

Comparative morphological evaluation of inflorescence characters in *Annonaceae*

Focko WEBERLING and Jürgen R. HOPPE

Abstract: The inflorescences of *Annonaceae* are monotelic and in this respect primitive: the basic branching type is a thyrsoïd formed by a terminal flower and a varying number of lateral cymosely branched partial inflorescences. The ramification of the cymose partial inflorescences is monochasial. It starts out of the axil of the usually adaxial prophyll (addorsed prophyll) which precedes the terminal flower and continues from the axils of the addorsed prophylls of secondary and higher order. Accordingly the consecutive flowers are all oriented in a vertical plane, thus forming a rhipidium. The rule of the addorsed position of the prophyll has some exceptions in which a transversally distichous order of scaly leaves and the subtended flowers results. In the proximal zone of the thyrsoïdal inflorescence the rhipidia can be preceded by branches which are themselves thyrsoïform. Towards the apex of the inflorescence a progressive reduction of the rhipidial partial inflorescences often takes place and consequently a reduction of the number of flowers. The thyrsoïds can be reduced to botryoids or umbel-like contracted botryoids, often described as "terminate racemes" or "terminate umbels". The ultimate stage of reduction is the single terminal flower, which occurs in many taxa, although at the time of anthesis it has usually shifted into a pseudolateral position.

Thyrsoïds in a permanent terminal position, i.e. at the end of a more or less extended leafy shoot, are very rare within the family. Frequently the originally terminal position of the inflorescences is changed because the lateral shoot originating in the axil of the preceding foliage leaf does not only overtop the flowering main shoot but beyond this is completely aligned in the direction of the main axis, creating the impression that it is the continuation of the main shoot, the inflorescence then being in lateral position. If the overtopping branches come to flower the same process may be repeated. By this way series of superposed shoot generations can be formed, each of them overtopping its mother axis. Altogether they give the impression of a homogenous monopodial axis, though in reality they form a sympodium. The relations between the different parts can be more complicated by concaulescence resulting in the formation of "extra-axillary" or "leaf-opposed" inflorescences. On the other hand there are some taxa with genuine "axillary inflorescences" - often distinguished as "truly axillary" inflorescences - which originate in the axils of foliage leaves of a proliferating synflorescences axis.

The ramification system may still be complicated by the occurrence of accessory shoots, which can develop in different ways. In some genera a long shoot - short shoot differentiation has taken place. The short shoots can be developed as flagelliform shoots ending in pendulous flowers. In other species cauliflory is observed, resulting from retardation of anthesis.

Introduction

The comprehensive account on *Annonaceae* by FRIES (1959) characterizes the inflorescences in more detail than is usually done in comparable treatments

of other families or taxa of lower rank. The reason for this is the fact that one can quite easily recognize the inflorescences of the *Annonaceae* at first sight as, in a straightforward descriptive sense, belonging to three basic types. So, in very early descriptions of the family the inflorescences are classified as being "terminal", "leaf-opposed" or "axillary" (BENTHAM 1862: 20; EICHLER 1878: 147).

FRIES (1919; 1959) described the characters of inflorescences in great detail, especially the taxa of higher rank. This should not lead to the opinion that these characters were regarded to be of great taxonomic value throughout the *Annonaceae*. FRIES himself states, that (in translation) "for the subdivision of the family the different position of the flowers does not appear to be applicable" (FRIES 1919: 47), whereas for the delimitation of genera, subgenera and species the "study of inflorescences ... might be of considerable value".

In many of the descriptions of genera or species the inflorescences are characterized as belonging to one of the "basic types" mentioned above. A detailed description of the branching pattern is mostly lacking, a fact which renders a comparison of the inflorescences of different species quite impossible.

Even less is known about the position of the inflorescences in the branching system of the plant as a whole, which is the case in most studies on inflorescences of woody plants. Therefore not very much is known about the arrangement of repetitive units (i.e. paracladia in the sense of TROLL) within the flowering region.

Based on the typology of inflorescences revealed by TROLL (1964, 1969, see also TROLL & WEBER 1955) a comparative survey is given of the inflorescence characters. The nature of the flower bearing elements which may be compared as identical structures can therefore be ascertained. This will show which characters might be investigated in future monographic treatments of the family. It may also contribute to find out the different morphological lines which may be interpreted in terms of phylogeny.

Modes of ramification

The basic branching type of the inflorescences of the *Annonaceae* is a *thyrsoid* in the sense of BRIGGS & JOHNSON (1979) and WEBERLING (1988 b: 231): a ramification system with cymosely branched partial inflorescences on a multinodate dominating main axis, which ends in a terminal flower (a determinate thyrses in the sense of TROLL 1964).

"C y m o s e b r a n c h i n g" is defined here as a branching exclusively from the axils of the prophylls. In *Annonaceae* only a single prophyll occurs, which in the vegetative as well as in the floral branches mostly appears in an adaxial position as a so-called a d d o r s e d prophyll, a position otherwise known as typical for the monocotyledons (cf. WEISSE 1926). Consequently the ramification of a cymose partial inflorescence is monochasial (fig. 1 I). It starts out of the axil of the adaxial prophyll which precedes the primary flower and continues from the axils of the addorsed prophylls of the flowers of secondary and higher order. Accordingly the consecutive floral branches of the partial inflorescence are all oriented in a vertical plane (the median plane corresponding to the relevant subtending bract of the partial inflorescence). This sort of a cymosely branched partial inflorescence is called a r h i p i d i u m (EICHLER 1875: 39).

There are, however, a few exceptions from the rule of the median position of the prophylls and ramification. Among them are the inflorescence of *Mezzettia leptopoda* with a transversally distichous order of scaly leaves and the subtended flowers (fig. 3 I, II; 4 I) and *Asimina triloba* (fig. 7) or some species of *Annona*, as e.g. *A. cherimola* MILL. (fig. 11 I, II) and *A. senegalensis* PERS. (fig. 11 III, IV); for further information see WEISSE (1927).

The thyrsoid stated before as the basic branching form of inflorescences in the *Annonaceae* thus is composed of a terminal flower and a varying number of lateral rhipidia as is shown by fig. 1 I. This is sometimes called a double-rhipidium. In the proximal zone of the thyrsoidal inflorescence the rhipidia can be preceded by branches which are themselves thyrsiform (and may be called sub-thyrsoids). The entire inflorescence thus turns out to be a double-thyrsoid (diplothyrsoid, fig. 1 II), which in this special form is sometimes called a pleiorhipidium. On the other hand towards the apex of the inflorescence a progressive reduction of the rhipidial partial inflorescences often takes place, i.e. a decrease in the extent of branching and consequently a reduction in the number of flowers. This can be seen in the inflorescences of *Artabotrys* (fig. 5 I - III) of *Guatteria anomala* (fig. 1 III) and of *Cananga odorata* (fig. 6 II, III). Reduction can also affect the number of the rhipidial partial inflorescences, until only the uppermost rhipidium remains (fig. 2 II). The remaining arrangement of flowers usually is called a "terminal rhipidium". This term, however, includes the terminal flower of the inflorescence as a part of the lateral rhipidial partial inflorescence and by this way obscures the comparison between inflorescences of different degree of reduction. The ultimate stage of reduction is the single terminal flower, which occurs in many taxa, although at the time of anthesis it has usually shifted into a pseudolateral

position. There are, however, also taxa with truly lateral flowers - a fact which we shall try to interpret later on.

Some taxa of the *Annonaceae* are described to have umbel-like inflorescences. In the strict sense this would mean that these inflorescences are indeterminate. This, however, is hardly to be expected within the *Annonaceae*. Thus the above mentioned inflorescences could be *botryoids* or contracted botryoids, often described as "terminate racemes" or "terminate umbels".

In case of the *Annonaceae* inflorescences of this ramification type should be derived from a thyrsoid by reduction of the rhipidial partial inflorescences to single lateral flowers. This apparently applies to the few-flowered axillary botryoids of the genus *Mezzettia* BECC. In *Mezzettia leptopoda* OLIV. the bases of the 5- or 4-flowered umbel-like inflorescences (fig. 3 I, IV) bear some (3) sterile scales, which - as an exception among the *Annonaceae* - are in a transversal-distichous order. The subtending scaly leaves of the flowers are fallen off already, nevertheless it can be seen from the buds (fig. 3 II), that they followed in the transversal-distichous order. The arrangement of the bases of the flower stalks seems to confirm the transversal-distichous position of the lateral flowers (fig. 3 IV). However, the frontal section through a young inflorescence in fig. 4 I reveals that the two lowermost flowers are accessory flowers, which accompany the only two axillary flowers of the inflorescence. Thus the regular ramification of the inflorescence is that of a 3-flowered botryoid or sciadioid, which can easily be derived from a thyrsoid: since the two uniflorous branches preceding the terminal flower do not bear any bracts, their further ramification appears to be inhibited. The result is a botryoidal branching system (raceme-like, but ending in a terminal flower). The statements of FRIES (1919: 36 - 38) for other species of *Mezzettia* can be interpreted in a similar way.

