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THE GENERA MITCHELLA AND DAMNACANTHUS

Evidence for their close alliance; comments on the campylotropy in the Rubiaceae and the circumscription of the Morindeae

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SUMMARY

The two species of *Mitchella* (Southeast Asian and North American) and several species of the Southeast Asian genus *Damnacanthus* are investigated. Vegetative character states (growth form, branching pattern, leaves) of the two genera are described and compared. *Damnacanthus* always exhibits heterophylly and some species have paired thorns. The latter are interpreted as paired lateral shoots in the proximal part of a sympodial branch unit, and it is speculated that the paired thorns may be modified inflorescence shoots.

Detailed information is also given on inflorescence structure and floral morphological and anatomical details of *Damnacanthus* and *Mitchella*. Particular emphasis is placed on the ovaries, the structure of which is remarkably similar in the two genera. The uniovulate locules are characterized by having campylotropous ovules which are inserted near the top of the septum; extensive obturator tissue covers part of the horizontally arranged curved ovule in cap-like manner. The micropyle of the ovule, obscured by the obturator, points upwards and to some degree also inwards, while the embryo sac is found in a ± horizontal position. The seeds, however, contain minute embryos, of which the radicles are pointing ± downwards. This apparently contradicting micropyle and radicle position finds its explanation in the unusual ovule structure and orientation and in the subsequent strong growth of the endosperm, through which the embryo is pushed to the position where it is found in mature seeds. The detailed structure of the drupaceous fruits and of the seeds of both genera are compared.

Chromosome numbers ($x = n = 11$, $2n = 22$) are presented for *Mitchella* and *Damnacanthus*, certain palynological information is added, and literature on reproductive biological aspects is reviewed and supplemented by original observations.

While *Mitchella* had been associated with various different tribes, *Damnacanthus* was in the past nearly always placed in the Morindeae. The investigated characters overwhelmingly support the close alliance between *Mitchella* and *Damnacanthus*. However, according to our present state of knowledge, the Morindeae appear to be a heterogeneous tribe, and at least a group of genera allied to *Prismatomeris* is probably to be removed. *Damnacanthus* and *Mitchella* do show certain agreements with the 'core' of the Morindeae, but their definite tribal placement should be withheld until a recircumscription of the Morindeae becomes available.

1. INTRODUCTION

The tribal position of *Mitchella* L. was debated for a long time. Due to contradictory and, in part, erroneous character descriptions in early literature, the genus was subsequently associated with various different tribes. Ironically, Baillon's overlooked and forgotten paper "Sur des radicules d'embryon à direction anormale" had

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already provided convincing evidence for the genus' taxonomic position. Baillon had clearly linked the problem of *Mitchella*'s placement with the apparently contradictory micropyle and radicle orientation in *Mitchella*. He (Baillon, 1879, 1880), moreover, had considered the genus *Damnacanthus* Gaertn. f. to be closely allied to *Mitchella* and placed both in his "série des *Chiococca*." In more recent publications, the genus *Damnacanthus* is generally found included in the tribe Morindeae, and there is virtually no reference to a possible alliance between *Mitchella* and *Damnacanthus* (see chapter 5 for further information). Although certain detailed studies exist on representatives of both genera, in-depth investigations of numerous important character states are still lacking. Up to now, neither Baillon's (1879) findings regarding ovule and seed structure nor his originally suggested close alliance between the two genera were ever checked for their correctness.

As good preserved material of *Damnacanthus* species and the two species of *Mitchella* became available recently, it was possible to carry out comprehensive comparative work on the two genera.

2. MATERIAL

In addition to field observations on Japanese *Damnacanthus* and *Mitchella* species (C.P.), herbarium material of the following institutions was studied: BKF, BR, L, MAK, TI, W, WU.

The following material (* = preserved) was used for detailed investigations and the preparation of the figures:

Damnacanthus biflorus (Rehd.) Masamune: Japan, Ryukyu Is., Tokuno-shima, between Boma and Nishiagina, *Hatusima 19357* (L) (fig. 3B); Amomio-shima, Chinase, Nase City, *Fukuoka 8003* (L).

Damnacanthus indicus Gaertn. f.: India, Assam, Khasi Hills, *Thakur Rup Chand 7403* (L).

Damnacanthus indicus Gaertn. f. subsp. *indicus* var. *indicus*: Japan, Shikoku, Kochi Pref., Taisho–Yuzuhara road, around Niida shrine, *Puff 880508-1/1** (WU) (voucher for chromosome count; figs. 2, 5B, 6C & D, 7, 8F & G, 13D).

Damnacanthus indicus Gaertn. f. subsp. *major* (Sieb. & Zucc.) Yamazaki var. *major*: Japan, Honshu, Aichi Pref., Mikawa Prov., Atsumi Peninsula, Irako-zaki, Jan. 22, 1968, *Kanai & Ohashi s.n.* (BR) (figs. 11A–D, 12B).

Damnacanthus macrophyllus Sieb. ex Miq. forma *giganteus* (Makino) Yamazaki: Japan, Shikoku, Kochi Pref., Taisho–Yuzuhara road, around Niida shrine, *Puff 880508-1/2** (WU) (figs. 4, 5A, 6A & B, 8A–E, 14E).

Damnacanthus okinawensis Hatusima (= *Damnacanthus biflorus* × *D. indicus* subsp. *major*): Japan, Ryukyu Is., Okinawa Is., Benoki-Yama, *Sonohara et al. SIRI 71701* (L) (fig. 3A).

Mitchella repens L.: U.S.A., Michigan, fruits from W.J. Beal Botanic Garden, Michigan State Univ. (figs. 11M–O, 12D & E, 13A & B).

Mitchella undulata Sieb. & Zucc.: Japan, Shikoku, Kochi Pref., Yokokura Mt, *Puff 880507-1/1** (WU) (voucher for chromosome count); Honshu, Tottori Pref., Mt Daisen, Oct. 16, 1988, *Suzuki s.n.** (WU) (fig. 11E); *Meyer et al. 16894* (MAK) (figs. 11F–L, 12A & C); Tokyo Pref., Hachiioji-City, Mt Imakuma, June 30, 1989 & July 18, 1989, *Suzuki s.n.** (WU) (figs. 6E & H, 9A & B, D & G, 13C, 14A–D); Hokkaido, Mt Ashibetu, Aug. 2, 1988, *Suzuki s.n.** (WU) (figs. 6F & G, 9C).

3. METHODS

Chromosome counts were obtained from acetocarmine squashes of vegetative material or flower buds preserved in the field in 3 parts ethanol and 1 part glacial acetic acid. Material preserved in the field in 70% ethanol was used for both microtome sections and, after critical-point drying, for most SEM-graphs. For other standard methods employed see Robbrecht (1988).

4. COMPARISONS OF THE CHARACTER STATES OF DAMNACANTHUS AND MITCHELLA

4.1. Vegetative characteristics

4.1.1. Growth form, branching pattern, and the thorns of Damnacanthus (fig. 1)

Mitchella species are perennial herbs with evergreen leaves whose stems may be slightly woody at the base (hence Holm, 1907, prefers the term 'undershrub' for *Mitchella repens*). Plants tend to have a "strongly clumped spatial dispersion. This distribution pattern results from the tendency of these prostrate perennials to spread by production of trailing stems with adventitious roots" (Hicks et al., 1985).

Plants of *Mitchella* produce rather long unbranched primary shoots, beset with leaf pairs which are all of the same shape and ± the same size ("The shoots of *Mitchella* [*repens*] ... appear to be somewhat uniform, since their foliage is identical": Holm, 1907: 168). Lateral branches originate on older parts of these shoots, which may be solitary or paired at a node. Lateral branches may, in turn, produce lateral branches of a higher order. Primarily the basal shoot portions, i.e. those in contact with the substrate, often develop adventitious roots.

The lateral branch system of a main axis must not be confused with the sympodial-dichasial or -monochasial branching pattern of the main elements (in the case of sympodial-dichasial branching, a slightly anisotomous development is usually recognizable, see fig. 1A). The material available to us did not provide conclusive evidence whether sympodial branching is always forced by the production of a terminal inflorescence or whether it can also be due to termination of main axis growth without inflorescence formation. The situation becomes further complicated and sometimes rather confusing by inflorescences produced terminally on lateral branches of varying orders.

There is, thus, no regular sympodial-di- or monochasial branching pattern with ± identical repeated sympodial elements as in *Damnacanthus* (see below).

Damnacanthus is a shrubby genus with conspicuously heterophyllous evergreen leaves. Several species are characterized by being armed with paired thorns (fig. 2A–

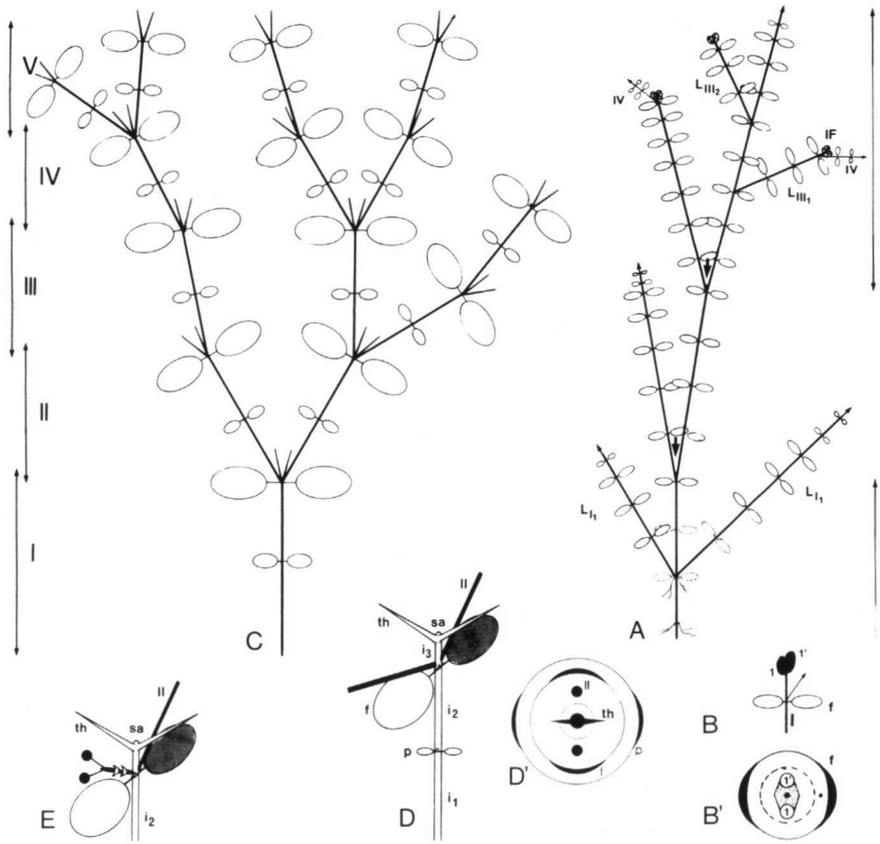


Fig. 1. Schematic representation of the growth form and inflorescence position of *Mitchella* (A–B') and *Damnacanthus indicus* (C–E). – A: three shoot generations (I, II, III), two with lateral branches (LI_1, $LIII_1$ ...); both lateral branches and sympodial branch units bear terminal inflorescences (IF); arrows point to position of no longer existing (old) inflorescences and mark the beginning of a sympodial-dichasial branching; note inflorescences being overtopped by a new generation of shoots (IV) and adventitious roots in the nodal areas of the oldest part of the plant. – B: paired flowers (1, 1') borne terminally on axis I; a developing shoot is shown in the axil of one of the foliage leaves (f). – B': ground plan of B; note that the paired, fused flowers are arranged in right angles to the median of the foliage leaves and are believed to have originated from a node without bracts (dotted circle). – C: heterophyllous branch consisting of several shoot generations (I–V); note that branching may be sympodial-dichasial or -monochasial. – D: sympodial branch unit comprised of a pair of prophylls (p) and a pair of foliage leaves (f); no bracts are present below the pair of thorns (th), i.e. at the third node; i_1, i_2, i_3, internodes; sa, shoot apex; shown in black: the next sympodial branch units (II). – D': ground plan of D; the dotted circle represents the third node without bracts. – E: a new vegetative (II) and a fertile, 2-flowered sympodial branch unit arising from the axils of the foliage leaves of a sympodial branch unit (compare with D). – Further explanations in the text.

D; in literature frequently referred to as spines. Since they are, as will be explained below, modified shoots, the morphologically more accurate term thorn is used here). The thorns may be very conspicuous and to c. 2 cm long or very rudimentary and hardly detectable. There are, however, also thornless *Damnacanthus* species (see Chao, 1978; Yamazaki, 1987b). Presumably, they represent the end point of a reduction series, i.e. thorns are reduced to such an extent that they are no longer discernible. *Damnacanthus macrophyllus,* investigated by us in detail, for example, had without exception clearly detectable although very minute thorns (fig. 4); the species is described as having "branches without or with very short spines" (Yamazaki, 1987b).

