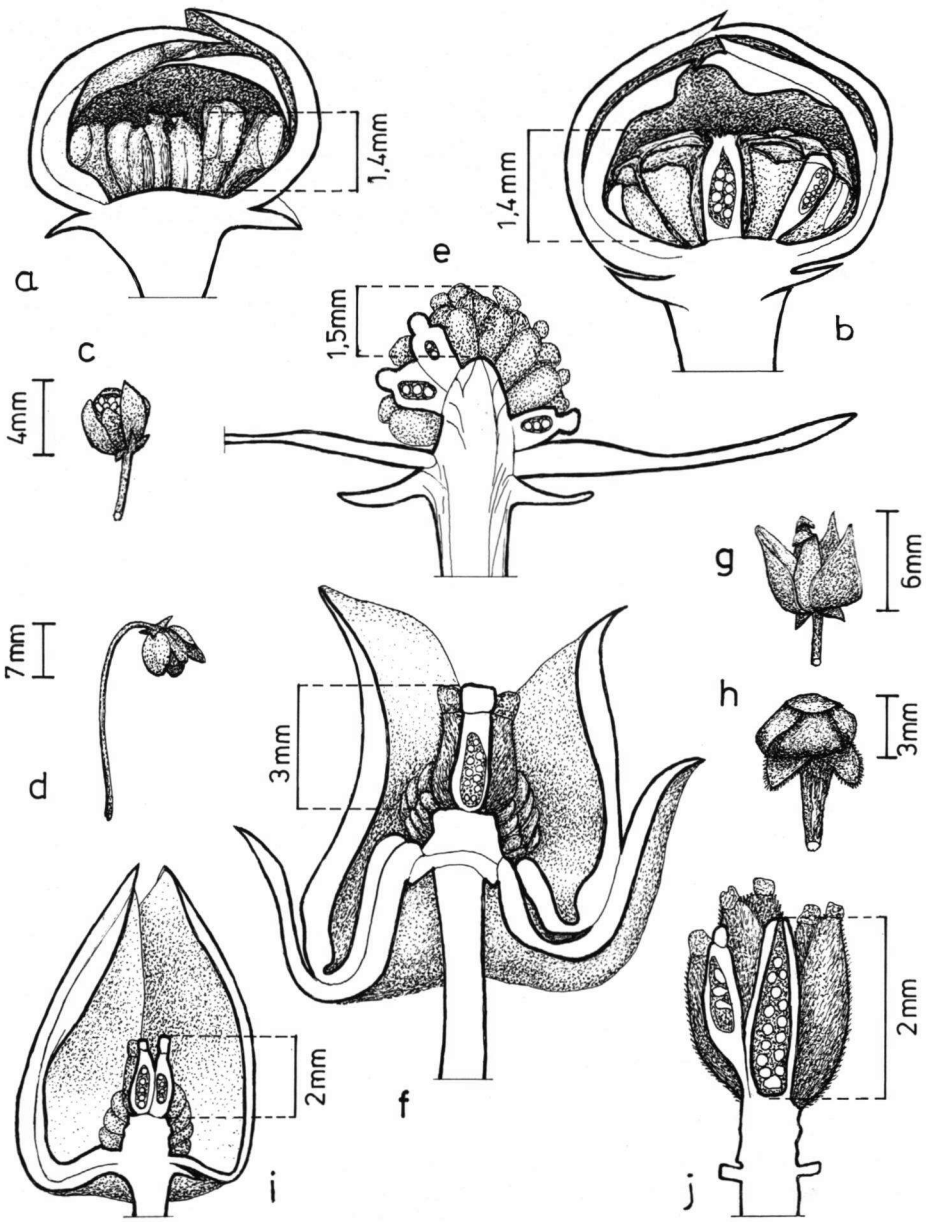


Fig. 34. Sageraea-group — a. *Sageraea lanceolata* (Wood SAN 16115): longitudinal section; b. *Sageraea glabra* (Merrill 4021): longitudinal section; c. & d. *Stelechocarpus burahol* (Lörzing 5585): flowers; e. *Stelechocarpus burahol* (U-82, Cult. Hort. Bog. s.n.): longitudinal section; f. *Alphonsea teysmannii* (Okada 3204): longitudinal-section; g. *Alphonsea sp.* (Sangkhachand 1544): flower; h. *Sageraea lanceolata* (Fraser 162A): bud; i. *Alphonsea javanica* (Kostermans 13977): longitudinal section; j. *Alphonsea javanica* (Nikil SAN 35977): longitudinal section of torus and carpels.

Specimens examined:
A. glabrifolia: Maxwell 75-507 (L). — *A. javanica:* Haviland 2105 (L); Kostermans 9907, 13977 (L); Nikil SAN 35771 (L). — *A. kinabaluensis:* Chew & Corner 4861 (K); Gibot SAN 79588 (L). — *A. lutea:* Teijsmann s.n. (L). — *A. madraspatana:* Mooney 3427 (L). — *A. maingayi:* Maingay 98 (L). — *A. sclerocarpa:* Mueller-Dombois et al. 69042607 (K). — *A. teysmannii:* Okada 3204 (U). — *A. sp.:* Sangkhachand 1544 (L).

Phoenicanthus Alston in Trimen, Handb. Fl. Ceylon 6 (1931) 6.

Buds broadly ovoid (petals). *Sepals* (aestivation not observed), 3, connate, 1 mm long, fleshy, veins not prominent, indument absent, margins ciliate. *Petals* imbricate, 6, free, both whorls equal in length, 4 mm long, 1.3 × as long as wide, 4 × length of sepals, fleshy, veins not prominent, indument absent, margins ciliate. *Torus, stamens,* and *carpels* not observed.

Type – *P. obliqua* (J.D. Hooker & T. Thomson) Alston.

Distribution – 2 species in Sri Lanka.

Note – *Phoenicanthus* is tentatively placed in this group, because the inner structures of the flowers could not be examined. The description by Huber (1985) indicates a place of the genus in this group as the most likely. According to Huber (1985) *Phoenicanthus* should have 6 or 9 stamens, 1–3 carpels, and 1 or 2 ovules.

Specimens examined:
P. coriacea: Thwaites 2612 (BM). — *P. obliqua:* CP 2703 (BHU).

Sageraea Dalzell, Hooker's J. Bot. Kew Gard. Misc. 3 (1851) 207.

Buds spheroid to depressed ovoid (petals). *Sepals* (aestivation not observed), 3, free or connate, 1–1.5 mm long, fleshy, veins not prominent, indument absent, margins ciliate. *Petals* white, imbricate, 6, free, outer whorl longer, outer ones 5–6 mm long, inner ones 3–3.5 mm long, 2 × as long as wide, 4–5 × length of sepals, fleshy, veins not prominent, indument absent, margins ciliate. *Torus* flat. *Stamens* c. 12, 1.2–1.7 mm long, extrorse or latrorse; apical prolongation absent. *Carpels* free, 2–5, 1.4 mm long, glabrous, style absent, stigma spheroid; ovules 8, lateral, 2-seriate. *Flowers* bisexual.

Type – *S. laurina* Dalzell.

Distribution – Tropical Asia, 7–9 species.

Note – *Sageraea* (fig. 34a, b, h) seems closely related to *Stelechocarpus*. In both genera the surface of the petals is warty.

Specimens examined:
S. elliptica: Mujin 33834 (L); Tarmiji 73433 (L); Rahmat si Toroes 3430 (L). — *S. glabra:* Escritor 20808 (L); Merrill 4021 (L). — *S. lanceolata:* Fraser 162A (K); Wood SAN 16115 (L).

Stelechocarpus J.D. Hooker & T. Thomson, Fl. Ind. 1 (1855) 94.

Buds broadly depressed ovoid (petals). *Sepals* (aestivation not observed), 3, free or connate, 1.5–6 mm long, fleshy, veins not prominent, indument present or absent, hairs simple, margins ciliate or not. *Petals* green, or pinkish-brown outside,

Table 18. List of character states found in the genera of the Sageraea-group.

Taxa: A = *Alphonsea*, P = *Phoenicanthus*, S1 = *Sageraea*, S2 = *Stelechocarpus*, T = *Tridimeris*.

	A	P	S1	S2	T
Flowers:					
3-merous	+	+	+	+	–
2-merous	–	–	–	–	+
ciliate margins only	–	+	+	+	+
hairs simple	+	–	–	+	+
bisexual	+	?	+	–	+
unisexual	–	?	–	+	–
Sepals:					
valvate	+	?	–	–	?
imbricate	–	?	?	?	?
connate	+	+	–,+	–,+	–,+
1–3 mm long	+	+	+	+	+
3–6 mm long	–	–	–	+	–
Petals:					
imbricate	–	+	+	+	+?
valvate	+	–	–	–	–?
inner whorl smaller	(+)	–	+	(+)	–
3.5–10 mm long	+	+	+	+	+
10–18 mm long	+	–	–	+	–
Stamens:					
numerous	+	?	–	+	+,–
anthers extrorse	+	?	+	+	+
anthers latrorse	–	?	+	–	–
apex discoid	–	?	–	+	+
apex tongue-shaped	(+)	?	–	–	+
apex not prolonged	+	?	+	+	–
1–1.7 mm long	+	?	+	+	?
Carpels:					
1–7 in number	+	?	+	–	+
numerous	–	?	–	+	–
Ovules:					
2–3, lateral, 1-seriate	–	?	–	+	?
8–20, lateral, 2-seriate	+	?	+	–	?

pink inside, imbricate, 6, free, both whorls equal in length or outer slightly longer, 5–15 mm long, 1–2 × as long as wide, 2–3 × length of sepals, fleshy, veins prominent or not, indument absent, margins ciliate or not. *Torus* (depressed) ovoid. *Stamens* numerous, 1–1.5 mm long, extrorse; apex discoid, fleshy, or apical prolongation absent. *Carpels* free, numerous, 1–1.5 mm long, hairy, style absent, stigma spheroid, bilobed, or cylindrical; ovules 2–3, lateral, 1-seriate. *Flowers* unisexual.

Type – *S. burahol* (Blume) J.D. Hooker & T. Thomson.

Distribution – Tropical Asia, 3–5 species.

Note – *Stelechocarpus* (fig. 34c, d) is most related to *Sageraea*, but differs from it in the usually larger, and unisexual flowers (fig. 34e). The stamens and carpels resemble those of *Uvariopsis*, which has unisexual flowers as well. However, the aestivation, the number of petals, and the indument are different. In *S. burahol* the petals do not always fully enclose the carpels and stamens.

Specimens examined:

S. burahol: J. & M.S. Clemens 20347 (K); U-82, Cult. Hort. Bog. s.n. (U); Iboet 402 (U); Lörzing 5585 (U). — *S. cauliflorus:* Chew W.L. 684 (L); Henderson 23802 (K); Ridley 7279 (K).

Tridimeris Baillon, Adansonia 9 (1869) 219.

Buds not observed. *Sepals* (aestivation not observed), 2, connate or free, 1.5–2 mm long, fleshy, veins not prominent, indument present or absent, hairs simple, margins ciliate. *Petals* green, imbricate?, 4, free, both whorls equal in length, 3.5–8 mm long, 1–1.2 × as long as wide, 2–5 × length of sepals, fleshy, veins not prominent, indument present or absent, hairs simple, margins ciliate or not, thin. *Torus* broadly cylindrical. *Stamens* few to numerous, 1.2 mm long, extrorse; apex tongue-shaped or discoid, fleshy. *Carpel* 1, hairy, style absent, stigma flat, lobed? (incompletely observed). *Flowers* bisexual.

Type – *T. hahniana* Baillon.

Distribution – 1 species in Mexico.

Note – *Tridimeris* closely resembles *Ruizodendron* (Cremastosperma-group) in the indument of the sepals and the almost glabrous petals, the texture of the sepals and petals, and the stamens. They differ in the length of the petals which are very long in *Ruizodendron* and the number of ovules, many in *Tridimeris* (Fries, 1959), one in *Ruizodendron*, as can be deduced from the number of seeds in fruit.

Specimens examined:

T. hahniana: Hahn s.n. (P); Schatz et al. 1198 (U).

15. Sapranthus-group (fig. 35; table 19)

Buds ovoid (sepals) or apert? *Sepals* valvate or apert?, 3 or 4, free or connate, 1–13 mm long, fleshy, sometimes thin, veins prominent or not, indument present, hairs simple. *Petals* reddish, purplish, blackish, pinkish, greenish, yellowish, or creamy, apert? to valvate, or imbricate, 6 or 8, free or sometimes inner ones fused with the outer ones, both whorls equal in length or one whorl shorter, 7–110 mm long, 0.7–13 × as long as wide, 3–15 × length of sepals, almost membranous to

fleshy, veins prominent or not, indument present, hairs simple, inner petals often basally glandular inside. *Torus* cushion-shaped to broadly cylindrical, or depressed ovoid, sometimes with a slightly concave apex. *Stamens* numerous, 0.8–2.4 mm long, extrorse; apex discoid or sometimes tongue-shaped, fleshy, rarely hairy. *Carpels* free, few to numerous, 1–4.5 mm long, hairy, style absent or present, short, stigma shallowly or narrowly obconical, obovoid, broadly ovoid, ellipsoid, spheroid, or discoid; ovules 2–14, lateral, 1- or 2-seriate. *Flowers* bisexual.

Distribution – 4 genera in Mexico and Central America, and some in adjacent Colombia.

Notes – This group is characterized by usually long petals (fig. 35c, d, e, f, g), often with a distinct longitudinal venation (fig. 35d). The flowers open when they are still immature. These genera have a moderate number of stamens and carpels (fig. 35a, b, h, k), and several to many, lateral ovules.

Although the genera are usually easy to distinguish, some species represent intermediate forms.

The Sapranthus-group seems to have affinities to several other groups or genera. Genera with long, narrow petals, like *Ancana* (Meiogyne-group), *Piptostigma* (not included in a group), *Polyalthia* (Polyalthia-group), and *Ruizodendron* (Cremastosperma-group), remind of the flowers of the Sapranthus-group. The stamens of *Stenanona* remind of those of *Bocageopsis, Onychopetalum* (both Unonopsis-group), and *Oxandra* (Cremastosperma-group).

Desmopsis Safford, Bull. Torrey Bot. Club 43 (1916) 184.

Buds not observed, apert? *Sepals* apert?, 3, free or connate, 1–4 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* creamy to yellow to green or pinkish, apert?, 6, free, both whorls equal in length, 7–60 mm long, 0.7–13 × as long as wide, 7–15 × length of sepals, fleshy, the veins prominent or not, indument present, hairs simple. *Torus* broadly cylindrical with a slightly concave apex, sometimes with a depressed ovoid apicule. *Stamens* numerous, 1–2 mm long, extrorse; the apex discoid, fleshy. *Carpels* free, 5–15, 1–1.5 mm long, hairy, style absent, stigma shallowly obconical; ovules 2, lateral, 1-seriate. *Flowers* bisexual.

Type – *D. panamensis* (B.L. Robinson) Safford.

Distribution – 16 species ranging from Mexico to Panama, and adjacent Colombia.

Notes – *Desmopsis* (fig. 35a, b, e) is diverse in its flowers, and includes some species which seem intermediate between *Desmopsis* and the other genera of the Sapranthus-group. *Desmopsis* may be closely related to *Ephedranthus* as in both genera similar stamens are found.

One undescribed species from Mexico, of which the status is still uncertain and which possibly belongs to *Desmopsis*, shows features of *Desmopsis, Guamia* (Meiogyne-group), *Haplostichanthus* (Polyalthia-group), *Pseudoxandra* (Cremastosperma-group), and *Unonopsis* (Unonopsis-group). It differs from the other species of *Desmopsis* by the buds with reduplicate-valvate sepals and more or less valvate petals.

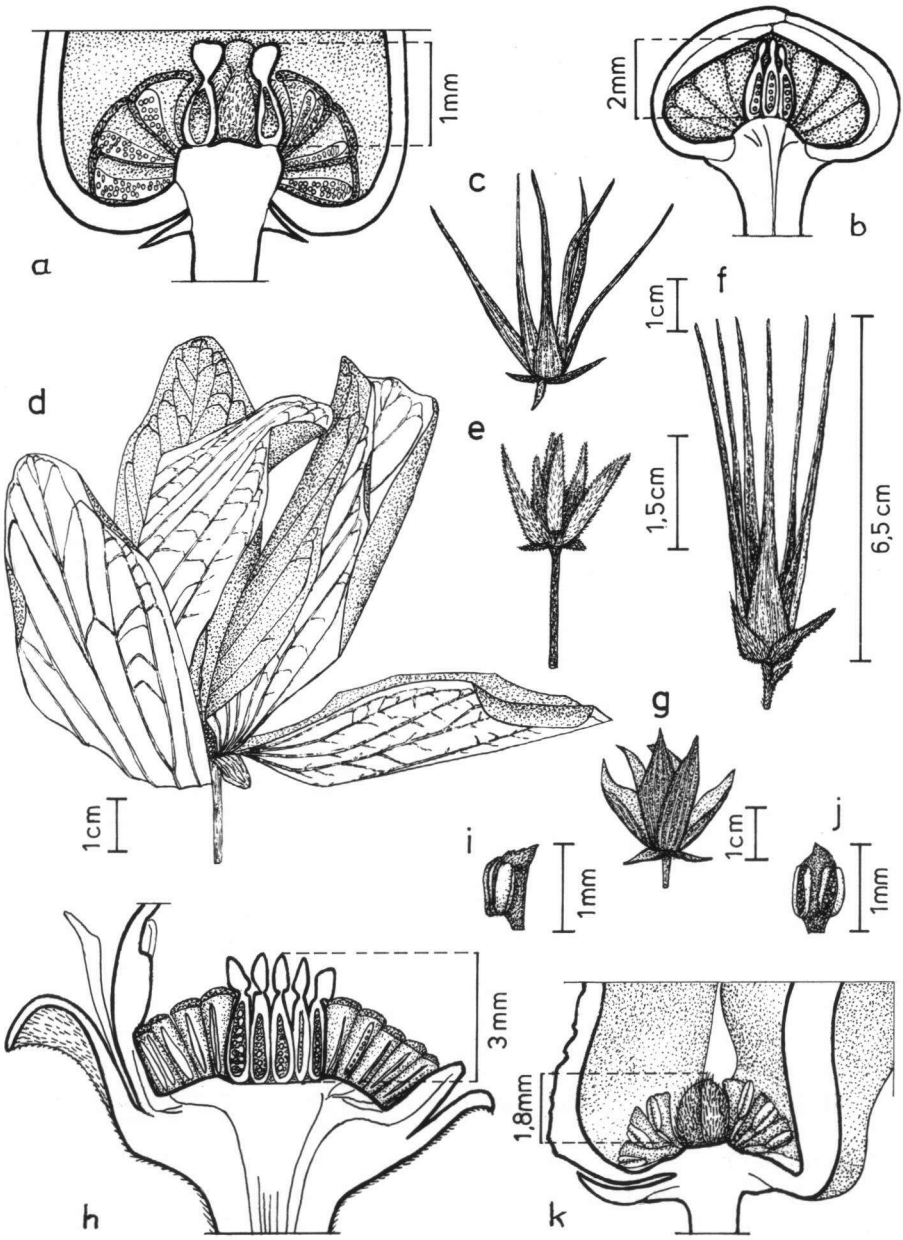


Fig. 35. Sapranthus-group — a. *Desmopsis mexicana* (Hinton 15823): longitudinal section; b. *Desmopsis? sp. nov.* (van Rooden 770): longitudinal section; c. *Stenanona costaricensis* (Wilbur & Stone 10215): flower; d. *Sapranthus longepedunculatus* (Hinton 9182): flower; e. *Desmopsis sp.* (van der Werff & Herrera 7085): flower; f. *Stenanona panamensis* (Grayum 4504): flower; g. *Sapranthus microcarpus* (Standley 21622): flower; h. *Sapranthus palanga* (van Rooden 868): longitudinal section; i., j. & k. *Stenanona costaricensis* (Wilbur & Stone 10215): stamens (i & j) and longitudinal section (k).

Specimens examined:
D. bibracteata: Calderón 314 (GH); Jiménez 416 (US); Opler 1704 (MEX); Pittier 3367 (GH, NY), 5747 (US); C. Wright s.n. (US). — *D. brevipes:* Croat 244 (MO); Standley & Valerio 44576 (US), 45176 (US), 46641 (US); Warscewicz 226 (B); von Wedel 694 (GH, S, US). — *D. erythrocarpa:* Contreras 5912 (DUKE, MO), 5976 (DUKE), 7808 (US), 8973 (DUKE, US), 10186 (DUKE). — *D. galeottiana:* Calzada 773 (F). — *D. heteropetala:* Pittier & Durand 7967 (BR). — *D. lanceolata:* Matuda 2299 (F), 6145 (MICH). — *D. maxonii:* Busey 650 (U); Maxon 5564 (US); Pittier 3154 (US); Standley 36774 (US), 36834 (US). — *D. mexicana:* Hinton 15823 (MICH, MO, UC, US, W), 15836 (MICH, UC, US). — *D. stenopetala:* Contreras 6729 (DUKE); Schipp 698 (F, GH, MO, NY, S, Z); von Türckheim 8496 (F, GH), 11868 (B). — *D. sp.:* van der Werff & Herrera 7085 (U). — *D.? sp. nov.:* van Rooden 769, 770 (U); Schatz & Ibarra 1127 (U).

Reedrollinsia J.W. Walker, Rhodora 73 (795) (1971) 461.

Buds not observed. *Sepals* (aestivation not observed), 4, connate, 7 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* reddish, (aestivation not observed), 8, free, outer whorl longer, outer ones 85 mm long, inner ones 65 mm long, 22 × as long as wide, 12 × length of sepals, fleshy, veins prominent, indument present, hairs simple. *Torus* not observed. *Stamens* numerous, 2–2.4 mm long, extrorse; apex discoid, glabrous or fleshy. *Carpels* numerous (incompletely observed). *Flowers* bisexual.

Type – *R. cauliflora* J.W. Walker.

Distribution – 1 species in Mexico.

Note – *Reedrollinsia* differs from the other genera of this group in the number of sepals and petals (4 and 8 respectively), and its connate sepals. Its long petals are not as narrow as those of *Stenanona*. Also the number of stamens and carpels is much higher than in the other genera of the Sapranthus-group.

Specimen examined:
R. cauliflora: Walker 357 (U).

Sapranthus B.C. Seemann, J. Bot. 4 (1866) 369.

Buds ovoid (sepals). *Sepals* valvate, 3, free or connate, 6–11 mm long, fleshy, thin, veins prominent, indument present, hairs simple. *Petals* dark purple, almost black, maroon, purple-brown, reddish, pink, or greenish to yellow, imbricate, 6, free, both whorls equal in length or inner ones longer, 18–110 mm long, 2–5 × as long as wide, 3–10 × length of sepals, fleshy, thin, veins prominent, indument present, hairs simple, inner petals basally glandular inside. *Torus* broadly cylindrical to cushion-shaped or depressed ovoid with a slightly concave apex. *Stamens* numerous, 1.1–2 mm long, extrorse; apex discoid, fleshy, sometimes hairy or with glandular dots. *Carpels* free, few to numerous, 1.3–4.5 mm long, hairy, style absent or very short, stigma obovoid, broadly ovoid, or narrowly obconical, sometimes with hairs; ovules 3–14, lateral, 1- or 2-seriate. *Flowers* bisexual.

Type – *S. nicaraguensis* B.C. Seemann.

Distribution – About 8 species ranging from Mexico to Panama.

Note – *Sapranthus* has two flower types: one with large, purplish to brownish flowers, with many, 2-seriate ovules (fig. 35d), and one with much smaller (fig. 35g), usually greenish flowers and few ovules. The purplish flowers are often bad-smelling.

Specimens examined:

S. borealis: Narvaez Montes & Salazar 856 (US); Ortega 856 (MEX). — *S. campechianus:* Bartlett 12298 (A, MICH, NY, S, US); Croat 23556 (DUKE, GH, MO). — *S. foetidus:* Jones s.n. (PMA); Palmer 394 (A, F, UC, US). — *S. ligularis:* Calderón 325 (MO, NY, US); Heyde & Lux 4508 (GH, S, US). — *S. longepedunculatus:* Hinton 9182 (MICH, NY, U), 10318 (F, GH, MO, NY, US, W), 10344 (F, MO, S, W). — *S. microcarpus:* Calderón 2239 (US); Edwards 332 (A, F, UC, US); Garcia 46 (UC); Garcia Sálas 1414 (F); Reko 3111 (US); Standley 21223 (GH, US), 21622 (US), 21817 (GH, US), 22268 (GH, NY, US). — *S. nicaraguensis:* Calderón 422 (GH), 1471 (GH, US); Iltis G63 (WIS); Molina R. 105 (F, GH, MEX, US), 8637 (F, NY); van Rooden 200 (U): Shannon 5041 (GH, NY, US); C.L. Smith 111 (MO, NY); L.O. Williams & Molina R. 16766 (F). — *S. palanga:* Etienne s.n. (UC); Frankie 86a, c (F, MO); Greenman 5807 (MO); van Rooden 868 (U).

Table 19. List of character states found in the genera of the Sapranthus-group.

	Desmopsis	*Reedrollinsia*	*Sapranthus*	*Stenanona*
Flowers:				
perianth 4-merous	–	+	–	–
perianth 3-merous	+	–	+	+
hairs simple	+	+	+	+
bisexual	+	+	+	+
Sepals:				
valvate	?	?	+	+
connate	–,+	+	–,+	–
veins prominent	–	–	+	+
1–5 mm long	+	–	–	+
5–13 mm long	–	+	+	+
Petals:				
imbricate	?	?	+	?
valvate	?	?	?	?
connate	–	–	–	+
base glandular	–	–	+	+
veins prominent	+,–	+	+	+,–
7–110 mm long	+	+	+	+
Stamens:				
numerous	+	+	+	+,–
anthers extrorse	+	+	+	+
apex tongue-shaped	–	–	–	+
apex discoid	+	+	+	–
0.8–2.5 mm long	+	+	+	+
Carpels:				
2-numerous	+	+	+	+
Ovules:				
2–5, 1-seriate	+	?	+	–
> 5, 2-seriate	–	?	+	+

Stenanona Standley, Publ. Field Columbian Mus., Bot. ser. 4 (8) (1929) 205.

Buds ovoid (sepals). *Sepals* valvate, 3, free, 1.2–13 mm long, fleshy, thin, veins prominent, indument present, hairs simple. *Petals* (dark) red or rose-pink, apert?, 6, connate (inner with outer), both whorls equal in length, 12–41 mm long, 5–10 × as long as wide, 3–10 × length of sepals, fleshy, thin, veins prominent or not, indument present, hairs simple, inner petals basally glandular inside. *Torus* depressed ovoid, cylindrical, or cushion-shaped. *Stamens* few to numerous, 0.8–1.8 mm long, extrorse; apex tongue-shaped, sometimes those of inner ones elongate, fleshy. *Carpels* free, 2–12, 1.5–1.7 mm long, hairy, style absent, stigma discoid to flat and lobed, or very broadly obovoid; ovules 7, lateral, 1- or 2-seriate. *Flowers* bisexual.

Type – *S. panamensis* Standley.

Distribution – 2 species in Panama and Costa Rica.

Note – *Stenanona* is recognizable by its long and narrowly elongate petals (fig. 35c, f). The stamens differ from those of the other genera of the Sapranthus-group: the apices are tongue-shaped (fig. 35i, j) in *Stenanona*, and discoid in the other genera. The texture of the petals reminds of that of *Reedrollinsia*.

Specimens examined:

S. costaricensis: Kupper 569 (M, S); Miller & Sandino 1152 (U); Wilbur & Stone 10698 (DUKE, F), 10215 (DUKE, GH, NY, US). — *S. panamensis:* Cooper 427 (B, F, FHO, GH); Grayum 4504 (U); Schatz & Graham 1110 (U).

16. Unonopsis-group (fig. 36; table 20)

Buds (very) broadly to broadly depressed ovoid to spheroid or to ellipsoid (petals). *Sepals* valvate (rarely imbricate), 3, free or connate, 1–4 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* whitish to yellowish or greenish, valvate or slightly imbricate, 6, free, both whorls equal in length or outer ones slightly longer, 1.5–10 mm long, 0.5–2 × as long as wide, 2–10 × length of sepals, fleshy, veins not prominent, indument present, hairs simple. *Torus* broadly ovoid, ovoid with a concave apex, cylindrical, cushion-shaped, or sometimes flat. *Stamens* numerous to few, 0.6–5.4 mm long, extrorse; apex discoid or tongue-shaped, fleshy. *Carpels* free, 1 to numerous, 1.3–3.5 mm long, hairy or glabrous, style absent, stigma (narrowly) ellipsoid, broadly ovoid, cylindrical, shallowly obconical, or discoid to lobed; ovules 1–6, lateral or sometimes basal, 1-seriate. *Flowers* bisexual.

Distribution – 3 genera in tropical America.

Notes – The Unonopsis-group is characterized by small, usually whitish flowers, usually valvate sepals and petals (fig. 36d), and usually with few, lateral ovules (fig. 36a, c, e).

Bocageopsis and *Onychopetalum* cannot be maintained as distinct genera on the basis of their flowers as many intermediate specimens were found.

The flowers of the Unonopsis-group resemble in general appearance more or less those of the Cremastosperma-group. The latter, however, have imbricate sepals and petals and one ovule. Walker (1971a) found a similar pollen type in the Cremasto-

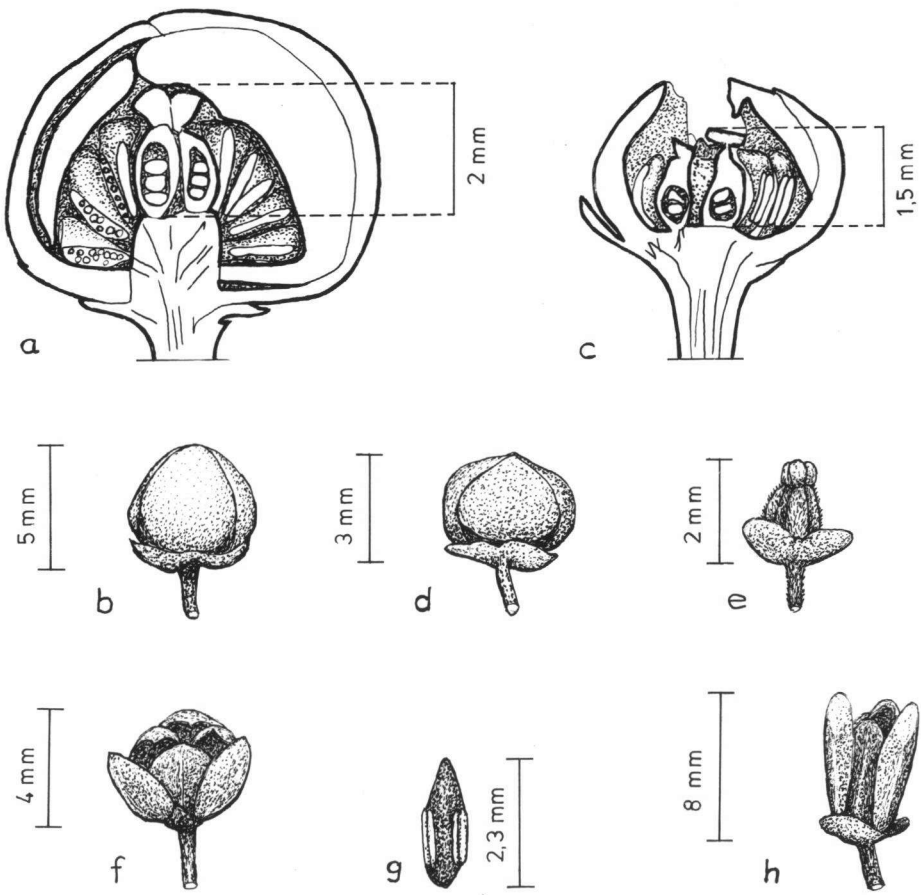


Fig. 36. Unonopsis-group — a. *Unonopsis sp.* (Maas 2789): longitudinal section; b. *Unonopsis floribunda* (Krukoff 4806): bud; c. *Bocageopsis multiflora* (Berg et al. P18612): longitudinal section; d., e. & f. *Bocageopsis multiflora* (Breteler 4780): bud (d), flower after anthesis (e), and flower (f); g. *Bocageopsis sp.* (Morawetz 32-7983): stamen; h. *Onychopetalum lanceolatum* (Maguire et al. 56665): flower.

sperma-group and the Unonopsis-group. The stamens of *Bocageopsis* (fig. 36g) and *Onychopetalum* resemble those of *Oxandra* (Cremastosperma-group), *Stenanona* (Sapranthus-group), and *Greenwayodendron* (not included in a group).

Bocageopsis R.E. Fries, Acta Horti Berg. 10 (2) (1931) 143.