At first sight the likewise axillary inflorescences of *Monanthotaxis whytei* (STAPF) VERDCOURT (fig. 11 V) seem to be botryoids as well, but their ramification proves them to be *sciadioids* (contracted thyrsoids, fig. 11 VI). In contrast to this species the inflorescences of *M. congoensis* BAILLON are described by LE THOMAS (1969) as "racèmes simples" and portrayed with a long rhachis (LE THOMAS 1969, pl. 45, 1). Probably fresh or pickled young inflorescences are necessary to find out, whether these "racemes" end in a terminal flower or not.

In 4 of the 5 species of *Tetrameranthus* R. E. FRIES the axillary inflorescences "remain single-flowered", only *T. umbellatus* WESTRA is described to have "(up to) 5-flowered umbels often arising from every axil" (WESTRA 1985: 480). According to the comments given by WESTRA one of the flowers

is a "first order flower" and comparable to the single flower of the other species. Consequently the inflorescence of *T. umbellatus* should be called a contracted botryoid.

A character of high diagnostic value is the occurrence and different position of an articulation on the flower stalk serving as abscission zone for fruits and nonfertilized flowers. The differences of diagnostic value especially refer to the location of the articulation in relation to the mostly present sterile bracts. It seems to be doubtful, however, whether the articulations in different position are comparable elements in a morphological sense.

Position and metatopic displacement of inflorescences.

Within the *Annonaceae* a thyrsoidal inflorescence as described in chapter 2 rarely can be found in a terminal position, i.e. at the end of a more or less extended leafy shoot. Perhaps some species of the large genus *Fissistigma* GRIFF. could serve as an example, such as *F. shangtzeense* or *F. xylopetalum* TSIANG et P.T.LI (cf. the drawings added to the original descriptions in TSIANG & LI 1965, pl. LXIII and LX).

We can also refer here to a well-known drawing of *Mitrephora maingayi* HOOK.f. et THOMS. (fig. 2 II) first published by FRIES (1911). However, the inflorescence shown by this picture is restricted to what is called a many-flowered "terminal rhipidium". As explained before, this means that the terminal thyrsoid is reduced to its terminal flower (which has fallen off here already) and one lateral rhipidium.

Other species of *Mitrephora* are said to have "axillary" flowers or inflorescences, though FRIES (1919) states that all the species investigated fundamentally displayed the same structure. The reason for this discrepancy is that in most cases the terminal inflorescence is overtopped by a rapidly developing lateral shoot, which, originating in the axil of the uppermost leaf pushes the terminal inflorescence aside. This may be demonstrated by the somewhat schematic drawing of the inflorescence of *Guatteria anomala* R. E. FRIES (fig. 1 III), which still keeps a more or less terminal position. In most cases the inflorescence appears to be in a truly lateral position, as it happens in many species of *Annona* (fig. 1 VII). Here the appearance and position of the bract b might even strengthen the impression of a true axillary position of a rhipidial inflorescence, though in reality this bract only subtends the floral branch terminated by flower 1. It follows the leaf a and precedes the bract c on the flowering shoot ending in flower T.

Annona cherimola MILL. (fig. 11 I, II) may serve as a further example for the overtopping of a terminal flower by a lateral shoot originating in the axil of the uppermost foliaceous leaf.

Often the leafy lateral shoot originating in the axil of the leaf does not only overtop the flowering main shoot but beyond this is completely aligned in the direction of the main axis, creating the impression that it is the continuation of the main shoot. The relations between the different parts can be more complicated by a concaulescence of the overtopping branch with the prolonged internode between leaf a and the bract b (fig. 1 VIII). If the overtopping branches come to flower the same process may be repeated. By this way series of superposed shoot generations can be formed, each of them overtopping its mother axis. All together they give the impression of a homogeneous monopodial axis, whereas in reality they form a sympodium. This also applies to the flowering branches of *Artabotrys* R. BR., a genus comprising many hook climbers which are especially interesting because of the transformation of the axes of their thyrsoidal inflorescences into hooks (fig. 5 II, III). The inflorescences were thoroughly investigated by TREUB (1883) and later by FRIES (1949), who recognized that their originally terminal position is altered by the development of a lateral shoot arising from the leaf axil below the inflorescence and continuing the branching system. At first sight this branching system can look like a monopodial branch bearing hooks below every third leaf, as in *A. suaveolens* BL. or *A. insignis* ENGLER et DIELS. This may be explained by fig. 5 IV taken from a branching diagram of *A. insignis* given by CREMERS (1973). The hooks, however, are transformed terminal inflorescences, each of them marking the distal end of a short shoot generation. In such cases the position of the inflorescences is usually described as "extraaxillary" or "leaf-opposed" like the "single lateral flowers" of *Richella* A. GRAY (*R. biglandulosa* (BL.) R. E. FR., fig. 1 V) and many species of *Hornschurchia* (fig. 1 IV). The position of the inflorescence of *Cyathostemma* (fig. 1 VI) again is said to be "extraaxillary". Nevertheless, early stages of the ontogeny of all these "extraaxillary" or "opposite" flowers and rhipidia reveal their original terminal position.

On the other hand there are many taxa with genuine "axillary inflorescences" i.e. originating in the axils of foliage leaves as e.g. in *Tetrameranthus* R. E. FR. (WESTRA 1985) or *Pseudoxandra* R. E. FR. (MAAS et al. 1986). They are often distinguished as "truly axillary" from the "extra-axillary" or "pseudo-axillary" inflorescences.

These different terms which are in use for the description of the diverse modifications of the position and shape of flower bearing branching systems

may be useful for a brief characterization of the diverse forms. They are, however, not sufficient to reveal the morphological relations between them.

Comparative studies

We might be well advised therefore, to return to our initial statement, that we should regard the terminal thyrsoid as the basic branching type of the inflorescences of the *Annonaceae*, although thyrsoids in a permanent terminal position are very rare within the family. We have, however, pointed out already, that the "extraaxillary" and "opposite" lateral single flowers are in reality terminal flowers. They occur in all generic groups of the *Annonaceae* (sensu FRIES 1959). They can be typical for whole groups, such as the *Trigynaea*-group, comprising the genera *Porcelia*, *Cardiopetalum*, *Cymbopetalum*, *Trigynaea*, *Hornschuchia* and *Bocagea*. However, these genera don't have single flowers exclusively as FRIES suggests (FRIES 1959, 157). There are recently described species of *Hornschuchia* which have highly elaborate thyrsoids (*H. obliqua* P. MAAS & VAN SETTEN; MAAS et al. 1988). On the other hand single flowers occur in many species of genera which are characterized as having inflorescences. The "extraaxillary" lateral flowers thus can be regarded as reduced thyrsoidal inflorescences of originally terminal position.

As we have seen e.g. in *Mitrephora maingayi* HOOK. f. et THOMS. (fig. 2 II), the terminal thyrsoid can be highly reduced and then only comprise one rich-flowered rhipidium below the terminal flower. Further reduction can affect the number of flowers of this remaining rhipidium. As an example the species of *Guatteria* may be mentioned (fig. 1 III). We can find many transitional forms between more or less reduced thyrsoids keeping a terminal position for a shorter or longer period of their ontogeny, depending on the more or less early and strong development of the axillary shoot, which continues the branching system.

Thyrsoids bearing one terminal rhipidium with a low number of flowers occur in many genera. In *Annona malmeana* R. E. FRIES (fig. 2 III) two-flowered terminal inflorescences in concaulescence with an overtopping lateral shoot were found by FRIES (1919, fig. 6), but also a uniflorous terminal inflorescence (fig. 2 IV). FRIES (1919: 28) also mentions small few-flowered terminal inflorescences for *Melodorum lanuginosum* and *M. verrucosum* HOOK. f. et THOMS. (*Fissistigma lanuginosum* and *F. verrucosum* (HOOK. f. et THOMS.) MERR.). Further examples are *Orophea* (*O. hexandra*; s. FRIES 1919, fig. 16; see also KESSLER 1988) or *Duguetia*, for which inflorescences are reported to have 2-3-4, but exceptionally 12 flowers, whereas *D. uniflora*

(DUN.) MART. always has single flowers (FRIES 1919: 16). Further examples can be found in the genus *Uvaria* (fig. 2 I).

There are, however, also taxa with truly axillary single flowers, rhipidia and even thyrsoids, which do not merit their lateral and axillary position to any kind of metatopic displacement. As mentioned already, axillary botryoids are characteristic for *Mezzetia leptopoda* OLIV. (fig. 3) and a few other taxa. The question thus must be answered, how the position of these flower bearing ramification systems is related to the architecture found in most taxa of the family.