The thorns of *Damnacanthus* are always associated with pairs of true ('large') foliage leaves. Their orientation is always in right angles to the pair of foliage leaves, and they are seemingly found in the axil of one of the leaves, or in the middle between two lateral branches and in the axils of the stipules (fig. 1C, 2B–D). There have been various morphological interpretations of these paired thorns, none of which are, in our opinion, correct:

Schumann (1891: 137) describes them as follows (translated): "The thorns are without doubt ... homologous to lateral branches. In dried material they are found in front of [i.e., in the same plane as] the stipules, thus they belong to the otherwise so rare stipular shoots ['Stipularsprosse']"; he, however, may not have been fully satisfied with his interpretation as he suggests that the correctness of the proposed homology should be tested by ontogenetical investigations of fresh material.

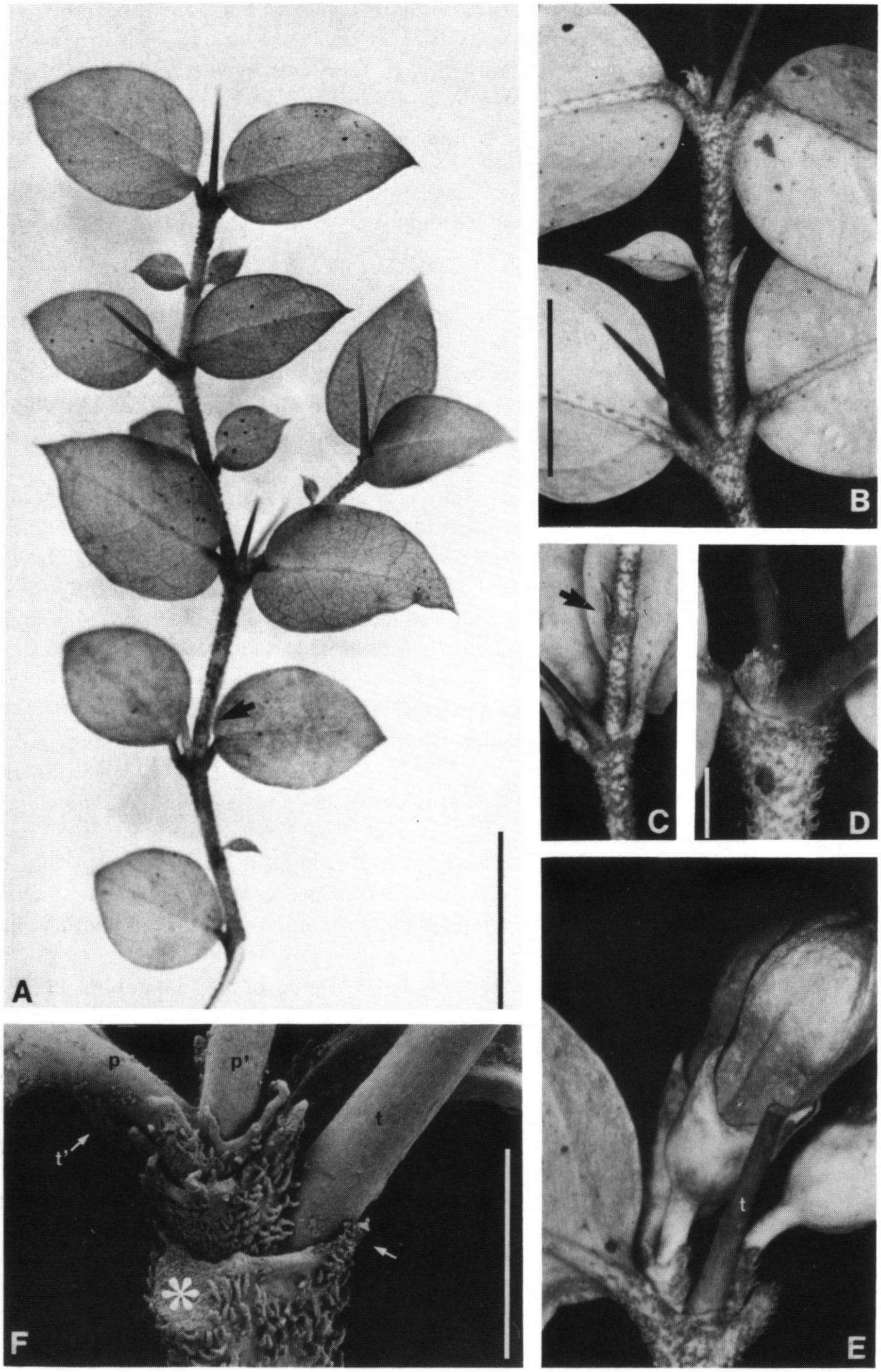
Johansson (1987a: 147) describes *Damnacanthus indicus* as having "narrow stipules which develop into spines". This interpretation is totally unrealistic as the pair of leaves associated with the paired thorns has normally developed stipules (see fig. 2F). Johansson unknowingly followed A.P. & A. De Candolle's (1833: 584) interpretation: "... ces stipules sont remplacés par des épines solitaires ..." (as *Baumannia geminiflora*).

Kumazawa (1979: fig. 11.8) also asserts that the thorn of *Damnacanthus* should be interpreted as a metamorphosis of the leaf, and compares the situation with that in *Carissa* (Apocynaceae). For both genera, his interpretations are very likely to be incorrect (see below).

Yamazaki (1987a) considers the thorn to be a metamorphosed lateral branch; his interpretation is, however, difficult to follow. He talks of the thorn being "transformed from the compound of the lateral branch and the cover leaf" [= bract?] ... and "the greater part of the spine" being "constituted by the lateral branch and the smaller part by the cover leaf being completely adhered to the base of the lateral branch." It seems that he has not fully understood the general growth pattern and how the position of the paired thorns can be accommodated in this pattern.

Our explanation is as follows (fig. 1C & D', abbreviations also used in the text below):

In *Damnacanthus,* a very regular sympodial branching pattern prevails (branching is either sympodial-monochasial or sympodial-dichasial – and then often slightly anisotomous). The entire shoot system is comprised of identical sympodial elements. Each such element is comprised of:


A
B
C
D
E
t
p
p'
t'
t
F

1) a pair of small leaf-like or ± scale-like prophylls (p; i.e., the first leaf pair of a sympodial element),
2) a pair of (larger) foliage leaves (f). Each such leaf morphologically always represents a bract ('Tragblatt') in whose axil a new sympodial element (II) originates (also see fig. 2C: bud), and
3) a pair of thorns (th; which may, however, be reduced to varying degrees). The paired thorns represent paired lateral branches (which are not supported by bracts) in the proximal portion of a sympodial element which ceases growth immediately after the production of the thorns.

The structure of such a sympodial unit is obscured by the fact that the axis above the pair of foliage leaves (i.e. the uppermost or third internode of a unit; i3) is extremely congested. Consequently, the paired thorns seem to be directly associated with the node bearing the foliage leaves.

Our interpretation of the branching pattern and thorn of *Damnacanthus* thus fully corresponds to the situation in *Carissa* (Apocynaceae) as outlined by Shah & Vasudeva Rao (1977), except that the paired thorns of *Carissa* are subtended by a pair of scale-like leaves, whereas those of *Damnacanthus* are not supported by bracts.

As the vegetative thorn-bearing sympodial unit is comparable to a sympodial unit bearing a 2-flowered inflorescence (see paragraph 4.2 for details), it may be speculated that the paired thorns are modified inflorescence shoots. An argument in favour of this speculation may be that the paired thorns originate at a node without bracts, a situation that is repeated in the inflorescences of *Damnacanthus* (see there for details). Similar modifications of inflorescence structures are also known from some other Rubiaceae, e.g. *Uncaria* (Cinchoneae–Mitragyninae; climbing hooks = inflorescence peduncle, Guillaumin, 1931), or *Catesbaea spinosa* (Catesbaeeae; paired axillary thorns = pedicels of solitary flowers, Robbrecht, 1988: fig. 4A). Also for *Carissa* (Apocynaceae; see above!), it has been argued that thorny branches are homologous to inflorescences (Brunard, 1970; Cohen & Arzee, 1980).

4.1.2. Roots

Peculiar moniliform roots are known from *Damnacanthus macrophyllus* (see reproduced historical illustrations in Yamazaki, 1987b). This is apparently unique in

Fig. 2. *Damnacanthus indicus* subsp. *indicus*. – A: part of plant showing several sympodial-monochasial and one sympodial-dichasial branching and heterophylly (arrow points to scale-like prophylls). – B & C: variation in shape and size of prophylls; B: sympodial branch unit arising in axil of one of the paired foliage leaves at the bottom, comprised of strongly anisophyllous prophylls, the foliage leaf pair at the top and paired thorns (bud: cf. D); C: scale-like prophylls (arrow). – D: proximal part of a sympodial branch unit with a pair of foliage leaves and paired thorns; note bud in the axil of the left foliage leaf, from which a new sympodial branch unit will develop. – E: '3-flowered' inflorescence, actually comprised of a 2-flowered and a 1-flowered inflorescence on either side of paired thorns (t, cut off thorn). – F: SEM-graph of the base of a 2-flowered sympodial branch unit showing 2 sets of paired bracts and the base of the pedicels (p, p') of the two flowers; also visible: scar of a removed foliage leaf (*), stipule (arrow), paired thorns (t, t'). – Scale bars: A: 10 mm; B = C: 5 mm; D = E, F: 1 mm. – Further explanations in the text.

the genus. The only other Rubiaceae with nodular roots known to us is *Psychotria ipecacuanha* (Schumann, 1891: fig. 39F). It is uncertain whether the root structure of these two taxa is comparable, however.

Neither the roots of *Mitchella repens* (see Holm, 1907) nor those of *Mitchella undulata* show any particularly unusual characteristics.

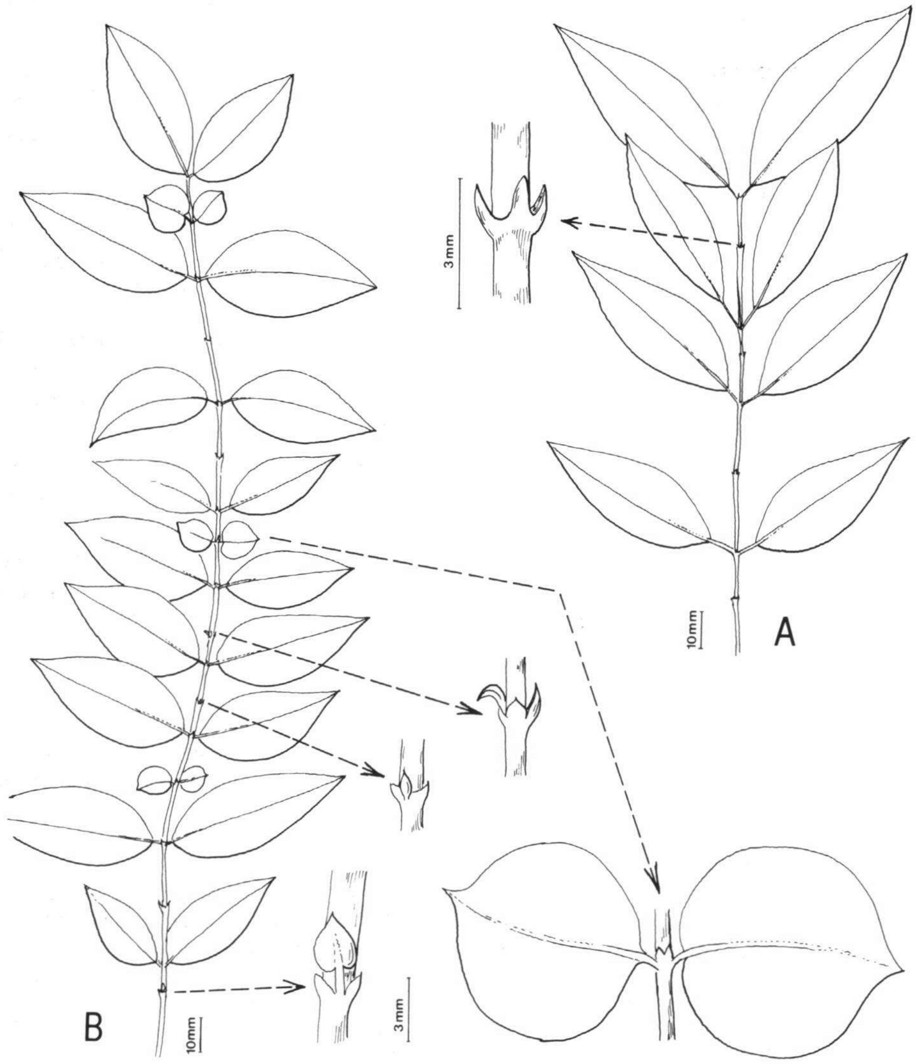


Fig. 3. Seemingly uniform, heterophyllous branch of *Damnacanthus okinawensis* (A) and of *D. biflorus* (B). In both A and B the branch is actually comprised of numerous sympodial units, each with a pair of variously shaped small prophylls and a pair of foliage leaves; in the illustrated parts, branching is strictly sympodial-monochasial. – Further explanations in the text.