Buds spheroid to very broadly ovoid (petals). *Sepals* valvate, 3, free or connate, 1 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* creamy or whitish(-green), valvate (or slightly imbricate), 6, free, both whorls equal

in length or outer ones slightly longer, 1.5–5 mm long or outer ones 4 mm long and inner ones 2.5–3 mm long, 0.5–1 × as long as wide, 2–5 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, sometimes apex inwards cuspidate. *Torus* broadly cylindrical to cushion-shaped. *Stamens* few (9 or more), 1–3 mm long, extrorse; apex long-acute, fleshy. *Carpels* free, 2–7, 1.3–1.5 mm long, hairy, style absent, stigma (narrowly) ellipsoid or discoid to lobed, glabrous; ovules 2–6, lateral, 1-seriate. *Flowers* bisexual.

Lectotype – *B. multiflora* (Martius) R.E. Fries.

Distribution – 3 species in South America.

Note – *Bocageopsis* (fig. 36d, f) has tiny, globose flowers.

Specimens examined:

B. canescens: Prance 5049; Prance et al. 5929 (U). — *B. mattogrossensis:* Dziewa 18 (U). — *B. multiflora:* Berg et al. P18612 (U); Breteler 4780 (WAG); Cid et al. 705 (U); Nelson 408 (U); Prance et al. 5791, 5827 (U); Solomon 6368 (U). — *B. sp.:* Morawetz 32-7983 (U).

Onychopetalum R.E. Fries, Acta Horti Berg. 10 (2) (1931) 148, f. 3.

Buds broadly ovoid to ellipsoid (petals). *Sepals* valvate or more or less imbricate, 3, connate, 1 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* white, valvate (or slightly imbricate), 6, free, both whorls equal in length, 4–7 mm long, 2 × as long as wide, 4–6 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, often apex inwards cuspidate. *Torus* very broadly ovoid, sometimes with a concave apex, cushion-shaped, or flat. *Stamens* up to 16, 2–5.4 mm long, extrorse; apex long-acute, fleshy. *Carpels* free, 1–2, 1.3–2.8 mm long, glabrous or hairs only along the edges, style absent, stigma cylindrical or ellipsoid; ovules 3–4, lateral, 1-seriate. *Flowers* bisexual.

Type – *O. amazonicum* R.E. Fries.

Distribution – 4 species in Amazonian Brazil and Bolivia.

Note – The flowers of *Onychopetalum* (fig. 36h) have longer and narrower petals than those of *Bocageopsis*, but the differences between the two genera are only gradual.

Specimens examined:

O. amazonicum: Fróes 32206 (S). — *O. krukoffii:* Krukoff 5326 (U). — *O. lanceolatum:* Maguire et al. 56665 (K, U). — *O. lucidum:* Krukoff 8214 (BR, U). — *O. sp.:* Prance et al. 5791 (U).

Unonopsis R.E. Fries, Kongl. Svenska Vetenskapsakad. Handl. 34 (5) (1900) 26, t. IV, 3–8.

Buds spheroid to broadly depressed ovoid (petals). *Sepals* valvate, 3, connate, 1–4 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* white, pale green or yellow, valvate, 6, free, both whorls more or less equal in length, 4–10 mm long, 1.5 × as long as wide, 4–5 × length of sepals, fleshy, veins not prominent, indument present, hairs simple. *Torus* broadly ovoid or cylindrical. *Stamens* numerous, 0.6–2.2 mm long, extrorse; apex discoid, fleshy. *Carpels* free, 4 to numerous, 1.8–3.5 mm long, completely hairy or ciliate, style absent, stigma

broadly ovoid or shallowly obconical, glabrous; ovules 1–5, lateral or sometimes basal, 1-seriate. *Flowers* bisexual.

Lectotype – *U. angustifolia* (Bentham) R.E. Fries.

Distribution – 27 species in Central and South America and the Antilles.

Note – *Unonopsis* (fig. 36a, b) resembles *Bocageopsis* and *Onychopetalum* in its flowers, but differs from the two genera in the discoid apices of the stamens. The flowers of *Unonopsis* are usually larger than those of the other two genera.

Specimens examined:

U. angustifolia: Spruce 2567 (BR). — *U. buchtienii:* Schultes & Cabrera 13795 (U). — *U. floribunda:* Krukoff 4806 (U), 8621 (U), 8989 (BR). — *U. glaucopetala:* Breteler 3799 (P); Sandwith 355 (U). — *U. grandis:* Spruce 3163 (BR). — *U. lindmanii:* Glaziou 20638 (BR); Regnell III-248 (BR). — *U. mathewsii:* Plowman & Kennedy 5810 (U). — *U. perrottetii:* Fanshawe 2164 (U). — *U. pittieri:* Burger et al. 10618 (U). — *U. williamsii:* Chagas 3570 (U). — *U. sp.:* Davidson & Jones 9869 (U); Maas et al. 2789 (U); Vásquez et al. 6975 (U).

Table 20. List of character states found in the genera of the Unonopsis-group.

	Bocageopsis	*Onychopetalum*	*Unonopsis*
Flowers:			
perianth 3-merous	+	+	+
hairs simple	+	+	+
bisexual	+	+	+
Sepals:			
valvate	+	+	+
imbricate	–	(+)	–
connate	+,–	+	+
1–4 mm long	+	+	+
Petals:			
valvate	+	+	+
imbricate	(+)	(+)	–
< 4 mm long	+	–	–
4–10 mm long	+	+	+
Stamens:			
< 16 in number	+	+	–
numerous	–	–	+
anthers extrorse	+	+	+
apex long-acute	+	+	–
apex discoid	–	–	+
< 2.5 mm long	+	+	+
2.5–5.5 mm long	+	+	–
Carpels:			
1–7 in number	+	+	+
numerous	–	–	+
Ovules:			
1, basal	–	–	+
1–6, lateral, 1-seriate	+	+	+

17. Uvaria-group (figs. 37, 38; table 21)

Buds spheroid to very broadly ovoid (sepals or petals); sepals sometimes entirely fused, often with an apiculate apex. *Sepals* valvate, reduplicate-valvate, or sometimes imbricate, (2 or) 3, free or connate, 2–25 mm long, fleshy, veins rarely prominent, indument present or rarely absent, hairs stellate (rarely simple). *Petals* reddish, brownish, yellowish, greenish, or creamy, imbricate (rarely valvate), (4 or) 6, free or connate, both whorls equal in length or inner slightly shorter or longer, 3–45 mm long, 1–2 × as long as wide, 1.5–5 × length of the sepals, fleshy, rarely almost membranous, veins usually not prominent, indument present, hairs stellate, inner petals often basally glabrous inside, sometimes with 2 marginal glands. *Torus* shallowly conical with a flat apex, broadly cylindrical, depressed ovoid, flat, sometimes with a slightly concave apex, or cushion-shaped. *Stamens* numerous, 0.6–7 mm long, extrorse or latrorse, staminodes sometimes present (outer stamens); apex discoid to tongue-shaped, glabrous, usually fleshy. *Carpels* free, numerous (rarely few), 1.2–5 mm long, hairy (usually stellate), style absent, stigma (shallowly) obconical, (narrowly) cylindrical, broadly obovoid, or sometimes ellipsoid, glabrous or hairy; ovules 1–16, lateral, 1- or 2-seriate. *Flowers* bisexual or rarely unisexual.

Distribution – 8 genera in tropical Asia, New Guinea, New Caledonia, Australia, Africa, and Madagascar.

Notes – This predominantly Asiatic group is characterized by valvate sepals (fig. 37i), imbricate petals, stellate indument, many stamens, many narrow carpels (fig. 37b, h), and laterally attached ovules (fig. 38a, b, c, e). The stamens are often latrorse and the apices tongue-shaped (fig. 38b, e). The torus is often shallowly conical with a flat apex (fig. 38a, b).

Several genera of this group seem closely related to *Uvaria*, and it is not certain whether all these genera should be maintained as distinct from *Uvaria*, especially *Anomianthus, Ellipeia, Ellipeiopsis,* and *Rauwenhoffia. Tetrapetalum* closely resembles some species of *Cyathostemma*, only differing in the number of sepals and petals.

The Uvaria-group has possibly affinities to the Uvariastrum-group, which it resembles in the carpels with numerous ovules, but the genera of the latter group have valvate petals and most of them have simple hairs. The Uvaria-group has some features in common with the Duguetia-group (valvate sepals and imbricate petals of similar size, stellate indument); however, in the Duguetia-group the carpels have one, basal ovule. *Rauwenhoffia* reminds of *Fissistigma* and *Sphaerocoryne* (both Friesodielsia-group) in general appearance of the flowers.

Anomianthus Zollinger, Linnaea 29 (1858) 324.

Buds (very) broadly ovoid (sepals). *Sepals* valvate, 3, free, 2.5–4 mm long, fleshy, veins not prominent, indument present, hairs stellate. *Petals* whitish to (brownish- or reddish-)yellow, imbricate (rarely valvate), 6, free or connate, both whorls equal in length, 11–25 mm long, 1–3 × as long as wide, 3–9 × length of sepals, fleshy, veins prominent or not, indument present, hairs stellate; inner petals basally glabrous inside, and with 2 marginal glands. *Torus* broadly cylindrical with a slightly concave apex and a depressed ovoid apicule. *Stamens* numerous, 1.3–2.3

mm long, extrorse or latrorse; apex tongue-shaped, glabrous, fleshy or not. *Carpels* free, numerous, 2–3.5 mm long, densely hairy or ciliate, style absent, stigma obconical, hairy; ovules (at least) 3–4, lateral, 1-seriate. *Flowers* bisexual.

Lectotype – *A. heterocarpus* (Blume) Zollinger = *A. dulcis* (Dunal) Sinclair.

Distribution – 1 species in tropical Asia (Thailand, Indochina, and Java).

Note – *Anomianthus* differs from *Uvaria* because of its 2 marginal glands on the inner petals, and the narrower petals.

Specimens examined:
A. dulcis: Docters van Leeuwen 364a (L); Hochreutiner 2516 (L); Pierre 385 (U); Poilane 3193, 6828, 8141, 22654, 32376 (P); Sukkri 15 (L).

Balonga A. Le Thomas, Adansonia sér. 2, 8 (1968) 106.

Buds not observed. *Sepals* (aestivation not observed), 3, free, 5–6 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* (aestivation not observed), 6, free, inner whorl slightly longer, outer ones 12–14 mm long, inner ones 15 mm long, 1.5 × as long as wide, 3 × length of sepals, fleshy, veins not prominent, indument present, hairs stellate. *Torus* broadly cylindrical, apex depressed ovoid with a broad margin. *Stamens* numerous, 1.2 mm long, extrorse; apex discoid, fleshy. *Carpels* free, numerous, densely hairy (incompletely observed). *Flowers* bisexual.

Type – *B. buchholzii* (Engler & Diels) Le Thomas.

Distribution – 1 species in West equatorial Africa (Cameroon and Gabon).

Note – *Balonga* was separated from *Uvaria* by Le Thomas (1968) because it has imbricate sepals, an elongate torus, and a low number of ovules per carpel (1 or 2), whereas the monocarps in fruit are laterally attached. This was reason for her to place the genus near *Ruizodendron*. In its flowers, however, *Balonga* seems closer to *Uvaria*. The elongate torus of *Balonga*, though, is aberrant in the Uvaria-group.

Specimen examined:
B. buchholzii: Zenker 4926 (BM, P).

Cyathostemma W. Griffith, Notul. Pl. Asiat. 4 (1854) 707, t. 650.

Buds very broadly ovoid to spheroid (sepals and/or petals). *Sepals* valvate or imbricate, 3, free or connate, 2–3 mm long, fleshy, veins not prominent, indument present or absent, hairs stellate or rarely simple. *Petals* brownish or (yellowish-) green, imbricate or valvate, 6, free or connate, both whorls equal in length, 3–7 mm long, 1–2 × as long as wide, 2 × length of sepals, fleshy, veins not prominent, indument present, hairs stellate or rarely simple, inner petals basally glabrous inside. *Torus* shallowly conical with a flat apex or flat with slightly concave apex. *Stamens* numerous, 0.6–2 mm long, latrorse to more or less introrse or extrorse; apex tongue-shaped or discoid, fleshy, (sometimes) with minute indument. *Carpels* free, numerous, 1.2 mm long, hairy, slightly stipitate, style absent, stigma ellipsoid, glabrous; ovules 4–8, lateral, 1- or 2-seriate. *Flowers* bisexual, rarely unisexual (and plants androdioecious?).

Type – *C. viridiflorum* W. Griffith.

Distribution – 10 species in tropical Asia (Thailand, Malaysia, Borneo, and Sumatra).

Note – *Cyathostemma* (fig. 37c, f) can be recognized by its small, open flowers: the petals do not fully enclose the stamens and carpels, but do not expand either.

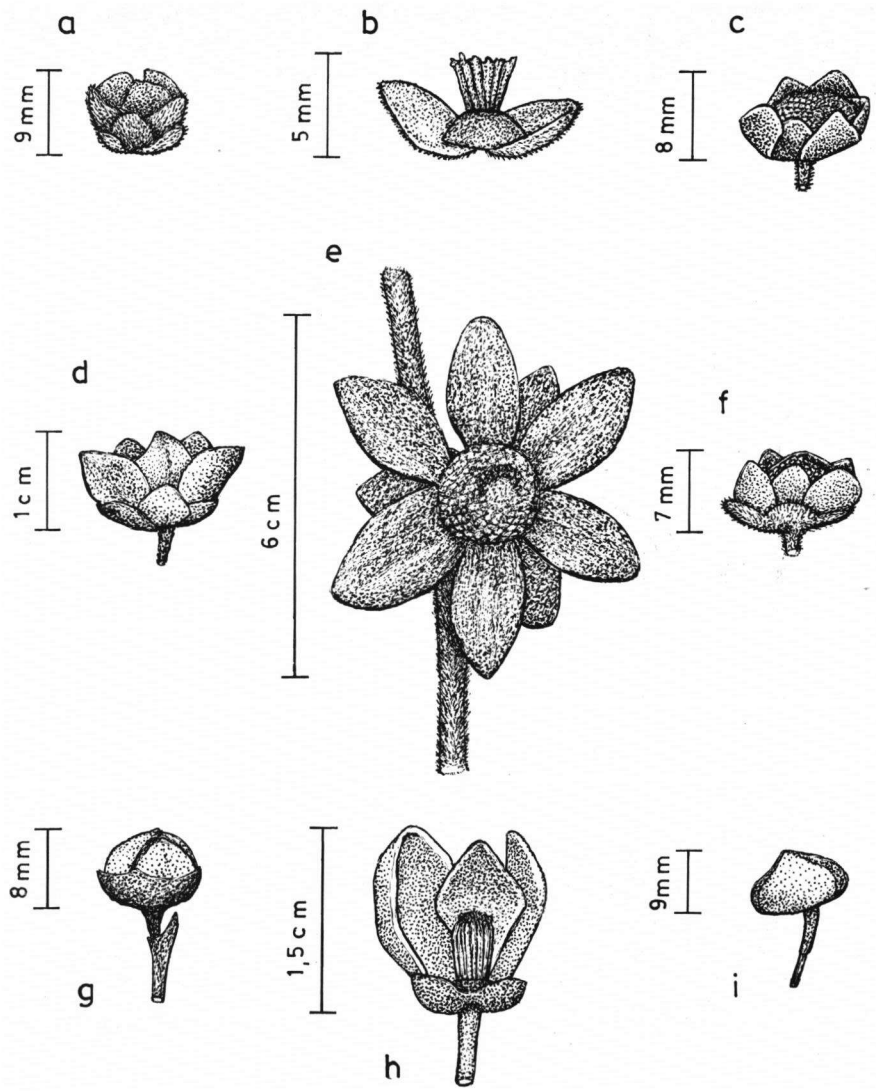


Fig. 37. Uvaria-group — a. & b. *Tetrapetalum volubile* (Ashton BRUN 606): flower (a) and flower after anthesis (b); c. *Cyathostemma nitidum* (Korthals s.n.): flower; d. *Rauwenhoffia siamensis* (Cult. Hort. Bog. XI-A-30): flower; e. *Uvaria grandiflora* (Champion s.n.): flower; f. *Cyathostemma excelsum* (Purseglove 4965): flower; g. *Uvaria* cf. *macrophylla* (Mauriasi et al. BSIP 8692): bud; h. *Rauwenhoffia leichhardtii* (Brass 7681): flower after anthesis, 3 petals left; i. *Uvaria sympetala* (Brass 8241): bud.

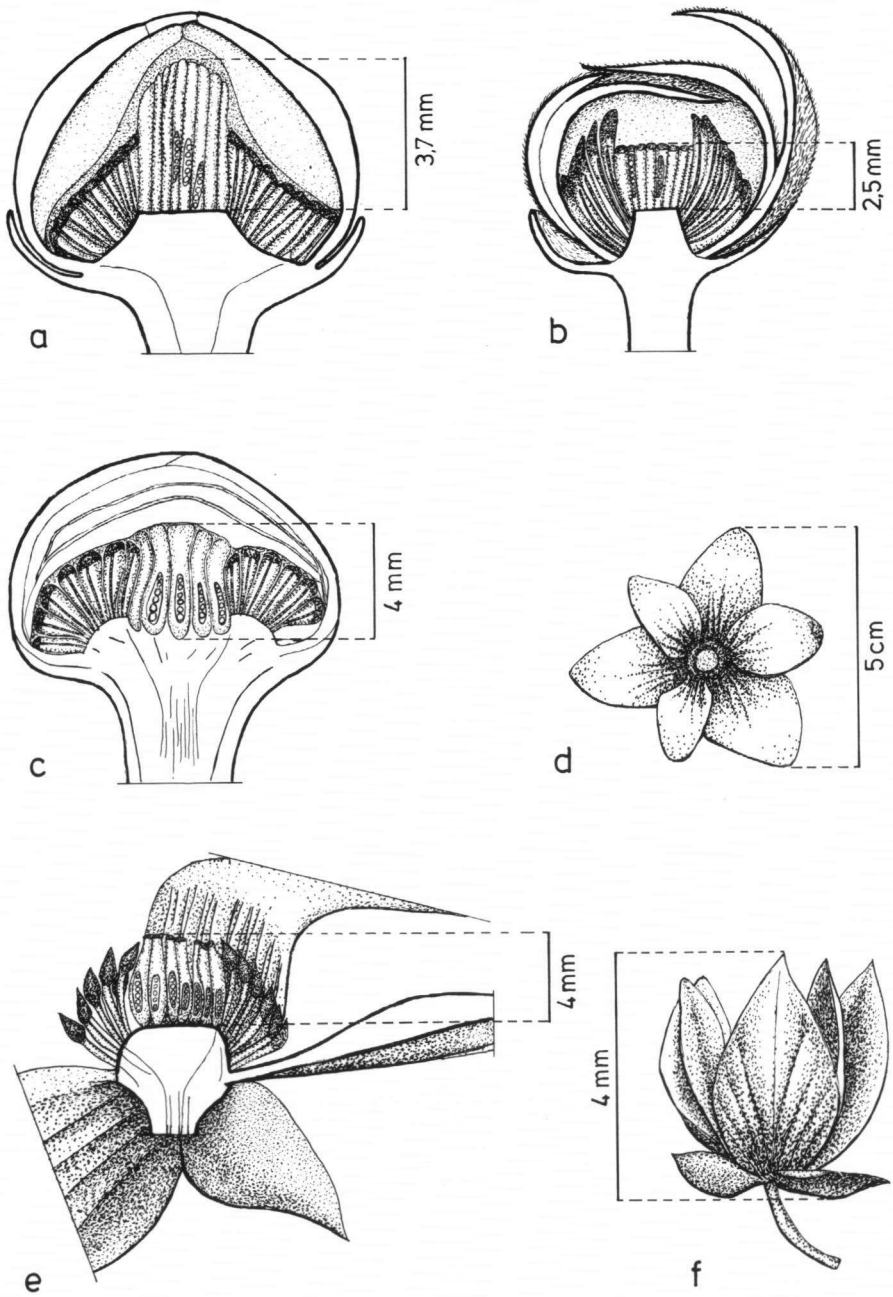


Fig. 38. Uvaria-group — a. *Rauwenhoffia leichhardtii* (Brass 7584): longitudinal section; b. *Uvaria littoralis* (Cult. Hort. Bog. XVI-E-3): longitudinal section; c. *Uvaria obanensis* (Bos 5555): longitudinal section; d. & e. *Uvaria* cf. *afzelii* (Cult. Hort. Wag. 432): flower (d) and longitudinal section (e); f. *Uvaria scabrida* (Bos 3353): flower.

Specimens examined:

C. argenteum: Kadim & Noor 551 (L). — *C. excelsum:* Ashton BRUN 5167 (L); Elmer 21081 (L); Endert 1551 (L); King 6210 (L); Kostermans 4733 (L); Purseglove 4965 (L). — *C. hookeri:* Haviland 2250 (BM); Othman Ismawi S37445 (L); Scortechini s.n. (L); van Steenis 1106 (B). — *C. micranthum:* Brass 8557 (L); Carr 11088 (L); Maxwell 75-396 (L). — *C. nitidum:* Korthals s.n. (L). — *C. viridiflorum:* Sinclair 39246 (L).

Ellipeia J.D. Hooker & T. Thomson, Fl. Ind. 1 (1855) 104.

Buds very broadly ovoid (petals). *Sepals* valvate, 3, free or connate, 3–5 mm long, fleshy, veins not prominent, indument present, hairs stellate. *Petals* yellowish, imbricate, 6, free, outer whorl longer, outer ones 9–19 mm long, inner ones 6 mm long, 1.3 × as long as wide, 3–4 × length of sepals, fleshy, veins not prominent, indument present, hairs stellate, inner petals basally glabrous inside. *Torus* broadly cylindrical or depressed ovoid. *Stamens* numerous, 1.4–1.9 mm long, extrorse or latrorse; apex discoid or depressed ovoid, glabrous, sometimes fleshy. *Carpels* free, numerous, 1.8–2.5 mm long, hairy, style absent, stigma obovoid, glabrous; ovule 1, lateral. *Flowers* bisexual.

Type – *E. cuneifolia* J.D. Hooker & T. Thomson.

Distribution – About 5 species in tropical Asia (Malaysia and Borneo).

Note – *Ellipeia* differs from *Uvaria* by its single ovule. Sinclair (1955), however, states that *Uvaria pauci-ovulata* has 1–3 ovules. Also the leaves of *U. pauci-ovulata* look very similar to those of *Ellipeia*. According to Scheffer (1885), *E. gilva* has ovules in 2 series, while he mentions 1 or 2 ovules for *E. coriacea*. The only difference between *Ellipeia* and *Uvaria* seems to be the difference in size of the inner and outer petals in *Ellipeia*, whereas they are (sub)equal in *Uvaria*.

Specimens examined:

E. cuneifolia: Griffith 431, 5191, s.n. (P); King 6045 (U), 6844 (P). — *E. gilva:* de Vriese s.n. (L).

Ellipeiopsis R.E. Fries, Ark. Bot. ser. 2, 3 (1955) 41.

Buds spheroid to very broadly ovoid (sepals). *Sepals* reduplicate-valvate, 3, free or connate, 5–7 mm long, fleshy, veins not prominent, indument present, hairs stellate. *Petals* yellowish, imbricate, 6, free, both whorls equal in length, 9–11 mm long, 1 × as long as wide, 1.5–2 × length of sepals, fleshy, veins not prominent, indument present, hairs stellate; inner petals basally glabrous inside, 2 marginal glands present. *Torus* cushion-shaped. *Stamens* numerous, 1.3–1.6 mm long, extrorse; apex discoid, glabrous, fleshy. *Carpels* free, numerous, 2 mm long, stellate hairy, style absent, stigma broadly obovoid or cylindrical, glabrous; ovule 1, lateral. *Flowers* bisexual.

Type – *E. ferruginea* (Hamilton ex J.D. Hooker & T. Thomson) R.E. Fries.

Distribution – 2 species in tropical Asia (Burma, Thailand, and Indochina).

Specimens examined:

E. cherrevensis: van Beusekom & Phengkhlai 1063 (L); Kerr 636 (L, P); Pierre 96 (P), 745 (P), 1790 (L, P). — *E. ferruginea:* without collector and number (K).

Rauwenhoffia R.H.C.C. Scheffer, Ann. Jard. Bot. Buitenzorg 2 (1885) 21.

Buds very broadly ovoid (sepals or petals) to spheroid, rarely to broadly ovoid-deltoid (sepals). *Sepals* valvate, (2 or) 3, free or connate, 2.5–6 mm long, fleshy, veins not prominent, indument present, hairs stellate. *Petals* yellowish to brownish, imbricate or valvate, 6, free or rarely connate, both whorls equal in length, 9–23 mm long, 2 × as long as wide, 3–4 × length of sepals, fleshy, veins not prominent, indument present, hairs stellate, inner petals basally glabrous inside. *Torus* shallowly conical with a flat apex. *Stamens* numerous, 1.4–1.8 mm long, extrorse; apex discoid, fleshy, with indument. *Carpels* free, numerous, 3.7 mm long, stellate hairy, style absent, stigma shallowly obconical to discoid, glabrous; ovules many, lateral, 2-seriate. *Flowers* bisexual.

Lectotype – *R. siamensis* R.H.C.C. Scheffer.

Distribution – 5 species in Thailand, Indochina, New Guinea, and Australia.

Notes – As pointed out by Ban (1974), the proper generic name for *Rauwenhoffia*-species (figs. 37d, h, 38a) may be *Melodorum*, published by Loureiro (1790), a type-specimen of which is kept at BM (*Melodorum fruticosum*).

Some *Uvaria*-species from Madagascar strongly resemble *Rauwenhoffia* in several aspects.

Specimens examined:

R. leichhardtii: Brass 7584 (BM, L), 7681 (L); Byrnes 2829 (L); Hollrung 413 (L). — *R. papuasica:* Schlechter 19368 (BR). — *R. siamensis:* Cult. Hort. Bog. XI-A-30 (K, L); Kerr 4308 (P), 7033 (K); Poilane 29373 (P).

Tetrapetalum Miquel, Ann. Mus. Bot. Lugduno-Batavum 2 (1865) 1.

Buds (spheroid to) very broadly ovoid (petals). *Sepals* (aestivation not observed), 2, free or more or less connate, 2–3 mm long, fleshy, veins not prominent, indument present, hairs stellate. *Petals* imbricate, 4, free, both whorls equal in length, 5–8 mm long, 1–1.5 × as long as wide, 2–3 × length of sepals, fleshy, veins not prominent, indument present, hairs stellate, inner petals basally glabrous inside. *Torus* shallowly conical with a flat apex or broadly cylindrical. *Stamens* numerous, 2 mm long, latrorse; apex tongue-shaped, fleshy. *Carpels* free, numerous, 1.8–2 mm long, stellate hairy, style absent, stigma narrowly cylindrical, stellate hairy, or obconical, glabrous; ovules 10, lateral, 2-seriate. *Flowers* bisexual.

Type – *T. volubile* Miquel.

Distribution – 2 species in tropical Asia (Borneo).

Note – *Tetrapetalum* (fig. 37a, b) differs from *Cyathostemma* only in its dimerous flowers. *Cyathostemma excelsum* of Borneo so closely resembles *Tetrapetalum volubile* that they may be one species in which 2-merous and 3-merous flowers occur.

Specimens examined:

T. borneensis: Elmer 21211 (P, U); Wood SAN 16166 (L). — *T. volubile:* Ashton BRUN 606 (K, L); Buwalda 6617 (L); de Vriese s.n. (L).

Table 21. List of character states found in the genera of the Uvaria-group.

Taxa: A = *Anomianthus*, B = *Balonga*, C = *Cyathostemma*, E1 = *Ellipeia*, E2 = *Ellipeiopsis*, R = *Rauwenhoffia*, T = *Tetrapetalum*, U = *Uvaria*.

	A	B	C	E1	E2	R	T	U
Flowers:								
perianth 3-merous	+	+	+	+	+	+	–	+
perianth 2-merous	–	–	–?	–	–	+	+	–
hairs simple	–	+	(+)	–	–	–	–	–
bisexual	+	+	+	+	+	+	+	+
male	–	–	(+)	–	–	–	–	–
Sepals:								
valvate	+	?	+	+	–	+	?	+
imbricate	–	?	+	–	–	–	?	–
reduplicate-valvate	-	–	–	–	+	–	–	+
connate	–	–	–,+	–,+	–,+	–,+	–,+	–,+
entirely connate in bud	–	–	–	–	–	–	–	–,+
2–5 mm long	+	–	+	+	–	+	+	+
5–10 mm long	–	+	–	–	+	+	–	+
> 10 mm long	–	–	–	–	–	–	–	+
Petals:								
imbricate	+	?	+	+	+	+	+	+
valvate	(+)	?	+	–	–	+	–	–
connate	+,–	–	–,+	–	–	–,(+)	–	–,+
whorls unequal in size	–	+	–	+	–	–	–	–,+
3–15 mm long	+	+	+	+	+	+	+	+
15–45 mm long	+	(+)	–	+	–	+	–	+
marginal glands present	+	–	–	–	+	–	–	–,+
Stamens:								
numerous	+	+	+	+	+	+	+	+
> 2.5 mm long	–	–	–	–	–	–	–	–,+
staminodes present	–	–	–	–	–	–	–	+,–
anthers latrorse	+	–	+	+	–	–	+	+
anthers extrorse	+	+	+	+	+	+	–	+
apex tongue-shaped	+	–	+	–	–	–	+	+
apex discoid	–	+	+	+	+	+	–	+
Carpels:								
1–3 in number	–	–	–	–	–	–	–	+
numerous	+	+	+	+	+	+	+	+
Ovules:								
1 in number (lateral)	–	?	–	+	+	–	–	
> 1 in number	+	?	+	–	–	+	+	+
1-seriate	+	?	+	+	+	–	–	+
2-seriate	–	?	+	–	–	+	+	+

Uvaria Linnaeus, Sp. Pl. (1753) 536.

Buds spheroid with often entirely fused sepals and an apiculate apex (sepals) to very broadly ovoid (petals) surrounded by a cup-shaped calyx. *Sepals* valvate or reduplicate-valvate, 3, free or connate, 2–25 mm long, fleshy, sometimes thin, veins not prominent, indument present, hairs stellate. *Petals* purplish-red to pink, brownish to yellowish to greenish, or creamy, imbricate, 6, free or connate, both whorls equal in length or outer ones longer, 5–45 mm long or outer ones 12–38 mm long, inner ones 9–30 mm long, 1–2 × as long as wide, 1.5–5 × length of sepals, fleshy, sometimes almost membranous, veins prominent or not, indument present, hairs stellate, inner petals basally glabrous or not inside, with or without marginal glands. *Torus* shallowly conical with a flat apex, cylindrical, flat, or depressed ovoid, sometimes with a slightly (to deeply) concave apex. *Stamens* numerous, 1–7 mm long, extrorse or latrorse, staminodes present (outer stamens) or not; apex tongue-shaped or discoid, fleshy, rarely with indument. *Carpels* free, numerous or rarely 2–3, 1.5–5 mm long, stellate hairy, style absent, stigma shallowly obconical to cylindrical, glabrous or hairy; ovules 3–30, lateral, 1- or 2-seriate. *Flowers* bisexual.

Lectotype – *U. zeylanica* Linnaeus.

Distribution – About 170 species in tropical Asia, New Guinea, Australia, New Caledonia, and tropical Africa incl. Madagascar.

Notes – *Uvaria* (figs. 37e, g, 38d, f) exhibits diversity in its flowers, associated with its geographic distribution. The Asiatic species usually have reddish to pinkish, purplish or brownish flowers, whereas the African species have yellowish, greenish, creamish, or brownish flowers. The apices of the stamens of the Asiatic species are usually tongue-shaped (fig. 38b), whereas they are mostly discoid (fig. 38c) in the African species. Staminodes are mainly found in the Asiatic species.

A number of species differ from the other *Uvaria*-species:

Uvaria elmeri (Borneo) has a very large ovule production, compared with other Annonaceae: it has up to 30 ovules per carpel, a very large number of carpels, and many flowers in a cauliflorous cluster.

Uvaria hahnii (Thailand): it differs from all other *Uvaria*-species in its long and relatively narrow, valvate petals, in the 2 marginal glands (as in *Anomianthus* and *Ellipeiopsis*), stamens with papillose, discoid apices (like those of *Disepalum*), and unlike most Asiatic *Uvaria*-species it lacks staminodes. There is more reason, based on the flowers, to exclude *U. hahnii* from *Uvaria* than to keep all other genera of the Uvaria-group apart from *Uvaria*.

Uvaria klaineana var. *chrysophylla* (Gabon) has a deeply concave torus and stamens like, e.g., *Letestudoxa* (Fusaea-group); it seems to have imbricate sepals. This species is the only *Uvaria*-species of which Le Thomas (1981) examined the pollen and it resembled that of *Afroguatteria, Letestudoxa,* and *Pseudartabotrys* (all Fusaea-group).

Uvaria diplocampta (Madagascar): it has thick sepals (like in *Rauwenhoffia*), yellow petals with basally a red spot (not mentioned for the other species or genera of the Uvaria-group), stamens of which the apices have a shiny texture (like in *Letestudoxa, Pachypodanthium* (Duguetia-group), and *Sphaerocoryne* (Friesodielsia-group), only 2 carpels, and a flat stigma.

Uvaria lemurica (Madagascar): very thick sepals, long and narrow petals (like *Anomianthus*), inner petals with 2 marginal glands (like *Anomianthus* and *Ellipeiopsis*), stamens of which the apices have a shiny texture and 3–3.5 mm long, resembling those of *Letestudoxa*, and 2–3 carpels.