The well known diagram of the inflorescences of *Xylopia brasiliensis* SPRENG., published by FRIES (1919, 1959) shows a few-flowered thyrsoid originating from the axil of a foliaceous leaf and accompanied by an axonoscopic vegetative bud (fig. 2 VIII). In his comment FRIES (1919: 39) wrote: "Die Blüten sitzen in Infloreszenzen, und diese sind achselständig und kommen in allen Blattachseln in der floralen Region des Triebes ohne sterile Intervalle vor." (The flowers are arranged in inflorescences; these are axillary and occur in the axils of all the leaves within the floral region of the shoot without any intervals.) According to FRIES (1919: 41/42) the same applies to *Unonopsis lindmanii*, *U. riedeliana* R.E. FRIES and other species of this genus. Their inflorescences differ in the degree of their ramification and the number of flowers, which is reported to be very high in *U. riedeliana*. However, the bract below the terminal flower (T in fig. 2 IX) remains sterile in all cases (FRIES 1919: 41).

Here we like to refer to *Xylopia frutescens* AUBL., a species characterised by highly symmetrically ramified branches (fig. 4 III). Each of the smaller branches bears some sterile foliaceous leaves in its basal part followed by an extended and uninterrupted zone, in which each of the leaves bears a reduced thyrsoidal inflorescence in its axil (fig. 4 II). These axillary inflorescences conform with those depicted by FRIES (1919) for *Xylopia brasiliensis* SPRENG. (fig. 2 VIII) even with respect to the presence of a vegetative axonoscopic accessory bud. The uppermost leaves of the twigs are sterile again; with other words: the apex of the twig continues to vegetative growth without - or before - developing a terminal thyrsoid and a terminal flower. This phenomenon of *p r o l i f e r a t i o n*, has been described (basing on results of W. TROLL) by WEBERLING (1981/89) for some *Myrtaceae*, but can be found in many other families (WEBERLING 1983; 1988 a, b; WEBERLING & HERKOMMER 1989; STECK & WEBERLING 1989).

Whereas the majority of species in *Xylopia* is characterised by thyrsoidal partial inflorescences in the axils of foliage leaves of a proliferating inflores-

cence, in a minority of species the axillary thyrsoids are reduced to single flowers, which may be stalked or even sessile. There are some intermediate forms demonstrating the transition between both extremes.

The same situation - within the same genus species with axillary thyrsoids and others with single flowers borne from the axils of foliaceous leaves - returns e.g. in *Bocageopsis*, as can be inferred from the description given by MAAS et al. (1986).

Thus the occurrence of single axillary flowers reported for so many taxa can be explained by reduction of axillary thyrsoids. The same applies to the axillary botryoids - as in *Mezzettia leptopoda* - which also can be derived by reduction of the ramification of a thyrsoid.

In *Cananga odorata* (LAM.) HOOK. f. et THOMS. well developed thyrsoids (fig. 6 III) occur in the axils of all the foliaceous leaves along the middle zone of the twigs, which then continue their development with sterile leaves, thus returning to vegetative growth again (fig. 6 I). We can also interpret this arrangement of inflorescences as a differentiation of the branching system into vegetative long shoots (macro-blasts) and flower bearing short shoots (brachy-blasts). However, in contrast with the long-shoot - short-shoot systems known from the temperate zones the unfolding and anthesis of the flower-bearing short shoots here occurs immediately after the development of the long shoot without any seasonal interruption, and the leaves subtending the short shoots are still alive. The short branches ending in umbel-like inflorescences described for *Mezzettia leptopoda* (fig. 3) seem to be in better agreement with the definition of a brachyblast, since for a shorter or longer period they are protected by a series of bud scales, though their subtending leaves often are still present at their flowering time.

In case of many species of *Asimina* ADANS., as in *A. triloba* (L.) DUN., *A. grandiflora* (BARTR.) DUN. and others, the macroblast-brachyblast differentiation appears to be clearer. The short uniflorous shoots at least in *A. triloba* (fig. 7) bear some scaly leaves at their bases and develop from the axils of decayed leaves on last-years shoots (see FRIES 1959: 72; A. GRAY 1848). In *A. pygmaea* (BARTR.) DUN. and *A. angustifolia* A. GRAY, however, the leathery subtending leaves of the flower bearing brachyblasts are still alive at the time of anthesis.

Whereas in *A. triloba* and *A. grandiflora* the uniflorous brachyblasts remain really short, they are developed as flagelliform shoots ending in pendulous flowers in the species of *Monodora* DUN., as *M. crispata* ENGL. (fig. 8), *M. tenuifolia* BENTH. (fig. 9 II) or *M. myristica* (GÄRTN.) DUN. (fig. 9 I), due to an elongation of the two distal internodes which can be more than 15 cm long.

The first internodes remain very short (fig. 8 I, II). The brachyblast character of the flowering shoots of *Monodora tenuifolia* was already confirmed by TROLL (1964: 124), who points to their exclusively bracteose foliation, though according to WEISSE (1927: 28) it happens that some foliaceous leaves or a transitional leaf precede the terminal flower. TROLL (1964: 124) regards the distal somewhat larger bract as a metaxyphyll. These brachyblasts are accompanied by two serial accessory buds (WEISSE 1926: 519).

According to WEISSE (1927: 29) and TROLL (1964: 124) a leafy shoot can arise from the axil of the uppermost of the basal scaly leaves and soon overtop the distal part of the flowering brachyblast. If these overtopping branches come to flower, the same process can be repeated. By this way again series of sympodial shoot generations can be formed, each of them overtopping its mother axis.

We have just mentioned the serial accessory buds which accompany the brachyblasts of *Monodora tenuifolia*. In this case the accessory buds are developed acropetally above the regular axillary shoot, a position called axonoscopic. The opposite, a basipetally development of accessory buds, called phylloscopic, could be seen in *Mezzettia leptopoda*. Here they occur in two different forms: as vegetative buds below the insertion of the brachyblast, and developed into flowers below the lateral flowers of the botryoid. In *Xylopia brasiliensis* we have met them as axonoscopic vegetative buds (fig. 2 VII, VIII), whereas in *Xylopia odoratissima* the vegetative accessory buds are reported to be phylloscopic. Thus position and differentiation of the accessory buds and even their orientation can be different, this can even refer to different shoots of the same plant, as in plagiotropic and upright growing shoots of *Xylopia odoratissima* (fig. 2 V, VI). The number of axillary buds can be considerably high. They are then often arranged in a zigzag-line, as is reported for the vegetative accessory buds of *Uvaria chamae* BEAUV. (FRIES 1919: 20).

As we have seen in *Mezzettia leptopoda* the occurrence of accessory flowers can considerably influence the habit of an inflorescence. This would prove all the more if they occur in high number (which might be the case in some species of *Cleistopholis* PIERRE).

In several species of *Xylopia* the "axillary inflorescences" can be affected by a retardation of anthesis (or even of flower-formation?) with the result of ramiflory or cauliflory, as was also described for some *Myrtaceae* by WEBERLING (1983, 1988 a). This apparently applies to *Xylopia stenopetala* OLIV. (fig. 10 III, after HOOKER, Ic. plant. 16, 1886) as well as to several other taxa, e.g. *Sageraea thwaitesii* HOOK.f. et THOMS. (fig. 10 I, see

BEDDOME 1874, pl. XLI), where axillary rhipidia - or thyrsoids - are portrayed originating in the axils of leaves as well as on leafless older twigs. The species of *Stelechocarpus* (BL.) HOOK.f. et THOMS. are exclusively ramiflorous or cauliflorous. A great number of examples has been described and portrayed by FRIES (1949) especially from the genera *Crematosperma*, *Xylopia* (*X. ulei* DIELS = *X. benthamii* R.E.FR.), *Guatteria* (*G. novogranatensis* R. E. FRIES) and *Duguetia* (*D. stelechantha* (DIELS) R. E. FR. In *Hornschuchia bryotrophe* NEES, which was also portrayed by FRIES (1919, fig.6) the highly ramified stem-borne floriferous branches rather appear as leafless flagelliform inflorescences, which according to FRIES arise from the base of the stem and extend over the soil. For the characterization and delimitation of *Duguetia* sect. *Geanthemum* by FRIES (see FRIES 1959: 57) the formation of stem-borne flagelliform inflorescences was even the deciding character. Among the species of this section there is also the well-known *Duguetia rhizantha* (EICHL.) HUB. (*Annona rhizantha* EICHL.), which was described and thoroughly investigated by EICHLER (1883) because of its long-stretched partly subterranean flowering branches (see also FRIES 1959: 21, fig. 11A). A similar architecture is reported for some Bornean species of *Polyalthia* BLUME [*P. flagellaris* (BECC.) AIRY SHAW] and *Uvariopsis* ENGL. (see FRIES 1959).