4.1.3. *Leaves and stipules*

Both *Damnacanthus* and *Mitchella* have evergreen coriaceous leaves. While the leaves of *Mitchella* are uniform, the occurrence of heterophylly is characteristic for *Damnacanthus*. Pairs of relatively large leaves (true foliage leaves) alternate with pairs of small leaves (fig. 1C). Depending on the species of *Damnacanthus*, the small leaves exhibit a diverse morphology and can be variable within an individual (figs. 2A, 3 & 4). They may be a) 'miniatures' of the large leaves but agree with them in shape, b) be different in shape but still foliage leaf-like, or c) be ± scale-like. In the latter case, they are mostly only comprised of the stipular sheaths bearing appendage-like blade rudiments ['Oberblätter']) on either side (fig. 4, insert). The degree of blade-'reduction' in the 'small' leaves may vary to some extent – even within single individuals (figs. 2A–C, 3A). Small leaves may also exhibit a certain degree of anisophylly (see fig. 2B).

In *Damnacanthus*, this alternation between large and small leaves is closely linked with the branching pattern in that the pairs of small leaves invariably represent prophylls – see paragraph 4.1.1 for further explanations.

According to our observations, prophylls are always present, but on branch systems where some or all of them are very reduced, i.e. ± scale-like, their presence may be overlooked unless examined carefully (cf. fig. 3).

Within the Rubiaceae, this kind of branching pattern-linked heterophyllous leaf arrangement appears to be confined to *Damnacanthus*. It is not comparable to the three types of heterophylly recognized in the family by Robbrecht (1988: 49).

Domatia are lacking on leaves of the genus *Mitchella* (as in all herbaceous angiosperms). They are probably also absent on leaves of *Damnacanthus* (lacking in all taxa examined by us; relevant records in literature were not found).

Indumentum: In the species examined, leaves and other vegetative parts are usually glabrous or puberulous. The short external hairs are of the cylindrical type (sensu Robbrecht, 1988) and one- to few-celled, with non-pitted outer walls. – For internal indumentum see paragraph 4.3.

Leaf anatomy: Anatomical findings published for *Mitchella repens* (Holm, 1907: figs. 10–14) also apply to *Mitchella undulata:* the epidermis cells have moderately thickened outer walls, and the upper epidermis cells are larger than the lower ones; the leaves are hypostomatic; the mesophyll, with raphide-containing idioblasts, is differentiated into one- to two-layered palissades and a loose spongy mesophyll.

The leaf anatomy of the investigated taxa of *Damnacanthus* is, in turn, similar to that of *Mitchella*. There are minor differences between the leaves of the investigated species *Damnacanthus indicus* and *Damnacanthus macrophyllus*. The more coriaceous-leaved *Damnacanthus indicus* has an upper epidermis with a quite thick cuticle and the cells are relatively small (but still larger than cells of the lower epidermis); as compared to *Damnacanthus macrophyllus*, the entire leaf is somewhat thinner because of the more 'compact' mesophyll. *Damnacanthus macrophyllus* has only a single layer of palissade cells which are ± invertedly triangular in outline rather than ± rectangular as in *Damnacanthus indicus*; the upper epidermis cells, also with a massive cuticle, are markedly larger than the lower ones.

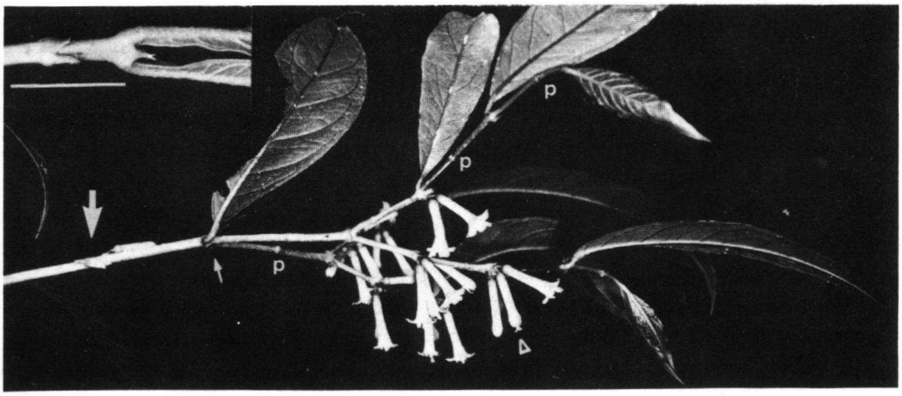


Fig. 4. Flowering branch of *Damnacanthus macrophyllus* (from colour transparency Puff JP-1018) comprised of several sympodial branch units. Note the alternation between pairs of scale-like prophylls (p) and pairs of foliage leaves, and the rudimentary thorn (thin arrow) associated with a foliage leaf pair. Inflorescences are associated both with foliage leaves (partly fallen off!) and prophylls (thick arrow). Note also stigmas protruding from flower-bud just about to open (open triangle). Insert: Part of a sympodial branch unit showing a pair of prophylls (left) and the base of a foliage leaf pair; note bifid stipules. – The portion shown is c. 30 cm long; scale bar (insert): 5 mm. – Further explanations in the text.

Node and petiole anatomy: The two species of *Mitchella* and the investigated taxa of *Damnacanthus* have unilacunar nodes with one trace per gap. The arc-shaped leaf trace gives off a small lateral bundle on either side shortly after leaving the gap; these laterals supply the stipular sheath. In *Damnacanthus* it is noteworthy that the vascular cylinder of a lateral branch (i.e. new sympodial unit) starts forming before the leaf trace gap closes again (fig. 5A). There may thus be a 'common gap' for leaf trace and vascular supply of the lateral shoot.

Stipules and colleters: The stipules of *Mitchella* are entire; those of *Damnacanthus* are either entire or bilobed, depending on the species (see fig. 4, insert).

In both *Mitchella* and *Damnacanthus* stipules are provided with ± elongated colleters of the standard type. For *Mitchella repens* they were described as "long, slender glandular hairs" by Holm (1907: fig. 14B), an inappropriate description as glandular hairs in the strict morphological-anatomical sense are absent in the Rubiaceae (see Robbrecht, 1988, for a discussion). Illustrations of the morphology of the colleters of *Mitchella undulata* are presented in Numata & Asano (1970: fig. *Mitchella undulata,* 12–13). – For colleters associated with floral organs see paragraph 4.3.

4.2. Inflorescences

Individual inflorescences of *Mitchella* are typically 2-flowered, whereby the ovaries of the two flowers are fused (fig. 6G; see paragraph 4.3 for details). There can be some variation in the inflorescence structure of *Mitchella repens* (number of flowers per inflorescence, arrangement, etc.; see Blaser, 1954). *Mitchella undulata* is es-

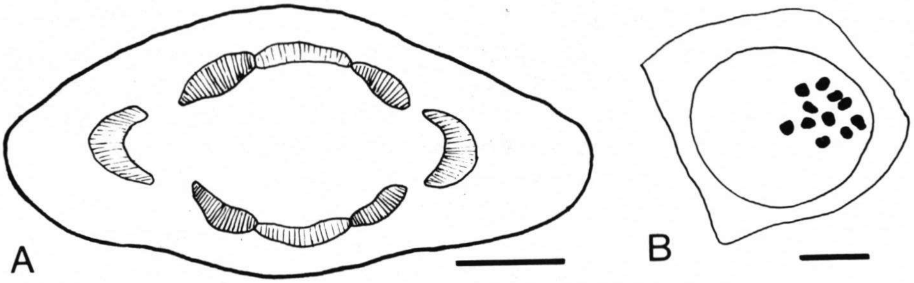


Fig. 5. A: node anatomy of *Damnacanthus macrophyllus*. B: chromosomes of *Damnacanthus indicus* subsp. *indicus* (pollen mother cell, metaphase 2). – Scale bars: A: 1 mm; B: 10 µm.

sentially identical; 2-flowered inflorescences are the rule, but odd flowering shoots (plants?) with only 1-flowered inflorescences were also observed.

Inflorescences of *Mitchella* are found terminally on shoots of varying orders (see fig. 1A & B).

Most interesting and of importance for the interpretation of the inflorescence of *Mitchella* is the exact position of the paired and fused ovaries/flowers (fig. 1B & B'): The long axis of the ovary pair is positioned in a right angle to the pair of foliage leaves below the inflorescence. This can still be observed in the fruiting stage (see Numata & Asano, 1970: fig. *Mitchella undulata,* 5).

The logical consequence of the position of the paired, fused ovaries (i.e., the 2-flowered inflorescence) of *Mitchella* is that the paired flowers cannot be interpreted as originally having been axillary, i.e. each having arosen directly in the axil of one of the leaves of the leaf pair below the inflorescence, followed by fusion. Blaser (1954) correctly pointed this out. Another argument against such a derivation is that in *Mitchella* inflorescences are often overtopped by one or two lateral shoots arising in the axil of the foliage leaves below the inflorescence (this is so at least in *Mitchella undulata*; see fig. 1A). Overtopping can start before the maturation of the fruits (see Numata & Asano, 1970: fig. *Mitchella undulata,* 5) and, consequently, fruiting inflorescences may be found in a seemingly axillary position.

The paired flowers can perhaps be derived from a 3-flowered 'naked' cyme (i.e. without bracts) by total reduction of the terminal flower (the flowers thus representing the two laterals). This hypothesis is supported by the occasional occurrence of a single terminal appendage between two fused ovaries (usually only clearly observable in very young bud stage and becoming obscured at later stages of development; observed in *Mitchella undulata*: fig. 6H). This appendage could be interpreted as the remains of the main axis (i.e. the pedicel of the terminal flower of an originally 3-flowered cyme). In *Mitchella repens,* Blaser (1954) occasionally observed two appendages at the top of a fused ovary pair (single appendages apparently also do occur in that species – see Dudley, 1883; Blaser, however, had doubts regarding the correctness of this observation). These two appendages are positioned in right angles to the plane that can be drawn through the pair of fused ovaries. She considers their presence to be an indication that the 2-flowered inflorescence of *Mitchella* might be derived from a (hypothetical) more-flowered (i.e. more than 3-flowered) inflorescence. She interprets the two appendages as rudimentary bracts of (a no longer present) second tier of flowers. Whether this interpretation is acceptable or not is not really relevant, however. Her and our interpretation agree in the essential part: the 2-flowered inflorescences are to be deduced from two (equal rank) lateral flowers which lost their pedicels and started to fuse to varying degrees (for *Mitchella repens,* Blaser described in detail the variation in the extent of the fusion). Moreover, these two flowers must originally have arisen at a node above the pair of foliage leaves but not directly in the axils of these leaves (if the latter case were true, the fused ovary pairs would be expected to lie in the same plane as the median of the foliage leaf pair).

Individual inflorescences of *Damnacanthus* are 2- or sometimes only 1-flowered due to suppression of the second flower (usually recognizable as rudiment); 2- (or 1-)flowered inflorescences may be either solitary or paired. Literature references to "3- or 4-flowered inflorescences" (e.g. Chao, 1978) are not fully accurate as such descriptions either refer to paired 2- (or 1-)flowered inflorescences (see fig. 2D & E) or to the presence of a 'normal' and a second accessory 2- (or 1-)flowered inflorescence (i.e. 2 sets of inflorescences, produced above each other). Accessory inflorescences, apparently originating from resting buds on older stems in the region of a sympodial-dichasial branching, are also occasionally present; consequently, such inflorescences, do not belong to the same age generation as the sympodial elements in its vicinity but are younger. Such a situation is illustrated for *Damnacanthus indicus* subsp. *major* in Hayashi (1985: 679; as *'Damnacanthus major'*).

Descriptions and illustrations of the inflorescence position of *Damnacanthus* given in literature are contradictory: Gaertner (1805: fig. 182), for example, depicted the infructescence of *Damnacanthus indicus* as being terminal above a pair of thorns, while Chao (1978) described the inflorescence of that species as being axillary. The complicated true situation is described below:

In *Damnacanthus indicus,* the 2- (or 1-)flowered inflorescences are seemingly found in the axil of a foliage leaf in place of a new sympodial element (fig. 1E). At nodes bearing a single 2- (or 1-)flowered inflorescence, vegetative branching is thus no longer sympodial-dichasial, as one axis of the dichasium is 'used up' by the formation of the inflorescence (except if the inflorescence present is an accessory one; see above). Upon closer examination, it becomes clear that the two flowers (or occasionally only one) are actually found proximally on a strongly congested short shoot which, from its base upwards, bears two sets of very reduced, almost scale-like bracts (see fig. 1E). As can be deduced from the orientation of the two flowers, they cannot originate in the axils of the upper pair of bracts but must come from a third, 'naked' node above. The apex of the flower-bearing short shoot ceases growth immediately after the production of the two lateral flowers rather than developing a terminal flower (2- rather than 3-flowered cyme!). The structure of individual inflorescences can thus be equated to vegetative sympodial branch units comprised of three plastochrons (see paragraph 4.1.1). The difference is that the flower-bearing shoot is more congested, bears ± scale-like bracts only (but no foliage leaves) and produces paired flowers instead of paired thorns.