Two unnamed specimens from Madagascar: very small sepals and relatively long and narrow petals, like in *Anomianthus*. However, they lack marginal glands on their inner petals as found in *Anomianthus*.

All the species from Madagascar mentioned here show features otherwise only found in *Anomianthus* and *Rauwenhoffia*. In Asia these genera are better delimited (except for *Rauwenhoffia* where problems occur with the generic delimitation between *Rauwenhoffia* and *Uvaria* in New Guinea).

Specimens examined:

AFRICA, MADAGASCAR INCLUDED — *U. acuminata:* Faden et al. 956 (WAG); T. & S. Pocs 6085 (WAG); Reitsma 139 (WAG). — *U. afzelii:* Cult. Hort. Wag. 432 (WAG); Versteegh & den Outer 168, 543 (WAG). — *U. amplexicaulis:* Herb. d'Alleizette s.n. (L); Perrier de la Bathie 1743 (B). — *U. angolensis:* Lye & Morrison 2638 (WAG); Stolz 1844 (L). — *U. caffra:* Schlechter 11997 (L). — *U. chamae:* Gledhill 456 (WAG); J.J.F.E. de Wilde 3742 (WAG). — *U. combretifolia:* Herb. d'Alleizette s.n. (L); Capuron 6751 (P). — *U. diplocampta:* Perrier de la Bathie 1758 (B). — *U. gabonensis:* Karmann s.n. (L). — *U. kirkii:* Drummond & Hemsley 3496 (B); Faulkner 1528 (B), 2410 (B); Milne-Redhead & P. Taylor 7520 (B); Mwasumbi LBM 10663 (B); Procter 2744 (WAG). — *U. klaineana* var. *chrysopetala:* Le Testu 6337, 8401 (P). — *U. lemurica:* Perrier de la Bathie 2272 (B). — *U. mocoli:* Herb. d'Alleizette s.n. (L). — *U. obanensis:* Bos 5555 (WAG). — *U. ovata* subsp. *ovata:* Adams 4796 (WAG); J.J.F.E. de Wilde 597 (WAG). — *U. ovata* subsp. *afzeliana:* Leeuwenberg 2994 (L). — *U. scabrida:* Bos 3353 (WAG). — *U. sp.* (Madagascar): Appert 772 (U); Lorence 2089 (K).

ASIA — *U. boniana:* K'tung 6178 (L). — *U. branderhorstii:* Brass 8239 (L). — *U. cauliflora:* Tong S 34349 (L). — *U. concava:* Iboet 384 (L). — *U. cordata:* Chew W.L. 170 (L); Larsen et al. 2600 (L); Maxwell 75-520 (L). — *U. elmeri:* Kartawinata 722 (L). — *U. grandiflora:* Champion s.n. (K); Kostermans 27199 (L); Lei 510 (L); Whitmore FRI 15781 (L). — *U. hahnii:* Maxwell 75-366, 76-200, 76-246 (L); — *U. latifolia:* Teijsmann s.n. (U?). — *U. littoralis:* Bakhuizen van den Brink 3094 (U), 3096 (L, U); Cult. Hort. Bog. XVI-E-3 (U); Okada 3366 (U). — *U. lobbiana:* Cockburn FRI 8439 (L). — *U.* cf. *macrophylla:* Gafui et al. BSIP 8884 (L); Mauriasi et al. BSIP 8692, BSIP 8884 (L). — *U. macropoda:* Jayasuriya 1274 (L), 2110 (L). — *U. ovalifolia:* Brass 8421 (L). — *U. pauci-ovulata:* Ngadiman 36432 (K). — *U. sympetala:* Brass 8241 (L). — *U. timorensis:* de Vriese & Teijsmann s.n. (L). — *U. zeylanica:* Thwaites CV 1030 (BR); Wallich s.n. (BR). — *U. sp.:* Morawetz 31-31185 (U).

18. Uvariastrum-group (figs. 39, 40; table 22)

Buds very broadly to narrowly ovoid or to deltoid-ovoid (sepals or petals); sepals rarely entirely fused in bud. *Sepals* valvate, reduplicate-valvate or apert?, 2, 3, (or 4), free or connate, 1–28 mm long, fleshy, veins rarely prominent, indument present, hairs usually simple, sometimes stellate or lepidote. *Petals* reddish, brownish, greenish, yellowish to whitish, valvate, sometimes reduplicate-valvate, rarely inner petals imbricate, (3, 4,) 6 (or 8), free, rarely connate, both whorls equal in length or rarely outer petals slightly longer, sometimes all petals in one whorl, 4.5–40 mm long, 1–4 × as long as wide, 1–11 × length of the sepals, fleshy, veins or prominent or not, indument present, hairs usually simple, rarely stellate or lepidote, inner petals

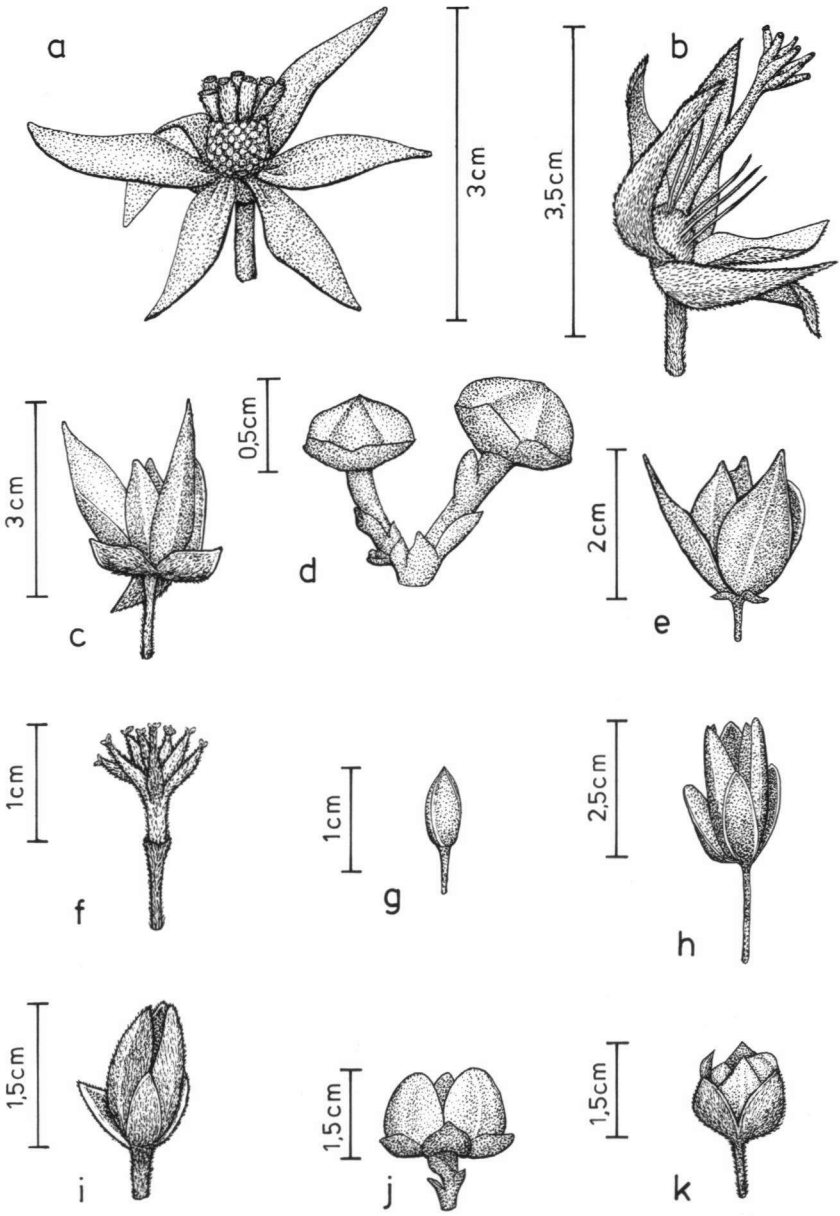


Fig. 39. Uvariastrum-group — a. *Monocyclanthus vignei* (van Meer 19): flower; b. *Mischogyne michelioides* (de Meneces 325): flower, most of the stamens dropped; c. *Uvariastrum insculptum* (J.J.F.E. de Wilde 3126): flower; d. *Dennettia tripetala* (Maitland 626): buds; e. *Meiocarpidium lepidotum* (Breteler 1398): flower; f., g. & h. *Mischogyne elliottianum* (Dalziel 761): carpels only (f), bud (g), and flower (h); i. *Mischogyne michelioides* (de Meneces 325): young flower; j. *Uvariodendron connivens* (Talbot 404): flower; k. *Uvariastrum insculptum* (J.J.F.E. de Wilde 3126): young flower.

sometimes glandular at the base inside. *Torus* broadly cylindrical, (depressed or broadly) ovoid, sometimes with slightly concave apex, flat, or depressed obovoid with slightly concave apex. *Stamens* numerous, 0.4–7 mm long, extrorse or latrorse; apex discoid to tongue-shaped or sometimes umbonate, rarely not prolonged, often fleshy, sometimes hairy. *Carpels* free, numerous to 1, 1.3–7.8(–20) mm long, hairy or rarely glabrous, style absent or rarely present, stigma (shallowly) obconical and sometimes grooved, bilobed, or flat and lobed, rarely cylindrical or ellipsoid; ovules 6–18, lateral, 1- or 2-seriate. *Flowers* bisexual or occasionally unisexual.

Distribution – 9 genera in tropical Africa.

Notes – This group is characterized by an enlarged torus (fig. 40), many, usually 2-seriate ovules, and valvate petals. The petals are (sub)equal. Two flower types occur in this group: one with large sepals and one with very small sepals.

Because of their indument, *Dielsiothamnus* (stellate hairs) and *Meiocarpidium* (scales) are with hesitation placed in this group.

The Uvariastrum-group is difficult to delimit from the Hexalobus-group. When both groups would be combined, the resulting group would be too heterogeneous. Compared with the Hexalobus-group, the Uvariastrum-group usually has thicker petals, which are always valvate, a larger torus, and more carpels. *Dielsiothamnus* in its flowers has a midway position between the Friesodielsia-group, the Hexalobus-group, the Uvaria-group, and the Uvariastrum-group.

Dennettia E.G. Baker in Rendle, E.G. Baker & Wernham, Cat. Pl. Oban (1913) 5, pl. 2.

Buds depressed ovoid to very broadly deltoid-ovoid (petals). *Sepals* apert?, 2 or 3, connate, 1.5–2 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* reddish, valvate, 3 or 4, free, in one whorl, 7–12 mm long, 1–1.5 × as long as wide, 5–6 × length of sepals, fleshy, veins not prominent, indument present, hairs simple. *Torus* depressed ovoid with a slightly concave apex and a constricted base, depressed obovoid and a slightly concave apex, or broadly cylindrical. *Stamens* numerous, 1.2–1.7 mm long, latrorse; apex discoid (slightly depressed), glabrous. *Carpels* free, numerous, 2.5–3 mm long, hairy, style absent, stigma shallowly obconical, grooved; ovules 14–16, lateral, 2-seriate. *Flowers* bisexual.

Type – *D. tripetala* E.G. Baker.

Distribution – 1 species in Africa (Nigeria and Cameroon).

Note – *Dennettia* (fig. 39d) has, like *Uvariopsis*, only 3 or 4 petals in one whorl. However, *Dennettia* has bisexual flowers and *Uvariopsis* unisexual ones.

Specimens examined:

D. tripetala: Geerling & Bokdam 2222 (BR, WAG); Maitland 626 (K); mr. & mrs. Talbot s.n. (BM).

Dielsiothamnus R.E. Fries, Ark. Bot. ser. 3 (1955) 35.

Buds not observed. *Sepals* (aestivation not observed), 3, connate, 6–9 mm long, fleshy, veins not prominent, indument present, hairs stellate. *Petals* brown-yellowish, (aestivation not observed), 6, free or sometimes connate, both whorls equal in

length, 7–9 mm long, 1–1.5 × as long as wide, 1 × length of sepals, fleshy, veins not prominent, indument present outside only, hairs stellate, inner petals with marginal glands? *Torus* cylindrical with a slightly concave apex, depressed ovoid, sometimes with a slightly concave apex, or flat. *Stamens* numerous, 1.3–2.3 mm long, extrorse; apex umbonate, glabrous, fleshy. *Carpel* 1, (length not measured), hairy, style absent, stigma shallowly obconical; ovules c. 12, lateral, 2-seriate. *Flowers* bisexual.

Type – *D. divaricatus* (Diels) R.E. Fries.

Distribution – 1 species in East Africa, ranging from Kenya to Moçambique.

Note – *Dielsiothamnus* differs from the other genera of this group by the stellate indument, the single carpel, and umbonate apices of the stamens. The stamens resemble in shape those of *Xylopia* and *Cananga,* but are not indurate. A single carpel is found in, e.g., *Isolona, Monodora* (both Hexalobus-group), *Cyathocalyx,* and *Dasoclema* (both Friesodielsia-group). The combination of one carpel per flower and a stellate indument is also found in *Dasoclema.*

Specimens examined:

D. divaricatus: Anderson 798 (K); Mendonça 1148 (BR); Schlieben 5451 (B, P); Torre & Paiva 9247 (WAG), 9581 (WAG), 11727 (BR).

Meiocarpidium Engler & Diels, Notizbl. Königl. Bot. Gart. Berlin 3 (1900) 54.

Buds very broadly deltoid-ovoid (petals). *Sepals* apert?, 3, free or more or less connate, 2–4 mm long, fleshy, veins not prominent, indument present, lepidote. *Petals* creamy, yellow, or brown, valvate or slightly reduplicate-valvate, 6, free, both whorls more or less equal in length, 14–23 mm long, (inner ones 14–20 mm long), 1.3–2 × as long as wide, 7–10 × length of sepals, fleshy, veins not prominent, indument present, lepidote on the outer petals, stellate hairs on inner petals. *Torus* depressed cylindrical-ovoid. *Stamens* numerous, 2.8–3.5 mm long, latrorse; apex discoid, hairy. *Carpels* free, few, 4 mm long, indument lepidote, style absent, stigma shallowly obconical, ovules 10–14, lateral, 2-seriate. *Flowers* bisexual.

Type – *M. lepidotum* (D. Oliver) Engler & Diels.

Distribution – 1 species in Central Africa (Cameroon and Gabon).

Note – *Meiocarpidium* (figs. 39e, 40a) is easy to recognize by the lepidote indument of the outer petals, which is only found in *Duguetia* and *Meiocarpidium.* These two genera are not related; they differ, among others, in the number and the attachment of the ovules. The stamens of *Meiocarpidium* remind of those of *Letestudoxa* in shape, but differ in texture.

Specimens examined:

M. lepidotum: Breteler 1398 (WAG); Le Testu 1415 (BR), 5032 (BR, P); Tessmann 609 (K); Zenker 84, 2947, 3027 (L).

Mischogyne Exell, J. Bot. 70, Suppl. 1 (1932) 213, f. 2.

Buds ovoid to narrowly ovoid (sepals). *Sepals* reduplicate-valvate, sometimes caducous, 3, free, 5–16 mm long, fleshy, thin, veins prominent or not, indument present, hairs simple. *Petals* white, valvate, 6, free, both whorls equal in length,

7–25 mm long, 1.5–2.5 × as long as wide, 1.5 × length of sepals, fleshy, thin, veins prominent, indument present, hairs simple. *Torus* broadly cylindrical or shallowly conical with a flat apex. *Stamens* numerous, 3.6–7 mm long, latrorse; apex tongue-shaped, fleshy or not, glabrous or hairy. *Carpels* free, c. 8 to numerous, 2–5 (–20) mm long, hairy, long-stipitate, style absent, stigma ellipsoid or bilobed, hairy or glabrous; ovules > 6, lateral, (number of series not observed). *Flowers* bisexual.

Type – *M. michelioides* Exell.

Distribution – 2 species in Africa, ranging from Sierra Leone to Angola.

Note – *Mischogyne* (fig. 39f, g, h, i) seems most related to *Uvariastrum*, in which *M. elliotianum* was included in the past. It differs from that genus by the longer and flattened stamens without a discoid apex. The carpels of *M. michelioides* are very long-stipitate, which makes that flowers of this species look very different from all other Annonaceae (fig. 39b).

Specimens examined:

M. elliotianum: Dalziel 761 (K); Jacques-Félix 465 (P); Morton A4230 (WAG); Oldeman 777 (WAG); Vigne 4336 (BR, P). — *M. michelioides:* Bamps et al. 4459 (BR, WAG); Gossweiler 9379 (B); de Meneces 325 (K); Teixeira & Andrade 589 (BR).

Monocyclanthus Keay, Kew Bull. (1953) 69, f. 1.

Buds ovoid (petals); petals also at the apex in one whorl. *Sepals* valvate, 3, connate, 2 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* outside yellow or greenish, inside deep purple or dark red apically to creamish-white basally, valvate, 6, free, all petals in one whorl and of equal length, 13–22 mm long, 2.5–4 × as long as wide, 8–11 × length of sepals, fleshy, veins prominent or not, indument present, hairs simple, inside glabrous. *Torus* depressed obovoid or ovoid. *Stamens* numerous, 0.9–1 mm long, extrorse or latrorse; apex discoid, fleshy, hairy. *Carpels* free, 6–16, 3 mm long, hairy, style absent, stigma obconical and grooved with involute margins and hairy, or bilobed and glabrous; ovules 7, lateral, 1-seriate. *Flowers* bisexual.

Type – *M. vignei* Keay.

Distribution – 1 species in West Africa (Ghana and Liberia).

Note – *Monocyclanthus* (fig. 39a) is easy to recognize by the one-whorled arrangement of the 6 relatively large petals.

Specimens examined:

M. vignei: Leeuwenberg & Voorhoeve 4934 (B, WAG); van Meer 19 (WAG); Vigne FH 4744 (K).

Polyceratocarpus Engler & Diels, Notizbl. Königl. Bot. Gart. Berlin 3 (1900) 56.

Buds very broadly ovoid (petals); sometimes sepals entirely fused. *Sepals* valvate, 3, connate, 2–3 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* greenish- or pale brown, creamy or white, valvate, 6, free, both whorls equal in length, 6–35 mm long, 2 × as long as wide, 3–10 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inside some-

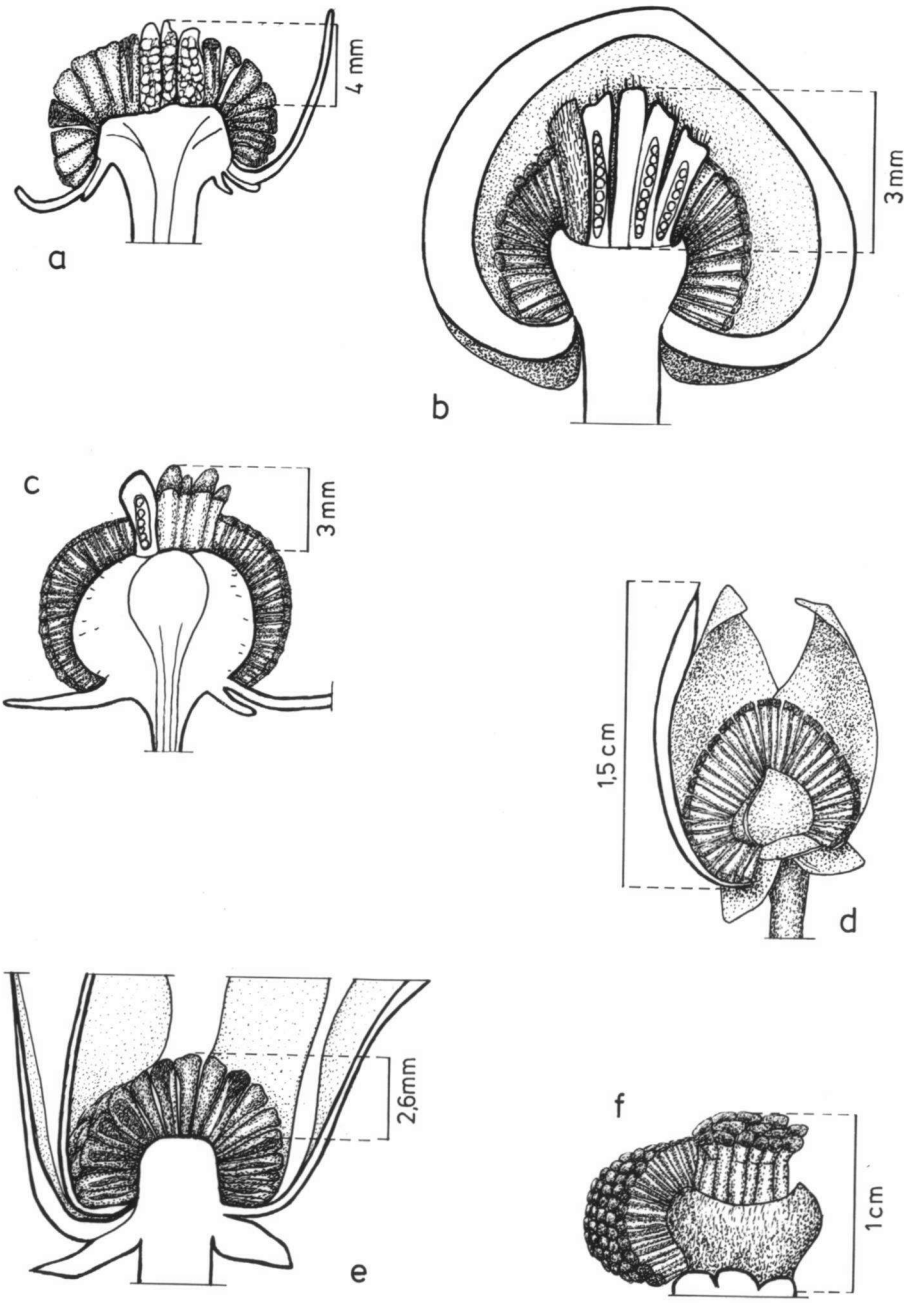


Fig. 40. Uvariastrum-group — a. *Meiocarpidium lepidotum* (Le Testu 5032): longitudinal section; b. *Dennettia tripetala* (mr. and mrs. Talbot s.n.): longitudinal section; c. *Monocyclanthus vignei* (Leeuwenberg & Voorhoeve 4934): longitudinal section; d. *Polyceratocarpus gossweilerii* (Breyne 987): 3 petals and part of stamens dropped; e. *Polyceratocarpus pellegrinii* (Le Testu s.n.): longitudinal section; f. *Uvariodendron connivens* (Talbot 404).

times glabrous, inner petals glabrous along the margin outside near the base. *Torus* shallowly conical and constricted, broadly cylindrical, or depressed obovoid with a slightly concave apex. *Stamens* numerous, 1.3–3.8 mm long, extrorse; apex discoid, fleshy. *Carpels* free, numerous, 4.5–7.8 mm long, hairy, style (almost) absent, stigma shallowly obconical or bilobed, glabrous; ovules 20, lateral, 1-seriate. *Flowers* bisexual or occasionally unisexual and plants androdioecious.

Type – *P. scheffleri* Engler & Diels.

Distribution – West and Central Africa, Angola, and Tanzania, 5–7 species.

Note – *Polyceratocarpus* deviates from the other genera of this group in the fruits and seeds (Van Setten, 1990), the pollen morphology (Le Thomas, 1981; Walker, 1971a), and the venation of the leaves. In its flowers (fig. 40d, e) *Polyceratocarpus* agrees very well with the present group.

Specimens examined:

P. gossweileri: Breyne 987 (BR). — *P. microtrichus:* Farron 4825 (P); Hallé 2279 (P). — *P. parviflorus:* Bos 6684 (BR); Le Testu 8569 (BR); J.J.F.E. de Wilde 3539 (B, WAG). — *P. pellegrinii:* Le Testu s.n. (BM, P). — *P. scheffleri:* Peter 18832 (K), 22024 (B). — *P. sp.:* J.J.F.E. de Wilde et al. 103 (WAG).

Uvariastrum Engler, Monogr. Afr. Pflanzen-Fam. 6 (1901) 31, t. 1B.

Buds shallowly triangular-ovoid (sepals). *Sepals* reduplicate-valvate, 3, free, 10–28 mm long, fleshy, thick, veins prominent or not, indument present, hairs simple. *Petals* (pale or orange-)yellow, or brown-green, valvate or sometimes inner ones imbricate, 6, free, outer whorl slightly longer, outer ones 13–35 mm long, inner ones 13–30 mm long, 2–3 × as long as wide, 1.5 × length of sepals, fleshy, veins prominent or not, indument present, hairs simple. *Torus* broadly cylindrical, or shallowly conical with a flat apex. *Stamens* numerous, 1.6–5.5 mm long, extrorse; apex discoid, hairy. *Carpels* free, numerous, 5–5.7 mm long, hairy, style absent, stigma flat and more or less lobed, glabrous; ovules 12–16, lateral, 2-seriate. *Flowers* bisexual or occasionally unisexual and plants androdioecious?.

Type – *U. pierreanum* Engler.

Distribution – West & Central Africa, Angola, Tanzania, and Zambia, 7–8 species.

Note – *Uvariastrum* (fig. 39c, k) is easy to recognize by the thick and large, reduplicate-valvate sepals together with valvate petals.

Specimens examined:

U. germainii: Lebrun 5977 (P). — *U. hexaloboides:* Angus 919 (BM, K); Milne-Redhead 3413 (K); Richards 4055 (K). — *U. insculptum:* Leeuwenberg 2785 (WAG); Staudt 740 (B); J.J.F.E. de Wilde 3126 (WAG). — *U. pierreanum:* Brenan & Richards 8827 (BR); Brenan 8901 (BR); Touzet 65 (BR); W.J.J.O. de Wilde & de Wilde-Duyfjes 1904 (B). — *U. zenkeri:* Letouzey 9121 (P); Zenker 481 (B, U).

Uvariodendron (Engler & Diels) R.E. Fries, Acta Horti Berg. 10 (1) (1931) 51.

Buds very broadly ovoid (sepals). *Sepals* valvate, 3 (or 4), free or connate, 7–28 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* green-

ish, whitish, or yellow-brown, valvate, 6 (or 8), free, both whorls more or less equal in length or inner ones slightly shorter, outer ones 8–40 mm long, inner ones 4–40 mm long, 1–2 × as long as wide, 1–1.3 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inside more or less glabrous. *Torus* depressed ovoid, sometimes with a slightly concave apex, or depressed obovoid with a slightly concave apex. *Stamens* numerous, 1–5 mm long, extrorse or latrorse; apex discoid, fleshy, sometimes hairy. *Carpels* free, numerous, 1.3–6 mm long, hairy or glabrous, style present or absent, stigma (shallowly) obconical, sometimes cup-shaped and grooved, cylindrical, or discoid, hairy or not; ovules 6–18, lateral, 1- or 2-seriate. *Flowers* bisexual.

Lectotype – *U. giganteum* (Engler) R.E. Fries.

Distribution – West, Central and East Africa, 12–13 species.

Note – *Uvariodendron* (figs. 39j, 40f) seems most related to *Uvariastrum*, but differs from that genus in the buds, which are enclosed by several large bracts.

Specimens examined:

U. angustifolium: Lovi 3964 (K); Staudt 742a (B); Vigne 1610 (K, P). — *U. anisatum:* R.B. & A.J. Faden 74/886 (K). — *U. calophyllum:* Biholong 279 (P); Onochie et al. FHI 30860 (K). — *U. connivens:* Talbot 404 (K). — *U. fuscum:* Mann 308 (P). — *U. giganteum:* Hallé 3156 (P). — *U. kirkii:* Peter 40249 (B). — *U. molundense:* Mildbraed 4373 (B).

Uvariopsis Engler, Notizbl. Königl. Bot. Gart. Berlin 2 (1899) 298.

Buds ovoid to spheroid (petals). *Sepals* apert?, 2 (or 3), free or connate, 1–7 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* yellow, rose, pinkish-brown, or brown outside, (pale) yellow or flushed with reddish inside, valvate, reduplicate-valvate, or rarely slightly imbricate, 3 or 4, free or connate, in one whorl, equal in length, 4.5–24 mm long, 1–4 × as long as wide, 4–5 × length of sepals, fleshy, sometimes thick, veins not prominent, indument present, hairs simple, inside hairy, basally glabrous or glandular. *Torus* (broadly) ovoid, shallowly conical, or depressed obovoid. *Stamens* numerous, 0.4–0.5 mm long, extrorse; apex discoid or not prolonged, glabrous. *Carpels* free, numerous, 2–2.5 mm long, hairy, style absent, stigma flat, lobed, glabrous; ovules 6–8, lateral, 2-seriate. *Flowers* unisexual.

Type – *U. zenkeri* Engler.

Distribution – West & Central Africa, 9–12 species.

Note – *Uvariopsis* is easy to recognize by its unisexual flowers with 3 or 4 petals. There are conspicuous differences in size between the flowers of the various species. Verdcourt (1986) discovered a species of *Uvariopsis, U. bisexualis,* with bisexual flowers.

Specimens examined:

U. bakerianum: Brenan 9409 (P); Letouzey 9017 (P). — *U. congensis:* Harris 167 (K). — *U. congolana:* Hallé 2817, 3039 (P); Louis 5762 (B). — *U. dioica:* Keay FHI 28066 (K); Winkler 909 (B). — *U. globulifera:* Breteler 2812 (WAG). — *U. letestui:* Hallé 3060 (P). — *U. solheidii:* Hallé 3474 (P). — *U. vanderystii:* Le Testu 8525 (P). — *U. zenkeri:* Zenker 481 (U), 575 (B).

Table 22. List of character states found in the genera of the Uvariastrum-group.

Taxa: D1 = *Dennettia*, D2 = *Dielsiothamnus*, M1 = *Meiocarpidium*, M2 = *Mischogyne*, M3 = *Monocyclanthus*, P = *Polyceratocarpus*, U1 = *Uvariastrum*, U2 = *Uvariodendron*, U3 = *Uvariopsis*.