As in many other cases of cauliflory or ramiflory the flowering of the originally axillary inflorescences can continue over a long time. At first the continuation of flower formation may be due to the development of buds arising from the axils of the prophylls of different order at the base of the stem-borne inflorescences, finally, however, it often seems to extend into the formation of a meristimatic cushion which appears to produce inflorescences which can no more be allocated to the branching system of the original axillary inflorescence (fig. 10 IV). In case of *Duguetia rhizantha* the continuance of flowering is due to the sympodial continuation of the flower bearing branches (EICHLER 1883, FRIES 1949), which in principle follows the same mode as described above for *Annona cherimola* (fig. 11 I, II) and many other taxa of the family.

Typological evaluation and summary

Notwithstanding the many variations of inflorescence pattern in *Annonaceae* the flower bearing systems of all taxa which were investigated by us or taken into consideration basing on results of other authors proved that the basic branching type of inflorescences is the terminal thyrsoid. This is equivalent to the statement that they are *monotelic synflorescences* in the sense of TROLL (1964/69). In relation to the polytelic type of inflorescences which until now has not been found within the family this character can be

regarded as primitive. The diverse variations are due to reduction of the degree of ramification and the number of flowers, to metatopic displacements, to the differentiation of macroblast-brachyblast systems, to proliferation and to specializations like ramiflory and cauliflory.

Reduction of ramification often leads to uniflorous terminal or axillary inflorescences. In many taxa the vigorous development of a distal, overtopping axillary shoot together with metatopic displacement of axes or leaves causes the shifting of an originally terminal inflorescence or a single terminal flower into (pseudo-)lateral or "extra-axillary" position. The genuine axillary thyrsoidal inflorescences or single flowers should not be conceived as separate elements but rather be regarded as integrant parts (partial inflorescences) of a more extensive proliferating synflorescence. Further differentiation within a proliferating synflorescence can lead to a specialization of the branching system into vegetative macroblasts and flower bearing brachyblasts. Retardation of anthesis of axillary partial inflorescences or brachyblasts can result in ramiflory and cauliflory. All these variations indicate diverse and multiple trends, which probably occurred independently within different lines of evolution within the family.

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Adresses of the authors:

Prof. Dr. Focko WEBERLING Arbeitsgruppe Biosystematik, Universität Ulm, Liststraße 3, D-89079 Ulm, Germany. - Dr. Jürgen R. HOPPE, Abt. Spezielle Botanik der Universität Ulm, D-89096 Ulm, Germany.

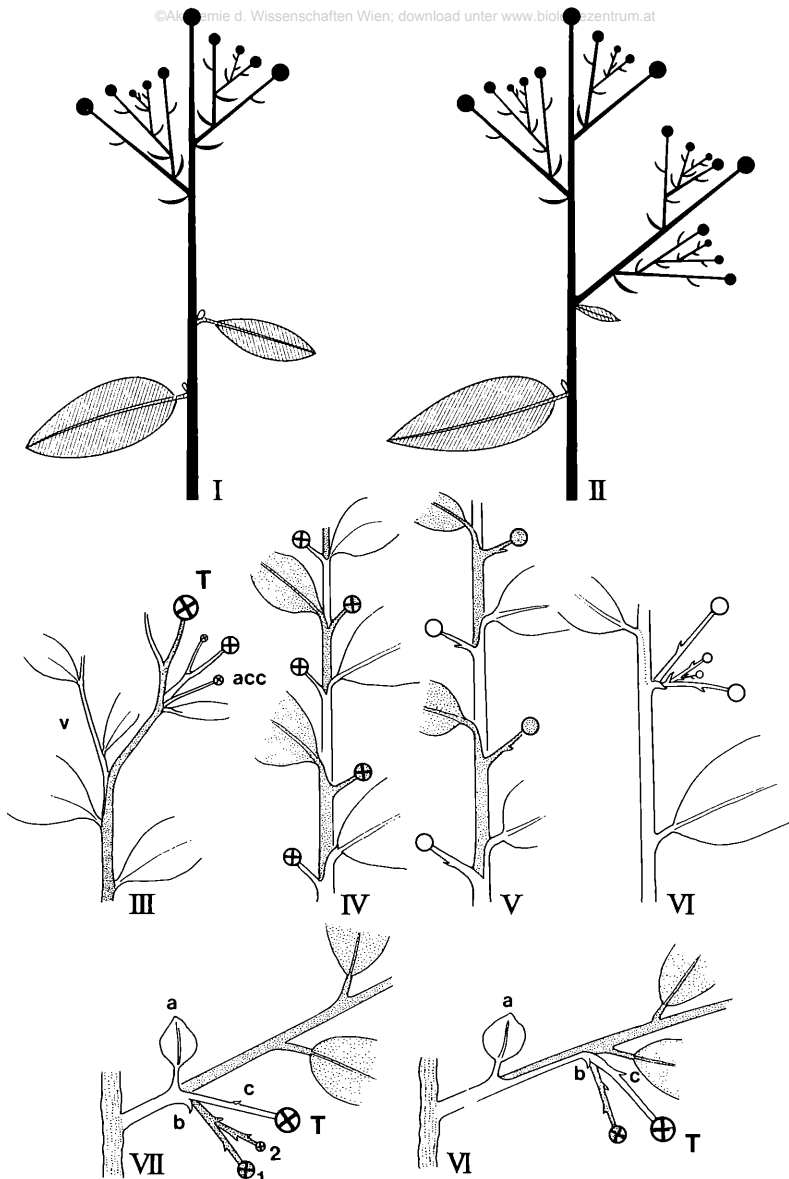


Fig. 1. I. Thyrsoid and II dithyrsoid as basic branching type of inflorescences of the *Annonaceae*; III *Guatteria anomala* R. E. FRIES, diagram of an inflorescence, T terminal flower, v vegetative branch, o outcropping the inflorescence, acc accessory flower of the lateral rhachidium; IV *Hornschuchia myrtillosa* NEES and *Richella biglandulosa* (BL.) R. E. FRIES (*Psychotria biglandulosa* SCHEFF.), V *Hornschuchia myrtillosa* NEES and *Richella biglandulosa* (BL.) R. E. FRIES, diagrams showing the ramification of flowering branches, the consecutive shoot generations are shaded in different manner; a - c consecutive leaves preceding the terminal flower T; 1, 2 consecutive flowers of the rhachidium. After FRIES 1939 (III), 1919 (IV - VI), and 1950 (VII, VIII).

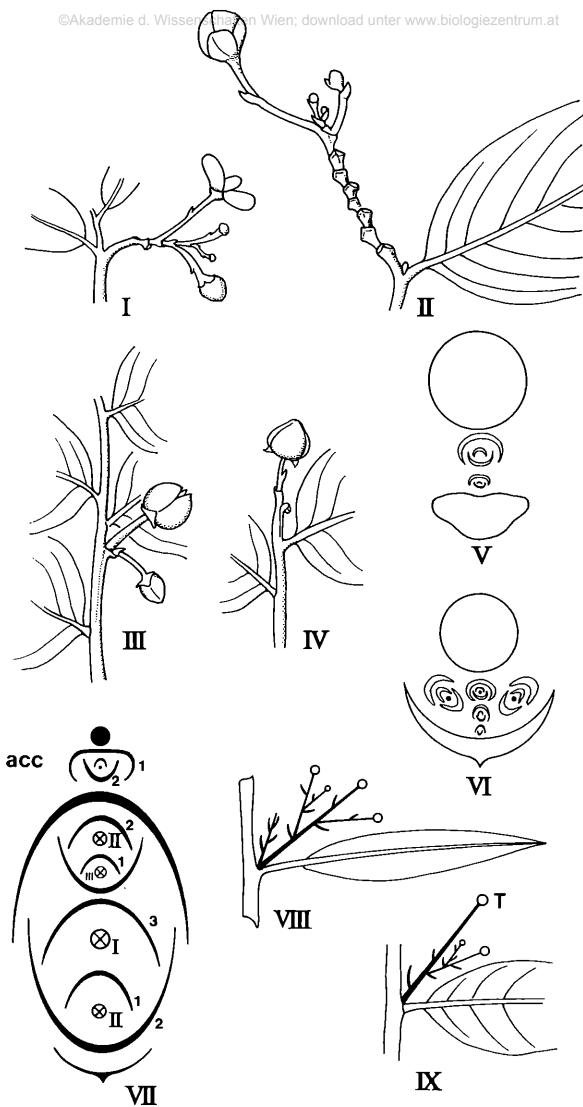


Fig. 2. I. *Uvaria macrophylla* ROXB., 6-flowered terminal thyrse with overtopping branch arising from the axil of the uppermost foliaceous leaf; II *Mitrephora maingayi* HOOK.f. et THOMS., terminal inflorescence with one many-flowered rhipidial branch; III, IV *Annona malmeana* R. E. FRIES, III two-flowered terminal inflorescence, overtopped by a branch arising from the axil of the uppermost foliaceous leaf, IV uniflorous inflorescence still in terminal position; V, VI *Xylopiya odoratissima* WELW., sections through axillary buds and accessory buds of a plagiotropic branch (V) and a vigorous upright growing shoot (VI); VII, VIII *Xylopiya brasiliensis* SPRENG., VII ramification of a thyrse with axonoscopic accessory vegetative bud (acc), VIII diagram in horizontal plane; IX *Unonopsis lindmani* R. E. FRIES, ramification of an axillary thyrse. After FRIES 1919.