At least in *Damnacanthus indicus*, *D. macrophyllus*, and *D. officinarum* Huang (possibly also in other species?) inflorescences are not only associated with foliage leaves but are sometimes also found in the axils of prophylls of a particular sympodial unit (i.e. between internode i1 and i2 in fig. 1D; also see fig. 4; Lo, 1979: fig. 1.1). In *Damnacanthus biflorus* inflorescences produced in the axils of scale-like prophylls appear to be even predominant, while inflorescences associated with foliage leaves seem to be rare.

Inflorescences arising in the axils of prophylls nevertheless have a structure homologous to fertile sympodial branch units arising in the axils of foliage leaves (as depicted in fig. 1E). For instance the two flowers of a 2-flowered inflorescence arising in the axil of a prophyll are found in the proximal portion of an extremely congested shoot with two sets of very reduced, scale-like leaves. Consequently, such seemingly axillary 2-flowered inflorescences are actually not axillary. Characterizations of the inflorescences of *Damnacanthus* as 'axillary' are, thus, purely descriptive but morphologically not accurate.

Are the inflorescences of Mitchella and Damnacanthus homologous?

According to our interpretation, the 2-flowered inflorescences of the two genera can be deduced from an originally 3-flowered cyme, of which the terminal flower is no longer developed. The two flowers present, thus, are 'equally ranked' laterals. In this respect there is a clear homology and, in our opinion, this could indicate and support a close alliance. In numerous other Rubiaceae, 2-flowered inflorescences are of a different structure, i.e. comprised of a terminal and a lateral flower of an originally 3-flowered cyme. According to our present state of knowledge, this seems to be the by far more common situation in the family (e.g. Puff, 1986: fig. 27 & 1989: fig. 3). The explanation frequently offered for the development of such 2-flowered inflorescences is supported by the often observed unequal development of lateral axes in the family (see, for example, Puff, 1986). As regards the entire shoot system and branching pattern, there are, nevertheless, very marked differences between the two genera in that *Damnacanthus* exhibits a much more complicated but yet very regular pattern. As regards the presumed homology between the 2-flowered inflorescences and paired thorns of *Damnacanthus*, see paragraph 4.1.1 for further details.

4.3. Flowers (figs. 6–10)

Characteristic for the genus *Mitchella* is the fusion of two neighbouring flowers by their ovaries (fig. 6G). The degree of fusion varies (see Blaser, 1954 for details on *Mitchella repens*), but normally the two ovaries are completely fused while the corollas of the two flowers are completely separate. *Damnacanthus* has discrete individual flowers which are typically arranged in 2-flowered inflorescences (see paragraph 4.2 for details).

Both *Mitchella* and *Damnacanthus* have 4-merous flowers.

4.3.1. Calyx, corolla and androecium

The calyx lobes are small, and lobes are not united below to form a basal tubular portion. Because of the fusion of two neighbouring ovaries, *Mitchella* typically has 8 calyx lobes, but due to further fusion this number may be smaller (fig. 6G & H). In *Mitchella,* small triangular appendages topped by colleters were frequently observed between the actual calyx lobes (stipular structures?; fig. 6H). In *Damnacanthus indicus,* there is a single row of colleters inside the calyx at its base (figs. 6C & D, 11B).

In both *Damnacanthus* and *Mitchella* the aestivation of the corolla lobes is 'typically' valvate (sensu Robbrecht, 1988). The corolla tube is ± cylindrical to narrowly funnel-shaped (fig. 6A, E) and c. 5–15 mm long. In both, the corolla tubes are hairy inside, either along their entire length or at least in the upper part. This internal indu-

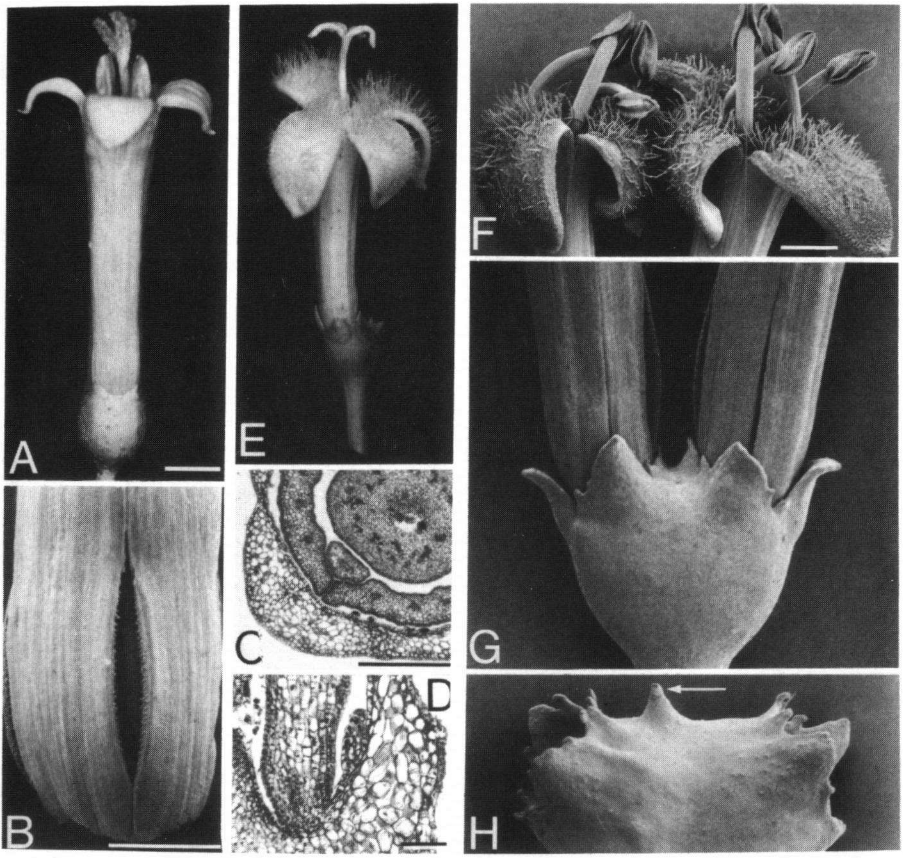


Fig. 6. Flowers and floral organs of *Damnacanthus macrophyllus* (A, B), *D. indicus* (C, D), and *Mitchella undulata* (E–H). – A: monomorphic flower. – B, G: fenestrated base of corolla tube. – E, F: long- and short-styled flowers (in E, the second corolla of a flower pair was removed). – C, D: cross and longitudinal section of calyx to show colleters on the inside (visible in C from bottom left to top right: calyx lobe, colleter, corolla lobes, filament, disk; in D from right to left: calyx lobe, colleter, corolla tube, small portion of disk). – G, H: fused ovaries with calyces (colleters partly visible); note appendage (arrow) in H. – Scale bars: A = E: 2 mm; B = G = H: 1 mm; C: 0.5 mm; D: 0.1 mm. – Further explanations in the text.

mentum also extends to the lobes in *Mitchella* (fig. 6E & F). It is made up of thin-walled, long, unicellular hairs which are mostly moniliform, at least in their proximal part. Characteristic for the corollas of both genera is that the tubes are fenestrated at the base (fig. 6B & G), i.e. have four splits which correspond to the border of the four otherwise fused petals. This phenomenon is known from several other Rubiaceae (see Robbrecht, 1988: 80 for a survey).

Fig. 7. Ovary, placentation and ovule of *Damnacanthus indicus*. – A & B: SEM-graphs of ovule and obturator, two views (the arrows indicate the plane of section D). – C: radial section of locule showing placenta (note raphide-containing idioblast; arrow), obturator and part of the ovule. – D: section tangential in relation to the vertical axis of the locule showing placenta with vascular bundle (vb), obturator, and part of ovule. – E–G: cross sections of locules (the planes are indicated by the arrows in D; the side of the locule facing the centre of the ovary is at the bottom); E: part of ovule and obturator; F: the ovule is sectioned in two places because of its curvature in the horizontal plane; G: the curved ovule, sectioned slightly lower than F, still shows a constriction but already appears as a unit. – Scale bars: 100 µm; A = B; C–G the same magnification. – Refer to fig. 10 for further information on ovule shape and orientation and also see text.

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Fig. 8. Ovary, placentation and ovule of *Damnacanthus macrophyllus* (A–E) and *D. indicus* (F, G). – A & B: SEM-graphs of ovule and obturator, two views. – C: median longitudinal section of locule showing placenta, obturator and ovule (compare with B; note embryo sac cavity in the centre of the ovule). – D: section tangential in relation to the vertical axis of the locule showing ovule and micropylar canal with the actual micropyle pointing upwards and towards the centre of the ovary (because of the curvature of the ovule, the embryo sac is not visible; the embryo sac would be in a plane parallel to and below the paper plane) and parts of the obturator near the upper margin. – E: cross section (the arrows in D indicate the plane and the portion pictured) showing, because of the curvature of the ovule, part of the 'main body' of the ovule on the left and the area of the micropyle on the right, separated by obturator tissue. Refer to fig. 10 for further information on ovule shape and orientation and also see text. – F: cross section of ovary showing vascular bundles running into the placentas; also note the bundles immediately outside the locules (one is marked with an arrow) which will continue upwards and run into the style. – G: cross section of lower half of style with four vascular bundles (arrows). – Scale bars: 100 µm; A = B; D = E = G.

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Fig. 9. Ovary, placentation and ovule of *Mitchella undulata*. – A, B: SEM-graphs of ovule and obturator, two views. – C, D: corresponding SEM-graph and LM picture of radial section of locule showing placenta, obturator and micropylar end of ovule (note area of the actual micropyle: arrow in C). – E, F: cross sections of locules (the planes are indicated by the arrows in D; the side of the locule facing the centre of the ovary is at the bottom; E & F are turned 90° in relation to D); E: the ovule is sectioned in two places because of its curvature in the horizontal plane, obturator tissue separates the two ovule portions and surrounds the portion on the left; F: the curved ovule, sectioned slightly lower than E, still shows a constriction but already appears as a unit (the micropylar canal is faintly recognizable: arrow!); obturator tissue is visible outside the ovule both on the bottom and top. – G: cross section of part of an ovary showing two locules and placenta surrounded by large-celled obturator tissue (note that obturator tissue and tissue in the centre of the ovary are of the same cell structure; compare with H). – H: radial section of ovary showing locule (compare with D), tissue of the same structure and staining properties as obturator tissue in the centre and above the locule (arrow) and a vascular bundle (vb), also note distinct small-celled layers surrounding the locule (the later endocarp). – Scale bars: 100 µm; A = B; D = E = F; G = H. – Refer to fig. 10 for further information on ovule shape and orientation and also see text.