	D1	D2	M1	M2	M3	P	U1	U2	U3
Flowers:									
hairs simple	+	–	–	+	+	+	+	+	+
hairs stellate	-	+	+	–	–	–	–	–	–
hairs lepidote	-	–	+	–	–	–	–	–	–
male	–	–	–	–	–	+	(+)	–	+
female	–	–	–	–	–	–	–	–	+
bisexual	+	+	+	+	+	+	+	+	(+)
Sepals:									
valvate	?	?	?	–	+	+	–	+	?
reduplicate-valvate	?	?	?	+	–	–	+	–	?
2 in number	+	–	–	–	–	–	–	–	+
3 in number	+	+	+	+	+	+	+	+	(+)
connate	+	+	–,+	–	+	+	–	–,+	–,+
1–5 mm long	+	–	+	–	+	+	–	–	+
5–10 mm long	–	+	–	+	–	–	–	+	+
10–28 mm long	-	–	–	+	–	–	+	+	–
Petals:									
valvate	+	?	+	+	+	+	+	+	+
reduplicate-valvate	-	?	+	–	–	–	–	–	+
connate	–	–,+	–	–	–	–	–	–	–,+
3 or 4 in number	+	–	–	–	–	–	–	–	+
6 in number	–	+	+	+	+	+	+	+	–
in one whorl	+	–	–	–	+	–	–	–	+
4–12 mm long	+	+	–	+	–	+	–	+	+
12–40 mm long	-	–	+	+	+	+	+	+	+
Stamens:									
numerous	+	+	+	+	+	+	+	+	+
> 2.5 mm long	–	–	+	+	–	–,+	–,+	–,+	–
anthers latrorse	+	–	+	+	+	–	–	+	
anthers extrorse	–	+	–	–	+	+	+	+	+
apex tongue-shaped	–	–	–	+	–	–	–	–	
apex umbonate	–	+	–	–	–	–	–	–	–
apex not prolonged	–	–	–	–	–	–	–	–	+
apex discoid	+	–	+	–	+	+	+	+	+
Carpels:									
1 in number	–	+	–	–	–	–	–	–	–
> 1 in number	+	–	+	+	+	+	+	+	+
Ovules:									
6–10 in number	–	–	–	+	+	–	–	+	+
> 10 in number	+	+	+	?	–	+	+	+	–
1-seriate	–	–	–	?	+	+	–	+	–
2-seriate	+	+	+	?	–	?	+	+	+

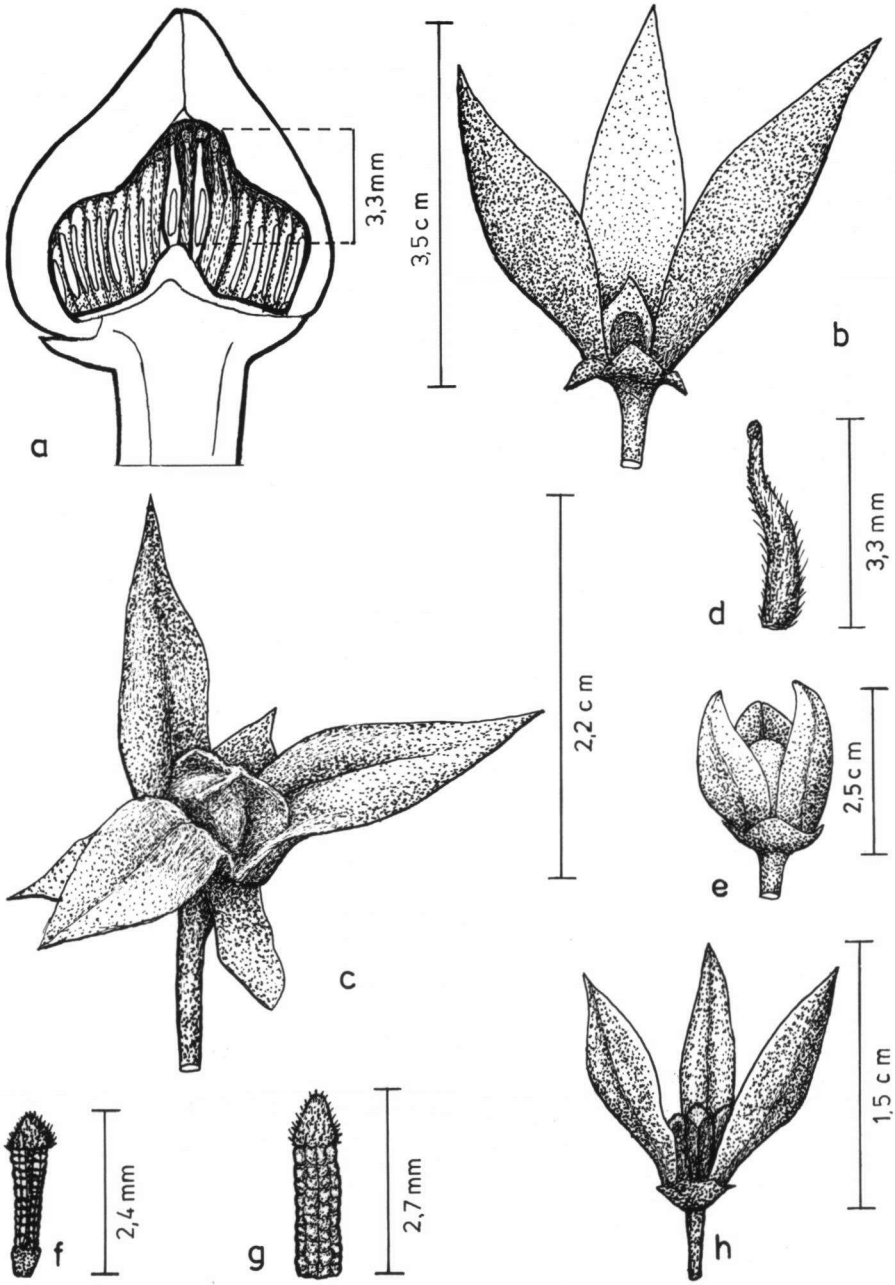


Fig. 41. Xylopia-group — a. *Boutiquea platypetala* (Zenker 2877): longitudinal section; b. *Boutiquea platypetala* (Letouzey 9436): flower; c. *Goniothalamus ridleyi* (Dransfield 4454): flower; d. *Boutiquea platypetala* (Zenker 2877): carpel; e. *Goniothalamus sp.* (van Beusekom & Phengkhlai 256): flower; f. *Goniothalamus tapis* (Jacobs 5243): stamen; g. *Neostenanthera gabonensis* (Beentje 601): stamen; h. *Neostenanthera gabonensis* (Hallé & Villiers 4799): flower.

19. Xylopia-group (figs. 41–43; table 23)

Buds (depressed or triangular-)ovoid (sepals), or narrowly pyramidal, triangular, lanceoloid, (narrowly) ellipsoid, or (broadly) (depressed) ovoid (petals). *Sepals* valvate or reduplicate-valvate (rarely slightly imbricate), 3, free or connate, 1–45 mm long, fleshy, sometimes very thin, veins not prominent, indument present or rarely absent, hairs simple. *Petals* whitish, yellowish, greenish, brownish, orange, reddish, pink, or purplish, valvate or rarely slightly imbricate, 6, free or rarely connate, both whorls equal in length or usually inner whorl (much) smaller, 3.5–165 mm long, 2–15 × as long as wide, 1–30 × length of sepals, fleshy, or sometimes thin, veins prominent, indument present, hairs simple; inner petals often connivent, sometimes basally glabrous, glandular, with denser indument, or differently coloured inside, sometimes 2 marginal glands present. *Torus* depressed ovoid with a deeply concave apex, flat, sometimes with a deeply concave apex, slightly concave, (very) shallowly conical with an ovoid or flat apex, broadly cylindrical with very shallowly conical apex, or slightly convex. *Stamens* numerous or rarely few, 0.7–4 mm long, usually indurate, extrorse or rarely more or less introrse, usually septate, rarely margins of slit inflexed, staminodes present or not; apex discoid, umbonate, or tongue-shaped, glabrous or hairy. *Carpels* free, 2 to numerous, 1.5–7 mm long, hairy, style present or sometimes absent, stigma lanceoloid, ellipsoid, cylindrical, discoid, or rarely obconical; ovules 1–8, basal or lateral, 1-seriate. *Flowers* bisexual.

Distribution – 6 genera throughout the tropics.

Notes – This group is characterized by usually valvate sepals and petals, inner petals which are usually smaller than the outer ones (figs. 41b, c, h, 42c), usually indurate stamens, and often septate anthers (fig. 42f, g).

Some genera within this group seem congeneric: *Richella* with *Goniothalamus* and *Boutiquea* with *Neostenanthera*. The latter two genera are placed in this group with hesitation. They differ from the other genera in the stamens which are not indurate, the shape of the torus (figs. 41a, 42f), and they always have one, basal ovule. In other respects they closely resemble *Goniothalamus*.

The Xylopia-group resembles the Fusaea-group in the indurate texture of the stamens and in the carpels with the presence of a style (fig. 43a, f, h). The Xylopia-group differs from that group because it usually has septate stamens and more than one ovule, which are laterally attached. The Xylopia-group resembles the Friesodielsia-group (e.g., *Fissistigma, Mitrella, Pyramidanthe,* and *Sphaerocoryne*) in the perianth: both have smaller inner petals, and sepals and petals of similar size. The two groups differ in the texture and shape of the stamens.

Boutiquea A. Le Thomas, Adansonia sér. 2, 5 (1966) 531.

Buds not observed. *Sepals* (aestivation not observed), 3, connate (or free), 1–2.5 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* (pale) yellowish(-greenish), valvate, 6, free, outer whorl much longer, outer ones 20–33 mm long, inner ones 8–10 mm long, 4 × as long as wide, 20–30 × length of sepals, fleshy, veins prominent, indument present, hairs simple; inner petals connivent. *Torus* very shallowly conical, apex broadly ovoid. *Stamens* numerous, 1.8–3 mm

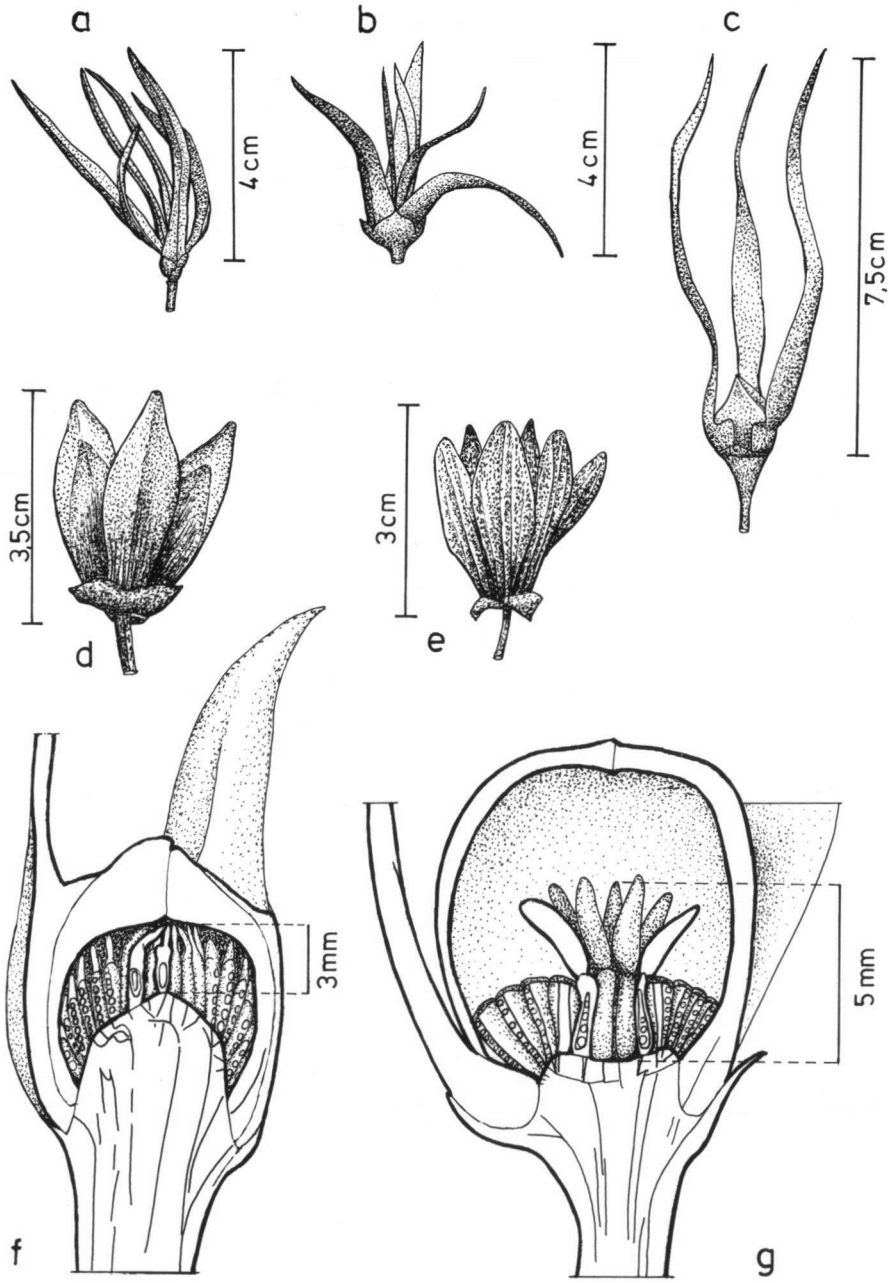


Fig. 42. Xylopia-group — a. *Xylopia longipetala* (Westphal 10172): flower; b. *Xylopia aromatica* (Prance 24789): flower; c. *Neostenanthera hamata* (de Koning 4795): flower; d. *Xylopia grandiflora* (Lorence 2225): flower; e. *Cananga latifolia* (van Beusekom & Phengkhlai 522): flower; f. *Neostenanthera gabonensis* (Beentje 601): longitudinal section; g. *Goniothalamus sp.* (van Beusekom & Phengklai 256): longitudinal section.

long, extrorse, septate?; apex more or less tongue-shaped, shiny. *Carpels* free, numerous, 3.3 mm long, hairy, style present or absent, stigma ellipsoid; ovule 1, basal. *Flowers* bisexual.

Type – *B. platypetala* (Engler & Diels) Le Thomas.

Distribution – 1 species in Cameroon, Africa.

Notes – *Boutiquea* (fig. 41b, d) closely resembles *Neostenanthera*, but differs from that genus by the fruits with sessile monocarps. In their flowers *Boutiquea* and *Neostenanthera* are not distinct.

Specimens examined:
B. platypetala: Letouzey 9436 (BR, P); J. & A. Raynal 10389 (P); Zenker 2877, 4402 (B).

Cananga (A.P. de Candolle) J.D. Hooker & T. Thomson, Fl. Ind. 1 (1855) 129 (nom. cons.).

Buds depressed ovoid (sepals). *Sepals* valvate or reduplicate-valvate, 3, free or connate, 3–10 mm long, fleshy, thin, veins not prominent, indument present, hairs simple. *Petals* (pale) green to yellow, valvate, 6, free, both whorls equal in length, 12–70 mm long, 5–14 × as long as wide, 4–6 × length of sepals, fleshy, thin, veins prominent, indument present, hairs simple, inner petals sometimes basally with denser indument inside. *Torus* slightly convex, sometimes with slightly concave apex. *Stamens* numerous, 1–2.7 mm long, indurate, extrorse or more or less introrse, not septate; apex umbonate, glabrous or hairy. *Carpels* free, numerous, 1.8–4.5 mm long, hairy, style absent, stigma obconical or cylindrical; ovules 4, lateral, 1-seriate. *Flowers* bisexual.

Type – *C. odorata* (Lamarck) J.D. Hooker & T. Thomson.

Distribution – 2 species in tropical Eastern Asia and Australia; cultivated all over the tropics.

Note – *Cananga* (figs. 42e, 43b) is placed in this group because the same type of stamens are found in *Goniothalamus*. The stamens are easy to recognize by the umbonate apices (fig. 43c). *Cananga* differs from the other genera in this group because the anthers are not septate (as in part of the *Goniothalamus*-species) and by the equal-sized petals.

Specimens examined:
C. latifolia: Herb. d'Alleizette s.n. (L); van Beusekom & Phengkhlai 522 (L); Maxwell 76-232 (L); Phengnaren 727 (L). — *C. odorata:* Backer s.n. (U); Baker & Burger 165 (U); Bristol 2063 (U); Cult. Hort. Bog. s.n. (L); Davidson & Donahue 8987 (L); Docters van Leeuwen 9549 (U); Hartshorn 1225 (U); Moore 241 (U); Versteeg 1073 (U); Yuncker 15086 (U).

Goniothalamus (Blume) J.D. Hooker et T. Thomson, Fl. Ind. 1 (1855) 105.

Buds ovoid(-deltoid) (sepals or petals). *Sepals* valvate or reduplicate-valvate, 3, free or connate, 3–45 mm long, fleshy, sometimes very thin, veins prominent or not, indument present, hairs simple. *Petals* (creamy-)white, reddish-cream, pink, red, purplish-chocolate, maroon, (light or red-)green, (pale or greenish-)yellow, or dark brown and inside yellow, valvate, 6, free, outer whorl much longer, outer ones 11–165 mm long, inner ones 4–27 mm long, 2–15 × as long as wide, 1–20 ×

length of sepals, fleshy, veins prominent or not, indument present, hairs simple; inner petals connivent. *Torus* cushion-shaped, slightly convex, or shallowly conical with a flat apex. *Stamens* numerous, 1.4–4 mm long, indurate, extrorse, septate or not, sometimes margins of slit inflexed; apex discoid, umbonate, depressed ovoid, or more or less tongue-shaped, glabrous or hairy, rarely fleshy. *Carpels* free, 8 to numerous, 1.8–5 mm long, hairy, style very long, stigma discoid or lanceloid, glabrous, or replaced by a ciliate rim; ovules 1–6, basal or lateral, 1-seriate. *Flowers* bisexual.

Type – *G. macrophyllus* (Blume) J.D. Hooker & T. Thomson.

Distribution – 86 species in tropical Asia, New Guinea, and the Pacific.

Notes – *Goniothalamus* (fig. 41c, e) is diverse in the size, shape, and texture of its sepals and petals, as well as in the shape of the stamens. The stamens (fig. 41f) are often similar to those of other genera: *Cananga, Letestudoxa* (Fusaea-group), *Pyramidanthe* (Friesodielsia-group), and *Xylopia*. Part of the species have large, showy sepals, a feature which is shared with *Sphaerothalamus* and one species of *Enicosanthum*.

Goniothalamus was thus far in most classifications placed near *Mitrephora* because of the connivent inner petals (fig. 42g). However, the structure of the flowers of these two genera is very different. The stamens are similar to those of *Xylopia* and *Cananga*. The affinity of *Goniothalamus* to *Xylopia* was already discovered by Walker (1971a).

The unnamed specimen from New Guinea (Kairo 780) resembles *Richella* in its perianth; it differs from that genus because it has at least 6 ovules.

Specimens examined:

G. australis: Morawetz 11-15185 (U). — *G. caloneurus:* Docters van Leeuwen 10123 (U); Lam 957 (U). — *G. cardiopetalus:* Sundara Raghavan 86311 (L). — *G. curtisii:* Kochummen KEP 95089 (L), FRI 2808 (L). — *G. dolichopetalus:* C. & C. Frake 36067 (L). — *G. elmeri:* Edaño 4169 (L); Elmer 14932 (U); Stern et al. 2131 (L). — *G. fulvus:* Lindong KEP 83452 (K, L). — *G. gardneri:* Waas 768 (L). — *G. giganteus:* Haviland 2107 (L). — *G. grandiflorus:* van Royen 16476 (L); Verdcourt 5089 (L); White NGF 9689 (L). — *G. macrophyllus:* Anderson & Ilias bin Paie S 28634 (K); Bakhuizen van den Brink 6171 (U). — *G. malayanus:* Chew W.L. 1359 (L); Sinclair s.n. (L). — *G. montanus:* Chew W.L. 182 (L). — *G. oblongipetalus:* Ramos & Edaño 30705 (L). — *G. obtusifolius:* Merrill 9215 (L). — *G. oligophlebius:* Castro 6542 (L). — *G. philippinensis:* Sulit 6554 (L). — *G. ridleyi:* Dransfield 4454 (L). — *G. roseus:* Saikeh Lantoh SAN 83189 (L). — *G. slingelandtii:* Teijsmann s.n. (U). — *G. suluensis:* Elmer 21537 (U); Maidin 10429 (L). — *G. sumatranus:* Dumas 1582 (L, U). — *G. tapis:* Jacobs 5243 (L). — *G. tenuifolius:* Chew W.L. 81 (L); F.S.C. 310 (L). — *G. thwaitesii:* Waas 1739 (L). — *G. umbrosus:* Anderson S 25443 (L). — *G. sp.:* van Beusekom & Phengkhlai 256 (L); Kairo 780 (L).

Neostenanthera Exell, J. Bot. 73, Suppl. 1 (1935) 5.

Buds narrowly pyramidal (petals). *Sepals* valvate, 3, free, 1–1.5 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* (pale) yellow, pale or yellowish-green, valvate, 6, free, outer whorl much longer, outer ones 12–105 mm long, inner ones 5–14 mm long, 2–8 × as long as wide, 6–70 × length of sepals, fleshy, veins not prominent, indument present, hairs simple; inner petals connivent, sometimes basally differently coloured inside. *Torus* shallowly conical or broadly cylindrical with very shallowly conical apex. *Stamens* numerous, 1.4–2.7

mm long, extrorse, septate; apex discoid to tongue-shaped, glabrous or hairy. *Carpels* free, numerous, 1.5–3 mm long, stipitate, hairy, style present, hairy or glabrous, stigma lanceoloid or cylindrical, glabrous; ovule 1, basal. *Flowers* bisexual.

Lectotype – *N. hamata* (Bentham) Exell.

Distribution – West and Central Africa, 4–9 species.

Note – *Neostenanthera* (figs. 41g, h, 42f, 43d) together with the closely related genus *Boutiquea*, differs from the other genera of Xylopia-group by the very short sepals, the more elevated torus (fig. 42f), the small, more or less tongue-shaped apex of the stamens, and the single, basal ovule. The stamens are not indurate, as in the other genera of the Xylopia-group, but the anthers are septate, and the inner petals are connivent like in *Goniothalamus*. The stamens and carpels resemble those of *Enantia*.

Specimens examined:

N. gabonensis: Herb. d'Alleizette s.n. (L); Beentje 601 (WAG); Hallé & Villiers 4799 (K); Leeuwenberg 4173 (WAG); J.J.F.E. de Wilde 587 (WAG); W.J.J.O. de Wilde 388 (WAG). — *N. hamata:* de Koning 4795 (WAG); Versteegh & den Outer 673 (WAG); J.J.F.E. de Wilde 3349 (WAG). — *N. myristicifolia:* Breteler 1220, 1799 (WAG). — *N. neurosericea:* Zenker 3105 (L).

Richella A. Gray, Proc. Amer. Acad. Arts 2 (1852) 325.

Buds not observed. *Sepals* (aestivation not observed), 3, connate, 2–4 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* green or dull yellow, valvate, 6, free, outer petals much longer, outer ones 10–33 mm long, inner ones 5–14 mm long, 2 × as long as wide, 7–11 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner petals connivent. *Torus* slightly concave. *Stamens* numerous, 1.3–2 mm long, indurate, extrorse, septate; apex discoid, glabrous or hairy. *Carpels* free, numerous, 2–2.7 mm long, with ciliate margins or hairy, style absent or present, stigma cylindrical, hairy; ovules 2, lateral, 1-seriate. *Flowers* bisexual.

Type – *R. monosperma* A. Gray.

Distribution – 3 species in the Pacific (Fiji, New Caledonia), and Borneo.

Note – *Richella* in its flowers resembles *Goniothalamus* rather than *Friesodielsia*, to which it usually is supposed to be related, e.g., by Fries (1959) who included *Friesodielsia* in *Richella*. Van Steenis (1964) only mentioned that *Richella* differs from *Oxymitra* (= *Friesodielsia*) in the seeds, which are winged in *Richella*.

Specimens examined:

R. monosperma: Gillespie 3652 (B); A.C. Smith 7292 (K). — *R. obtusata:* Bamps 6138 (BR); Mackee 38351 (BR).

Xylopia Linnaeus, Syst. Nat. ed. 10 (1759) 1250 (nom. cons.).

Buds at first (triangular- or broadly depressed) ovoid (sepals), later triangular, lanceoloid, (narrowly) ellipsoid, (broadly) ovoid, or rarely broadly depressed ovoid (petals). *Sepals* valvate or sometimes slightly imbricate, 3, connate, 1–12 mm long, fleshy, veins not prominent, indument present or absent, hairs simple. *Petals* creamy to white (sometimes flushed with red, purple, or chocolate), to (pale or greenish-)

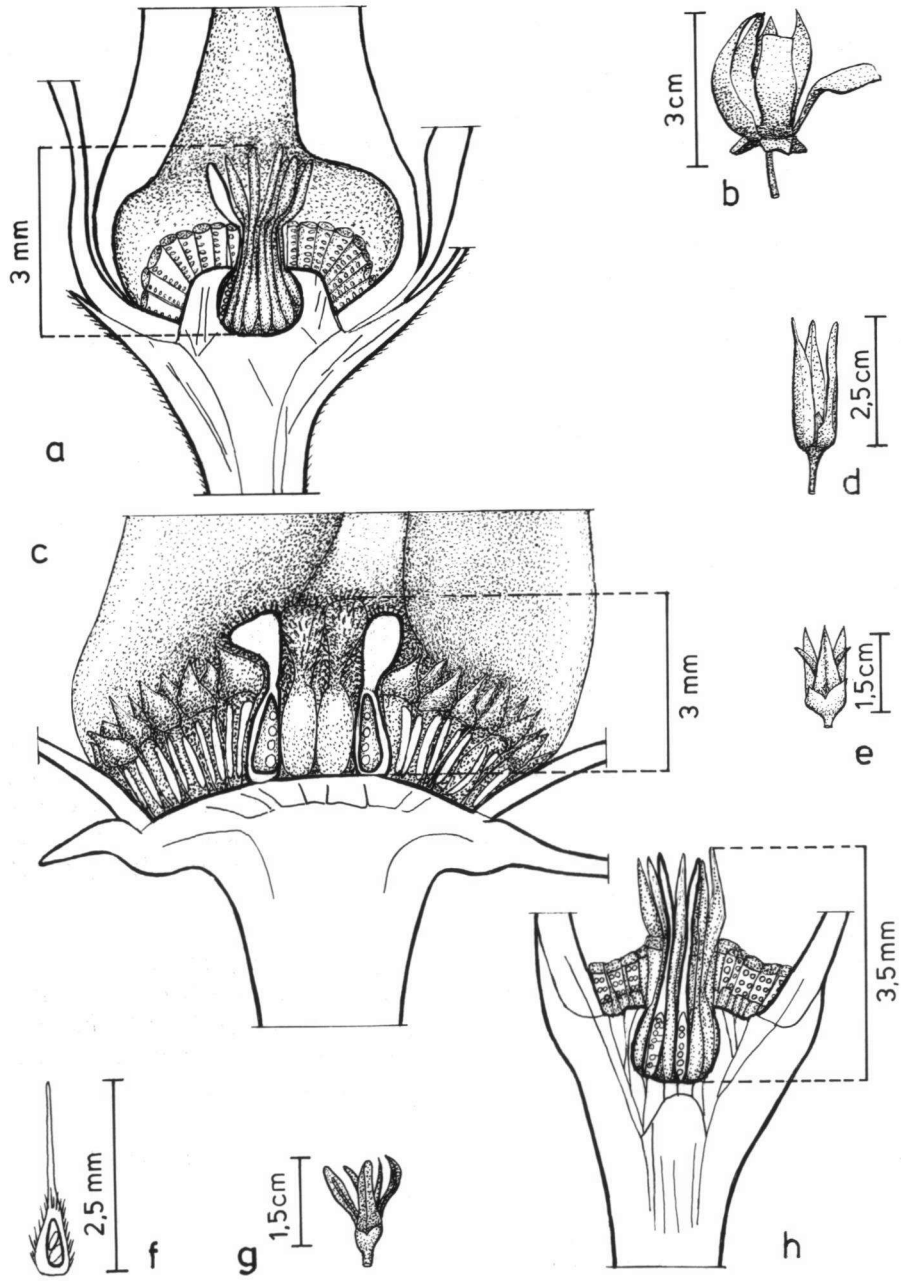


Fig. 43. Xylopia-group — a. *Xylopia aromatica* (Prance 24789): longitudinal section; b. & c. *Cananga odorata* (Cult. Hort. Bog. s.n.): flower (b) and longitudinal section (c); d. *Neostenanthera gabonensis* (Beentje 601): flower; e. *Xylopia ochrantha* (Berg 627): flower; f. *Xylopia staudtii* (J.J.F.E. de Wilde 7941): carpel; g. *Xylopia emarginata* var. *duckei* (de Bruijn 1614): flower; h. *Xylopia longipetala* (Westphal 10172): longitudinal section.

yellow, orange, or outside reddish, maroon, or greenish, inside white, sometimes with red or purple spot, or wine-coloured with a white spot, valvate or sometimes slightly imbricate, 6, free or connate, subequal or outer ones longer, 3.5–50 mm long or outer ones 7–55 mm long, inner ones 5–35 mm long, 2–6 × as long as wide, 3–11 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, or absent; inner petals sometimes basally glabrous or differently coloured inside, sometimes 2 marginal glands present. *Torus* depressed ovoid with a deeply concave apex, flat, slightly concave, flat with a deeply concave apex, or shallowly obconical with a concave apex. *Stamens* numerous to few, 0.7–3.5 mm long, indurate, extrorse, septate, staminodes present (inner or outer stamens) or absent; apex discoid or depressed ovoid, glabrous or hairy. *Carpels* free, 2 to numerous, 2.2–7 mm long, hairy, style usually present and long, stigma lanceoloid, rarely ellipsoid or cylindrical, sometimes not differentiated and with a ciliate rim only; ovules 1–8, basal or lateral, 1-seriate. *Flowers* bisexual.

Type – *X. muricata* Linnaeus (typ. cons.).

Distribution – About 160 species, pantropical.

Notes – *Xylopia* (figs. 42a, b, 43e, f, g) is rather uniform in its flowers, despite the large number of species. It is the only pantropical genus within the Annonaceae. In the flowers, most diversity is found in the Neotropics. The genus is remarkable by its concave torus (fig. 43a, h), which is, however, only observed in the neotropical and part of the African genera.

The two species formerly referred to *Pseudannona* (fig. 42d), *X. amplexicaulis* and *X. grandiflora*, both from Mauritius, differ from the remaining species of *Xylopia* in the larger size of the flowers.

Specimens examined:

AFRICA (MADAGASCAR AND MAURITIUS INCLUDED) — *X. aethiopica:* Bos 6296 (WAG); Corbisier 806 (U); Donis 2868 (U); Louis 1528 (U); Zenker 246 (U). — *X. amplexicaulis:* Blackburn s.n. (K); Lorence 2535 (K). — *X. banguyella:* Capuron 24356-SF (K). — *X. bemarivensis:* Capuron 22154-SF (B). — *X. ghesquiereana:* Capuron 22777-SF (K). — *X. grandiflora:* Herb. Lambert s.n. (BM); Lorence M23 (BR), 2225 (K); Wallich s.n. (BM). — *X. holtzii:* Torre & Correia 16681 (K). — *X. katangensis:* Fanshawe F3989 (K). — *X. lastelliana:* Perrier de la Bathie 4944 (B). — *X. longipetala:* Westphal 10172 (WAG); Zenker 408 (U). — *X. phloiodora:* Louis 448 (U). — *X. quintasii:* de Koning 985 (WAG); Zenker 359 (U). — *X. richardi:* Bernardi 15071 (K). — *X. rubescens:* Zenker 499 (U). — *X. staudtii:* J.J.F.E. de Wilde 7941 (WAG). — *X. tomentosa:* Dechamps et al. 1325 (WAG). — *X. torrei:* Torre & Paiva 9413 (K). — *X. sp.:* Perrier de la Bathie 4940 (B).

ASIA — *X. altissima*: Kostermans 7706 (L); Smythies et al. S 5906 (L). — *X. calosericea:* Streimann 51820 (L). — *X. caudata:* Banyeng ak Nudong S 25500 (L); Maxwell 75-41 (L). — *X. championii:* Kostermans 24720, 24989A (L). — *X. coriifolia:* Anderson 8100 (L); Kostermans 4683 (L). — *X. dehiscens:* Ramos & Edaño 29097 (L); Sulit 6475 (L); Wood SAN A3454 (L). — *X. densifolia:* Elmer 12471 (L); Martelino & Edaño 35553 (L). — *X. elliptica:* Kostermans 13109 (L); Puasa 4550 (L). — *X. ferruginea:* Kochummen FRI 16029 (L); Scortechini s.n. (U); Wood & Charington 16518 (L). — *X. magna:* Zainuddin Sohadi FRI 14609 (L). — *X. malayana:* Achmad 772, 871 (U); Cockburn FRI 7889 (L); Kostermans & Andong 16 (L); Okada 3262 (U).

NEOTROPICS — *X. amazonica:* Prance et al. 59162 (U). — *X. aromatica:* Heringer 2178 (U); Neill 4545 (U); Prance 24789 (U); A.S.L. Silva 320 (U); Vieira et al. 997 (U). — *X. benthamii:* Berg et al. P18553 (U); Morawetz 11-22883 (U); Zarucchi et al. 2614 (U). — *X. bocatorena:* Hartshorn 1187 (U). — *X. brasiliensis:* Reitz & Klein 4088 (U). — *X. crinita:* Liesner 7578 (U). — *X. cuspidata:* Huashikat 419 (U). — *X. discreta:* Narain LBB 13793 (U). — *X. emarginata:* de Bruijn 1614 (WAG); Davidse & González 12604 (U); dos Santos 237 (U); Sidney 1286 (U). —

X. frutescens: Davidse & González 16313 (U); van Donselaar 2810 (U); Wilson-Browne 554 (U). — *X. laevigata:* Harley et al. 15256 (U). — *X. ligustrifolia:* Foster 5588 (U); Terceros & Chori 366 (U). — *X. longifolia:* Forest Dep. Brit. Guiana 5188 (U). — *X. nitida:* Reeder & Roberts, LBB 12310 (U). — *X. ochrantha:* Berg 627 (U); Mori & Benton 13248 (U). — *X. polyantha* var. *longesericea:* de Bruijn 1594 (WAG). — *X. sericea:* Hatschbach & Ferreira 35264 (U). — *X. sp.:* Morawetz 11-22883 (U).

Table 23. List of character states found in the genera of the Xylopia-group.

Taxa: B = *Boutiquea*, C = *Cananga*, G = *Goniothalamus*, N = *Neostenanthera*, R = *Richella*, X = *Xylopia*.

	B	C	G	N	R	X
Flowers:						
3-merous	+	+	+	+	+	+
hairs simple	+	+	+	+	+	+
bisexual	+	+	+	+	+	+
Sepals:						
valvate	?	+	+	+	?	+
reduplicate-valvate	–	+	+	–	?	–
connate	+,–	+,–	+,–	–	+	+
1–5 mm long	+	+	+	+	+	+
5–12 mm long	–	+	+	–	–	+
12–45 mm long	–	–	+	–	–	–
Petals:						
valvate	+	+	+	+	+	+
whorls equal in size	–	+	–	–	–	(+)
inner whorl smaller	+	–	+	+	+	+
inner whorl connivent	+	–	+	+	+	–
outer whorl 7–35 mm	+	+	+	+	+	+
outer whorl 35–165 mm	–	+	+	+	–	+
inner whorl 4–35 mm	+	+	+	+	+	+
inner whorl 35–70 mm	–	+	–	–	–	+
Stamens:						
numerous	+	+	+	+	+	+,–
indurate	–	+	+	–	+	+
anthers extrorse	+	+	+	+	+	+
anthers almost introrse	–	+	–	–	–	–
anthers septate	+?	–	+,–	+	+	+
apex discoid	–	–	+	+	+	+
apex umbonate	–	+	+	–	–	–
apex tongue-shaped	+	–	–	+	–	–
staminodes present	–	–	–	–	–	+,–
0.7–4 mm long	+	+	+	+	+	+
Carpels:						
numerous	+	+	+	+	+	+,–
Ovules:						
1, basal	+	–	+	+	–	+
2–8, lateral, 1-seriate	–	+	+	–	+	+

20. Genera not included in one of the groups (figs. 44–48; table 24)

A number of genera has not been included in one of the groups because of unusual combinations of character states. Some of these genera may compose another group as can be concluded from non-floral character states. Le Thomas (1981), who studied the ultrastructure of pollen grains of African Annonaceae, placed the African genera discussed below within one lineage, together with *Artabotrys* and *Polyalthia*. *Ambavia, Cleistopholis, Mezzettia,* and *Tetrameranthus* share the uncommon chromosome number of 2n = 14 (Morawetz & Le Thomas, 1988). In their flowers all these genera are very different, although sometimes a similar structure is found in two of them. For instance, *Cleistopholis* and *Tetrameranthus* have similar carpels, and in young flowers of *Dendrokingstonia* a similar carpel is found as in *Piptostigma*. Until now, there is too little information available to draw any definite conclusions. These genera are described and commented here.