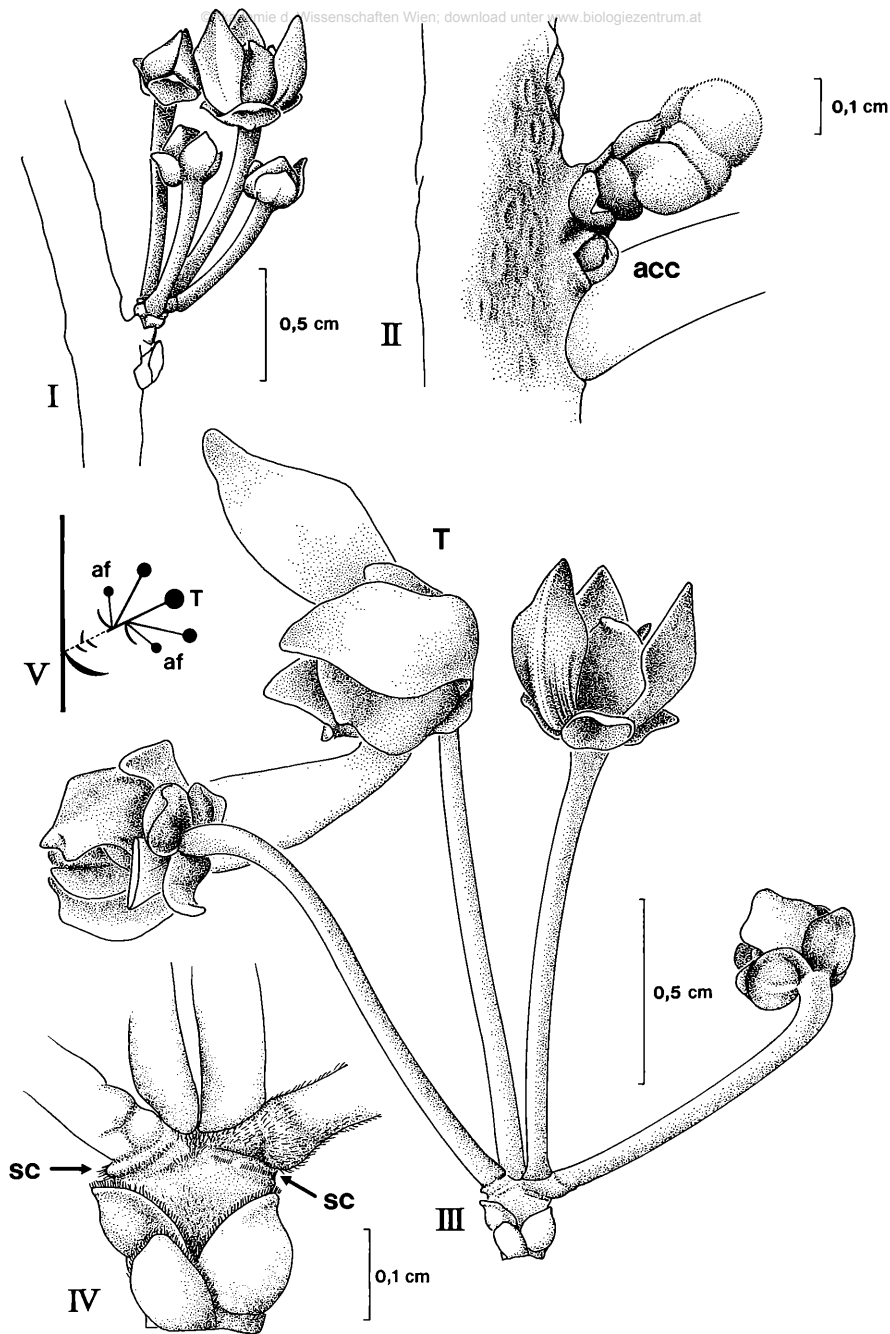


Fig. 3. *Mezzettia leptopoda* OLIV., axillary inflorescences (brachyblasts). I in natural position; III isolated, from the abaxial side; IV base of III on larger scale, sc scar of subtending bract; II bud of axillary inflorescence with accessory bud (acc); V diagram showing the ramification of an inflorescence; T terminal flower, af accessory flower (Mat.: Utrecht 1227).

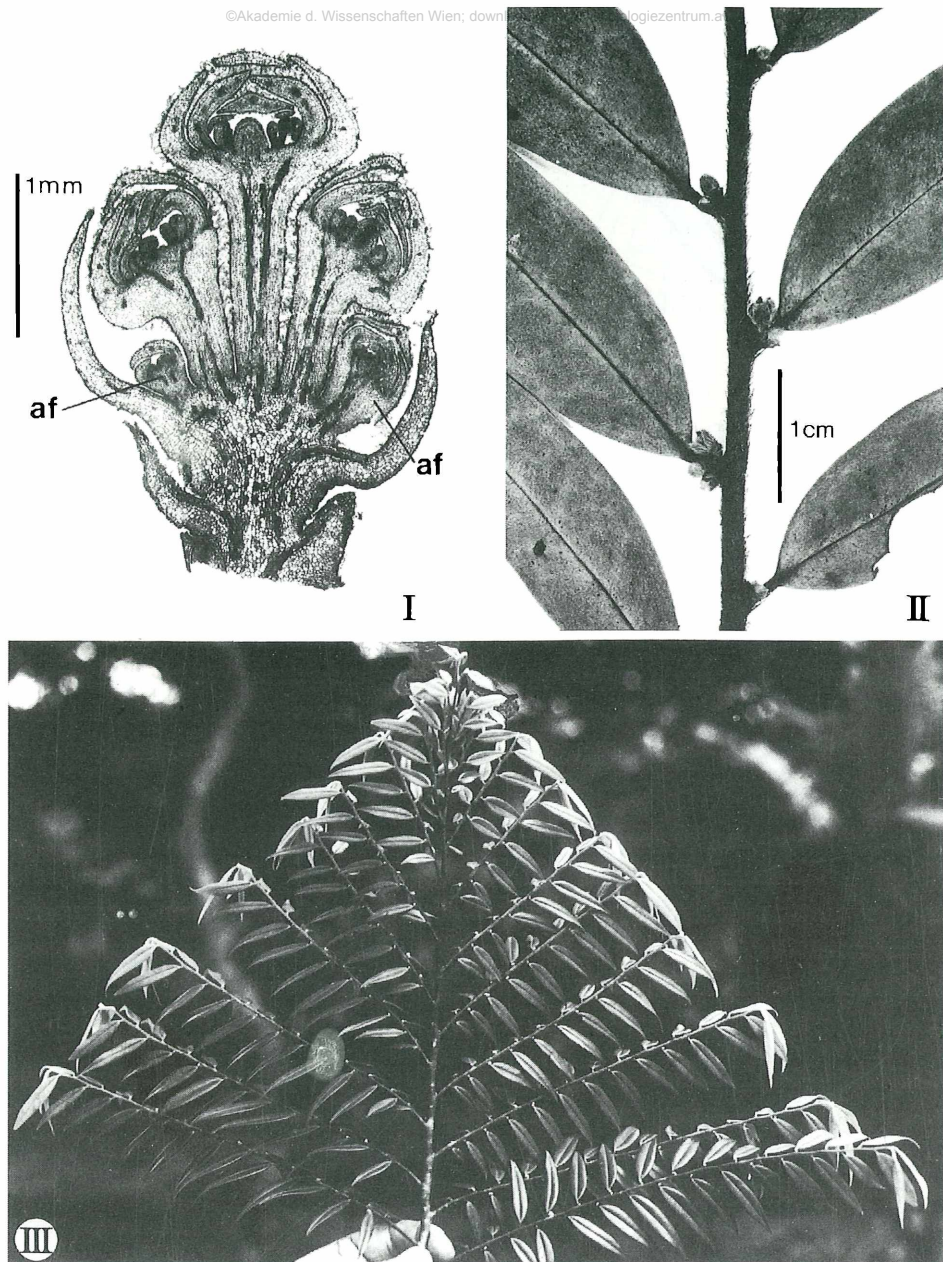


Fig. 4. I. *Mezzetia leptopoda* OLIV., frontal section of a botryoidal inflorescence, af accessory flower (same as in fig. 3 II; Mat.: Utrecht 1227); II, III *Xylopiya frutescens* AUBL., III symmetrically ramified branch with twigs which bear thyrsoïdal inflorescences in the axils of foliaceous leaves, II detail of a flower bearing twig (Mat.: WEBERLING 8562, CATIE, Turrialba, Costa Rica, cult., 1985).