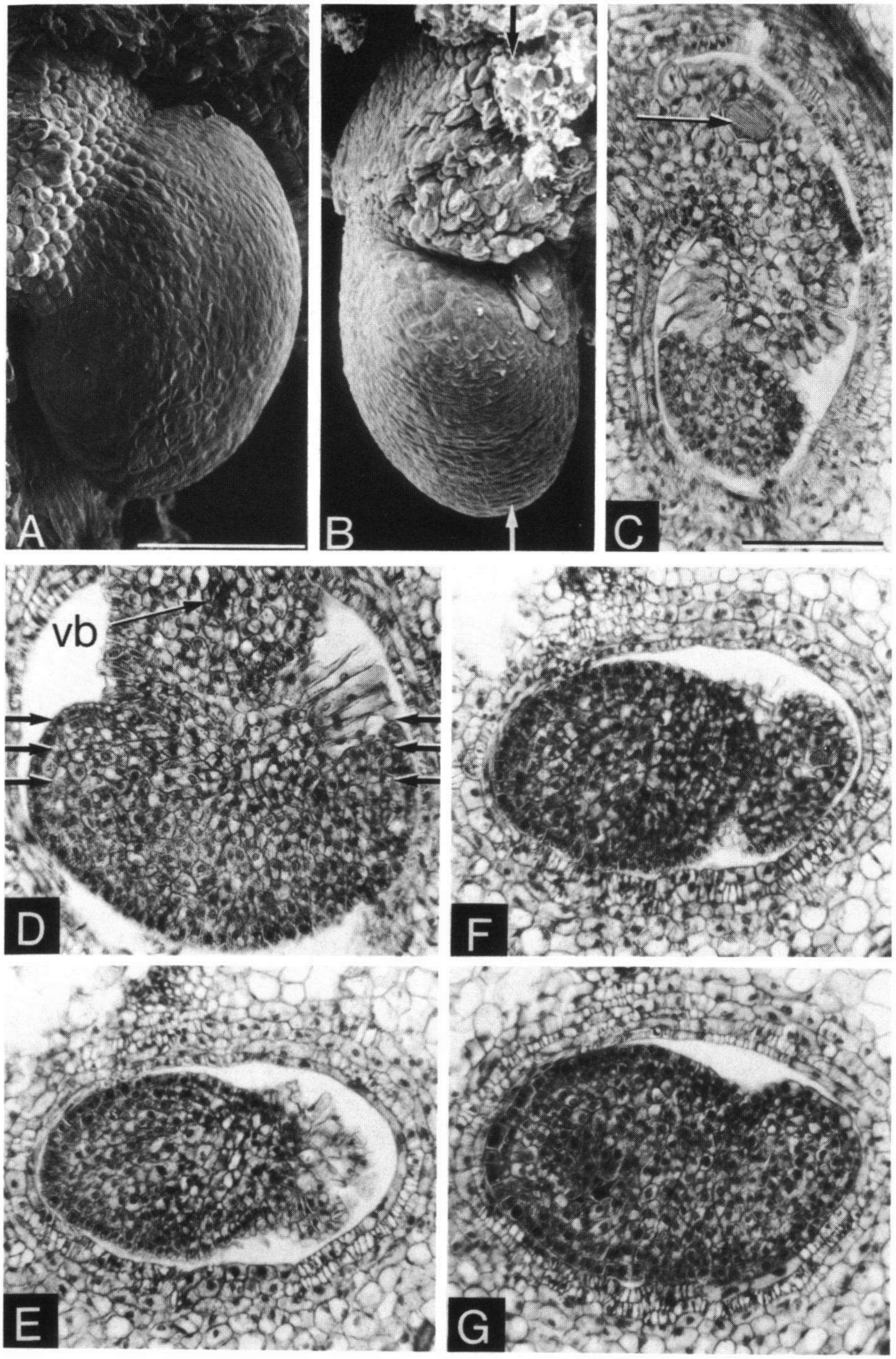

Fig. 7 — See legend on page 321.

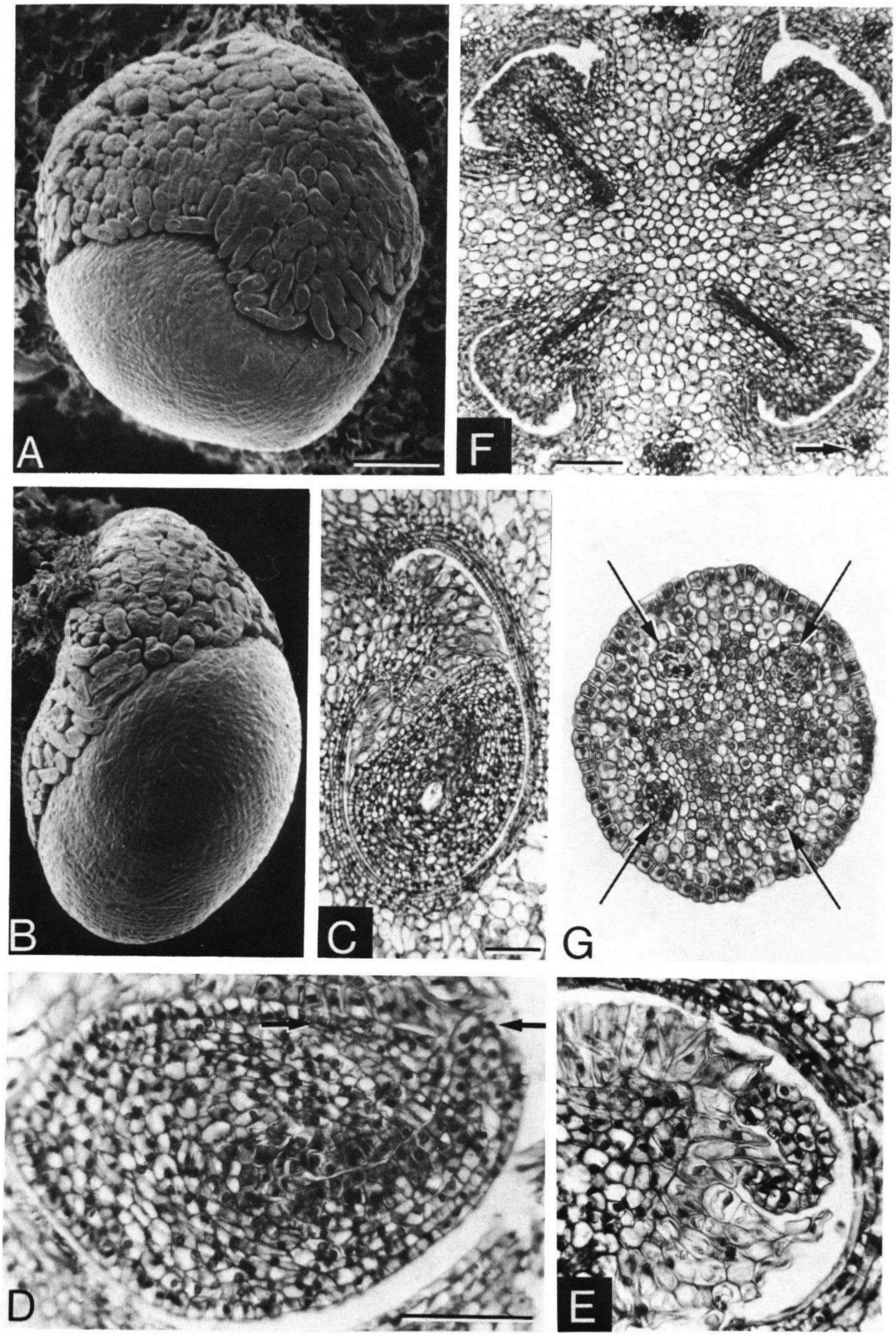

Fig. 8 — See legend on page 321.

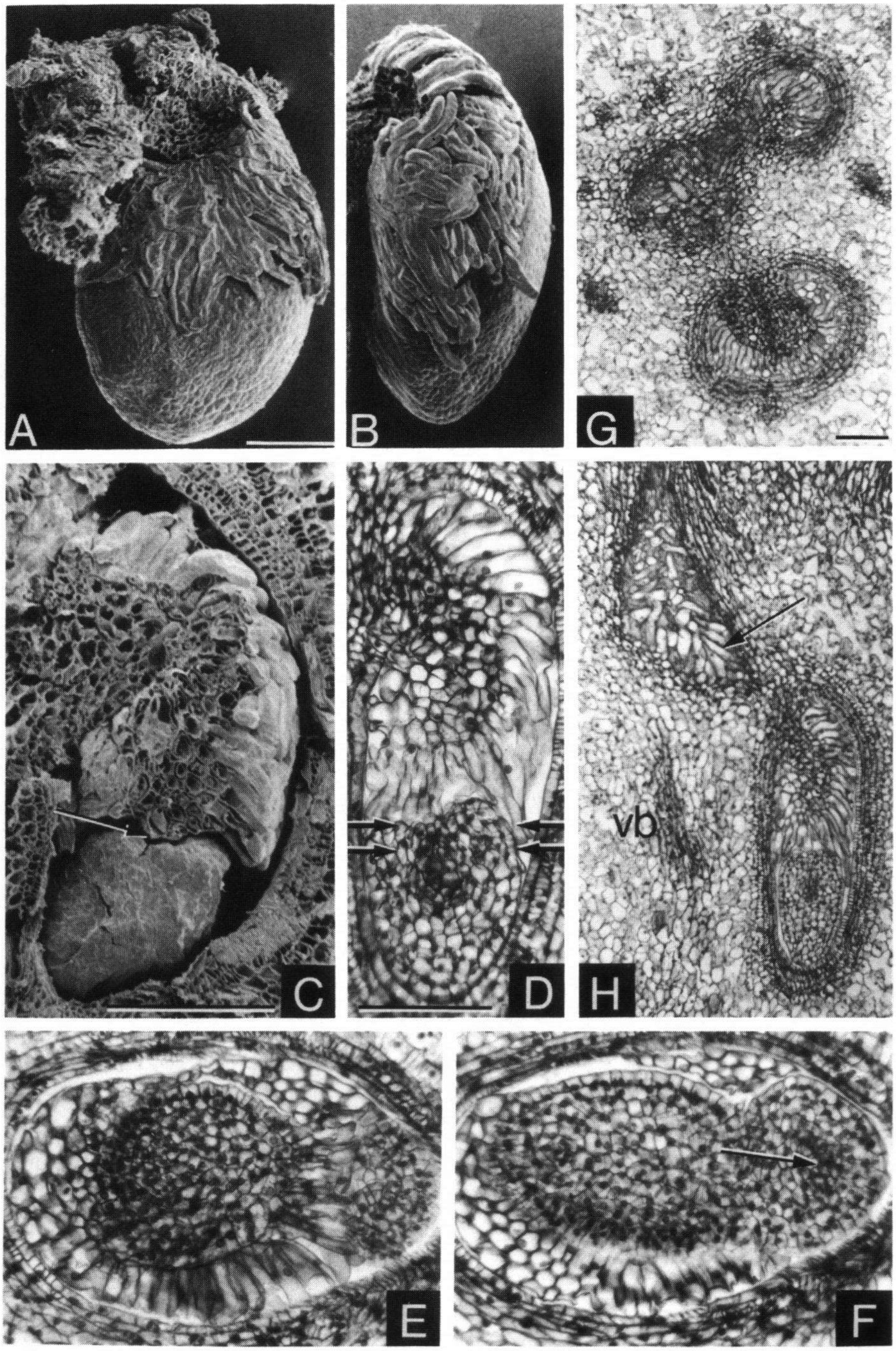

Fig. 9 — See legend on page 321.

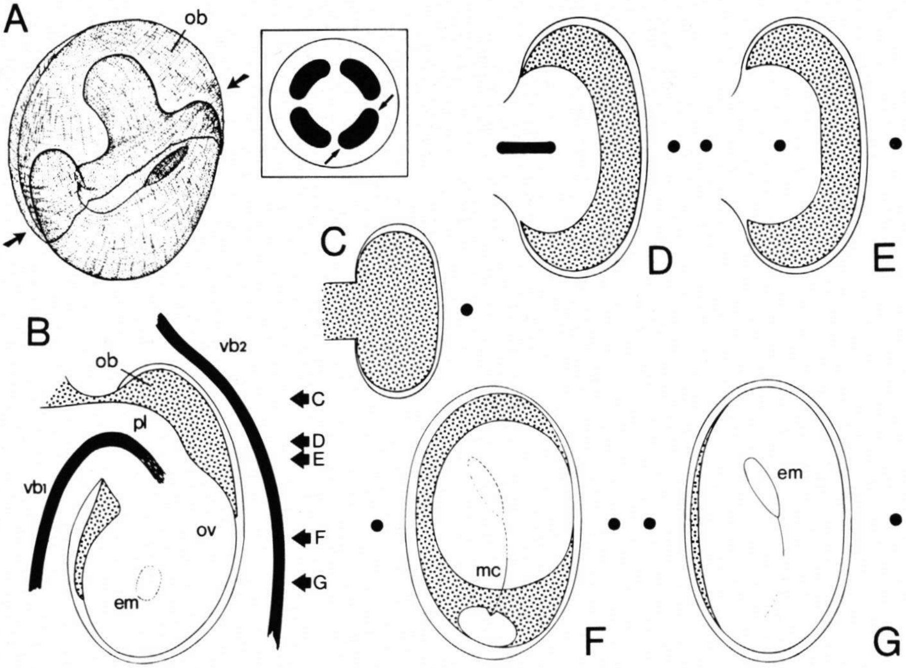

Fig. 10. Schematic representation of placentation, obturator and ovule of *Mitchella* and *Damnacanthus*. – A: three-dimensional reconstruction, oblique view; the obturator, ob, covers part of the ovule; the insert, a diagrammatic cross section of an ovary with four locules, gives an impression of its orientation. – B: median longitudinal section of locule (ovary wall with vascular bundle vb2, which will extend upwards into the style, on the right, and centre of ovary with vascular supply of ovule, vb1, on the left). – C–G: cross sections in the planes indicated in B. – em: embryo sac; mc: micropylar canal; ob: obturator tissue (dotted in B–G); ov: ovule; pl: placenta. – Further explanations in the text.

The insertion of the stamens is near the throat in the monomorphic *Damnacanthus*. The actual filaments are short (but strands corresponding in size and structure to the free parts of the filaments run down the entire length of the corolla tube. They are adnate to the tube except for the basal region, where the corolla tube has splits; see fig. 6C); the upper parts of the anthers are protruding from the throat (fig. 6A). In the heterodistylous *Mitchella* the anthers are also inserted near the throat, in long-styled flowers filaments are subobsolete, in short-styled morphs they are relatively long, raising the anthers well above the level of the throat (compare fig. 6E and F).