Ambavia Le Thomas, Compt. Rend. Hebd. Séances Acad. Sci., sér. D 274 (1972) 1655.

Buds (very) broadly ovoid (petals). *Sepals* imbricate, 3, free or connate, 0.5–2 mm long, fleshy, veins not prominent, indument present or absent, hairs simple, margins ciliate. *Petals* whitish, imbricate, 6, free, outer whorl slightly longer, outer ones 2–8 mm long, inner ones 2–6 mm long, 1–2 × as long as wide, 4–5 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner petals sometimes basally glabrous inside. *Torus* depressed ovoid. *Stamens* 9 or 12, 1–3.4 mm long, extrorse; apex discoid to tongue-shaped, glabrous or hairy, sometimes fleshy. *Carpels* free, 1–6, 1.2–2.7 mm long, glabrous, style absent, stigma discoid or flat; ovules 2, lateral. *Flowers* bisexual.

Type – *A. capuronii* (A. Cavaco & M. Keraudren) A. Le Thomas.

Distribution – 2 species in Madagascar.

Notes – In herbarium-specimens *Ambavia* (fig. 44b, c, d, g) is characterized by black sepals, which is typical of the Friesodielsia-group. *Ambavia* differs from that group because of its imbricate aestivation. Its carpels resemble those of *Cleistopholis*. The stamens of *A. capuronii* are reminiscent of those of *Anaxagorea*.

Both species of *Ambavia* look rather different in their flowers: they differ strongly in size, and *A. gerrardii* has bracts, whereas these are absent in *A. capuronii*.

Specimens examined:

A. capuronii: Service des eaux et forêts de Madagascar 15301-SF (P). — *A. gerrardii:* Herb. d'Alleizette s.n. (L); Perrier de la Bathie 13258 (B, P), 14221 (B); Service des eaux et forêts de Madagascar 16473-SF (P); Ürsch s.n. (L).

Anaxagorea A.F.C.P. de Saint-Hilaire, Nouv. Bull. Sci. Soc. Philom. Paris (1825) 91.

Buds (very broadly) ovoid to spheroid (petals); sometimes sepals entirely fused in bud. *Sepals* imbricate, valvate, or reduplicate-valvate, 2 or 3, free or connate, 2–13 mm long, fleshy, sometimes thin, veins prominent or not, indument present or

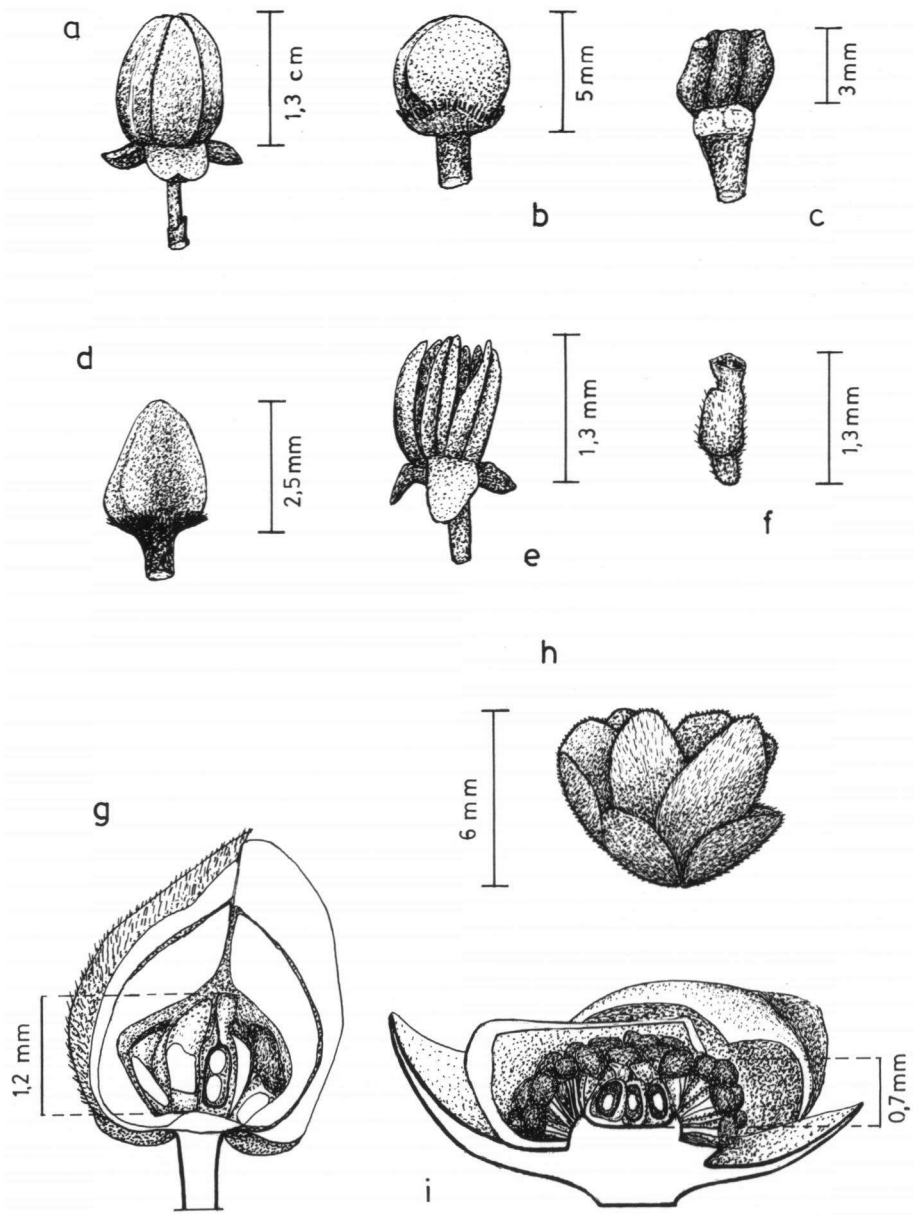


Fig. 44. Genera not included in one of the groups — a. *Anaxagorea brevipes* (Steyermark et al. 122286): bud; b. & c. *Ambavia capuronii* (Service des eaux et forêts de Madagascar 15301-SF): bud (b) and flower after anthesis (c); d. *Ambavia gerrardii* (Herb. d'Alleizette s.n.): bud; e. *Anaxagorea brevipes* (Steyermark et al. 122286): flower; f. *Anaxagorea javanica* var. *tripetala* (Kostermans 14010): carpel; g. *Ambavia gerrardii* (Service des eaux et forêts de Madagascar 16473-SF): longitudinal section; h. *Cleistochlamys kirkii* (Lovemore 48525): flower; i. *Cleistochlamys kirkii* (Schlieben 5431): longitudinal section.

absent, hairs simple or stellate, margins ciliate or not. *Petals* white to (greenish-)yellow, pale green, red, orange, maroon, cream-brown, or outside ferruginous-brown, inside creamy(-yellow), valvate or imbricate, 2, 3, or 6, free, both whorls equal in size or outer whorl longer, 6–16 mm long or outer ones 13–19 mm long, inner ones 7–14 mm long, 1–5 × as long as wide, 1–3 × length of sepals, fleshy, thick or thin, veins prominent or not, indument present or absent, hairs simple or stellate, margins ciliate or not; inner petals sometimes connivent, basally differently coloured inside. *Torus* cylindrical to cushion-shaped. *Stamens* numerous, 1.5–4.5 mm long, extrorse or latrorse, staminodes (inner stamens) present or not; apex discoid or tongue-shaped, sometimes fleshy, glabrous, apex of staminodes sometimes glandular. *Carpels* free, 1 to numerous, 2–4.5 mm long, (stellate) hairy or glabrous, style absent or present, stigma pyriform with ciliate rim, discoid, cylindrical, or depressed ovoid; ovules 2, basal. *Flowers* bisexual.

Type – *A. prinoides* (Dunal) Alph. de Candolle.

Distribution – 26 species in tropical Asia and Central and South America.

Notes – *Anaxagorea* (figs. 44a, e, f, 46a, d) shares a number of features with the Xylopia-group, e.g., the presence of staminodes (inner stamens), the vertical orientation of the stamens (parallel to the axis of the flower) with *Boutiquea* and *Neostenanthera,* the texture of the petals with *Neostenanthera.* It differs, among others, from the Xylopia-group in the more or less flattened stamens, which are not septate or indurate, the presence of stellate hairs in most of the species, and the 2 basal ovules. Two basal ovules are, beside *Anaxagorea,* only found in *Artabotrys* and *Polyalthia.*

The geographic distribution of *Anaxagorea* is unique within the Annonaceae: Asia and the Neotropics. There are many differences in the flower morphology between the Asiatic and the neotropic species, e.g., in the aestivation, the number of sepals and petals, the indument, the size of sepals and stamens, and the number of carpels.

Specimens examined:

ASIA — *A. borneensis:* Chew W.L. 648 (A). — *A. javanica* var. *dipetala:* Brand SAN 24583 (L). — *A. javanica* var. *javanica:* Forbes 2608 (BM); Kerr 9591 (K), 16285 (BM); Maxwell 75-752 (L); Smitinand & Sleumer 1181 (L); Zuang 53 (K). — *A. javanica* var. *tripetala:* Cockburn 71009 (L); Meijer SAN 28373 (L); Kostermans 14010 (K, L); Sinclair 7655 (E); Sinclair & Kiah bin 39928 (E); Stone 12126 (MO); Ahmad Talip SAN 70955 (L). — *A. luzonensis:* Bhargava 1948 (E); Callery 8 (P); Cuming 496 (C, MO); Elmer 17739 (A, MO, US); Kerr 12770 (BM); Pierre 600 (L); Stern 2068 (L, MO); Wai-Tak Tsang 949 (US).

NEOTROPICS — *A. allenii:* Croat 25137 (MO); Forero et al. 4762 (MO). — *A. brachycarpa:* Berry 1465 (MO); Foster 4261 (F); Nascimento 718 (U). — *A. brevipes:* Steyermark et al. 122286 (U). — *A. crassipetala:* Antonio 1371, 3053, 3562 (U); Hammel 1618 (U); Schunke V. 10006 (U). — *A. dolichocarpa:* Cremers 7653 (U); Lindeman et al. 707 (U); Maguire et al. 56025 (F); Steyermark 87350 (U). — *A. floribunda:* Klug 33 (NY). — *A. gigantophylla:* Maguire et al. 60311 (NY). — *A. panamensis:* Croat 11158 (F). — *A. petiolata:* Tillett 752-308 (VEN). — *A. prinoides:* Pires et al. 51374 (US); Rosa & Vilar 3125 (U); M.G. Silva & Bahia 3549 (NY). — *A. rufa:* Schultes & Cabrera 14464 (U); Gentry & Revilla 20424 (MO); Liesner 6815 (MO).

Cleistochlamys D. Oliver, J. Linn. Soc., Bot. 9 (1867) 175.

Buds spheroid (sepals); sepals entirely fused in bud. *Sepals* valvate, 3 (or 4), free or connate, 2–3 mm long, fleshy, slightly pellucid, veins not prominent, indument

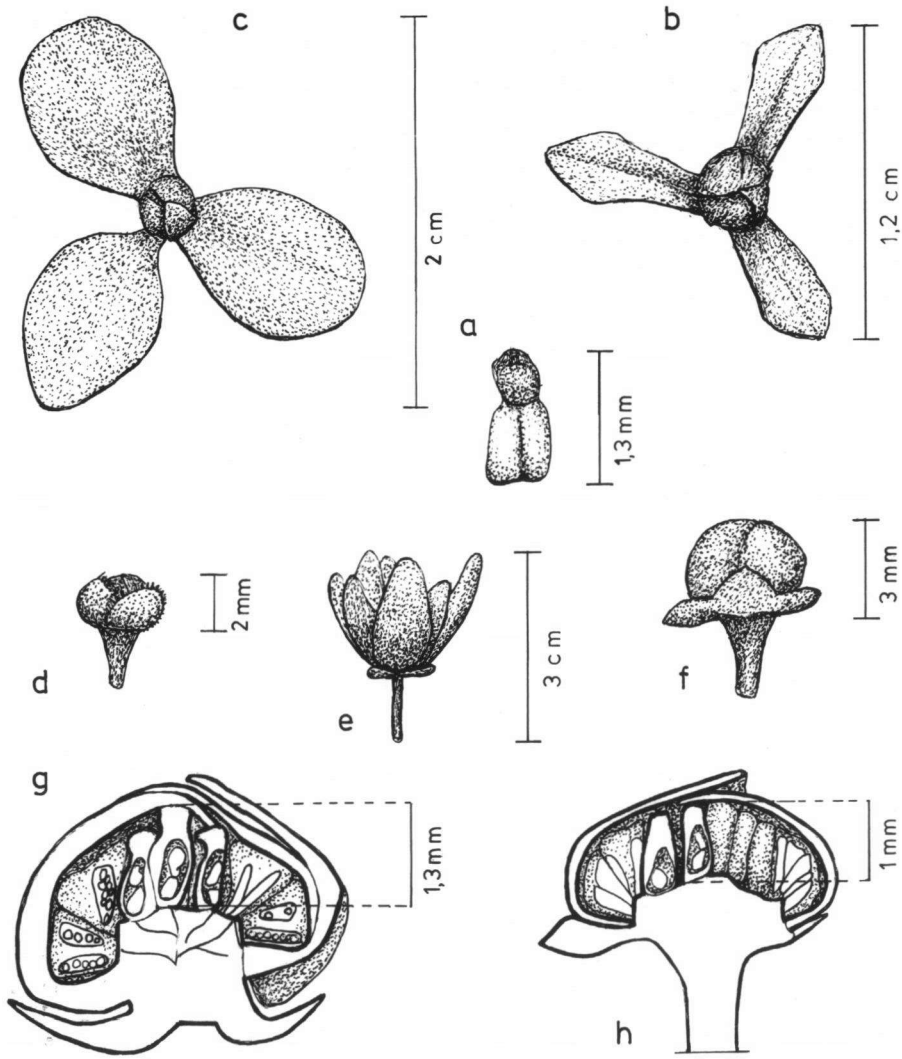


Fig. 45. Genera not included in one of the groups — a. *Cleistopholis patens* (van Meer s.n.): carpel; b. *Cleistopholis patens* (Versteegh & den Outer 76): flower; c. & d. *Cleistopholis glauca* (Lisowski 52356): flower (c) and bud (d); e. *Tetrameranthus duckei* (Ducke RB 23919): flower; f. *Cleistopholis glauca* (Lisowski 52356): bud; g. *Cleistopholis patens* (van Meer s.n.): longitudinal section; h. *Cleistopholis glauca* (Le Testu 8786): longitudinal section.

absent, margins ciliate or not. *Petals* (creamy-)white, imbricate, 6, free, both whorls equal in length, 4–6 mm long, 1.3–2 × as long as wide, 2 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inside glabrous or sparsely hairy. *Torus* cushion-shaped. *Stamens* (few to) numerous, 0.5–1 mm long, extrorse;

apex discoid, fleshy. *Carpels* free, few, 0.7–1 mm long, glabrous, style absent, stigma narrowly ellipsoid, glabrous; ovule 1, basal. *Flowers* bisexual.

Type – *C. kirkii* (Bentham) D. Oliver.

Distribution – 1 species in Eastern and Southern Africa.

Note – *Cleistochlamys* (fig. 44h, i) does not fit in any of the groups. The buds with entirely fused sepals in young stages, the imbricate petals, and the single basal ovule are shared with the Duguetia-group, the Fusaea-group, and the Guatteria-group. It differs from the latter two groups in the texture of the stamens (not indurate), and from the Duguetia-group in the hair type (stellate to scaly in the Duguetia-group). The genus has few stamens and carpels compared with the genera of the other 3 groups. The texture of the petals remind of that of some *Hexalobus*-species. The texture of the sepals is somewhat pellucid, which is otherwise not found within the Annonaceae.

Specimens examined:

C. kirkii: Edwards & Vahrmeijer 4277 (WAG); Fanshawe 9837 (P); Lovemore 48525 (K); Mendonça 4342 (WAG); Schlieben 5431 (B), 5675 (B, P); Torre & Paiva 11244 (B); Vollesen 2957 (WAG).

Cleistopholis Pierre ex Engler, in Engler & Prantl, Nat. Pflanzenfam. Nachtr. II–IV (1897) 160.

Buds depressed ovoid (petals). *Sepals* imbricate, 3, free, 0.7–1.5 mm long, fleshy, veins not prominent, indument absent, margins ciliate or not. *Petals* pale green or greenish-yellow, imbricate, sometimes inner ones valvate, 6, free, outer whorl much longer, outer ones 4–16 mm long, inner ones 1.5–3 mm long, 2–6 × as long as wide, 4–12 × length of sepals, fleshy, veins prominent or not, indument absent. *Torus* cylindrical or cushion-shaped. *Stamens* few (to numerous), 0.5–1 mm long, latrorse; apex discoid, rarely tongue-shaped, fleshy. *Carpels* free, 5 to numerous, 1–1.3 mm long, glabrous, style absent, stigma discoid, spheroid, or broadly ovoid; ovules 2, lateral. *Flowers* bisexual.

Lectotype – *C. patens* (Bentham) Engler & Diels.

Distribution – 4 species in West and Central Africa.

Note – *Cleistopholis* (fig. 45, except 45e) differs from all other genera because of the much smaller inner petals which are not expanded, whereas the aestivation of the sepals and petals is imbricate. As a rule in Annonaceae, a strong difference in size between inner and outer petals is associated with valvate petals. The carpels resemble those of *Ambavia* and *Sageraea*. Because of the absence of indument, except for ciliate margins, and the imbricate aestivation of the petals, *Cleistopholis* reminds of the Cremastosperma-group and the Sageraea-group. In one specimen of *C. glauca* similar stamens as in *Ambavia* were found.

Specimens examined:

C. glauca: Arends et al. 487 (U); Leeuwenberg 6467 (L); Le Testu 2250, 8584, 8786 (BR); Lisowski 52356 (WAG). — *C. patens:* Herb. d'Alleizette s.n. (L); Leeuwenberg 2622 (U); van Meer s.n. (WAG); Versteegh & den Outer 76 (U). — *C. staudtii:* W.J.J.O. de Wilde 1342 (U); Zenker 4880 (L).

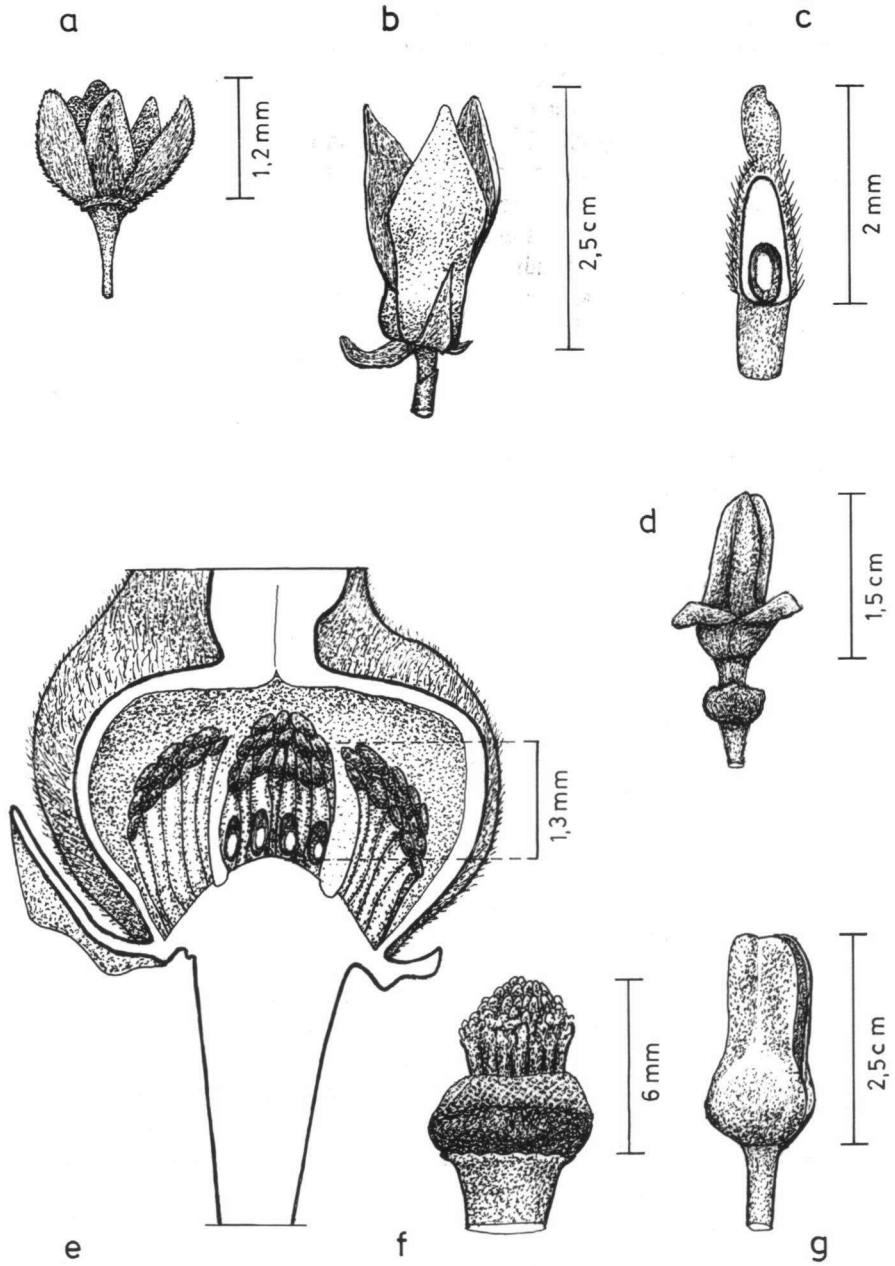


Fig. 46. Genera not included in one of the groups — a. *Anaxagorea dolichocarpa* (Lindeman et al. 707): flower; b. *Enantia polycarpa* (Versteegh & den Outer 686): flower; c. *Enantia chlorantha* (Zenker 441): carpel; d. *Anaxagorea crassipetala* (Antonio 3562): bud; e. *Enantia letestui* (Le Testu 8432): longitudinal section; f. & g. *Enantia chlorantha* (Le Testu 1783): flower after anthesis (f) and bud (g).

Dendrokingstonia Rauschert, Taxon 31 (1982) 555 (= *Kingstonia* J.D. Hooker & T. Thomson).

Buds broadly ellipsoid-ovoid (petals). *Sepals* imbricate, 3, free, 1–1.5 mm long, fleshy, veins prominent, indument present, hairs simple. *Petals* imbricate, 6, free, both whorls equal in length, 3 mm long, 2–3 × length of sepals, fleshy, veins not prominent, indument present, hairs simple. *Torus* flat. *Stamens* 7–9, 0.8 mm long, extrorse or latrorse; apex discoid, fleshy. *Carpel* free, 1, 1 mm long, hairy, style absent, stigma shallowly obconical (cup-shaped); ovules 2–4, lateral, 1-seriate. *Flowers* bisexual.

Type – *D. nervosa* (J.D. Hooker & T. Thomson) Rauschert.

Distribution – 1 species in tropical Asia (Malaysia and Sumatra).

Note – *Dendrokingstonia* reminds of the Mitrephora-group and the Sageraea-group in the small flowers in clustered inflorescences. It differs from both groups in the single carpel with a very shallowly obconical (cup-shaped) stigma, and from the Mitrephora-group in the imbricate aestivation. The carpel resembles in shape that of *Monocarpia* and *Piptostigma*.

Specimens examined:
D. nervosa: Boschbouwproefstation 2734 (L); Lörzing 5523 (L).

Enantia D. Oliver, J. Linn. Soc., Bot. 9 (1867) 174, nom. illeg., non Falconer 1841.

N.B.: Just when completing the present paper, the illegitimate generic name of *Enantia* D. Oliver was replaced by *Annickia* van Setten & Maas (1990).

Buds broadly deltoid to triangular (sepals). *Sepals* reduplicate-valvate, 3, free, 3.5–10 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* green or purple, valvate, 3, free, outer whorl absent, 15–28 mm long, 2 × as long as wide, 2–6 × length of sepals, fleshy, thick, veins not prominent, indument present, hairs simple. *Torus* depressed ovoid or shallowly conical with a flat apex. *Stamens* numerous, 2–3 mm long, extrorse; apex discoid to tongue-shaped, glabrous. *Carpels* free, numerous, 1.3–3 mm long, stipitate, hairy, style absent, stigma spheroid, glabrous; ovule 1, basal. *Flowers* bisexual.

Type – *E. chlorantha* D. Oliver.

Distribution – 10 species in tropical Africa.

Note – *Enantia* (fig. 46b, c, e, f, g) is the only annonaceous genus without outer petals. *Enantia* most resembles *Anaxagorea, Boutiquea,* and *Neostenanthera*: they all have the same structure of stamens and carpels, as well as more or less the same texture of sepals and petals. Le Thomas (1969) reported stellate hairs in some species.

Specimens examined:
E. chlorantha: Brenan et al. 8610 (K); Le Testu 1783 (BR); Zenker 441 (U). — *E. kummeriae:* Greenway 921 (K). — *E. letestui:* Le Testu 8432 (BM, BR). — *E. pilosa:* Gossweiler 6209 (BM); Tailfer 55 (BR). — *E. polycarpa:* Versteegh & den Outer 686 (U, WAG).

Greenwayodendron B. Verdcourt, Adansonia sér. 2, 9 (1969) 89.

Buds (lanceoloid to) ovoid (petals). *Sepals* imbricate, 3, free or connate, 2–2.5 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* white

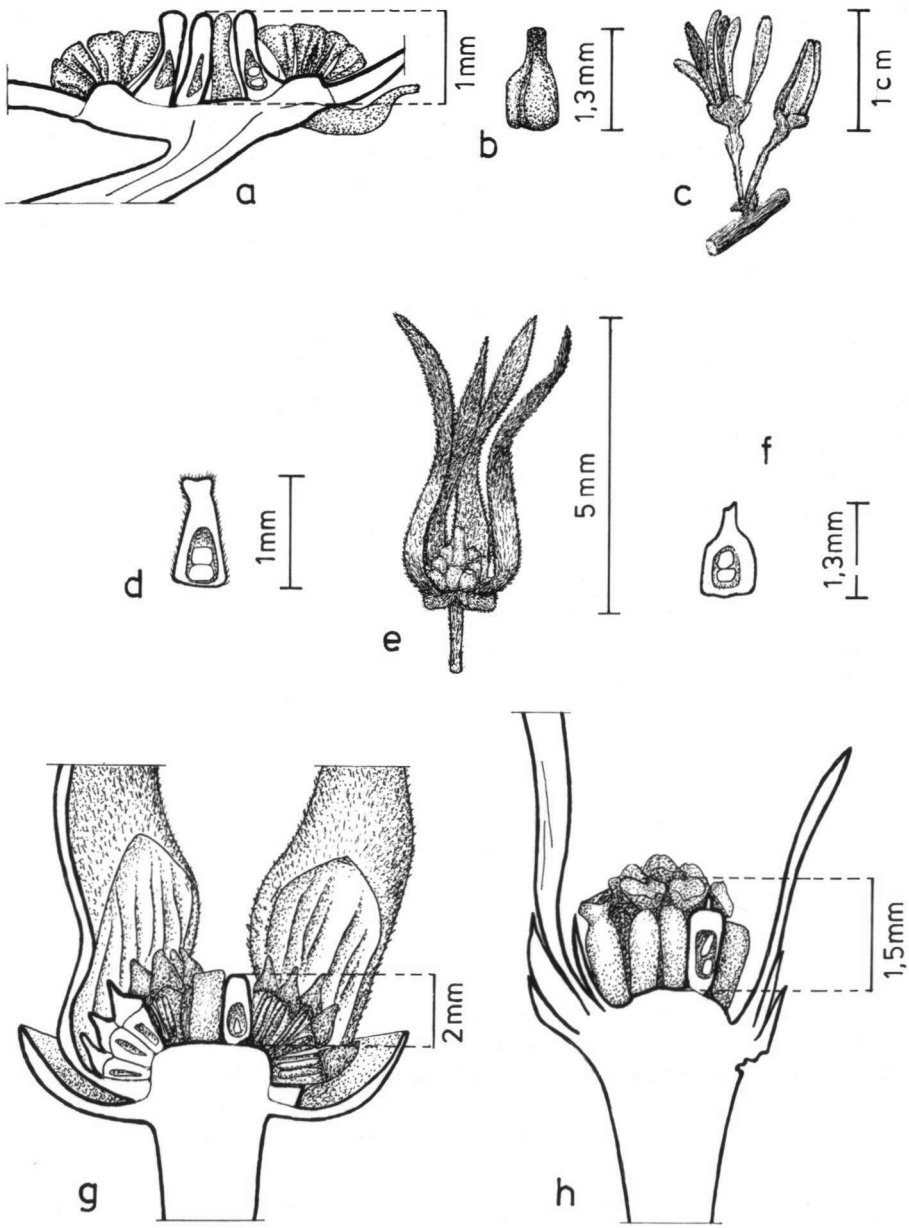


Fig. 47. Genera not included in one of the groups — a. *Tetrameranthus umbellatus* (Tunqui 62): longitudinal section; b. *Mezzettia leptopoda* (U-1227, Cult. Hort. Bog. s.n.): carpel; c. *Greenwayodendron olivieri* (Bos 1953): flower and bud; d. *Tetrameranthus umbellatus* (Tunqui 62): carpel; e. *Mezzettia havilandii* (Cuadra A1304): flower, 2 petals fallen off; f. *Mezzettia leptopoda* (U-1227, Cult. Hort. Bog. s.n.): carpel; g *Tetrameranthus duckei* (Morawetz et al. 21-9883): longitudinal section; h. *Greenwayodendron suaveolens* (Donis 2944): longitudinal section.

with greenish apex, pale green, or green-black, imbricate, 6, free, both whorls equal in length, 6–22 mm long, 6–10 × as long as wide, 3–8 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner petals basally glabrous inside. *Torus* slightly convex, shallowly conical, or very shallowly conical with conical apex. *Stamens* c. 16, 1.8–2.5 mm long, extrorse; apex discoid to tongue-shaped, fleshy or shiny. *Carpels* free, numerous, 1.5 mm long, sometimes stipitate?, glabrous, style absent, stigma shallowly obconical (cup-shaped) or spheroid; ovules 2, lateral, 1-seriate. Androdioecious.

Type – *G. suaveolens* (Engler & Diels) Verdcourt.

Distribution – 2 species in West and Central Africa.

Notes – Stamens of *Greenwayodendron* (fig. 47c, h) resemble those of *Bocageopsis, Onychopetalum* (both Unonopsis-group), and *Oxandra* (Cremastosperma-group). The imbricate aestivation of sepals and petals agrees with the Cremastosperma-group, too, while also androdioecious plants occur in the latter group. *Greenwayodendron,* however, differs from the Cremastosperma-group because of the 2 lateral ovules and the cup-shaped stigma in *G. suaveolens*. The torus of *G. olivieri* resembles that of *Boutiquea,* its carpels resemble those of *Enantia.*

Greenwayodendron was correctly separated from *Polyalthia* by Verdcourt (1969a). The shape of the buds, the different type of stamens, and the androdioeciousness make that *Greenwayodendron* differs too much from *Polyalthia* to be included in that genus.

Specimens examined:

G. olivieri: Andoh FH 5458 (K); Bamps 2533 (K); Bos 1953 (WAG); Geerling & Bokdam 2342 (WAG); de Koning 6660 (WAG); Morton A4178 (K); Versteegh & den Outer 414 (U); Zenker 1306 (BM). — *G. suaveolens:* Donis 2944 (WAG); Le Testu 9408 (WAG); Louis 10916 (K); Peter 18863 (WAG); J.J.F.E. de Wilde 8674 (WAG).

Lettowianthus Diels, Notizbl. Bot. Gart. Berlin-Dahlem 13 (1936) 266, t. 9, II.