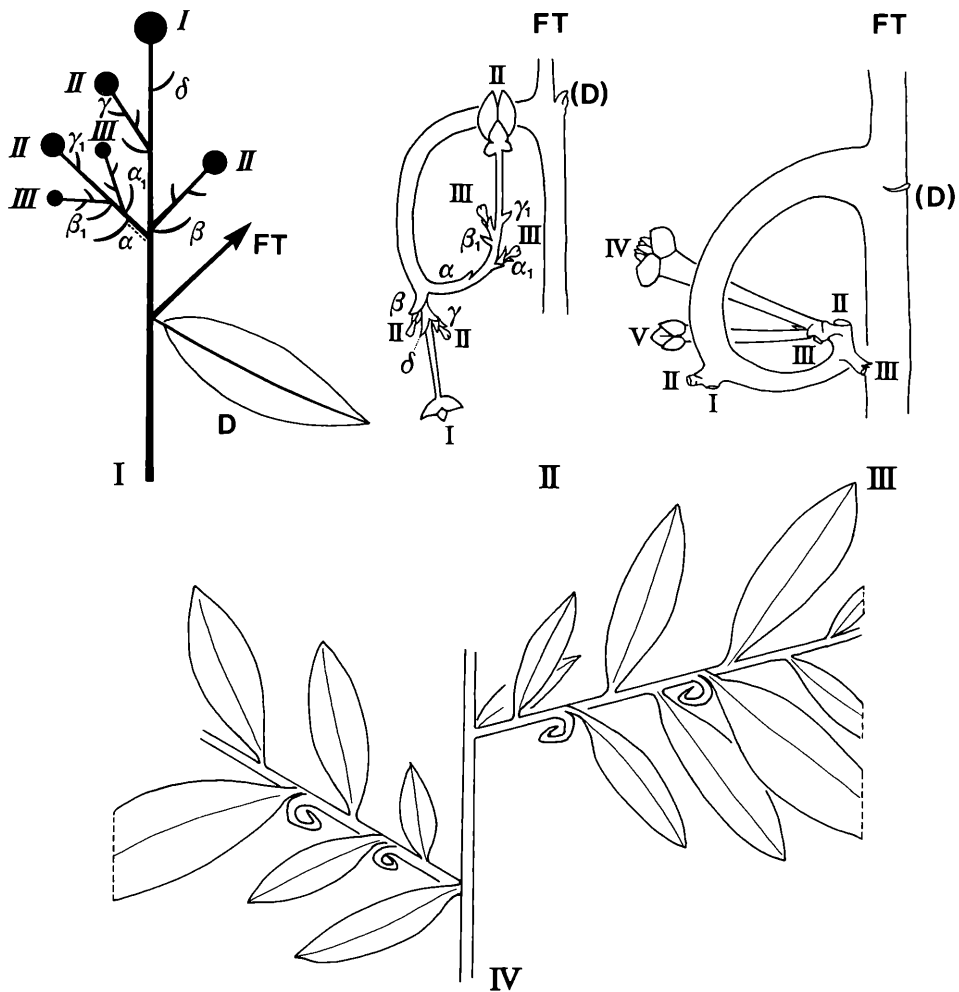


Fig. 5. *Artabotrys*, ramification and position of inflorescences. I diagram showing the ramification of a thyrsoideal according to fig. II; II, III hook-like inflorescences of *A. blumei* HOOK.f. et THOMS. (II) and *A. odoratissimus* R.BR. (after FRIES 1919); I terminal flower of the main axis, II and III terminal flowers of higher order, FT next sympodial axis, $\alpha - \delta$ and $\alpha_1 - \gamma_1$ consecutive leaves of the main axis and the secondary axis, respectively; IV *A. insignis* ENGLER et DIELS, part of a macroblast with two sympodially branched lateral axes, each shoot generation ending in a hook like inflorescence axes (after CREMERS 1973, altered).

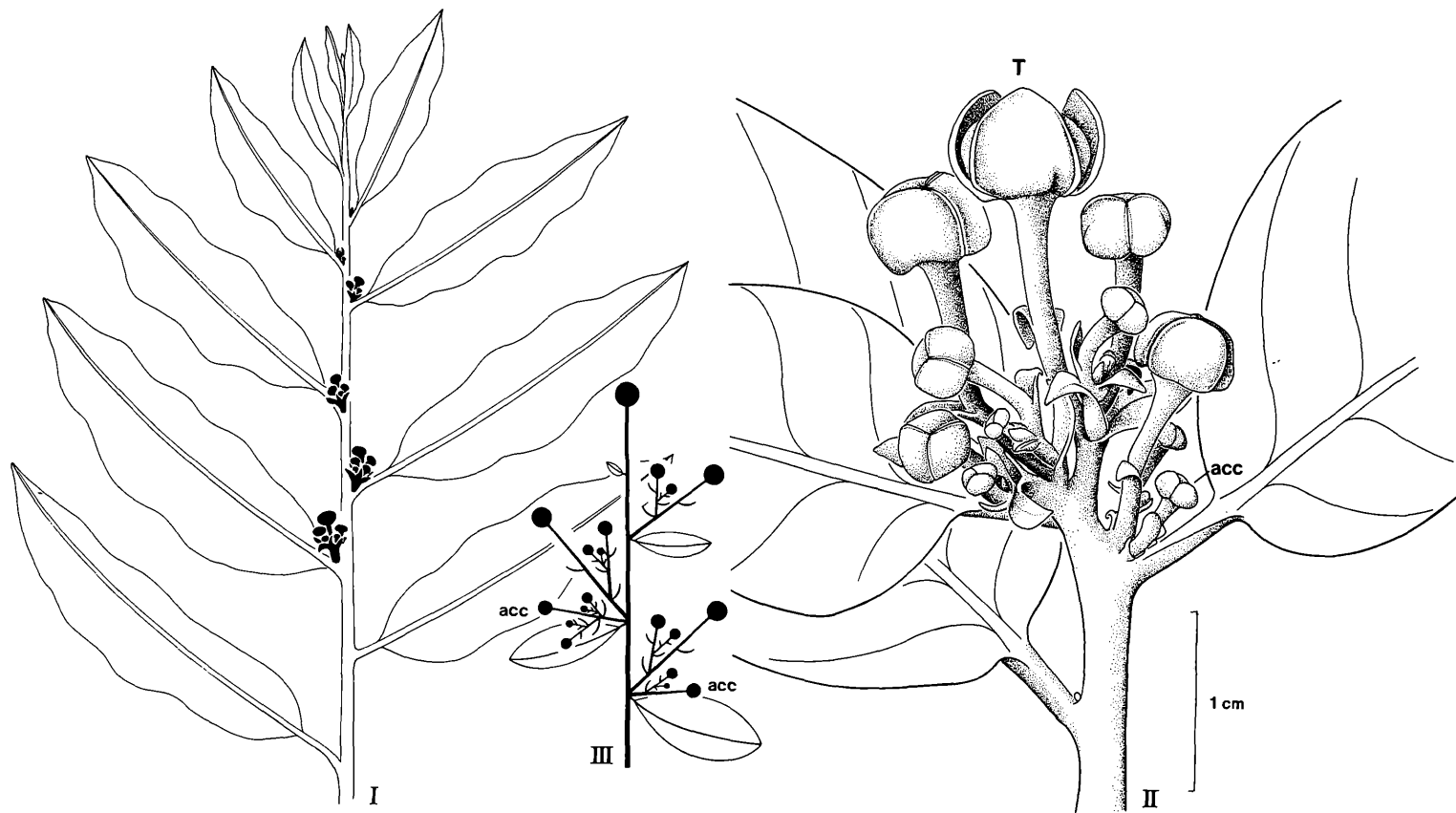


Fig. 6. *Cananga odorata* (LAM.) HOOK.f. et THOMS.; I flowering twig with thyrsoidal partial inflorescences in the axils of foliaceous leaves, slightly schematized; II thyrsoidal partial inflorescence (a flowering brachyblast), acc accessory flowering branch; III diagram showing the ramification of a thyrsoidal brachyblast (Mat. WEBERLING, s.n. San José, Costa Rica, cult., 1990).