4.3.2. Gynoecium

In both *Damnacanthus* and *Mitchella* there is a common style several times as long as the four papillate stigma lobes (fig. 6A & E). Stigmas are either included or exserted in the distylous *Mitchella* and slightly exserted in *Damnacanthus* (fig. 6A, E & F) (see also paragraph 4.6).

Ovary, placentation and ovules (figs. 7–10)

Each ovary has four uniovulate locules (in *Damnacanthus* falsely interpreted as two biovular locules by Johansson, 1987b: 21). Although the ovaries of the paired flowers of *Mitchella* are fused, this fusion does not fundamentally change the structure of each of the two ovaries involved. Cross sections reveal that there are two sets of four uniovulate locules, and that the fusion only takes place in adjoining ovary wall portions.

In both genera, the ovary is crowned by a rather massive ring-like disk which surrounds the base of style (fig. 6C).

Tissue differentiation and vascularization of the ovary

Cross sections of *Damnacanthus* and *Mitchella* ovaries show little tissue differentiation (see figs. 8F, 9G & H). Inside the ovary epidermis, there is homogeneous parenchymatic tissue. Only the later endocarps are already discernible as several layers of elongated and slightly thicker-walled cells surrounding the four (eight) locules (compare fig. 9H and tangential section, fig. 13C). The region of the septa is comprised of parenchymatic tissue indistinguishable from that of the ovary wall (see fig. 8F). Numerous vascular bundles are prominent in the ovary wall (see Blaser, 1954, for details on vascularization in *Mitchella repens*). While it was not attempted to trace all bundles in the ovaries of *Damnacanthus* to their final 'destination', it could be ascertained that 1) the four major bundles found in the style (fig. 8G) originate from bundles which, lower down in the ovary, are found outside the dorsal side of the locules (see figs. 8F and 10), and that 2) bundles running into the placenta and supplying the ovules come up from the central part of the ovary.

Placenta and obturator

In both genera, the placenta is inserted in the upper part of the septum, near the top (figs. 7C, 9C, D & H). In both *Damnacanthus* and *Mitchella* a conspicuous and massive obturator* is inserted in the indistinct transition zone between placenta and funicle of the ovule. This pollen guiding tissue is made up of ± elongated large cells, covers part of the ovule in cap-like manner, and can extend downwards for a considerable distance (figs. 8B, 9B). Under the dissecting microscope the massive obturator is easily confused with the ovule itself, unless viewed carefully. In *Damnacanthus*, the extent of the obturator appears to be species-specific. At least in the two *Damnacanthus* species studied in detail, rather marked differences were observed (obturator rather small in *Damnacanthus indicus*, but very extensive in *Damnacanthus macrophyllus*, compare figs. 7 and 8). It also seems noteworthy that tissue of the same cell structure (and with the same staining properties) as obturator tissue extends to the centre of the ovary and from there upwards into the base of the style (fig 9G & H). It is presumably this rather loose and relatively large-celled tissue, through which the pollen tube grows towards the micropyle.

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* In relevant rubiaceous literature (e.g., Fagerlind, 1937), the term *strophiole* is commonly used for outgrowths of a comparable kind. As 'strophiole' refers to a strictly funicular outgrowth, the term obturator is chosen instead.

Ovule structure

Probably because the obturator obscures part of the ovule, including the micropyle, the exact structure, shape, and orientation of the ovule remained unknown up to now, although Baillon's (1879) overlooked article already gave valuable clues.

In order to document the true (and rather complicated) situation, serial cross, longitudinal and tangential microtome sections and supplementary SEM investigations were undertaken. As a result of these efforts, we can now present definite proof for the campylotropous nature of the ovules in the genera *Mitchella* and *Damnacanthus*.

As schematically shown in figure 10, the long axis of an ovule is ± in a horizontal plane and the long side faces towards the centre of the ovary (figs. 10A & G; 9F). The long axis, however, is curved upwards and, less markedly, also towards the centre (figs. 10A & F; 7F & G). Consequently, the slightly curved embryo sac is found in a ± horizontal position in the ovule (compare fig. 10 A & G) and the micropylar canal curves upwards. The actual micropyle, too, points upwards and to some degree also inwards (i.e. towards the centre of the ovary; fig. 10F); it is overtopped by the outer integument on the abaxial side of the ovule (figs. 10A & F; 8D & E), which is several times larger than the outer integument on the adaxial side (the inner integuments are scarcely recognizable). The orientation of the micropyles of different ovules of a single ovary can either be upwards and ± inwards and to the right, or upwards and ± inwards and to the left. In both genera, left/right micropyle orientation within single ovaries are variable and not clearly defined. All four ovules of an ovary may have the micropyle pointing in the same direction (i.e. all pointing to the right if viewed from above), or micropyles of two ovules from neighbouring locules may be facing each other, while micropyles of the remaining ovules may have an identical orientation.

Baillon (1879), without going into much detail and without supporting illustrations, vaguely circumscribed the situation for *Mitchella* and *Damnacanthus* described above as 'incompletely anatropous', an interpretation that is hardly acceptable in the strict anatomical sense but shows that he was aware of the unusual situation.

The situation described for *Mitchella* and *Damnacanthus* is highly remarkable in that it is, apart from *Theligonum* (tribe Theligoneae; see Wunderlich, 1971), the only well documented record of campylotropy in the Rubiaceae (the family is characterized by anatropous ovules). The campylotropous ovule of *Theligonum* and its further development is not comparable to that of the genus pair dealt with here, however. In *Theligonum*, the development of a campylotropous ovule appears to be linked to and the consequence of the unique unicarpellate gynoecium in the genus and seems to be derived from the typical anatropous ovules found in the presumably allied tribes Anthospermeae and Paederieae (see Puff, 1982). Also the seeds of *Theligonum* with their large embryos and relatively little endosperm suggest an affinity to the mentioned tribes, but bear no resemblance to *Damnacanthus* and *Mitchella*.

Detailed anatomical studies of ovaries, placentation and ovules of the vast majority of Rubiaceae are largely missing. In our opinion, it is not unlikely that through such investigations further examples of campylotropy could turn up.

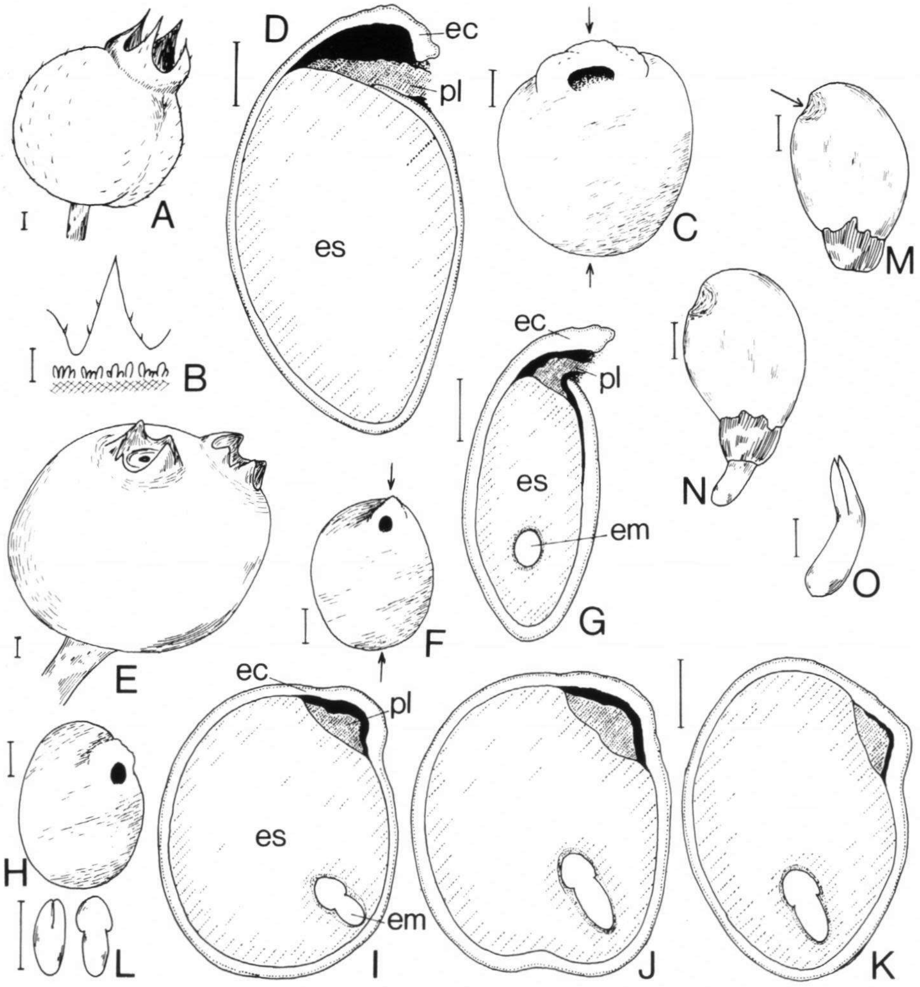

Fig. 11. Fruits, pyrenes, seeds and embryos of *Damnacanthus indicus* (A–D), *Mitchella undulata* (E–L) and *Mitchella repens* (M–O). – A: fruit with persistent calyx. – B: row of colleters at the base of calyx inside. – C, F: pyrenes with median 'hollow' (point of entrance of placenta), adaxial view. – D, G: section of pyrenes in the plane indicated by the arrows in C and F, showing 'hollow' in side view (in D, embryo not in the plane of the section; in G, embryo radicle cut obliquely). – E: 'compound' drupe with persistent calyces. – H: pyrene with slightly eccentrical 'hollow', adaxial view. – I–K: pyrenes sectioned in a plane parallel to orientation of drawing H, off-median to show variability in embryo position. – L: two views of an embryo (radicle pointing downwards). – M: start of germination after artificial removal of endocarp, seed-coat breaks open at the base, the endosperm starts protruding (arrow points to the position of placenta). – N: protruding radicle (about one week later). – O: seedling immediately after complete emergence from the seed. – Abbreviations: ec, endocarp; em, embryo; es, endosperm; pl, placental remnants; air-spaces are shown in black. – All scale bars: 0.5 mm. – Further explanations in the text.

4.4. Fruits, seeds and embryos (figs. 11–13)

Both *Mitchella* and *Damnacanthus* have drupaceous fruits. They are mostly brightly red coloured (and endozoochorous). It is, furthermore, noteworthy that in both genera the persistent calyx lobes also become ± fleshy and red in fruit. For a colour illustration of fruiting *Damnacanthus indicus* subsp. *indicus* and subsp. *major* see Hayashi (1985: 679; subsp. *major* as *'Damnacanthus major'*).

In *Damnacanthus,* fruits are mostly paired but have separate pedicels. In *Mitchella,* there are 'compound' drupes, i.e. two fused fruits form a dispersal unit (fig. 11E). Typically, fruits have 4 pyrenes or stones (twice that number in *Mitchella*) but, due to abortion, this number can be reduced (see two-lobed fruit with two fertile pyrenes of *Damnacanthus indicus,* fig. 11A, or fig. 182 in Gaertner 1805). In *Damnacanthus,* it was observed that aborted seeds are enclosed by endocarps anatomically identical but considerably smaller than those of pyrenes containing fertile seeds.

The fruits of both *Mitchella* and *Damnacanthus* agree in having the following anatomical characteristics:

- a skin-like exocarp;
- a fleshy and rather thick mesocarp with numerous raphide-containing idioblasts;
- pyrenes with a quite massive sclerenchymatic endocarp. The surface of the endocarp is slightly striate, due to the elongated shape of the fibres (sclereids) running diagonally. In the two genera, the fibres are provided with numerous minute circular pits (fig. 12B–D), only well observable with the SEM. Whether these pits might play a role in the easier uptake of water during germination remains unknown (see also comments on germination behaviour below).

The ± flattened pyrenes have an apical opening where the placenta enters the locule (figs. 11C, F, H, 12A); above the opening, the endocarp is ± thickened to a crescent-shaped rim. The pyrenes of *Mitchella* frequently are ± irregularly shaped; the apical opening in particular may be found in differing positions, i.e. in the median plane (see fig. 11F), or shifted to a ± eccentrical lateral position (cf. fig. 11H). The pyrenes lack any preformed germination slits.

4.4.1. Seeds

The seeds of both *Mitchella* and *Damnacanthus* normally closely adhere to the hard endocarp. In both genera, the testa is virtually identical. The exotestal cells have characteristic thickenings both on the radial and outer tangential walls (fig. 13A). In *Damnacanthus,* however, there seems to be a tendency towards a parenchyma-like exotesta with rather reduced, delicate thickenings (e.g., *Damnacanthus biflorus*: no thickenings along outer tangential wall, very small local thickenings along radial wall). Below the exotesta, several layers of crushed endotesta cells are often recognizable. Hayden (1968), describing the exotestal cells of *Mitchella* [*repens*] as showing 'scalariform pitting', probably only referred to the thickenings of the outer tangential walls. She noted a strong resemblance to those of *Morinda* (tribe Morindeae).