Buds depressed ovoid (sepals). *Sepals* imbricate, 3 or 4, free or connate, 8–16 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* yellow, green, or red, imbricate, 6, 8, or 12, free, whorls equal in length, 30–35 mm long, 2.5–3.5 × as long as wide, 2–3 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner petals basally glabrous inside. *Torus* shallowly conical with a flat apex or cylindrical. *Stamens* numerous, 3–4 mm long, extrorse or latrorse; apex discoid, fleshy. *Carpels* free, numerous, 4 mm long, stipitate, hairy, style absent, stigma obconical, glabrous; ovules 2, lateral. *Flowers* bisexual.

Type – *L. stellatus* Diels.

Distribution – 1 species in Tanzania, Africa.

Note – *Lettowianthus* is exceptional because of the unusual combination of many, relatively long stamens together with an imbricate aestivation of sepals and petals. The large mass of stamens resembles that of *Asimina, Malmea,* and several genera of the Uvariastrum-group. The indument resembles that of *Ambavia gerrardii, Cananga latifolia,* and *Tetrameranthus umbellatus* (however stellate in *Tetrameranthus*), while also the texture of sepals and petals is similar to the latter two species. The carpels are stipitate in the flowers, which is also observed in *Disepalum* p.p., *Enantia,* and

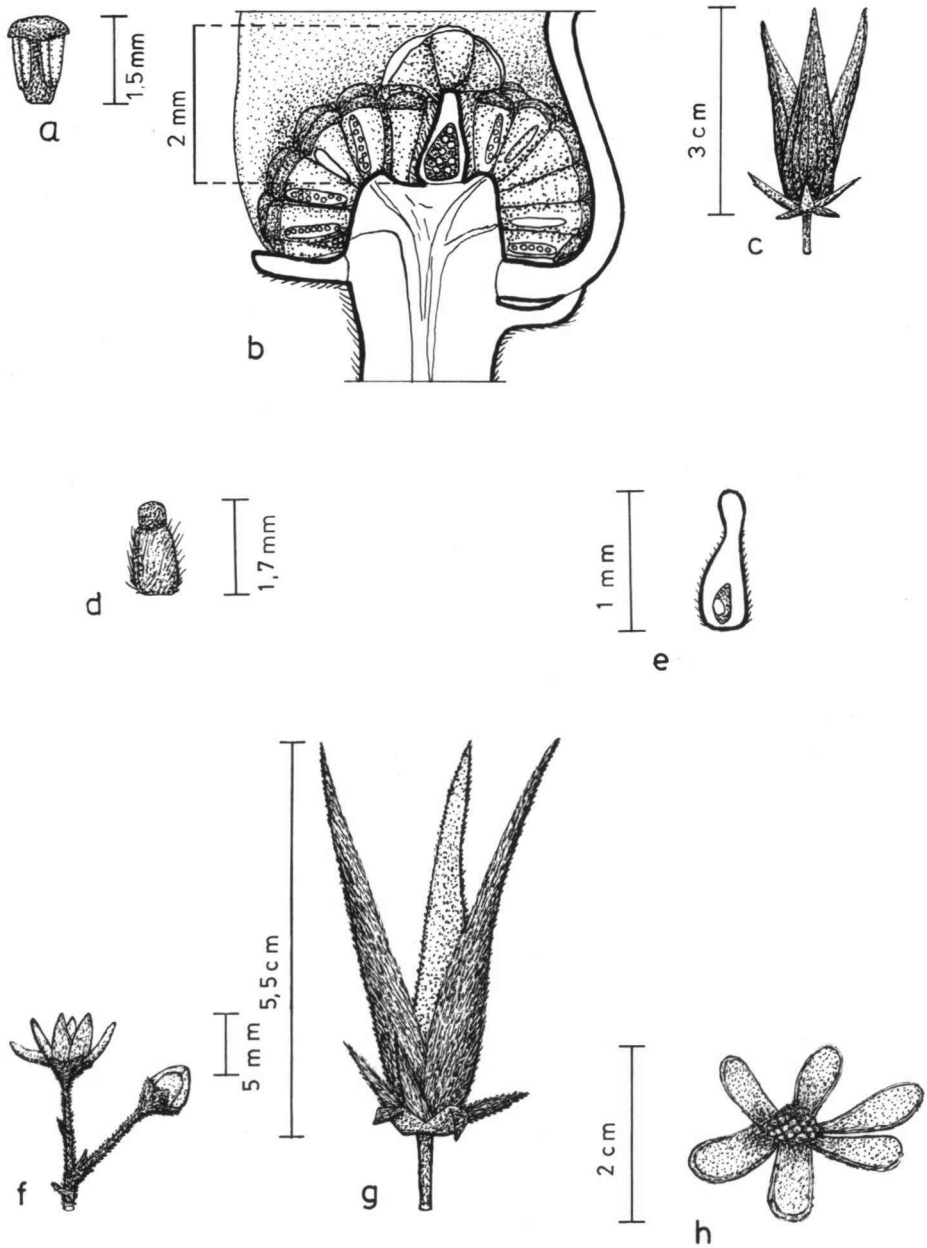


Fig. 48. Genera not included in one of the groups — a., b. & c. *Piptostigma fugax* (van der Laan 218): stamen (a), longitudinal section (b), and flower (c); d. *Neo-uvaria acuminatissima* (Kostermans 13933): carpel; e. *Neo-uvaria acuminatissima* (Lörzing 5546): carpel; f. *Neo-uvaria sp.* (Kostermans 6812): flower and bud; g. *Piptostigma oyemense* (Hallé 2264): flower; h. *Neo-uvaria foetida* (Ramos 24371): flower.

Neostenanthera. The more or less cushion-shaped apices of the stamens resemble those of *Asimina* and *Polyceratocarpus*. The stigma reminds of those of *Dendrokingstonia* (in young flowers), *Piptostigma,* and *Polyalthia* p.p.

Specimens examined:
L. stellatus: Burtt 4994 (BR, K); Haerdi 221/0 (BR); Schlieben 5579 (B, BR, P); Vollesen 3111 (WAG).

Mezzettia Beccari, Nuovo Giorn. Bot. Ital. 3 (1871) 187.

Buds ovoid (petals). *Sepals* imbricate, 3 (or 4), free, 1–2.5 mm long, fleshy, veins not prominent, indument present, hairs simple. *Petals* (pale) yellow, imbricate, 6 (or 8), free, both whorls equal in length, 4–18 mm long, 6–10 × as long as wide, 4–7 × length of sepals, fleshy, veins not prominent, indument present, hairs simple, inner petals basally more or less glabrous inside. *Torus* slightly convex with a slightly concave apex. *Stamens* 7–12, 0.7–0.9 mm long, slightly indurate, introrse (to more or less latrorse); apex depressed ovoid, shiny. *Carpel* 1, 1.3–1.5 mm long, glabrous, style and stigma terete, grooved; ovules 2, lateral, 1-seriate. *Flowers* bisexual.

Lectotype – *M. umbellata* Beccari.

Distribution – 4 species in tropical Asia (Malaysia, Sumatra, and Borneo).

Note – *Mezzettia* (fig. 47b, e, f) is the only annonaceous genus with truly introrse stamens (in part of its species), whereas also monosporangiate thecae seem to occur.

Specimens examined:
M. havilandii: Cuadra A1304 (K); Muin Chai SAN 29839 (L). — *M. leptopoda:* Cult. Hort. Bog. s.n., U-1227 (U); I.A.R.A. 12865 (L); Neth. Ind. For. Service 32393 (L). — *M. macrocarpa:* Wood SAN 17069 (L). — *M. parviflora:* Cult. Hort. Bog. IV-H-32 108 (B); Endert 26 (U).

Neo-uvaria Airy Shaw, Bull. Misc. Inform. (1939) 278.

Buds broadly ellipsoid to spheroid (petals). *Sepals* valvate, 3, connate, 1.3–3 mm long, fleshy, veins not prominent, indument present, hairs simple or stellate. *Petals* pale or creamy-white, pale brownish-yellow, pale whitish-brown, or buff outside, cream inside, valvate or imbricate, 6, free, both whorls equal in length or outer whorl longer, petals sometimes almost in one whorl, 5–10 mm long, 2 × as long as wide, 3–4 × length of sepals, fleshy, thick, veins not prominent, indument present, hairs simple or stellate, inner petals sometimes basally glabrous inside. *Torus* (almost) flat. *Stamens* few to numerous, 1.2 mm long, extrorse or latrorse; apex discoid, sometimes elongate in inner stamens, fleshy, sometimes hairy. *Carpels* free, c. 5–12, 1–1.5 mm long, hairy, style absent, stigma cylindrical, broadly obovoid, or ellipsoid, glabrous; ovule 1, basal. *Flowers* bisexual.

Type – *N. foetida* (Maingay ex J.D. Hooker & T. Thomson) Airy Shaw.

Distribution – 2 or 3 species in Malaysia, Indonesia, and the Philippines.

Notes – *Neo-uvaria* (fig. 48d, e, f, h) reminds of the Polyalthia-group and the Sageraea-group, but differs from the latter group because it has one basal ovule, and from both groups because of the stellate indument in part of the species and the very thick, fleshy petals.

Neo-uvaria paralellivenia differs from the other species of *Neo-uvaria* because the petals are distinctly unguiculate, and because of the imbricate aestivation.

Specimens examined:
N. acuminatissima: Lörzing 5546 (L); Kostermans 13933 (K). — *N. foetida:* Ramos 24371 (K, L); Saikeh SAN 64766 (L); Sinclair et al. 9250 (L). — *N. paralellivenia:* Okada 3391 (U). — *N. sp.:* Kostermans 6812 (P).

Piptostigma D. Oliver, J. Linn. Soc., Bot. 8 (1865) 158, t. 2.

Buds (broadly) ovoid (sepals or petals). *Sepals* valvate, 3, free, 1–6 mm long, fleshy, thin, veins not prominent, indument present, hairs simple. *Petals* olive-green, (pale or reddish-)yellow, or rose striked with red, valvate, 6, free, inner whorl much longer, outer ones 1.5–20 mm, inner ones 28–60 mm long, 4–15 × as long as wide, 7–30 × length of sepals, fleshy, thin, veins prominent, indument present, hairs simple, inner petals basally glabrous inside. *Torus* (broadly) cylindrical. *Stamens* numerous, 1–1.5 mm long, extrorse; apex discoid, fleshy. *Carpels* free, few to numerous, 2 mm long, hairy, style absent, stigma obconical or flat and lobed; ovules 5–9, lateral, 2-seriate. *Flowers* bisexual.

Lectotype – *P. pilosum* D. Oliver.

Distribution – Africa, from Ivory Coast to Angola, 13–15 species.

Notes – *Piptostigma* (fig. 48a, b, c, g) resembles the Miliusa-group in the very small, sepal-like outer petals. *Piptostigma* only differs from the Miliusa-group in the different stigma (obconical instead of ellipsoid) and in the geographic distribution: Africa, whereas the Miliusa-group includes Asiatic genera.

It has short broad stamens which are typical of, e.g., *Dendrokingstonia* and the Meiogyne-group. The stigma resembles that of *Dendrokingstonia* (in young flowers).

Specimens examined:
P. fasciculata: Toussaint 2151, 2367 (BR). — *P. fugax:* van der Laan 218 (WAG). — *P. glabrescens:* Andoh 5666 (WAG); Bos 6415, 6594 (WAG); Zenker 505 (WAG). — *P. multinervium:* Zenker 21 (U). — *P. oyemense:* Hallé 2264 (P). — *P. pilosum:* Bos 6683 (WAG). — *P. sp.:* Leonard 286 (BR); W.J.J.O. de Wilde & de Wilde-Duyfjes 2132 (BR).

Tetrameranthus R.E. Fries, Acta Horti Berg. 12 (3) (1939) 554, f. 41.

Buds broadly depressed ovoid (sepals). *Sepals* partly valvate and partly imbricate, 4, free, 3–5 mm long, fleshy, veins not prominent, indument present, hairs stellate. *Petals* yellow to green, imbricate (or valvate?), 8, free, both whorls equal in length, 7–27 mm long, 2–5 × as long as wide, 2–4 × length of sepals, fleshy, veins not prominent, indument present, hairs stellate, basal part of inner petals glandular inside, sometimes basally glabrous along the margin outside. *Torus* broadly cylindrical, depressed obovoid, or flat with a slightly concave apex. *Stamens* numerous, 1.5–2 mm long, latrorse; apex umbonate or discoid, fleshy. *Carpels* free, 6 to numerous, 1–2 mm long, (stellate) hairy or papillose, style absent, stigma flat and lobed, spheroid, or depressed ovoid, glabrous or hairy; ovules 1 or 2, lateral. *Flowers* bisexual.

Type – *T. duckei* R.E. Fries.

Table 24. List of character states found in the genera not placed in a group.

Taxa: A1 = *Ambavia*, A2 = *Anaxagorea*, C1 = *Cleistochlamys*, C2 = *Cleistopholis*, D = *Dendrokingstonia*, E = *Enantia*, G = *Greenwayodendron*, L = *Lettowianthus*, M = *Mezzettia*, N = *Neouvaria*, P = *Piptostigma*, T = *Tetrameranthus*.

	A1	A2	C1	C2	D	E	G	L	M	N	P	T
Flowers:												
3-merous	+	+	+	+	+	+	+	+	+	+	+	–
2-merous	–	+	–	–	–	–	–	–	–	–	–	–
4-merous	–	–	(+)	–	–	–	–	+	–	–	–	+
hairs stellate	–	+	–	–	–	–	–	–	–	+	–	+
hairs simple	+	+	+	–	+	+	+	+	+	+	+	–
indument absent	(+)	+	–	+	–	–	–	–	–	–	–	–
male	–	–	–	–	–	–	+	–	–	–	–	–
bisexual	+	+	+	+	+	+	+	+	+	+	+	+
Sepals:												
imbricate	+	+	–	+	+	–	+	+	+	?	–	+
valvate	–	+	+	–	–	–	–	–	–	+	+	+
reduplicate-valvate	–	+	–	–	–	+	–	–	–	–	–	–
connate	–,+	–,+	–,+	–	–	–	–,+	–,+	–	+	–	–
0.5–5 mm long	+	+	+	+	+	+	+	–	+	+	+	+
5–16 mm long	–	+	–	–	–	+	–	+	–	–	(+)	–
Petals:												
imbricate	+	+	+	+	+	–	+	+	+	+	–	+
valvate	–	+	–	(+)	–	+	–	–	–	+	+	+?
outer whorl absent	–	–	–	–	–	+	–	–	–	–	–	–
inner whorl absent	–	–,+	–	–	–	–	–	–	–	–	–	–
inner whorl smaller	+	–,+	–	+	–	–	–	–	–	–,+	–	–
outer whorl smaller	–	–	–	–	–	–	–	–	–	–	+	–
1.5–10 mm long	+	+	+	+	+	–	+	–	+	+	–	+
10–60 mm long	–	+	–	+	–	+	+	+	+	–	+	+
Stamens:												
numerous	–	+	(+)	+,–	–	+	–	+	–	+,–	+	+
anthers extrorse	+	+	+	–	+	+	+	+	–	+	+	–
anthers latrorse	–	(+)	–	+	+	–	–	+	+	+	–	+
anthers introrse	–	–	–	–	–	–	–	–	+	–	–	–
apex discoid	(+)	+	+	+	+	+	+	+	(+)	+	+	+
apex tongue-shaped	+	+	–	–,(+)	–	+	+	–	–	–	–	–
apex semi-globose	–	–	–	–	–	–	–	–	+	–	–	–
apex umbonate	–	–	–	–	–	–	–	–	–	–	–	+
staminodes present	–	–,+	–	–	–	–	–	–	–	–	–	–
0.5–1 mm long	–	–	+	+	+	–	–	–	+	–	–	–
1–4.5 mm long	+	+	–	–	–	+	+	+	–	+	+	+
Carpels:												
1 in number	(+)	(+)	–	–	+	–	–	–	+	–	–	–
> 1 in number	+	+,–	+	+	–	+	+	+	–	+	+	+
Ovules:												
1, basal	–	–	+	–	–	+	–	–	–	+	–	–
2, basal	–	+	–	–	–	–	–	–	–	–	–	–
(1–)2, lateral	+	–	–	+	+	–	+	+	+	–	–	+
> 2, lateral	–	–	–	–	+	–	–	–	–	–	+	–

Distribution – 6 species in Amazonian Brazil, Colombia, and Peru.

Notes – *Tetrameranthus* has an unusual combination of character states. It has 4-merous flowers (fig. 45e), stellate hairs, and 2 lateral ovules (fig. 47d). The aestivation of the sepals and the petals is rather indistinct.

It is difficult to indicate affinities of *Tetrameranthus* to other genera. Perhaps it is most related to *Cleistopholis* with which it shares the same type of carpel. *Tetrameranthus* shares with *Duguetia* the stellate hairs and the glandular base of the inner petals, but *Duguetia* has only one, basal ovule. *Tetrameranthus umbellatus* and *T. laomae* have very small greyish hairs on their flowers, comparable with those of *Ambavia, Cananga latifolia,* and *Lettowianthus*. The hairs of these three genera, however, are simple.

Tetrameranthus is not very coherent in its flower morphology, despite its low number of species. The differences in flower morphology which are found between, for instance, *T. duckei* and *T. umbellatus,* are such as are usually found between genera. For instance, the different shapes of the apices of the stamens: in part of the species it is umbonate, in the other species it is discoid. They also differ in the shape of the torus (fig. 47a, g). The differences found in the flowers of these two species correspond with a different chromosome number (Morawetz, 1986b).

Specimens examined:

T. duckei: Ducke 1908 (F, NY), RB 23919 (S), RB 35313 (S); Ferreira 79/57 (S); Morawetz et al. 21-9883, 21-23883 (U); Prance et al. 2721 (INPA, NY, US); Rodrigues & L. Coêlho 2937 (U). — *T. laomae:* Soria S64 (F). — *T. macrocarpus:* Schultes & Cabrera 17091 (GH, US). — *T. pachycarpus:* Klug 1216 (US). — *T. umbellatus:* Morawetz & Wallnofer 14-81085 (U); Tunqui 62 (U). — *T. sp.:* Lleras et al. P17302 (U).

5. DISCUSSION OF CLASSIFICATION ON THE BASIS OF FLORAL FEATURES

5.1. DISTRIBUTION OF CHARACTER STATES

In their flowers, the Annonaceae are very uniform on one hand, but they exhibit an enormous diversity and a reticulate distribution of character states on the other hand.

Usually the genera can be recognized easily on the basis of their flowers. The genera accepted in this study are characterized either by a unique combination of character states (most commonly) or by a unique feature. Most genera are quite uniform in their flower morphology. This even applies to genera with a large number of species, e.g., *Rollinia* (c. 45 species) and *Guatteria* (c. 250 species).

Some genera, however, show a strong diversity in their flowers. In *Ambavia* the two species are different in the size of the flowers and the shape of the stamens. In *Anaxagorea* the flowers of the Asiatic species differ rather strongly from those of the neotropical species. In *Annona* the petals vary in shape, size, and number. *Friesodielsia* exhibits diversity in shape and size of its perianth. In *Papualthia* the species from New Guinea have small flowers and those from the Philippines have middle-sized flowers. In *Sapranthus* large purplish flowers with many ovules per carpel occur beside much smaller greenish flowers with few ovules. Also in *Tetrameran-*

thus two types of flowers are found. In *Uvaria* the Asiatic species have reddish flowers and stamens with tongue-shaped apices, whereas the African species have greenish flowers and stamens with discoid apices.

Similarity in nearly all character states is found in the flowers of *Desmos* and *Sapranthus,* which similarity is, however, not paralleled in non-floral features. These two genera mainly differ in the texture of the apices of the stamens. Several more examples exist of genera which show a striking similarity but differ in few but essential character states. *Cremastosperma* and *Guatteria,* both with imbricate petals of the same shape and size, differ only in the aestivation of the sepals and the texture of the stamens. Non-floral features indicate that these genera are not related. Such striking similarities between genera may explain why, for instance, earlier taxonomists included *Chieniodendron* in *Fissistigma.*

Unique combinations of character states occur in, e.g., *Ophrypetalum* (large sepals, imbricate petals with fringe on the inner side, a deeply concave torus, many small stamens without an apical prolongation of the connective, and carpels with a conspicuous style) and *Tetrameranthus* (stellate hairs, 4-merous flowers, stamens with a conical apex in part of the species, and 1–2 lateral ovules).

Distinctive character states are present in a number of genera. Some of these peculiar or unique features are:

— the ring of staminodes (innermost stamens) with glandular tips in part of the *Anaxagorea*-species;
— the rather pellucid and (in bud) entirely fused sepals of *Cleistochlamys* (fig. 1k);
— the relatively small inner petals which tightly enclose the stamens and carpels in *Cleistopholis*;
— the sepals which are located distinctly below the torus in the flowers in *Disepalum*; *Disepalum* has also otherwise the most aberrant flowers within the Annonaceae (fig. 1h);
— the absence of the outer whorl of petals in *Enantia*;
— the ring-shaped arrangement of staminodes (outer stamens) in *Fusaea*;
— the petals being folded in buds of *Hexalobus*;
— the conspicuous scales on the sepals and outer petals of *Meiocarpidium*;
— the introrse stamens and the possibly monosporangiate thecae in *Mezzettia* p.p. (fig. 7j);
— the gynophore in *Mischogyne* which is extremely long in *M. michelioides* (fig. 39b);
— the relatively large wings on the inner petals of *Petalolophus*;
— the very large purplish petals in *Sapranthus* p.p. (fig. 35d).

5.2. Longitudinal sections of the flowers

All genera show a distinctive configuration of torus, stamens, and carpels in the longitudinal sections of their flowers. Most genera are uniform in this respect, only in *Tetrameranthus* two different types are present (fig. 47a, g). Genera which are considered as being related, show a close similarity in their longitudinal sections.

In most genera the stamens and the carpels form a hemispherical to ovoid mass. Usually the carpels do not or hardly surpass the stamens. Only in *Artabotrys, Duguetia, Goniothalamus* (fig. 42g), *Ophrypetalum, Pseudoxandra,* and *Xylopia* (fig. 43a) the long stigmas conspicuously surpass the stamens. In *Alphonsea* and *Toussaintia* (fig. 25e) the carpels are placed on a long cylindrical torus. Contrary, in *Bocageopsis, Onychopetalum,* and *Oxandra* the small carpels are hidden by the long stamens. In *Dennettia, Meiocarpidium, Monocyclanthus, Polyceratocarpus,* and *Uvariodendron* torus, stamens and carpels together tend to form one globose mass (fig. 40).

A distinctive configuration is found in a number of genera. *Cleistochlamys* is distinct by the deeply concave torus and the fringe of the inner petals filling the 'floral chamber'. *Hexalobus* is easily recognized by the many transverse foldings of the petals.

Some genera are not distinct from other genera in their longitudinal sections. This applies to *Rauwenhoffia* versus *Uvaria, Guatteriopsis* versus *Guatteria,* and *Bocageopsis* versus *Onychopetalum.* One, unnamed species from Mexico, discussed under *Desmopsis* (fig. 35b), shows a striking similarity with the Australian genus *Haplostichanthus* (fig. 32b). Some specimens of *Meiogyne* resemble some specimens of *Unonopsis.* Another example is *Pachypodanthium* of which at least one species is not distinct from *Duguetia* in this respect.

Closely related genera, which are different in their perianth, may be strongly similar in their longitudinal sections. This applies to the 'Annona-gruppe' of Fries (1959). *Annona, Anonidium, Raimondia,* and *Rollinia* show a characteristic configuration in their longitudinal sections. *Annona* and *Rollinia* are alike in this respect, whereas *Anonidium* most resembles the African *Annona*-species and *Raimondia. Cymbopetalum* and *Porcelia* are different in their perianth, too, but closely resemble each other in their longitudinal sections. Also *Asteranthe* resembles these two genera in this respect.

Occasionally, genera which are not related show a comparable configuration of stamens and carpels. This is observed between *Cremastosperma* and *Guatteria.* This more or less applies also to *Alphonsea* and *Fissistigma* of which the carpels are placed on a rather elongate torus. These two genera, however, have different stamens.

5.3. The value of floral characters for classification

It is not possible to recognize satisfactory groups on the basis of unique character states unless great discrepancies with non-floral characters are accepted. All informal groups as used in this paper are therefore based on a combination of character states (table 3), in which the frequent (not always consistent) presence or absence is decisive. As a result the following character states characterize certain groups and are considered as important for classification:

Structure of the bud – In some groups the buds are formed by the petals, e.g., Cremastosperma-group, Meiogyne-group, Miliusa-group, Sageraea-group, and Unonopsis-group. The Duguetia-group and the Fusaea-group have buds enclosed by the sepals. More diverse in this respect are the Cymbopetalum-group and the Uvariastrum-group. Some genera show intermediate forms, e.g., in the Friesodielsia-group, the Uvaria-group, and the Xylopia-group. This character seems to be nearly

as important as the aestivation of the petals in the classification of Fries (1959), but it is not possible to subdivide the Annonaceae on this basis into two clearly delimited groups (table 3). This character more or less correlates with the chromosome number (table 26).

Flower break – The moment (in terms of morphology) at which the flower bud opens, is often characteristic for a group. For instance, in genera of the Unonopsis-group the buds open at the onset of the anthesis. In the Sapranthus-group unopened flower buds were rarely seen. In many genera of the Friesodielsia-group only unopened flowers were observed.

Aestivation – The sepals are considered as more important than the petals in this respect but should be used in combination with the petals. The neotropical Cremastosperma-group has imbricate sepals and petals. On the other hand, many Asiatic and African genera with imbricate sepals and petals are difficult to place and are not placed in a group. The aestivation of the petals only is not valuable in defining groups as in most groups both genera with imbricate and with valvate petals are found, e.g., in the Fusaea-group, the Guatteria-group, the Hexalobus-group, the Meiogyne-group, the Polyalthia-group, the Sageraea-group, and the Uvaria-group.

Indument – Stellate hairs are typical of the Uvaria-group and the Duguetia-group. It makes the positions of *Meiocarpidium* (scales) and *Dielsiothamnus* (stellate hairs) in the Uvariastrum-group somewhat uncertain. The same applies to the position of *Dasoclema* (stellate hairs) in the Friesodielsia-group.

Texture of sepals and petals – The groups are usually uniform in this respect. In the Hexalobus-group (the petals) and the Sapranthus-group (the whole perianth) the texture is relatively thin. There is a tendency that in groups with relatively small flowers the sepals and petals have about the same texture, whereas in groups with larger flowers texture of sepals and petals is often different.

Venation of sepals and petals – A longitudinal venation is usually prominent in the Sapranthus-group.

Length of the sepals – Each group has a maximum length which is different for each group. In the Cremastosperma-group, the Mitrephora-group, the Monanthotaxis-group, and the Unonopsis-group the sepals do not exceed a length of 5 mm. In the Fusaea-group a maximum length of 25 mm is measured. This character is associated with the structure of the bud.

Shape of the petals – This feature is quite uniform in many groups, e.g., the Cremastosperma-group (except *Ruizodendron*), the Meiogyne-group, the Miliusa-group, the Monanthotaxis-group, the Sapranthus-group, the Unonopsis-group, the Uvaria-group, and the Uvariastrum-group. Many genera of the Mitrephora-group have connivent inner petals with a narrow unguiculate base.

Size of outer and inner petals – Most groups are uniform in this respect. The inner and outer petals may be of equal size (e.g. Uvariastrum-group) or different in size. In the Xylopia-group and the Friesodielsia-group the inner petals are usually smaller. In the Miliusa-group the outer petals are much smaller and about the same size as the sepals.

Floral glands – A glandular base of the inner petals is typical of the Meiogyne-group.

Shape of torus – The shape of the torus is uniform in most groups. In the Uvariastrum-group the torus is enlarged into various shapes. In the Annona-group and the Duguetia-group the relatively long and narrow apex bearing the carpels is clearly set off from the broad basal part where the stamens are placed. A flat torus is common in the Monanthotaxis-group.

Diameter of the torus – This character was not measured in the present study, but is essential in separating the Fusaea-group and the Guatteria-group.

Number of stamens – Most groups are uniform in this respect. In the Monanthotaxis-group and the Sageraea-group few stamens are common. In the Fusaea-group, the Hexalobus-group, and the Uvariastrum-group the number is very large.

Shape of the stamens – Some groups are uniform in this respect, whereas other groups are more diverse (e.g. Monanthotaxis-group). Distinctive stamen types are present in, e.g., the Fusaea-group (except in *Afroguatteria*), the Guatteria-group, the Uvaria-group, and the Xylopia-group.

Texture of stamens – Although never used in this respect before, this feature defines some groups: in the Fusaea-group, the Guatteria-group, and the Xylopia-group the stamens are indurate.

Shape of the apex of the stamen – This feature is usually of minor importance. In the Meiogyne-group, however, the apex of the inner stamens is elongate.

Texture of the apex of the stamen – This feature is often uniform within a group. The apices are often shiny in the Friesodielsia-group; they are fleshy in, e.g., the Sapranthus-group. Rigid apices occur in the Duguetia-group, the Fusaea-group, and the Xylopia-group.

Septate anthers – These are present in the Cymbopetalum-group and the Xylopia-group.

Margins of thecae – Thecae with involute margins (after dehiscence) are found in several genera of the Guatteria-group.

Number of carpels – This character is mostly uniform within a group. Large numbers are typical of, for example, the Annona-group, the Duguetia-group, the Fusaea-group, and the Uvaria-group. The Hexalobus-group is characterized by one to few carpels.

Shape of carpels – Certain types are more frequent in certain groups. Because of the diversity within the groups it is difficult to give good examples. A style is commonly found in the Duguetia-group, the Fusaea-group, and the Xylopia-group. Also the shape of the stigma is often important.

Number of ovules – This feature is useful in the classification of genera. The Annona-group, the Duguetia-group, and the Fusaea-group (except *Disepalum*) always have one, basal ovule. Also in the Cremastosperma-group there is only one ovule: the placentation, however, may be basal or lateral, or even apical. A large number of ovules is found in the Cymbopetalum-group, the Hexalobus-group, and the Uvariastrum-group. The placentation here is always lateral, and mostly 2-seriate.

5.4. Geographical differences

Between the continents considerable differences in the differentiation and the geographic distribution of the groups of genera can be observed:

The neotropical genera can be grouped easily. For most neotropical groups it is possible to follow the classification of Fries (1959): the Annona-group, the Cremastosperma-group, the Cymbopetalum-group, the Guatteria-group, the Sapranthus-group, and the Unonopsis-group are based on (part of) Fries's groups. Only the 'Duguetia-gruppe' of Fries (1959) with, among others, *Duguetia, Fusaea,* and *Malmea* in one group, and also the 'Xylopia-gruppe' with, among others, *Anaxagorea, Diclinanona,* and *Xylopia* in one group, did not satisfy. *Anaxagorea, Diclinanona,* and *Tetrameranthus* are not or tentatively placed in a group. *Tridimeris* could be accommodated only in a group with some Asiatic genera.

In Africa many genera show in their flower morphology only vague relationships to other genera, and thus give great problems for the classification. Problematic genera which are either tentatively or not included in one of the groups are, e.g., *Afroguatteria, Ambavia, Artabotrys, Cleistochlamys, Cleistopholis, Dielsiothamnus, Enantia, Greenwayodendron, Lettowianthus, Meiocarpidium, Ophrypetalum,* and *Toussaintia.* Several genera extend into Asia (*Artabotrys, Friesodielsia, Polyalthia, Sphaerocoryne, Uvaria*) or the Neotropics (*Annona*). Others have their nearest and only relatives in the Neotropics: *Mkilua* (*Porcelia*) and *Pachypodanthium* (*Duguetia*).

In Asia the majority of the genera is uniform with regard to their stamens and carpels, whereas the perianth shows many intermediates from one type to another. Consequently, it is very difficult to delimit groups. In particular this applies to the genera placed here in the Miliusa-group, the Mitrephora-group, the Polyalthia-group, and the Sageraea-group. Genera which are difficult to place, are *Dasoclema, Dendrokingstonia, Mezzettia, Monocarpia,* and *Neo-uvaria.*

5.5. The genus delimitation on the basis of floral features

Starting from the genera accepted by Fries (1959) (see for exceptions Chapter 2), on the basis of the flowers selected in this study, many problems with the generic delimitation are encountered. Although most specimens can easily be referred to a genus, only a minority of the genera seems well-separated from other genera.

Some genera show a continuous variation from one extreme to another. As a result, *Papualthia* from New Guinea is by its flowers not distinguishable from the Australian genus *Haplostichanthus.* The same applies to the flowers of *Bocageopsis* and *Onychopetalum.* One species of *Meiogyne* cannot be distinguished from *Oncodostigma* by its flowers.

Some (small) genera fall within the variation range of another genus: *Boutiquea,* among others, is florally not different from *Neostenanthera,* and *Richella* does not really differ from *Goniothalamus. Boutiquea* differs from *Neostenanthera* in the fruits (Le Thomas, 1965). *Ephedranthus* in its flower morphology falls within the range of *Malmea*; they can, however, be distinguished by their leaves. *Guamia,* as far as examined, does not differ from *Oncodostigma.* The same applies to *Guatteriella* versus *Guatteria.*

Only quantitative differences are found between *Platymitra* and *Orophea. Cyathostemma* and *Tetrapetalum* only differ in the number of petals. *Mkilua* and *Porcelia* only differ in the ovule number and the size of the inner petals which are smaller in *Mkilua. Cardiopetalum* and *Froesiodendron* differ, apart from the size of the flowers,

in the texture of the apices of the stamens. *Annona* and *Raimondia* only differ in the sex distribution.