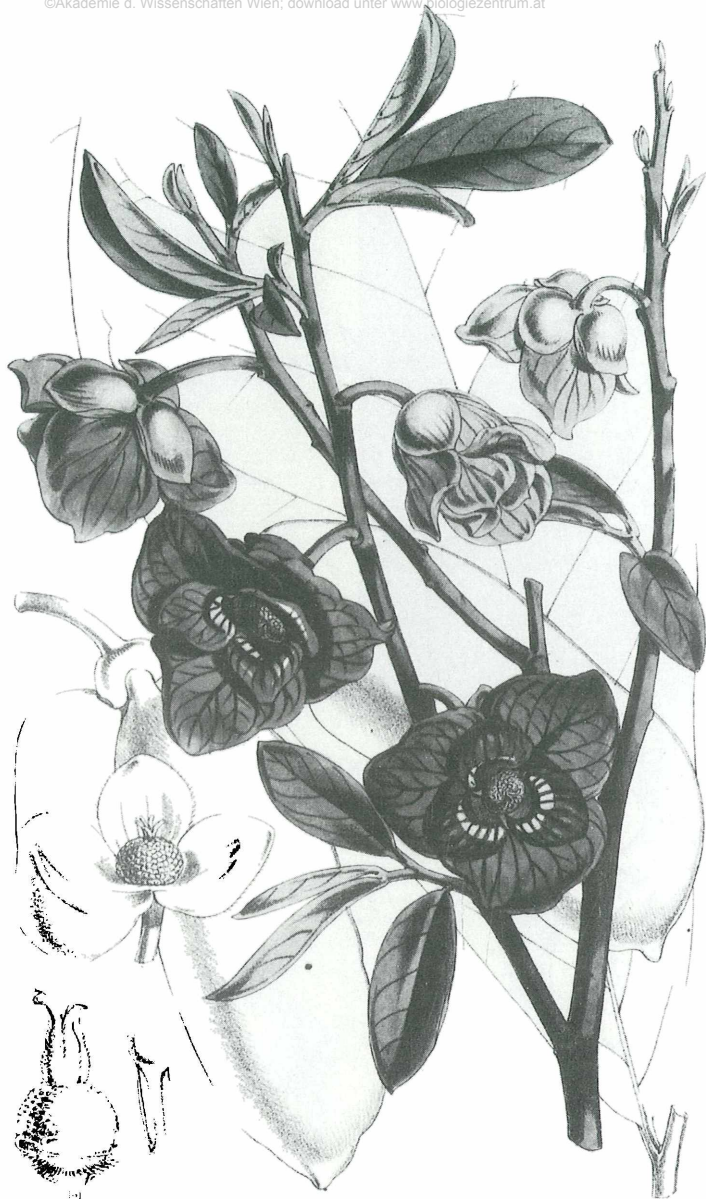


Fig. 7. *Asimina triloba* (L.) DUN. (Bot. Mag. 96, t. 5854, 1870)

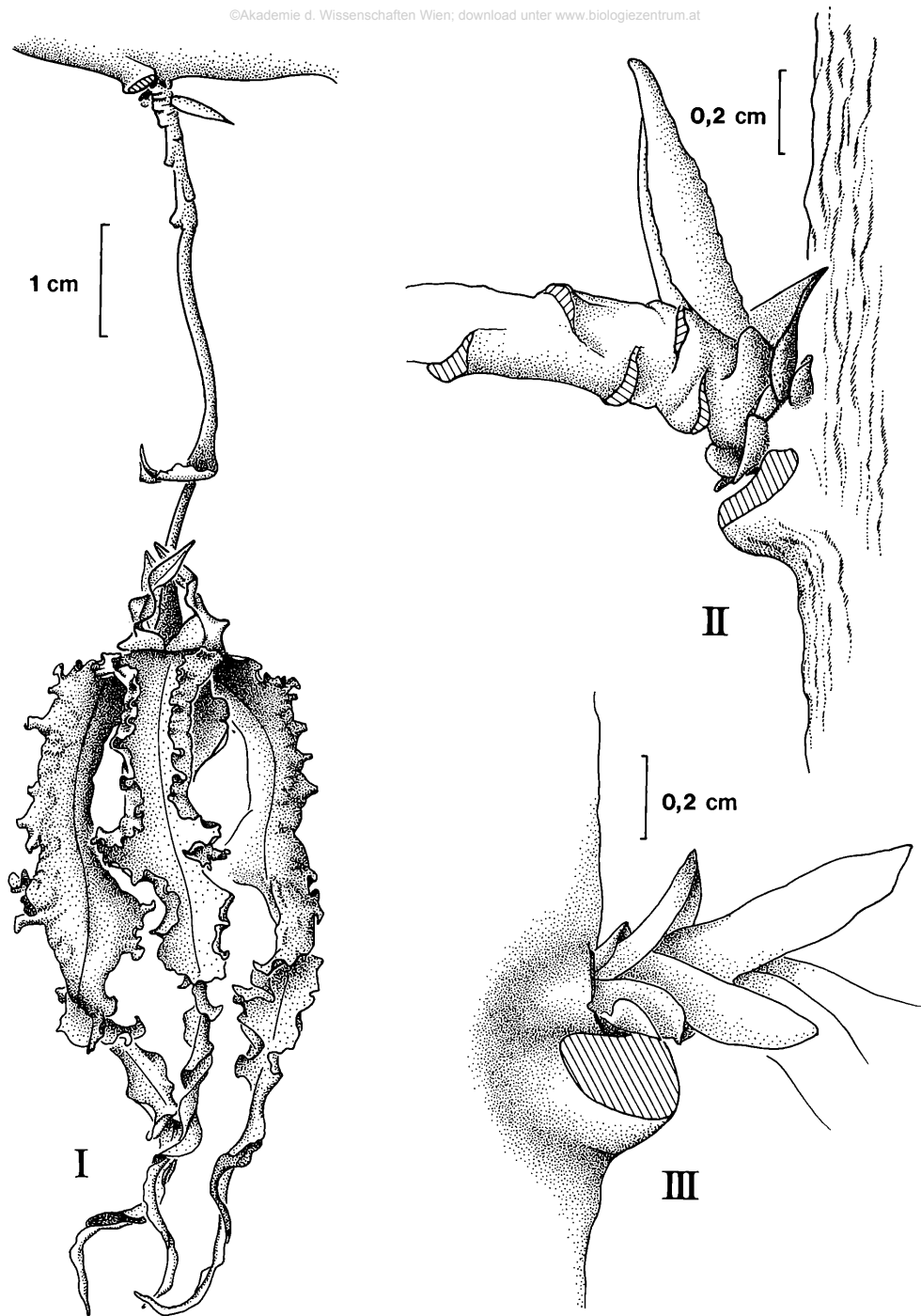


Fig. 8. *Monodora crispata* ENGL., I flagelliform brachyblast, II base of I on larger scale, III young brachyblast with distichously arranged more or less scaly leaves (Mat.: Bot. Gard. Utrecht).

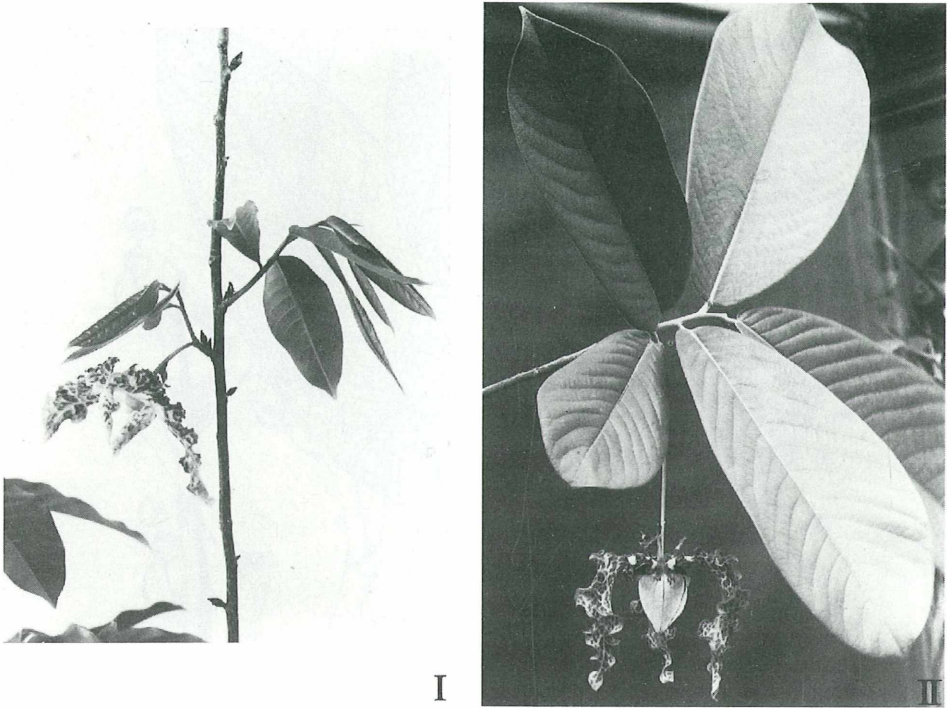


Fig. 9. I. *Monodora myristica* (GÄRTN.) DUN.; II *M. tenuifolia* BENTH., flagelliform brachyblasts (I orig. W. TROLL, II Bot. Gard. Tübingen).