The endosperm of *Damnacanthus* and *Mitchella* is soft and oily, very similar in these genera (compare fig. 13B & D) and very extensive as compared to the embryo.

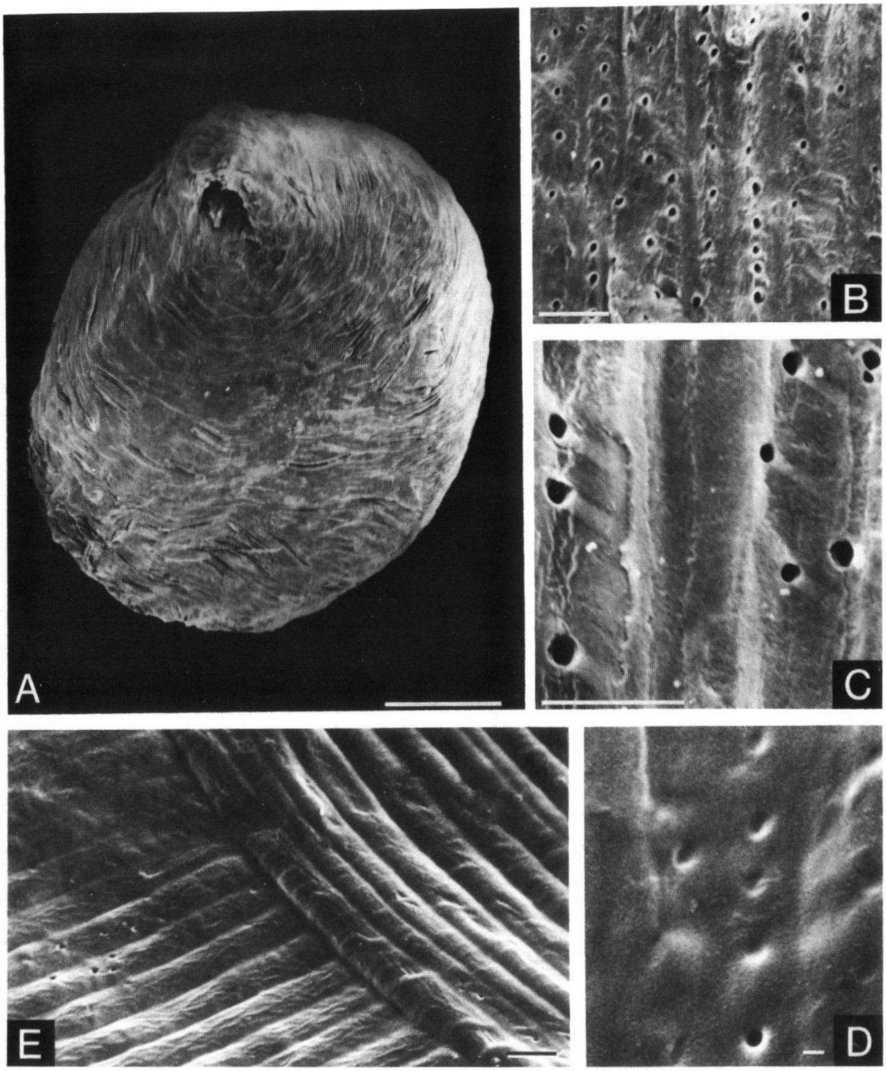

Fig. 12. SEM-graphs of pyrene of *Mitchella undulata* (A) and endocarp surfaces of *M. undulata* (C), *M. repens* (D, E) and *Damnacanthus indicus* subsp. *major* (B). – A: pyrene with 'hollow' (cf. fig. 11 H). – B, C: details of outer and D, E: inner endocarp surface showing pits and layering of the sclerenchymatic endocarp (E). – Scale bars: A: 0.5 mm; B, C, E: 10 µm; D: 1 µm.

4.4.2. *Embryos*

In mature and near mature seeds of both genera the embryo is found in the lower part of the seed. Its radicle points *downwards* and, as illustrated for *Mitchella undulata* (fig. 11I–K; sections of pyrenes from one and the same collection), there is slight variation both in the angle at which the embryo is oriented and in its position within the endosperm.

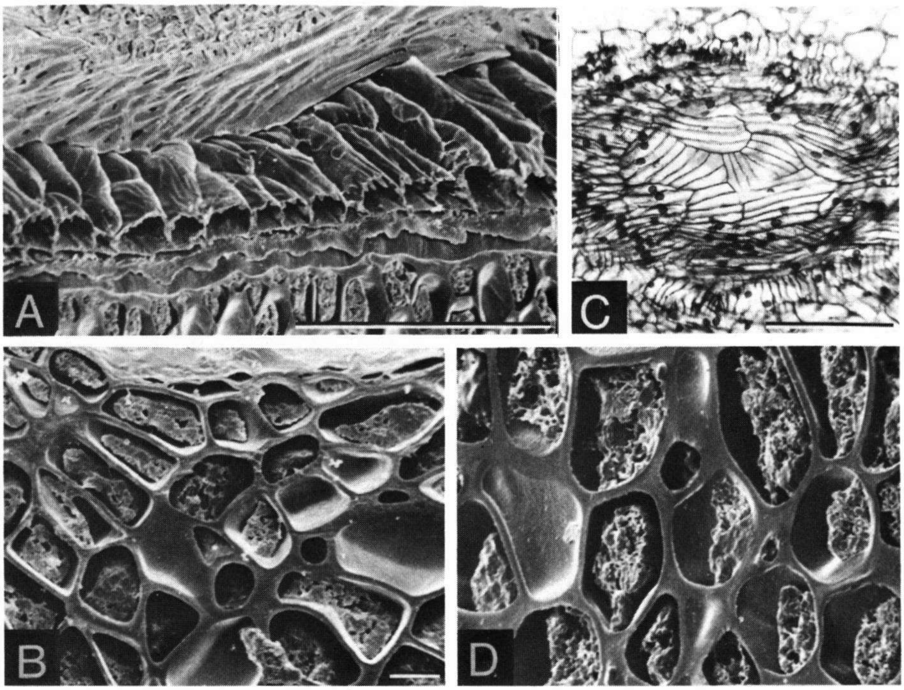

Fig. 13. Sections of endocarp, testa and endosperm of *Mitchella repens* (A, B), *M. undulata* (C), and *Damnacanthus indicus* (D). – A: mature diaspore; visible from top to bottom: sclerenchymatic endocarp layers, elongated exotesta cells with thickenings, crushed endotesta cell layers, endosperm. – B, D: endosperm cells. – C: ovary at anthesis, tangential section of later endocarp showing characteristic cell orientation. – SEM-graphs except for C. – Scale bars: A, C: 100 µm; B = D: 10 µm.

Damnacanthus and *Mitchella* thus have ovules with micropyles pointing upwards (see fig. 10) and embryo radicles pointing downwards. This situation is unusual in the Rubiaceae. It has been the principal cause for misinterpretations and, subsequently, for wrong tribal placements (see chapters 5 and 6 for details) because, normally, seeds with embryo radicles pointing downwards allow the deduction that basally attached anatropous ovules were present in ovaries.

This apparently contradicting micropyle and radicle position in the genera in question was largely clarified by Baillon (1879) but, unfortunately, his article had been completely overlooked. The situation finds its simple explanation in the campylotropy of the ovules of *Damnacanthus* and *Mitchella*. As described and illustrated above (fig. 10), embryo sacs are oriented in a ± horizontal plane in the ovules. After fertilization, strong growth of the endosperm takes place. At first, endosperm tissue fills out the entire embryo sac and, later on, extensive centrifugal growth of the endosperm, especially towards the chalazal part of the ovule, continues so that eventually the endosperm shows a marked increase in extent (the general situation in the Rubiaceae; see Wunderlich, 1971). As compared to numerous other Rubiaceae where em-

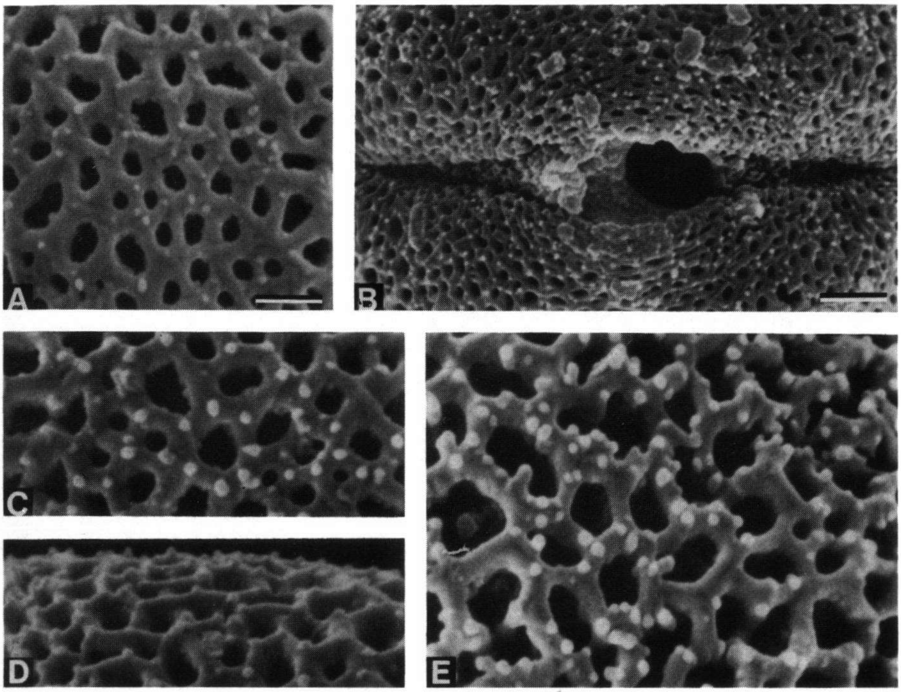

Fig. 14. Acetolysed pollen of *Mitchella undulata* (A–D) and *Damnacanthus macrophyllus* (E). – A, C–E: mesocolpium; A: from long-styled; C, D: from short-styled morph (D, side view to show depth of exine). – B: aperture from long-styled morph. – Scale bars: A = C = D = E: 1 µm; B: 2 µm.

bryos are only surrounded by a thin layer of endosperm, growth of the cellular endosperm is much more extensive in the genera dealt with here. Due to intensified growth, particularly on the chalazal side of the former ovule, the embryo is pushed into the position where it is found in mature seeds. The slight variation in the embryo position between different seeds (see fig. 11I–K and above) is easily explained by minor asymmetries and differences in endosperm growth. During seed development, the placenta does not increase in size (and is only recognizable as a 'plug' of tissue in the area of the opening of a pyrene; see fig. 11D, G, I–K). Because of its position, the placenta does not have any influence on the shape of the mature seed (in contrast to selected other Rubiaceae, where certain placenta positions can cause a campylotropous shape of a *seed*; see Fagerlind, 1937).

In *Damnacanthus indicus* polyembryony was observed in one out of several seeds dissected.

Characteristic for the two genera are embryos which are minute in relation to the size of the entire seeds (*Mitchella undulata*: fig. 11I–L; *Damnacanthus indicus*: Gaertner, 1805: fig. 182F). The cotyledons are very small as compared to the radicle. The gap between the two cotyledons is often found to be filled with loose tissue which must be interpreted as belonging to the endosperm (in the Rubiaceae, the endosperm normally shows a differentiation into a nuclear and a cellular portion during seed development. The latter is normally found around the developing embryo; it is presumably tissue belonging to this phase that is found between the cotyledons). Upon emergence of the embryo/seedling from the seed, the radicle is still longer than the cotyledons and thicker than the cotyledons in side view (fig. 11 0).

Based on experiments with *Mitchella repens,* the following information on germination behaviour can be given: trials with untreated pyrenes were invariably unsuccessful. Pyrenes kept on wetted filter paper for several months (in some cases over half a year) did not germinate at all. However, germination, succeeded, although only in few cases, after artificial removal of the sclerified endocarp (fig. 11M–O). Nevertheless, germination was slow: only approximately two months after sowing the first emergence of a radicle was observed. One week thereafter the embryo/seedling had completely emerged from seed. In nature, germination may come about only after (partial?) deterioration of the endocarp (pyrenes without 'preformed germination slits'!); presumably this may take a very long time (several seasons?).

4.5. Pollen (fig. 14)

Pollen of both *Mitchella* and *Damnacanthus* is colporate (fig. 14B). *Damnacanthus* has 3–6-colporate microreticulate grains with suprategillar elements ("exines with minute granules", Johansson, 1987a). Palynological investigations of *Damnacanthus indicus* and *D. henryi* (Johansson, 1987a) are supplemented by data for *Damnacanthus macrophyllus*; his findings, including the observation that colpi can partially touch each other at the polar ends, are confirmed. However, *Damnacanthus macrophyllus* differs from *D. indicus* (see Johansson, 1987a: fig. 8) in having more and somewhat larger ± globose suprategillar elements and a slightly different exine-net structure (fig. 14E). *Mitchella* has strictly 3-colporate, microreticulate grains (Robbrecht, 1982: *Mitchella undulata*; a report of '3-colpate' pollen in that species, Ikuse, 1956, is without doubt erroneous).