In a number of cases intermediate species are found between two, normally distinct genera, e.g., between *Guatteria* and *Guatteriopsis* which generally differ in the aestivation of the petals. Some *Annona*-species have dorsally thickened petals, thus tending to *Rollinia* with its gibbous to winged petals. A few *Monanthotaxis*-species have larger flowers which resemble some *Friesodielsia*-species (e.g., *F. obovata*) with smaller flowers.

A number of genera seem to form one genus with several distinct flower morphological variants. *Annona, Raimondia,* and *Rollinia* may form one genus on the basis of their distinct fruit-type, being diverse in their flowers. *Desmopsis, Sapranthus,* and *Stenanona* are not well-separated, either. *Ancana, Chieniodendron, Guamia, Meiogyne, Oncodostigma,* and *Polyaulax,* four of them being monotypic genera, seem to represent distinct species of one genus when judged from their flowers. *Enicosanthum, Papualthia,* and *Trivalvaria* may be only sections of *Polyalthia,* which differ in size of the flowers, fusion of perianth-parts, or ovule number. *Uvaria,* which shows diversity in its flowers, may include *Anomianthus, Balonga, Cyathostemma, Ellipeia, Ellipeiopsis, Rauwenhoffia,* and *Tetrapetalum,* as well.

In some cases problems with the generic delimitation are restricted to one particular area. A number of (widespread) genera are distinct in Asia, but are difficult to separate in New Guinea. This is observed between *Pseuduvaria* and *Mitrephora,* between *Mitrella* and *Fissistigma,* and between *Rauwenhoffia* and *Uvaria.* A comparable situation is found in Madagascar, where some *Uvaria*-species show features of *Anomianthus* and *Rauwenhoffia,* genera which in Asia are distinct from *Uvaria.*

5.6. The classification of Fries (1959) reconsidered

The interpretation of character states recognized in the present study is largely the same as interpreted by Fries (1959), see table 1. The main differences with Fries concern the number of petals of *Fenerivia* (see descriptive part), the carpel with unusual placentation in *Isolona* and *Monodora,* and in some cases the aestivation (see below).

The character states, mainly of the petals, selected by Fries (1959) and earlier taxonomists to define groups or tribes within the Annonaceae, are in many cases not supported by character states of stamens and carpels. Many character states seem to have developed independently in two or more (groups of) genera, thus resulting in a strongly reticulate distribution of character states.

Often genera from several continents sharing one particular character state, but not having any further similarity, were combined by Fries in one group. As result, many unnatural groups were created, e.g., the 'Asimina-gruppe', the 'Desmos-gruppe', the 'Monanthotaxis-gruppe', the 'Unonopsis-gruppe', and the 'Uvaria-gruppe'.

Within the 'Orophea-gruppe', of which the flowers are characterized by mitriform inner petals, *Goniothalamus* differs considerably in the shape of stamens and carpels from, e.g., *Mitrephora, Orophea,* or *Pseuduvaria. Goniothalamus* in this respect resembles more *Boutiquea, Neostenanthera,* and *Richella. Neostenanthera* (including the later described *Boutiquea*) was placed in the 'Artabotrys-gruppe'.

On the other hand, the 'Duguetia-gruppe' and the 'Uvaria-gruppe', both defined by, among others, imbricate petals, seem to be unnatural because they combine genera with simple hairs and those with stellate hairs. Although never used in classifications before, the presence of stellate hairs correlates well with other characters and deserves more attention.

The 'Monanthotaxis-gruppe' is based on the arrangement of the petals in one whorl. This is, however, also found in some genera placed in other groups by Fries (1959): *Diclinanona* p.p., *Disepalum*, and *Isolona*. *Popowia* (African species, in the present study referred to *Monanthotaxis*), placed in the 'Orophea-gruppe', with petals in two whorls, closely resembles *Monanthotaxis* s.s. and *Enneastemon* (in the present study included in *Monanthotaxis*).

Malmea is placed in the 'Duguetia-gruppe' because of its leaf-opposed inflorescence. In floral characters it closely resembles *Cremastosperma* and *Ephedranthus* of the 'Asimina-gruppe' with axillary inflorescences.

Two groups are based on non-floral characters: the 'Annona-gruppe' (with fruits composed of fused carpels) and the 'Trigynaea-gruppe' (with bractless pedicels). Despite diversity in the flowers (Trigynaea-gruppe) or the perianth (Annona-gruppe) they seem to be natural groups.

Tetrameranthus, placed in a separate tribe because of the spiral arrangement of the leaves, on the basis of the flowers indeed is not easy to place near other genera. However, this applies to some other genera as well.

Isolona and *Monodora* are accommodated in a separate subfamily Monodoroideae because of their gynoecium with ovules covering the whole ovary wall, which is generally considered as a syncarpous ovary with a parietal placentation. In other floral features these two genera do not resemble each other, but in floral structure they are not different from the other genera within the Annonaceae. In general shape their gynoecium resembles that of some unicarpellate species of *Cyathocalyx*. Only the placentation differs: 2-seriate in *Cyathocalyx martabanicus* (own observation) and *C. sumatranus* (Sinclair, 1955), and probably laminal in *Isolona* and *Monodora*. Leins & Erbar (1980, 1982) did not find indications of syncarpy in *Monodora* on the basis of ontogenetical studies. Van Setten (1990) found fruits with seeds in up to 5 rows in *Cyathocalyx*, *Dielsiothamnus*, and *Uvariastrum*.

The aestivation is an essential character in the classification of Fries (1959). In several cases the aestivation as observed in the present study differs from the observations of Fries, and this would have consequences for the position of that genus in his classification. *Mischogyne* ('Uvaria-gruppe', imbricate petals) appears to have valvate petals. In *Asimina* ('Asimina-gruppe', imbricate sepals) valvate sepals are found, while they appear to be imbricate in *Lettowianthus* ('Hexalobus-gruppe', valvate sepals). *Kingstonia* (= *Dendrokingstonia*) and *Mezzettia* ('Polyalthia-gruppe', valvate sepals and petals) have imbricate sepals and petals. Moreover, for several genera it is not possible to ascertain the aestivation with certainty.

A subdivision of the Annonaceae in Uvarieae and Unoneae, based on the aestivation of the petals (imbricate and valvate respectively) seems to make the classification of Fries unnatural. In a number of genera both valvate and imbricate petals are observed, e.g., in *Anaxagorea*, *Duguetia*, *Neo-uvaria*, and *Trivalvaria*. The closely related genera *Guatteria* and *Guatteriopsis* differ only in the aestivation of the petals,

imbricate and valvate respectively. *Rauwenhoffia* (of which the Asiatic species appeared to be imbricate) with valvate petals and *Uvaria* with imbricate petals are placed in different groups, but in other features they are very similar, and in New Guinea the two genera cannot be distinguished very well.

5.7. Comparison with non-floral features

Generally, the Annonaceae show a greater diversity in their flowers than in other parts of the plants. It is therefore usually easier to recognize affinities between genera on the basis of non-floral features than on the basis of the flowers. On the other hand, many genera are very similar in non-floral features, and can be distinguished only by their flowers. Comparison with non-floral features learns that more attention should be paid to the texture of the perianth, the stamen type, and the ovule number in classifications of the family. The non-floral features as compared with the flower morphology are briefly discussed below.

Leaves – The only studies available on this subject are those of the leaf venation patterns (Klucking, 1986) and the leaf anatomy of neotropical genera (Van Setten & Koek-Noorman, 1986). There is no agreement between the leaf venation patterns as recognized by Klucking and the flower morphology. Judged from the flower morphology other characters than those used by Klucking are important in a subdivision of venation patterns for taxonomical purposes. Much more agreement is present with the leaf anatomy. Observations by the author on the leaves with regard to shape, texture, indument, and venation patterns, learn that there is often agreement between flower morphology and leaf morphology. The leaves are helpful in recognizing affinities between genera and the delimitation of groups. In particular this applies to the Asiatic genera which are rather difficult to classify.

Fruits – Only a preliminary outline on the fruit and seed morphology is available (Van Setten, 1990). As far as conclusions can be drawn at this moment, there is a general agreement between flowers and fruits and seeds. Van Setten (1990) presents a scheme of transformation series in the fruits and seeds, which is briefly discussed below:

The groups of *Ancana, Enicosanthum,* and *Alphonsea,* on the basis of their flowers are related, but the genera are grouped in a somewhat different way. These three groups comprise genera of the Cremastosperma-group, the Meiogyne-group, the Polyalthia-group, the Sageraea-group, and the Sapranthus-group. The position of *Porcelia* within one of these groups is not supported.

A position of *Enantia* near *Bocageopsis* and *Unonopsis* is not supported by the flowers.

Van Setten's group comprising *Ambavia, Cleistopholis, Lettowianthus, Mezzettia,* and *Tetrameranthus* is very diverse in its flowers, although there are some indications for a relationship between these genera, e.g., in the imbricate aestivation, the latrorse anthers, and the 2 ovules of which one subbasal.

Placing *Monocarpia, Piptostigma,* and *Polyceratocarpus* in one group with *Mitrephora, Platymitra,* and *Pseuduvaria,* is not supported by the flowers.

Van Setten's groups of *Annona, Guatteria,* and *Duckeanthus* (*Fusaea*) are supported by the flower morphology although the group of *Duckeanthus* has to be divided into a group with stellate hairs (*Duguetia* and *Pachypodanthium*) and one with simple hairs (*Fusaea* and its relatives).

The group of *Dasymaschalon* seems correct but is diverse in its flowers. *Sphaerocoryne* is closer to *Mitrella* and *Pyramidanthe* (both group of *Fissistigma*) in its flowers, whereas *Friesodielsia* shows some intermediate features with *Fissistigma.* Thus the groups of *Dasymaschalon* and *Fissistigma* have to be combined on the basis of the flowers.

The group of *Cyathostemma* agrees with the Uvaria-group.

The groups of *Dennettia* and *Isolona* comprise several genera of the Hexalobus-group and the Uvariastrum-group.

With regard to the genus-concept, there are several cases of (related) genera which are diverse in their flower morphology and uniform in their fruits and seeds, and vice versa. *Annona* and *Rollinia* cannot be distinguished on the basis of their fruits but are different in their flowers. The same applies to *Duguetia* and *Pachypodanthium. Desmos* and *Dasymaschalon* are often considered as one genus on the basis of their moniliform fruits, the latter genus being reduced to a section of *Desmos* (e.g., Sinclair, 1955). They resemble each other in stamens and carpels but are different in their perianth. On the other hand, *Boutiquea* and *Neostenanthera* differ in their fruits whereas their flowers are not different. Within *Orophea* two types of fruits occur (Keßler, 1988) whereas the flowers are uniform.

Seeds – Seed anatomy of the Annonaceae was studied by Christmann (1987). He presents a classification based on seed anatomy, which is, however, not supported by the flower morphology. This seems due to the priority of the characters he selected. The presence or absence of oil cells in the seeds corresponds with the informal classification presented in the present paper.

Karyology – For several genera counts of chromosome numbers are available (table 26). Thus far, the counts within each group do not contradict each other and each group is characterized by only one basal number. More information about the relation between flower morphology and karyological data is given in Chapter 7.

Pollen morphology – General morphology was studied by Walker (1971a, b, 1972) and the ultrastructure of the pollen of the African genera by Le Thomas (1980/81). There is a general agreement between flower and pollen morphology, but the pollen morphological groups have to be divided into smaller groups on the basis of the flower morphology. The system of Walker, as one of the most elaborate classifications, is discussed more in detail below:

Malmea-tribe – The position of *Enantia* in this tribe is not supported by the flower morphology. The remaining genera can be divided into two groups on the basis of the aestivation, representing the Cremastosperma-group and the Unonopsis-group.

Uvaria-tribe – This large tribe should be subdivided into smaller groups on the basis of the flowers. This tribe comprises the Duguetia-group, the Friesodielsia-group,

the Meiogyne-group, the Miliusa-group, the Mitrephora-group, the Sageraea-group, the Sapranthus-group, and the Uvaria-group in the present paper. *Polyceratocarpus* on the basis of the flowers should be transferred to the *Hexalobus*-tribe and *Letestudoxa* and *Pseudartabotrys* to the *Fusaea*-subfamily because of the close similarity with *Duckeanthus* and *Fusaea*.

Guatteria-tribe – There is support from the flower morphology, although the flowers of *Heteropetalum* are somewhat different from the other genera.

Fusaea-subfamily – The position of *Meiocarpidium* within this tribe is not supported by the flowers and this genus should be transferred to the *Hexalobus*-tribe. This 'subfamily' is rather heterogeneous in its flowers. It includes, among others, the genera of the Xylopia-group.

Hexalobus-tribe – This tribe includes genera with large ovule numbers, except *Cleistochlamys* which has one basal ovule. This tribe includes the Hexalobus-group and the Uvariastrum-group of the present study (except *Cleistochlamys* which is not included in a group).

Asimina-tribe – There are no floral character states present which can separate this tribe from the *Hexalobus*-tribe.

Annona-tribe – This tribe is supported by the flowers. *Anonidium* is somewhat different in its flowers from the remaining genera.

Cymbopetalum-tribe – The position of *Disepalum* in this tribe is not supported by the flower morphology. The remaining genera form a coherent group which is, however, diverse in its flowers.

Generally, data on flowers, fruits and seeds, pollen, leaves, etcetera, more or less agree. A number of genera, however, exhibit unusual combinations of character states in this respect, among others, *Afroguatteria, Cleistochlamys, Enantia, Greenwayodendron, Monocarpia, Piptostigma, Polyceratocarpus,* and *Toussaintia.*

6. THE FLOWER AS REPRODUCTIVE SYSTEM

6.1. Flower production

Considerable differences were observed in the number of flowers present in one herbarium specimen. The position and the type of inflorescence seem to play an important role in this respect. The number of flowers produced per plant, of course, depends also on the frequency and the duration of the flowering periods and of the age of the plant.

Genera with (initially) terminal inflorescences generally have only one mature flower at a time on their branches, occasionally accompanied by one or two immature flowers (buds), in few-flowered inflorescences or solitary. This is observed in, e.g., *Annona, Dasymaschalon, Desmopsis, Desmos, Duguetia, Enicosanthum, Fusaea, Letestudoxa, Malmea, Pseudartabotrys, Rollinia, Sapranthus, Uvaria,* and *Woodiellantha.*

A regular distribution of flowers with only one or two flowers per leaf axil, and the flowers maturing successively, is observed in, e.g., *Ancana, Haplostichanthus, Oncodostigma, Papualthia* (Philippine species), and *Polyaulax.*

An abundance of flowers is often present in genera with axillary flowers, or which are truncifloroous. In particular in genera with the flowers clustered in many-flowered inflorescences this is evident. Often only one flower at a time is mature. This applies to, e.g., *Bocaceopsis, Cleistopholis, Dendrokingstonia, Mezzettia, Mezzettiopsis, Mitrephora* p.p., *Monanthotaxis, Onychopetalum, Platymitra, Pseuduvaria* p.p., and *Unonopsis*.

Abundant flowers are also found in genera with one or few flowers per inflorescence, but with many inflorescences on one branch with several flowers in the same stage, e.g., *Asimina, Cardiopetalum, Cleistochlamys, Goniothalamus* p.p., *Guatteria, Hexalobus* p.p., *Porcelia, Toussaintia,* and *Xylopia.*

In genera with androdioecious or unisexual flowers there is often a difference between (herbarium) specimens with male flowers and those with bisexual or female flowers. Herbarium-specimens with male flowers have an abundance of flowers. Those with bisexual or female flowers have few flowers. This is observed in *Diclinanona, Greenwayodendron,* and *Oxandra.*

Flowering may occur irregularly, as reported for *Deeringothamnus* (Norman, 1982) or in distinct flowering periods as reported for *Annona* (Gottsberger, 1989a) or *Asimina* (Norman, 1982). In *Annona* the flowering period lasts 1 or 2 months (Gottsberger, 1989a), whereas Schatz (1985) observed a flowering period of 7 months in a species of *Cymbopetalum.* In *Cleistochlamys* and *Hexalobus* flowering begins at the start of the rainy season (Coates Palgrave, 1977; Codd, 1951; White, 1962). *Cananga* in Malaya flowers seasonally after dry periods, usually twice a year (Corner, 1988).

Sometimes plants already flower when they are a very small shrub (less than c. 60 cm tall). This was observed in the greenhouse in Utrecht on specimens of *Desmos, Polyalthia, Uvaria,* and *Uvariopsis,* and in herbarium-specimens of *Deeringothamnus* and *Ellipeiopsis.* This is also found in an African *Annona*-species, which, according to Deroin (1989), behaves like a hemicryptophyte due to fire during the dry season. On the other hand, a species of *Sapranthus* is reported to flower only when the plants are at least 3–4 m tall (Janzen, 1983). They only start bearing fruits when reaching a height of 20 m.

6.2. Anthesis

Anthesis in this paragraph is defined as the period from the moment that the carpels start to be receptive until the moment that the stamens are shed off. Anthesis may start at the moment of flower break or at other moments, as already mentioned in chapter 3, and generally goes along with discoloration of the petals and emission of odours. The process of anthesis is largely the same for all genera. Nevertheless, a great diversity in certain aspects of the anthesis can be observed between the various genera. The timing of certain processes varies between the genera. Flower break may be early or late in the development of the flower, and seems to be associated with the aestivation of the sepals and petals. The length of the female and the male phase may vary as well. At the end of the anthesis various flower parts are shed off, but the moment and which flower parts, may differ between the genera.

The aestivation of sepals and petals is probably associated with the development of the flower and flower break. There are indications that most imbricate flowers

open (long) before anthesis. This is confirmed for *Asimina* by Willson & Schemske (1980) and for *Guatteria* (Gottsberger, 1970; Morawetz, 1988). Several imbricate flowers unfold their petals first and close them at anthesis in a reduplicate-valvate manner. This was observed in specimens of *Cremastosperma, Duguetia, Guatteria, Malmea, Pseudoxandra, Sapranthus,* and *Uvaria.* Also in genera with an apert aestivation such as *Desmos* (observation in the greenhouse of Utrecht) and *Polyalthia* (Morawetz, 1988) the petals close at anthesis. In several genera the petals continue to elongate when the flowers are open, e.g., *Asteranthe, Cananga, Desmopsis, Desmos, Diclinanona, Isolona, Monodora, Polyalthia,* and *Stenanona.*

Many valvate flowers seem to open their flowers at the onset of the anthesis. This is observed for herbarium-specimens of, e.g., *Alphonsea, Annona, Bocageopsis, Fissistigma, Miliusa, Papualthia* (species from New Guinea), *Phaeanthus, Pyramidanthe, Rollinia, Unonopsis,* and *Xylopia.* The same applies to genera which in bud are enclosed by large reduplicate-valvate sepals, such as *Cardiopetalum, Cleistochlamys, Duguetia, Enicosanthellum, Froesiodendron, Fusaea, Hexalobus, Letestudoxa,* and *Uvaria.*

In some genera with connivent inner petals large openings between the unguiculate bases of the inner petals appear when the flower is maturing. Finally also the inner petals spread. Such flowers are observed in *Haplostichanthus, Mitrephora, Orophea,* and *Pseuduvaria.*

Several valvate flowers seem to be cleistopetalous, and may be cleistogamous. This is observed in *Annona* p.p., *Artabotrys, Dasymaschalon, Goniothalamus,* and *Pseudartabotrys.* In some genera with large reduplicate-valvate sepals enclosing the flower bud, this seems to occur as well, e.g., *Pachypodanthium* and one species of *Toussaintia. Cleistopholis,* with imbricate perianth, seems to be cleistogamous as well. All these observations are based on herbarium specimens. It can, however, not be excluded that these genera open their flowers only in the evening when the flowers are not collected. Gottsberger (1990) mentions nocturnal anthesis for flowers which are pollinated by scarab beetles (night active visitors).

The female phase is indicated by a glistening exudate on the stigmas. In some genera, the stigmatic part which is small in immature flowers, expands, e.g., in *Duckeanthus* and *Guatteria.* In *Dendrokingstonia* and *Monocarpia* the stigma considerably enlarges when the flower is receptive. The male phase is indicated by discoloration of the stamens and the dehiscence of the anthers. In *Annona*-species with a floral chamber temperature elevation is observed during anthesis (Gottsberger, 1989a; Webber, 1981). In one species of *Monodora* the female phase lasts 7–8 days and the male phase 4–5 days (Lamoureux, 1975). For *Asimina* 4–6 and 2–3 days are reported for the female phase and 1 or 2 days for the male phase (Norman & Clayton, 1986; Willson & Schemske, 1980). In an African species of *Annona* the female phase lasts a few hours, early in the morning, the male phase being late in the afternoon of the same day (Deroin, 1988a). The female phase and the male phase may be overlapping or not, as turns out from field observations.

The flower parts are usually dropped after anthesis. All flower parts may be dropped or one of the organs may be persistent. *Asimina, Cardiopetalum, Deeringothamnus, Diclinanona,* and *Disepalum* are just a few examples of genera of which the sepals are persistent. In *Fissistigma* the outer petals may be persistent and the inner ones

caducous. The released stamens may be catched for a while by the still present petals as in *Annona* (Gottsberger, 1989a) and *Polyalthia* (Okada, 1990) or dropped immediately as in the open flowers of *Rollinia* (Murray & Johnson, 1987). Endress (1985) mentions that abscissing stamens remain attached to the torus by extended spiral thickenings in flowers of *Annona, Asimina,* and *Monodora.* In an African species of *Uvaria* which has open flowers at maturity, the abscissing stamens remain attached to the torus as well (Deroin, 1988a). In a number of genera the stigmas are still present when stamens and perianth are shed off. This is observed in (herbarium specimens of), e.g., *Alphonsea, Annona, Bocageopsis, Cyathocalyx, Goniothalamus, Mischogyne, Pachypodanthium, Richella, Tetrapetalum, Uvariodendron* p.p., and *Xylopia.* Flowers of which the stigmas drop early are observed in, e.g., *Ambavia, Cardiopetalum, Haplostichanthus, Hexalobus, Isolona, Lettowianthus, Monodora, Oncodostigma, Papualthia, Phaeanthus, Polyalthia, Sapranthus, Toussaintia,* and *Uvariastrum.*

6.3. Pollination mechanisms

The Annonaceae are considered to be predominantly beetle-pollinated. Although beetles are supposed to be the effective pollinators, in some genera also flies, thrips, and bees are noticed as visitors. Flies and bumble-bees were observed in *Asimina* (Kral, 1960; Uphof, 1933; Willson & Schemske, 1980). Flies were also observed in *Goniothalamus* (Hidaka, 1983) and *Pseuduvaria* (Morawetz, 1988), whereas Drosophilidae and Sciaridae lay their eggs in *Annona*-flowers (Webber, 1981). Thrips (Thysanoptera), beside beetles, are observed in flowers of *Guatteria* and *Xylopia* (Gottsberger, 1970). Thrips pollinate the flowers of *Belliolum* (Winteraceae) in New Caledonia (Thien, 1980), of which the flowers remind of those of *Bocageopsis, Onychopetalum,* and *Oxandra* because of their stamen type. *Belliolum,* however, has a larger number of petals. Stingless bees (Meliponidae) visited flowers of *Rollinia* and *Tetrameranthus,* collecting pollen during the male phase (Webber, 1981). No pollinators at all were observed in flowers of, e.g., *Deeringothamnus* (Norman, 1982) and a *Sapranthus*-species (Janzen, 1983).

The flowers have various constructions or phenomenons to attract pollinators and to advantage pollination. Several genera form a 'pollination chamber' or 'floral chamber' during anthesis. This was for the first time reported by Gottsberger (1970) for, among others, *Guatteria.* In many other genera such a smaller or larger 'floral chamber' is present. Corner (1988) mentions that beetles are trapped for several days in the flowers of *Anaxagorea, Cyathocalyx, Goniothalamus,* and *Xylopia.* Many genera to a larger or smaller extent form such a 'chamber' by bending or pressing their petals over the stamens and carpels. Such a 'floral chamber' attracts beetles, which use the flower as hiding and mating place. Mating behaviour, however, is rare in *Asimina* (Norman & Clayton, 1986), whereas Gottsberger (1989a) supposes that in *Annona* the flowers function as 'rendez-vous places' for beetles of both sexes. Okada (1990) suggests that in a *Polyalthia*-species of which the petals are bent over the reproductive organs, the petals primarily have a function in catching the abscissing stamens.

Alimentation for the pollinators is offered as food bodies in flowers such as in *Asimina* and *Sapranthus* or by thick, fleshy petals such as in *Annona.* Gnawed petals

are found in, e.g., *Annona, Guatteria* and *Xylopia* (Gottsberger, 1970, 1989a). In *Asimina* the beetles were mainly attracted in the male phase and they consumed pollen and corrugated tissue of the inner petals (Norman & Clayton, 1986).

Emission of odours is generally reported during anthesis. Webber (1981) found that odours in flowers of *Annona* turned from pleasant during day-time into disagreeable and more alcoholic during the evening. This corresponds with the attraction of different visitors. In *Annona* the odour becomes stronger when the temperature rises (Webber, 1981). In *Cymbopetalum* scarab beetles are attracted by the odour in the female phase (Schatz, 1985).

In flowers with a floral chamber the beetles are released when the petals and stamens are shed off. In some *Annona*-species the release of pollen-dusted beetles occurred half an hour earlier than the peak of the female phase (Gottsberger, 1989a).

Both allogamy and autogamy occur within the Annonaceae. Allogamy is advantaged by temporal or spatial separation of female and male phase, by dropping the stigmas before the pollen is released, or by dicliny.

An interphase of 6–24 hours between the female and male phase is reported for a species of *Asimina* (Norman & Clayton, 1986). In another *Asimina*-species they observed sometimes an overlap of one day and sometimes an interphase of one day.

Synchrony of anthesis within one tree is observed in two species of *Rollinia,* thus avoiding geitonogamy (Murray & Johnson, 1987; Webber, 1981). Every 48 hours a new set of flowers starts flowering. Murray & Johnson (1987) mention that the 'stigmatic cap' falls before the stamens are released. Such a synchronization of the flowering process is also observed in *Eupomatia* (Eupomatiaceae) (Endress, 1984a) and may occur in several more Annonaceae.

Flowers pollinated with pollen from the same plant (geitonogamy) do not set fruit in an African species of *Annona* (Deroin, 1989). Only flowers early in the flowering season, when there is only one open flower per plant, set fruit. Later flowers have a function in the reproduction of the pollinators by offering them pollen as food supply and a mating place.

In *Cananga* the stamens are tightly pressed by the petals so that the pollen cannot be released, despite the dehisced anthers, before the petals are shed off, together with the stigmas (Periasamy, 1954). Bagged flowers of *Cananga* do not set fruit (Deroin, 1988b).

In many species of *Anaxagorea* the inner staminodes surpass the stamens and carpels, thus avoiding autogamy. Endress (1984a) found in *Eupomatia* (Eupomatiaceae) the receptive stigmas secluded by the inner staminodes as well.

Dicliny is another way to promote cross-pollination. Examples of genera with androdioecious or unisexual flowers have already been mentioned in Chapter 3.

Autogamy is advantaged by pressing the petals over the reproductive organs in flowers with long, persistent stigmas. After anthesis, when the petals and stamens are released, the pollen may stick to the stigmas. This is observed in species of *Artabotrys* (Burck, 1906), *Dasymaschalon* (Knuth, 1904), *Desmos* (Burck, 1890), *Duguetia* (Gottsberger, 1970), *Goniothalamus* (Burck, 1890), *Polyalthia* (Okada, 1990), *Uvaria* (Winkler, 1906), and *Xylopia* (Gottsberger, 1970). Nearly all these genera have long stigmas which conspicuously exceed the stamens.

Data on self-compatibility and self-incompatibility within Annonaceae are few. Webber (1981) carried out experiments which show that all *Annona*-species studied and one *Rollinia*-species are self-compatible. Of these species only one *Annona*-species is autogamous; for the other species pollination by insects or other agents is necessary. In a species of *Polyalthia* bagged flowers set fruit in almost the same frequency as the controls (Okada, 1990). Also in one *Asimina*-species fruit set is possible, but this species is almost completely dichogamous (Norman & Clayton, 1986). Bawa et al. (1985) report self-compatibility for species of *Anaxagorea* and *Cymbopetalum*, whereas Bawa (1974) reports self-incompatibility for a *Sapranthus*-species. Flowers of an African *Annona*-species do not set fruit under geitonogamous conditions, but it is uncertain whether this is due to self-incompatibility (Deroin, 1989).

Hybrids were observed in *Asimina* between several species (Kral, 1960; Norman & Clayton, 1986). This happened in cases of disturbance which caused flowers to be produced at times different from the normal flowering period. Schatz (1985) found a putative hybrid of two sympatric species of *Cymbopetalum*. Both species have overlapping flowering periods although with a different peak period. No hybrids were observed in *Annona* species in spite of overlapping flowering periods and the fact that the flowers are pollinated by the same beetle species (Gottsberger, 1989a).

6.4. Androecium

As already mentioned before (Chapter 3), there are considerable differences in the shape, relative size, and diameter of the stamens (fig. 6). They may be divided more or less into three categories: short and broad stamens, long and narrow stamens, and flattened stamens. These three types are associated with the number of stamens within the flower, as appears from the longitudinal sections of the flowers. When the number of stamens is large, the diameter of individual stamens is usually small, or the stamens are flattened. When there are a low or a moderate number of stamens, the diameter of each stamen is usually relatively wide.

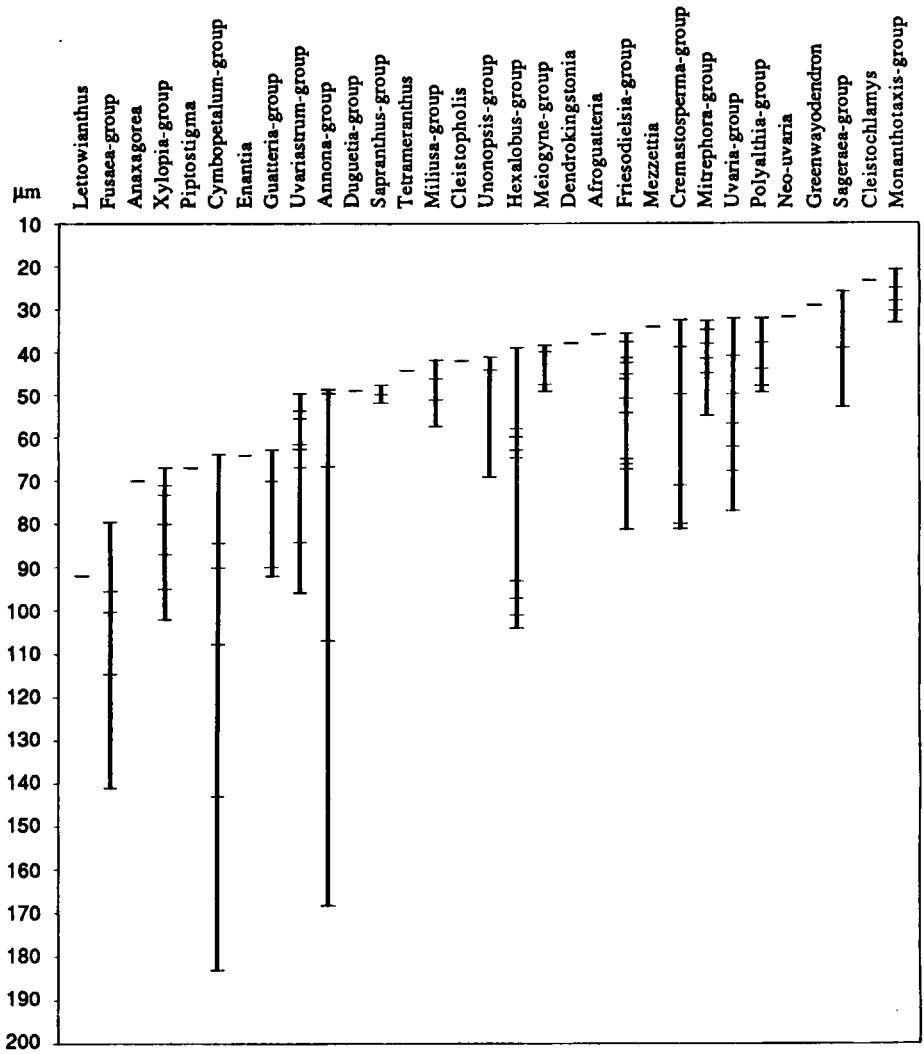
In most genera with a moderate or low number of stamens, the thecae are hardly immersed in the tissue of the stamens. In genera with a larger number of stamens, the thecae tend to lay deeper in the tissue of the stamen. This is found in, e.g., *Anonidium, Asteranthe, Fusaea, Guatteria, Guatteriopsis, Letestudoxa, Meiocarpidium, Porcelia,* and *Pseudartabotrys*. In *Guatteria* and *Guatteriopsis* the stamens look very stream-lined. Possibly the position of the thecae plays a role in preventing or promoting autogamy.