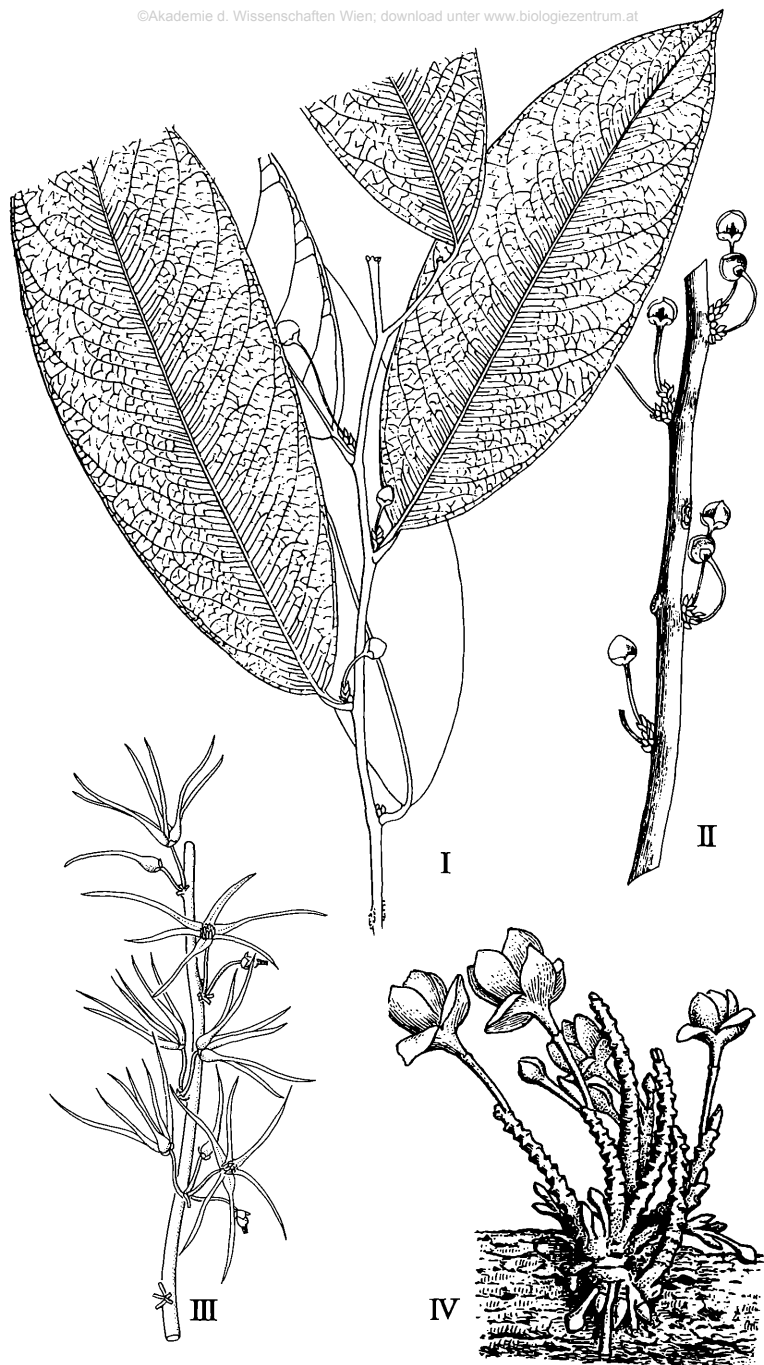


Fig. 10. I, II. *Sageraea thwaitesii* HOOK.f. et THOMS, younger (I) and elder part of a flowering branch (after BEDDOME 1874); III *Xylopi stenopetala* OLIV. (after HOOKER 1886); IV *Duguetia stelechantha* (DIELS) R. E. FRIES, cauliflorous inflorescence (after FRIES 1919).

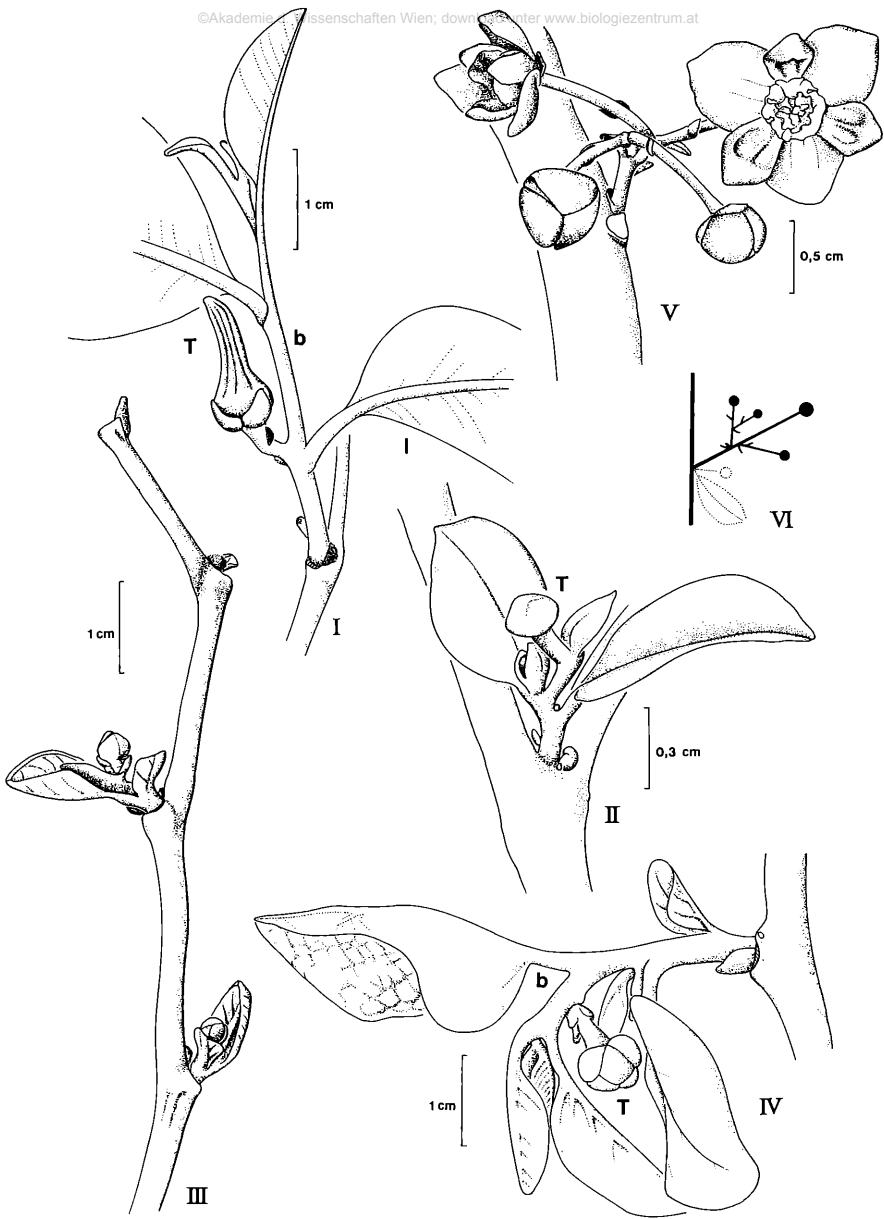


Fig. 11. I, II. *Annona cherimola* MILL., I axillary shoot ending in flower T and overtopped by an axillary branch b originating in the axil of leaf l; II young axillary flowering shoot. III, IV *Annona senegalensis* PERS., III last years macroblast with two developing brachyblasts, IV further developed brachyblast with terminal flower T and overtopping axillary shoot b; V, VI *Monanthes whytei* (STAPF) VERDCOURT, axillary inflorescence (V) and diagram of its ramification (VI) (Mat. I, II Bot. Garden Ulm; III, IV Bot. Garden Nelspruit, RSA, leg. WEBERLING 1985; V, VI Bot. Garden Utrecht, de Wit s.n.).

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