The average longest size of the pollen per genus, as they are measured by Walker (1971a, 1971b, 1972), within each informal group varies between certain limits (table 25). These average longest sizes of the pollen grain more or less seem to be associated with the number of stamens.

Small pollen is generally found in flowers with (relatively) few stamens, for instance, in *Cleistochlamys, Dendrokingstonia, Ellipeia, Greenwayodendron, Mezzettia, Mitrella, Monanthotaxis, Neo-uvaria, Platymitra, Popowia, Pseudephedranthus, Pseuduvaria, Sageraea, Stelechocarpus,* and *Woodiellantha*. Many of these genera have small flowers.

Table 25

Average length of the longest pollen grain axis of each genus in microns, ranged per group according to the present informal classification. Data are taken from Walker (1971a, b, 1972). Each genus is represented by one small bar. The measurement for *Afroguatteria* is kept separate from the Fusaea-group in this table because of the aberrant size of its pollen. The extra measurements for some groups refer to taxa which in the present paper are included in other taxa: *Saccopetalum* (= *Miliusa*, Miliusa-group), *Enneastemon* and *Popowia* (African species) (included in *Monanthotaxis*, Monanthotaxis-group), and *Rolliniopsis* (= *Rollinia*, Annona-group).



Intermediate-sized pollen is measured in, e.g., *Alphonsea, Anaxagorea, Artabotrys, Cremastosperma, Cyathocalyx, Desmopsis, Heteropetalum, Hexalobus, Isolona, Sapranthus, Unonopsis*, and *Uvaria*. These genera usually have middle-sized flowers.

Large pollen is usually found in genera with a large number of stamens: *Annona, Asimina, Cardiopetalum, Cymbopetalum, Deeringothamnus, Disepalum, Duckeanthus, Fusaea, Goniothalamus, Guatteria,* and *Xylopia.* Most of these genera have large flowers.

Some genera deviate from the general trend. *Afroguatteria,* despite the large diameter of the torus has small pollen. The diameter of its stamens is very small. *Hornschuchia* has large pollen despite its few stamens.

In general larger pollen is associated with a larger number of stamens with often longer anthers. Flowers with relatively few, short and broad stamens usually have very small pollen and much pollen per stamen, while flowers with many, but relatively long and narrow stamens, have larger pollen and less pollen per stamen.

6.5. Gynoecium

The number of ovules, the number of carpels, and the number of flowers per inflorescence appear to be correlated. In other words, there is a tendency to keep the production of ovules per inflorescence more or less constant within the Annonaceae.

In genera with only one, basal ovule per carpel, the number of carpels is usually very large. This may be observed in *Annona* and related genera, *Boutiquea, Disepalum, Duckeanthus, Duguetia, Enicosanthellum, Fusaea, Guatteria* and related genera, *Letestudoxa,* and *Neostenanthera.*

In genera with a large number of ovules there are often few carpels. This is observed in, e.g., *Alphonsea, Asimina, Asteranthe, Dielsiothamnus, Exellia, Hexalobus, Isolona, Monodora, Platymitra,* and *Sageraea.*

Genera with several ovules per carpel often have a moderate number of carpels, e.g., *Dasymaschalon, Desmopsis, Desmos, Meiogyne, Mitrephora, Monanthotaxis, Oncodostigma, Pseuduvaria, Stenanona, Unonopsis,* and *Xylopia.*

Some genera have few ovules and few carpels, e.g., *Bocageopsis* and *Onychopetalum. Dendrokingstonia* and *Mezzettia* both have one carpel, while *Dendrokingstonia* has 2–4 ovules and *Mezzettia* 2 ovules. These genera, however, have many flowers in clustered inflorescences.

There are a few exceptions of genera which strongly deviate from the number of ovules usually produced per inflorescence. *Cleistochlamys* has solitary flowers, each with only several carpels and one, basal ovule per carpel. A similar situation is found in *Oreomitra*: 3–6 carpels, and one, lateral ovule per carpel (Diels, 1912).

In contrast, *Cymbopetalum, Fissistigma, Porcelia, Uvaria* p.p., and perhaps some genera of the Uvariastrum-group seem to produce a relatively large number of ovules per inflorescence. In one *Uvaria*-species, *U. elmeri,* 30 ovules per carpel are counted, while the number of carpels is very large, and the flowers are clustered in a many-flowered inflorescence.

The explanation for the unusual placentation in the carpel of *Isolona* and *Monodora* (Chapters 3 and 5; Leins & Erbar, 1980, 1982) may be the number of ovules produced per inflorescence. *Isolona* and *Monodora* have only one carpel per flower and few flowers per inflorescence (solitary in *Monodora*, c. 2 flowers in *Isolona*). This makes that all ovules have to be packed in one carpel. The number of ovules is so large that it is not possible to maintain a 2-seriate placentation.

The number of ovules per inflorescence which is more or less constant for all genera, is no longer present in the fruiting phase (pers. comm., A.K. van Setten). Genera with many flowers in a many-flowered inflorescence often produce only one or very few monocarps in fruit. On the other hand, in many genera with many carpels with one ovule per carpel, the number of developed seeds is very large. The number of seeds within the fruits is generally lower than the number of ovules for that particular species. Abortive ovules, however, are observed only once, in a flower of *Onychopetalum*.

Table 26. The groups of genera with their chromosome numbers.

Data are taken from Morawetz (1988), Morawetz & Le Thomas (1988), Morawetz & Waha (1986), and Okada (1987). Okada (1987) also gives a count for *Desmopsis* (2n = 16), based on an older study, but from the flower morphological point of view this number may be erroneous and requires verification.

x = 9:

(1)		
Cremastosperma-group:	*Cremastosperma*	2n = 18
	Oxandra	2n = 18
Meiogyne-group:	*Ancana*	2n = 18
	Oncodostigma	2n = 18
Miliusa-group:	*Miliusa*	2n = 18
	Phaeanthus	2n = 18
Mitrephora-group:	*Fitzalania*	2n = 18
	Mitrephora	2n = 18
	Orophea	2n = 18
	Platymitra	2n = 18
	Popowia (Asia)	2n = 18
	Pseuduvaria	2n = 18
Polyalthia-group:	*Haplostichanthus*	2n = 18
	Polyalthia	2n = 18, 36
Sageraea-group:	*Alphonsea*	2n = 18
	Stelechocarpus	2n = 18
Sapranthus-group:	*Sapranthus*	2n = 18
Unonopsis-group:	*Bocageopsis*	2n = 18
	Unonopsis	2n = 18
Remaining genera:	*Neo-uvaria*	2n = 18
(2)		
Cymbopetalum-group:	*Cymbopetalum*	2n = 18, 27, 42, 80
	Porcelia	2n = 18

(Table 26 continued)

x = 8:

Duguetia-group:	*Duguetia*	2n = 16, 24, 32, 48
Friesodielsia-group:	*Artabotrys*	2n = 16
	Cyathocalyx	2n = 16, 64
	Dasymaschalon	2n = 16
	Desmos	2n = 16
	Fissistigma	2n = 16
	Friesodielsia	2n = 16
	Mitrella	2n = 16
	Sphaerocoryne	2n = 16
Fusaea-group:	*Disepalum*	2n = 16
	Fusaea	2n = 16
Hexalobus-group:	*Asimina*	2n = 16
	Isolona	2n = 16
	Monodora	2n = 16
Uvaria-group:	*Rauwenhoffia*	2n = 16
	Uvaria	2n = 16
Uvariastrum-group:	*Uvariopsis*	2n = 16, 24
Xylopia-group:	*Cananga*	2n = 16
	Goniothalamus	2n = 16
	Neostenanthera	2n = 16
	Xylopia	2n = 16
Remaining genera:	*Anaxagorea*	2n = 16, 48
	Enantia	2n = 16

x = 7:

(1)		
Annona-group:	*Annona*	2n = 14, 28, 42
	Rollinia	2n = 14, 28, 42, 56
(2)		
Guatteria-group:	*Guatteria*	2n = 28
	Guatteriella	2n = 28
	Guatteriopsis	2n = 28
(3)		
Remaining genera:	*Ambavia*	2n = 14
	Cleistopholis	2n = 14
	Mezzettia	2n = 14
	Tetrameranthus	2n = 14, 28

Table 27. Distribution of the aestivation types.

The groups are arranged according to table 25. For the Monanthotaxis-group and *Lettowianthus* no data on chromosome numbers are available, but their chromosome number can be postulated from their affinities with other groups or genera.

1 = Sepals and petals imbricate;
2 = Sepals and petals apert;
3 = Sepals and petals valvate;
4 = Sepals apert, petals imbricate;
5 = Sepals apert, petals valvate;
6 = Sepals valvate, petals imbricate;
7 = Sepals and outer petals valvate, inner petals imbricate.

	1	2	3	4	5	6	7
x = 9:							
Cremastosperma-group	+	–	–	+	–	–	–
Meiogyne-group	–	–	+	+	+	–	–
Miliusa-group	–	–	+	–	+	–	–
Mitrephora-group	–	–	+	+	+	–	–
Polyalthia-group	+	+	+	+	+	–	–
Sageraea-group	–	–	+	+	–	–	–
Sapranthus-group	–	+	+	–	–	+	–
Unonopsis-group	–	–	+	–	–	–	–
Neo-uvaria	–	–	+	+	–	–	–
Cymbopetalum-group	+	–	+	–	–	+	–
x = 8:							
Duguetia-group	–	–	+	–	–	+	–
Friesodielsia-group	–	+	+	–	+	?	–
Fusaea-group	–	–	+	–	–	+	–
Hexalobus-group	–	+	+	+	–	+	–
Uvaria-group	–	–	+	+	–	+	–
Uvariastrum-group	–	–	+	–	+	–	+
Xylopia-group	–	–	+	–	+	–	–
Anaxagorea	+	–	+	–	–	–	–
Enantia	–	–	+	–	–	–	–
probably x = 8:							
Monanthotaxis-group	–	–	+	–	+	–	+
x = 7:							
Annona-group	–	–	+	–	+	–	+
Guatteria-group	–	–	+	–	–	+	–
Ambavia	+	–	–	–	–	–	–
Cleistopholis	+	–	–	–	–	–	–
Mezzettia	+	–	–	–	–	–	–
Tetrameranthus	+	–	+	–	–	+	–
probably x = 7:							
Lettowianthus	+	–	–	–	–	–	–
x = unknown:							
Cleistochlamys	–	–	–	–	–	+	–
Dendrokingstonia	+	–	–	–	–	–	–
Greenwayodendron	+	–	–	–	–	–	–
Piptostigma	–	–	+	–	–	–	–

7. EVOLUTIONARY DIVERSIFICATION IN FLOWERS OF ANNONACEAE

7.1. FLOWER MORPHOLOGY AND KARYOLOGY

The relationship between flower morphology and chromosome numbers seems to be very strict. Also the distribution of certain non-floral character states seems more or less to be correlated with the chromosome numbers. The groups of genera for which chromosome base numbers of x = 9 are found (table 26), differ from those with x = 8 in the presence or absence of certain character states. The groups for which a chromosome base number of x = 7 are found, combine in their morphology features typical of either x = 9 or x = 8. The Cymbopetalum-group with base number x = 9 differs in its morphology from the other groups with that base number. It has to be stressed that there are no floral character states present which may delimit the genera of the various chromosome base numbers. There is rather a shift in the distribution of floral character states and the degree of morphological diversity.

Genera of the groups for which a chromosome number of 2n = 18 is found (table 26), generally have small to middle-sized flowers, small sepals, whereas the sepals are fairly equal to the petals in aestivation (table 27), texture, and indument. They lack a number of character states found in the genera with chromosome number 2n = 16 (table 28). *Neo-uvaria* (2n = 18), however, possesses stellate hairs, together with unusual thick petals. It is, therefore, uncertain whether *Neo-uvaria* should be included in one of the groups with 2n = 18, which it otherwise closely resembles in its morphology. Also in genera of the Polyalthia-group occasionally some features can be found that are typical of genera with 2n = 16. The genera of the groups with 2n = 18 are quite uniform in their stamens and carpels, compared with the groups with 2n = 16. With exception of the Polyalthia-group, which extends into East Africa and Madagascar, all these groups are restricted to Asia and the Neotropics (table 29). The scheme presented by Van Setten (1990) indicates that in these genera symmetrical and pitted seeds with needle-shaped ruminates prevail.

The Cymbopetalum-group with chromosome base number x = 9, is in some ways different in its morphology from the other genera with this chromosome base number. Septate anthers, which characterize the Cymbopetalum-group, are not found in the other groups with 2n = 18. This group contains both small and large-sized flowers as well as genera with an imbricate perianth (like the above mentioned groups of genera) and genera with large valvate sepals and imbricate petals (like genera with 2n = 16). A possible explanation is given in paragraph 7.4. Its geographic distribution is East Africa and the Neotropics.

Genera of groups with 2n = 16, which morphologically cannot be distinguished from the Annona-group (x = 7), the Guatteria-group (2n = 28), and the Cymbopetalum-group (x = 9), generally have middle-sized or larger flowers, often middle-sized or larger, valvate sepals, which usually differ in aestivation, texture, and/or indument from the petals. Character states like stellate hairs, indurate stamens, septate anthers, fused or stipitate carpels, and cup-shaped stigmas are exclusively or more frequently found in these groups (tables 28 and 30). Other character states, although sometimes found in a group of 2n = 18, are more frequent. Sizes or numbers of flower parts vary between wider limits, whereas fusion of flower parts is more

Table 28. The relationship between the distribution of a number of character states and chromosome number.

The groups are arranged according to table 26. For the Monanthotaxis-group and *Lettowianthus* no data on chromosome numbers are available, but their chromosome number can be postulated from their affinities with other groups or genera.

1 = Stellate hairs or scales;
2 = Petals in one whorl;
3 = Torus enlarged;
4 = Stamens indurate;
5 = Anthers septate;
6 = Carpels fused;
7 = Carpels stipitate.

	1	2	3	4	5	6	7
x = 9:							
Cremastosperma-group	–	–	–	–	–	–	–
Meiogyne-group	–	–	–	–	–	–	–
Miliusa-group	–	–	–	–	–	–	–
Mitrephora-group	–	–	–	–	–	–	–
Polyalthia-group	–	–	–	–	–	–	–
Sageraea-group	–	–	–	–	–	–	–
Sapranthus-group	–	–	–	–	–	–	–
Unonopsis-group	–	–	–	–	–	–	–
Neo-uvaria	–,+	–	–	–	–	–	–
Cymbopetalum-group	–	–	–	–	+	–	–
x = 8:							
Duguetia-group	+	–	+	–	–	–,+	–
Friesodielsia-group	–,+	–	–,+	–	–	–	–
Fusaea-group	–	–,+	+	+	–	–,+	–,+
Hexalobus-group	–	–,+	–,+	–	–,+?	–	–
Uvaria-group	+	–	–	–	–	–	–
Uvariastrum-group	–,+	+,–	+,–	–	–	–	–
Xylopia-group	–	–	–,+	+	+,–	–	–,+
Anaxagorea	–,+	–	–	–	–	–	–
Enantia	–,+	–	–	–	–	–	+
probably x = 8:							
Monanthotaxis-group	–	+,–	–	–	–	–	–
x = 7:							
Annona-group	–,+	–	+,–	–	–	+,–	–
Guatteria-group	–	–	–	+	–	–	–
Ambavia	–	–	–	–	–	–	–
Cleistopholis	–	–	–	–	–	–	–
Mezzettia	–	–	–	+?	–	–	–
Tetrameranthus	+	–	–	–	–	–	–
probably x = 7:							
Lettowianthus	–	–	–	–	–	–	+
x = unknown							
Cleistochlamys	–	–	–	–	–	–	–
Dendrokingstonia	–	–	–	–	–	–	–
Greenwayodendron	–	–	–	–	–	–	–
Piptostigma	–	–	–	–	–	–	–

frequent. The geographic distribution of the groups with 2n = 16 is pantropical (table 29), with at least one genus in each group occurring in Africa. Asymmetrical seeds with a smooth surface and lamellate ruminates are prevalent (scheme Van Setten, 1990). Syncarpous fruits, oil cells, and arils are absent in genera of the groups with 2n = 18. This also applies to lianas or scandent shrubs (except in *Oreomitra*?; Diels, 1912). Lianas are mainly found in the genera of the Friesodielsia-group, the Monanthotaxis-group, and the Uvaria-group. *Anaxagorea* and *Enantia*, both x = 8, remind in the unusual combinations of character states of the other genera, not included in a group (see below). On the other hand, in their flower morphology they resemble the other genera with x = 8.

Within the genera with base number x = 7, judged from the flower morphology, 3 groups can be recognized: the Annona-group, the Guatteria-group, and some of the genera which are not included in a group. The Annona-group and the Guatteria-group, in fact, cannot be distinguished from the groups with 2n = 16 on the basis of their flowers. Occasionally a feature is present which is more common in a genus with 2n = 18. The Guatteria-group is restricted to the Neotropics, whereas the Annona-group occurs both in Africa and the Neotropics. The other genera with x = 7, *Ambavia, Cleistopholis, Mezzettia,* and *Tetrameranthus,* have a perianth type (e.g., imbricate aestivation) that is typical of the groups with 2n = 18. At the same time they possess character states that are absent in genera with 2n = 18, such as stellate hairs in *Tetrameranthus* or introrse stamens in *Mezzettia*. The same applies to the other genera which are not included in a group, but for which no chromosome counts are available. The geographical distribution of this last x = 7-group is pantropical.

7.2. Inference of character state polarity

When combining all data available, it is possible to infer the polarity of the character state transformations in the evolution of flowers of Annonaceae. Basic assumption is that the Annonaceae are highly cantharophilous and that they have evolved from a more generalized flower type, in accordance with the views of Gottsberger (1974).

Gottsberger (1974) assumed that primitive Angiosperm flowers possessed relatively few stamens and carpels loosely arranged on the floral axis. More specialized (cantharophilous) genera should have enlarged and more robust flowers, with an increased number of stamens and carpels, in reduced inflorescences or solitary. As pointed out in chapter 6, the number of ovules produced per inflorescence is more or less constant within the family. This implies that either many carpels with few ovules, a moderate number of carpels with several ovules, or several carpels with many 2-seriate ovules could be the original situation.

Smaller flowers with relatively few stamens and carpels predominate in the groups with a chromosome number of 2n = 18. These groups lack a number of character states present in the other groups or show a lower frequency of certain character states (tables 28 and 30). Also fusion of organs is less common in the 2n = 18 groups than in the other groups. The 2n = 18 groups are restricted to Asia and the Neotropics, only *Polyalthia* extends into Madagascar and East Africa (table 29). The remaining groups seem to have an original distribution centre in Africa and have relationships

Table 29. The geographic distribution of the groups.

The groups are arranged according to table 26. For the Monanthotaxis-group and *Lettowianthus* no data on chromosome numbers are available, but their chromosome number can be postulated from their affinities with other groups or genera.

1 = South America;
2 = Central America;
3 = North America;
4 = African continent;
5 = Madagascar;
6 = Asia;
7 = Australia, New Guinea, and/or Pacific.

	1	2	3	4	5	6	7
x = 9:							
Cremastosperma-group	+	+	–	–	–	–	–
Meiogyne-group	–	–	–	–	–	+	+
Miliusa-group	–	–	–	–	–	+	+
Mitrephora-group	–	–	–	–	–	+	+
Polyalthia-group	–	–	–	+	+	+	+
Sageraea-group	–	+	–	–	–	+	–
Sapranthus-group	–	+	–	–	–	–	–
Unonopsis-group	+	–	–	–	–	–	–
Neo-uvaria	–	–	–	–	–	+	–
Cymbopetalum-group	+	+	–	+	–	–	–
x = 8:							
Duguetia-group	+	–	–	+	–	–	–
Friesodielsia-group	–	–	–	+	+	+	+
Fusaea-group	+	–	–	+	–	+	–
Hexalobus-group	+	–	+	+	+	–	–
Uvaria-group	–	–	–	+	+	+	+
Uvariastrum-group	–	–	–	+	–	–	–
Xylopia-group	+	+	–	+	+	+	+
Anaxagorea	+	+	–	–	–	+	–
Enantia	–	–	–	+	–	–	–
probably x = 8:							
Monanthotaxis-group	–	–	–	+	+	–	–
x = 7:							
Annona-group	+	+	–	+	+	–	–
Guatteria-group	+	–	–	–	–	–	–
Ambavia	–	–	–	–	+	–	–
Cleistopholis	–	–	–	+	–	–	–
Mezzettia	–	–	–	–	–	+	–
Tetrameranthus	+	–	–	–	–	–	–
probably x = 7:							
Lettowianthus	–	–	–	+	–	–	–
x = unknown							
Cleistochlamys	–	–	–	+	–	–	–
Dendrokingstonia	–	–	–	–	–	+	–
Greenwayodendron	–	–	–	+	–	–	–
Piptostigma	–	–	–	+	–	–	–

with either Asia or the Neotropics. When mainly found in Asia or the Neotropics, these groups have at least one representative in Africa. The first distribution type (Asia + Neotropics) more or less agrees with that of other ancient families such as Magnoliaceae, Chloranthaceae, Winteraceae, and many small (relict) families restricted to East Asia or the Pacific. The second distribution type (pantropical) reminds of that of the Myristicaceae, a family which, based on the character state polarity discussed below, seems to be a derived family (in their flowers). On the basis of their pollen, Walker (1971a) regards the *Malmea*-tribe (genera of Cremastosperma-group and Unonopsis-group, beside *Enantia*), and especially *Pseudoxandra*, as most primitive. Thus, several carpels with few ovules seem to be the original situation, when the views of Gottsberger (1974) are combined with the arguments just mentioned.

In contrast, Morawetz (1986a) presumed that 2n = 16 is the original chromosome number for Annonaceae and for primitive Angiosperms in general. This would imply that with a step from 2n = 16 to 2n = 18 there is a loss of many character states such as stellate hairs, septate stamens, fused carpels, etc. (table 28), together with a decrease of divergence whereas a specialization to a certain character state complex is absent. The base number x = 8 is found in some other families within the Magnoliales (Degeneriaceae, Himantandraceae) and Laurales (Chloranthaceae, Trimeniaceae) (Morawetz, 1986a, 1988).

When 2n = 18 is considered to be the basic chromosome number for Annonaceae, the following character state polarities can be postulated in Annonaceae-flowers (in general):

- from small and middle-sized flowers to large flowers (often solitary or in few-flowered inflorescences) or occasionally to very small flowers;
- from a less clearly differentiated perianth to a perianth which is clearly differentiated into sepals and petals;
- from an indument of simple hairs to an indument of stellate hairs or scales;
- from small sepals to large sepals;
- from all petals in two whorls to all petals in one whorl;
- from a small torus to an enlarged torus;
- from stamens with a more or less fleshy texture to stamens with an indurate texture or with a rigid apex;
- from stamens with extrorse anthers to those with latrorse or introrse anthers, or with anthers which are immersed in the tissue of the stamen;
- from free and sessile carpels to fused carpels or to stipitate carpels;
- from carpels with massive stigmas to carpels with cup-shaped or bilobed stigmas or with a distinct style;
- from few carpels with few, lateral ovules to many carpels with one ovule or to one to several carpels with many, 2-seriate ovules.

7.3. Parallel developments

Parallel developments are repeatedly observed in the flowers, not only in single character states but also in whole sets of (possibly apomorphic) character states.

Table 30. The relationship between the distribution of a number of character states and chromosome number.

The groups are arranged according to table 26. For the Monanthotaxis-group and *Lettowianthus* no data on chromosome numbers are available, but their chromosome number can be postulated from their affinities with other groups or genera.

1 = Buds enclosed by the sepals;
2 = One whorl of petals absent;
3 = Anthers latrorse;
4 = Apex of stamens rigid, papilose, or shiny;
5 = Style (conspicuously) present;
6 = Stigma bilobed;
7 = Stigma cup-shaped.

	1	2	3	4	5	6	7
x = 9:							
Cremastosperma-group	–	–	–	–	–,+	–	–
Meiogyne-group	–	–	–	–	–	–	–,+
Miliusa-group	–	–	–	–	–	–	–
Mitrephora-group	–	–	–	–	–	–	–
Polyalthia-group	–	–	–	–,+	–	–	–
Sageraea-group	–	–	–,+	–	–	–	–
Sapranthus-group	–,+	–	–	–	–	–	–
Unonopsis-group	–	–	–	–	–	–	–
Neo-uvaria	–	–	+,–	–	–	–	–
Cymbopetalum-group	–,+	–	–	+,–	–,+	–,+	–,+
x = 8:							
Duguetia-group	+	–	–	+	+,–	–	–
Friesodielsia-group	–,+	–,+	–	+,–	–,+	–,+	–,+
Fusaea-group	+	–	–,+	+,–	+,–	–	–
Hexalobus-group	+,–	–	–,+	–,+	–,+	–,+	+,–
Uvaria-group	+,–	–	+,–	–	–	–	–,+
Uvariastrum-group	–,+	–,+	+,–	–	–	–,+	+,–
Xylopia-group	+,–	–	–	+	+,–	–	–
Anaxagorea	–,+	+,–	–,+	–	–,+	–	–
Enantia	+	+	–	–	–	–	–
probably x = 8:							
Monanthotaxis-group	–	–	+,–	–	–	+,–	–
x = 7:							
Annona-group	–,+	–,+	–	–,+	+,–	–	–
Guatteria-group	+	–	–	+	+,–	–	–,+
Ambavia	–	–	–	–	–	–	–
Cleistopholis	–	–	+	–	–	–	–
Mezzettia	–	–	+,–	+	+	–	–
Tetrameranthus	+	–	+	–	–	–	–
probably x = 7:							
Lettowianthus	+	–	+,–	–	–	–	–
x = unknown							
Cleistochlamys	+	–	–	–	–	–	–
Dendrokingstonia	–	–	–,+	–	–	–	+
Greenwayodendron	–	–	–	–,+	–	–	–,+
Piptostigma	+,–	–	–	–	–	–	–

Parallel developments exist between genera which occur in different continents and between genera with different chromosome numbers. The similarity in character states in the flowers of *Desmos* (Asia; 2n = 16) and *Sapranthus* (Central America; 2n = 18) was already mentioned in Chapter 5. Another example is *Piptostigma* (Africa; chromosome number unknown) which has similar character states as the genera of the Miliusa-group (Asia; 2n = 18). *Piptostigma* only differs in the shape of its stigma and its longer petals from the genera of the Miliusa-group. The Fusaea-group and the Guatteria-group share the same set of derived character states, differing only in the diameter of the torus and the more streamlined stamens in the Guatteria-group. In several cases good distinguishing floral characters are absent between genera or groups of genera, which show a similar flower morphology that, however, may be the result of parallel developments, although past continental connections cannot be precluded. This applies, among others, to *Tridimeris* (Mexico) placed in the Sageraea-group (Asia), *Disepalum* and *Enicosanthellum* (both Asia) placed in the Fusaea-group (Africa and South America), and *Asimina* and *Deeringothamnus* (North America) included in the Hexalobus-group (Africa). In general one may conclude that in each continent more or less the same type of flowers has evolved in genera that has no or only a remote relationship.

7.4. Reversal developments

One of the main developments within Annonaceae-flowers is the progression towards larger flowers in more advanced groups of genera. In some highly advanced groups, however, we find very small flowers, e.g., *Bocagea, Hornschuchia,* and *Trigynaea* in the Cymbopetalum-group. Large pollen (the Cymbopetalum-group has pollen in polyads) in flowers with few stamens is very unusual in Annonaceae (Chapter 6). In Africa, where middle-sized to large flowers predominate, we find the small-flowered genera of the relatively advanced Monanthotaxis-group. Also in the Annona-group a reversal development seems present from large flowers in *Anonidium* and part of *Annona* to small flowers in *Raimondia, Rollinia,* and part of the *Annona*-species. This is paralleled by a similar reversal development in the pollen from tetrads to monads (Walker, 1971a), the presence of apocarpous fruits in some species of *Rollinia* formerly referred to *Rolliniopsis,* and probably also in flower biology (Gottsberger, 1989b).

7.5. The relation with flower biology

The relationship between flower morphology and flower biology is still a matter of speculation. The number of studies and single observations on the flower biology in Annonaceae is increasing (see for references Gottsberger, 1988), but they are mainly restricted to neotropical genera and to genera with more 'specialized' types of flowers (e.g., *Annona, Asimina, Cananga, Duguetia, Guatteria, Rollinia, Tetrameranthus,* and *Xylopia*). The only study on genera of the 'less advanced' groups (2n = 18), concerns single observations by Morawetz (1988) on *Haplostichanthus* (visited by small beetles) and *Pseuduvaria* (visited by small flies).

It can be expected that the different levels of specialization in the flowers correspond with a shift in the composition of visitors or with the frequency of flower visits. A number of possible differences in the pollinators being attracted between the 'more specialized' and the 'less specialized' Annnonaceae are discussed below.

Different pollinators – Gottsberger (1974) mentions that the Annonaceae, which are considered as more specialized on cantharophily, attract more specialized visitors (beetles) than the more 'open' flowers of Winteraceae which attract a wider array of visitors (thrips, flies, etc.) (Gottsberger et al., 1980; Thien, 1980). All Annonaceae, however, show features that are considered as typical of cantharophilous flowers. Protogyny, petal movements and flower closure, short duration of anthesis, shedding off flower parts, and occasionally the presence of staminodes, are features which are found in many Magnoliidae at least in part pollinated by beetles (Endress, 1984a; Thien, 1980).

Different beetle taxa – Gottsberger (1990) reports for the neotropical genera visitors of different taxa in small flowers and in large flowers. The larger Scarabaeidae visit the larger flowers, whereas smaller flowers attract smaller beetles such as Nitidulidae or Chrysomelidae. The size of the flower, the flowers being pendulous or upright, the presence or absence as well as the size of the floral chamber, and the odours all seem to play a role in the visitors which are attracted.

Different flower-pollinator-relationships – Some genera may have more specialized relationships with their pollinator. The beetles in that case are no longer casual visitors, but have a mutual relationship with the flowers they pollinate. In Chapter 6 the example is mentioned of an African *Annona*-species of which only flowers early in the flowering season set fruit. Flowers later in the flowering season play a role in the reproduction of the pollinators by offering them food and a mating place. *Annona*, indeed, is considered as a specialized genus on the basis of the arguments mentioned in paragraph 7.2. *Annona*, however, on the basis of the scarce data available on the flower biology, seems to be a genus that has developed a diversity in flower biological strategies (Chapter 6). And this corresponds with the greater diversity in flower morphology within the genus, compared with most other Annonaceae.

Recapitulating the above, it is not possible to indicate a clear difference in the degree of specialization in flower biology within the Annonaceae. There seems to be rather a great diversity in the beetle taxa being attracted between the various genera and between the various species within genera than an evolutionary development. Much more study, however, is necessary on phenology, flower biology, and ecology of Annonaceae.

8. CONCLUSIONS

1) The flower morphology of the genera of the Annonaceae was relatively well-documented before the start of the present study. Nevertheless, a few new characters have been discovered which are important to classification (e.g., texture of the stamens and their apices, moment of flower break). Field studies on phenology or flower biology or the use of SEM-techniques are promising in revealing new facts on flower morphology of Annonaceae.

2) The importance of floral characters, especially those of the petals, to classifications of Annonaceae has been overestimated in the past. Non-floral features rather than the flowers indicate affinities between genera. The petals are relatively important in the classification of the Asiatic genera, which predominated in the 19th century. Since the number of neotropical and African genera known has increased, characters of stamens and carpels should be taken into consideration as well.
3) A subfamily Monodoroideae, with *Isolona* and *Monodora,* is not supported by the flower morphology. The only groups maintained of the groups or tribes of previous classifications, are the Annona-group, the Guatteria-group, and the Cymbopetalum-group, present in the classifications of Fries (1959) and Walker (1971a).
4) The neotropical genera are relatively easy to classify and one may rely largely on the classification of Fries (1959). The African and Asiatic genera are more difficult to classify. In fact, the Meiogyne-group and Uvaria-group are the only clear-cut groups outside the Neotropics. Especially the classification of the Asiatic genera will always remain a matter of personal opinion. Any classification of the Asiatic genera, however, should be consistent with the chromosome numbers given by Okada (1987).
5) The delimitation of most genera is disputable and needs further study. Flowers generally play a role in the recognition and the delimitation of genera. Flower morphology, however, in most cases, will result in too narrow genus-concepts. The Australian genus *Ancana,* included by Fries (1955) in *Fissistigma,* should be reestablished or united with *Meiogyne* and related genera.
6) The present study reveals that the chromosome number, as far as data are available presently, is a very important character. Diversity in flower structures, but also of fruit and seed structures and other characters as well as geographic distribution is largely correlated with the chromosome number. More data on chromosome numbers are urgently needed, especially of genera which are difficult to place (e.g., *Dendrokingstonia, Greenwayodendron, Piptostigma*).
7) Studies on the flower biology of Annonaceae are almost restricted to those genera which are obviously most adapted to beetle pollination (or to beetles with a larger size). For the greater part of the family such studies are lacking.

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