In order to clarify whether pollen from long- and short-styled morphs of the heterodistylous *Mitchella* exhibits differences in the exine structure and exine surface, *Mitchella undulata* was reinvestigated. It was found that density and size of the suprategillar elements differ markedly. As compared to pollen from a long-styled morph, grains from short-styled flowers (of the same population) have distinctly more and larger 'warts' in comparable regions of the grain (i.e., the mesocolpium). While the size of the exine mesh does not seem to differ significantly, the structure of the exine is not entirely the same in that pollen because the short-styled morph has a more 'massive' (i.e. thicker and 'deeper') exine (compare fig. 14A and C & D).

These differences partially disagree with findings in other heterostylous Rubiaceae where, as known to date, long-styled morphs tend to have wider exine-nets and no suprategillar elements in the mesocolpium, while short-styled flowers have 'finer' exine-nets and wart-like suprategillar elements (see, for example, Puff & Robbrecht, 1989: 539 and figs. 18 & 19).

Interestingly, pollen of the monomorphic *Damnacanthus*, with flowers having stigmas exserted (and thus similar to the long-styled morph of *Mitchella*), agrees more with pollen from *short*-styled flowers of *Mitchella*.

4.6. Reproductive biology

The reproductive biology of *Mitchella repens* is well documented (Ganders, 1975; Keegan et al., 1979; Hicks et al., 1985). The cited literature includes detailed information on the heterostyly in the species, observations on the odd occurrence of self-compatible homostylous plants in essentially distylous populations, and provides evidence disproving the supposed dioecy mentioned for the species by older authors. The second species of the genus, *Mitchella undulata*, is also hetero(di)stylous.

See also paragraph 4.5 for details on differences between pollen from long- and short-styled flowers.

Damnacanthus differs in the absence of heterostyly. The genus has monomorphic, but not homostylous, flowers (see fig. 6A; terminology according to Ernst, 1955). The flowers have stigma lobes which are slightly exserted, while the anthers are positioned at the throat (their tips are protruding). In *Damnacanthus macrophyllus*, for example, stigmas start protruding from the corolla just as it opens (fig. 4); nevertheless, flowers are protandrous.

4.7. Chromosomes

Mitchella has a chromosome number of $2n = 22$. The published chromosome number for *Mitchella repens* (Atchison, 1947) was based on counts from 18 collections all originating from the eastern U.S.A. Chromosomes of the Asian *Mitchella undulata* were counted for the first time ($2n = 22$); metaphase chromosomes are indistinguishable from those of *Mitchella repens* (see Atchison, 1947: fig. 9C).

Chromosome counts of *Damnacanthus indicus* subsp. *indicus* yielded a number of $n = 11$ (fig. 5B). This is the first count for the genus.

See chapters 2 and 3 for vouchers and methods.

4.8. Distribution

Mitchella occurs both in North and Central America and in eastern Asia. This is a well known type of disjunction, cited and discussed in numerous publications and known for a long time (e.g., Gray, 1846; see also Hong, 1983). The American *Mitchella repens* occurs from Newfoundland to Minnesota in the North and from Florida to Texas in the South and has also outlying populations in Mexico and Guatemala [Hicks, 1982 (not seen), cited in Hicks et al., 1985]. The very closely related (and barely distinct) *Mitchella undulata* occurs from Japan westwards to Korea and adjacent parts of the U.S.S.R. in the North and to northern Taiwan in the South.

Damnacanthus is confined to eastern Asia and occurs from central and southern Japan westwards to Taiwan, China, Indo-China, and India. The genus has about ten species (Lo, 1979; Yamazaki, 1987b), of which *Damnacanthus indicus* is the one most widely distributed, occurring over the entire range of the genus.

5. TAXONOMIC HISTORY

5.1. *Prelinnean and early taxonomic history*

Linnaeus (1753) erected the genus *Mitchella* for a North American species previously known as *Chamaedaphne* (Mitchell, Gen. pl. Virg., not seen by us). Still, the name *Chamaedaphne* Mitchell was validly published in 1769 (Stafleu & Cowan, 1981: entry 6129), but is now rejected against *Chamaedaphne* Moench (Ericaceae).

Gaertner (1805) established the genus *Damnacanthus* on material sent to him [see De Candolle (1830: 473) and Zuccarini (1846)] by Thunberg under the wrong identification *'Carissa spinarum'* *. He called the single species *D. indicus*, thinking it came from India (s.l.), the country of origin of *'Spina spinarum'* (Thunberg's material must have come from Japan, however). Although Gaertner's statement "A Cl. Thunberg. sub nomine Carissae spinarum." in the protologue of *Damnacanthus* could, at first sight, suggest that his specific epithet *indicus* is superfluous, this is obviously not the case. This is further corroborated by another part of the protologue where Gaertner makes mention of Rumphius' name, viz. as a probable second species of *Damnacanthus*: "*Spina spinarum* Rumph. amb. 7. p. 37. t. 19. fig. 1. diversa hujus generis species esse videtur." This suggestion cannot be followed. *Spina spinarum* is neither a representative of the Rubiaceae, nor a *Carissa*, since it has alternate leaves with serrate margin. For a full elucidation, see Merrill [1917: 377, 425; "*Spina spinarum* I mas Rumph. = *Flacourtia indica* (Burm. f.) Merrill].

5.2. *Early nineteenth century history*

Only fruiting material was available to Gaertner (1805) to describe *Damnacanthus*. It was redescribed some time later, as *Baumannia* **, by A.P. & A. De Candolle (1833), using flowering material from unknown origin, cultivated by the brothers Bauman, Swiss horticulturists.

Gaertner accepted that *Damnacanthus* is related to *Canthium* (now in the Vanguerieae); in the same work on fruit morphology he described and depicted *Mitchella*, but apparently was not struck by the strong similarity between the fruits of the two genera. He did not at all discuss the relationship of *Mitchella*. A.P. & A. de Candolle (1833) were very careful to find out the position of *Baumannia* in the classification of the Prodromus (De Candolle, 1830), and believed its affinity could be with the Cordiereae or the Guettardeae, "selon que la nature du fruit mûr le décidera." Within these tribes they indicated *Nertera* and *Mitchella* (both in Guettardeae) as possible relatives, retaining the latter as the most probable ally. The two genera discussed here were thus for the first time associated with each other in the protologue of *Baumannia*. When Zuccarini (1846) studied Von Siebold's Japanese collections, he

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* A name of Linnaeus (1771), erroneously based on Rumphius' prelinnean name *Spina spinarum*. The description of *Carissa* in the 'Mantissa' applies partly to *Flacourtia* (first two paragraphs), partly (from "Folia opposita ..." onwards) to *Carissa* as presently defined (Leeuwenberg, pers. comm.).

** In the past, *Baumannia* was erroneously attributed to A.P. De Candolle alone, also by Farr, Leusink & Stafleu (1979); the name has two times been used again, for a genus of the Onagraceae by Stapf, and for a genus of the Rubiaceae-Knoxieae (= *Neobaumannia* = *Knoxia*) by Schumann (see Farr, Leusink & Stafleu, op. cit.).

Table 1. Position of *Damnacanthus* (+ its synonym *Baumannia*) and *Mitchella* by various authors.

	Mitchella	*Damnacanthus*
Gaertner (1805) (protologue of *Damnacanthus*)	relationship not commented	aff. *Canthium*
Reichenbach (1828)	'Coffeaceae'	as synonym of *Canthium*
Richard (1830)	associated with *Nertera*, as 'Guettardaceae dubieae'	as synonym of *Canthium*
De Candolle (1830)	'Trib. Guettardaceae subtr. Guettardeae'	'Trib. Coffeaceae subtrib. Coffeeae', associated with *Canthium*
De Candolle (1833) (protologue of *Baumannia*)	'Trib. Guettardaceae subtr. Guettardeae'	[as *Baumannia*] 'Trib. Guettardaceae subtr. Guettardeae', aff. *Mitchella*
Endlicher (1838)	'Guettardeae subtr. Euguettardeae'	[as *Damnacanthus*] 'Psychotrieae subtr. Coffeeae' [as *Baumannia*] 'Guettardeae subtr. Euguettardeae', aff. *Mitchella*
Lindley (1846)	'Guettardidae'	[as *Damnacanthus*] 'Psychotridae' [as *Baumannia*] 'Guettardidae', aff. *Mitchella*
Zuccarini (1846)	not mentioned	discovered synonymy *Baumannia* = *Damnacanthus*; supported position proposed by De Candolle (1833)
Hooker (1873)	Anthospermeae	Morindeae
Baillon (1880)	Chiococceae	Chiococceae, aff. *Mitchella* (? only a section of *Mitchella*)
Schumann (1891)	Anthospermeae	Morindeae
Bremekamp (1952, 1966)	not mentioned	not mentioned
Verdcourt (1958)	not mentioned	not mentioned
Blaser (1954)	corroborated Baillon's views	
Hayden (1968) Hayden & Dwyer (1969)	excluded from Anthospermeae aff. *Morinda*	not mentioned
Fosberg (1982)	excluded from Anthospermeae, "perhaps more related to Morindeae"	not mentioned
Puff (1982)	excluded from Anthospermeae; Paederieae group 2	not mentioned
Robbrecht (1982)	pollen not consistent with Paederieae	not mentioned
Johansson (1987a, b)	not mentioned	Morindeae
Robbrecht (1988)	incertae sedis	Morindeae

identified complete material (flowers and fruits) and thus discovered that *Baumannia* in fact was a redescription of *Damnacanthus*. This synonymy was accepted by all later authors.

The further history of the taxonomic position of *Damnacanthus* and *Mitchella* is quite intricate, and various positions have been proposed (table 1). In the first half of the nineteenth century, most authors maintained *Mitchella* and *Baumannia* closely associated in the 'Euguettardeae', then an artificial grouping of genera with drupaceous fruits and one-seeded pyrenes, including elements now placed in various tribes such as Psychotrieae, Vanguerieae, Guettardeae, and Chiococceae. At that time, *Damnacanthus* was classified far from *Mitchella* and *Baumannia,* in equally artificial taxa such as the "trib. Coffeaceae subtrib. Coffeeae", where it was frequently associated with *Canthium,* following the suggestion in the protologue. However, Zuccarini (1846), having discovered that *Baumannia* is a synonym of *Damnacanthus* (see above), did not accept the genus' alliance to *Canthium,* but stressed the correctness of the position of *'Baumannia'* as proposed by A.P. & A. de Candolle.

5.3. *Mitchella and Damnacanthus in the classical systems of the Rubiaceae*

In Hooker's (1873) classification, present-day tribal concepts of the Rubiaceae started to arise; he placed *Damnacanthus* in the Morindeae and classified *Mitchella* in a distant position, in the Anthospermeae. Some years later, Baillon (1879, 1880) stressed the close relationship between the two genera, and even, with some doubt, considered to reduce *Damnacanthus* to a section of *Mitchella.* His view was convincingly documented and founded on great detail of placentation and fruit structure, but was nevertheless neglected by all consequent authors. Baillon's placement of the genus pair was different also; he included it in his "série des *Chiococca.*"

Schumann (1891) apparently ignored or overlooked Baillon's strong argumentation. His classical system of the Rubiaceae is mainly founded on Hooker's (1873), and he maintained *Mitchella* in the Anthospermeae and *Damnacanthus* in the Morindeae.

5.4. *Mitchella and Damnacanthus in present-day literature*

In the more recent classification systems of the Rubiaceae, little or no attention has been paid to the two genera discussed here. Bremekamp (1952, 1966) seemingly never mentioned them in his long series of publications on the family. Verdcourt (1958) made only occasional mention of *Mitchella,* without discussion of its systematic position. In Robbrecht's (1988) review of the family and revision of its classification, *Damnacanthus* is maintained in the Morindeae, but *Mitchella* is considered to be of uncertain position. This reflects recently published views on *Mitchella.*

Only a few other modern authors have dealt with the genera in question. Blaser (1954), dealing with morphological and anatomical aspects of inflorescences and flowers of *Mitchella,* confirmed the association of the genus with tribes with descending ovules and expressed agreement with Baillon's (1880) findings. Hayden (1968) in her comparative study of New World rubiaceous seeds concluded that there is a strong resemblance between the fruits of *Mitchella* and those of Morindeae. Fosberg (1982) and Puff (1982), unaware of each others efforts, dealt with the delimitation of the Anthospermeae. Both excluded *Mitchella* from that tribe. Fosberg (1982) excluded the genus because of its pendulous ovules and left its position more or less undecided, being inclined to consider it "perhaps more related to the tribe Morindeae." Puff (1982) transferred *Mitchella* from the Anthospermeae to the Paederieae, basing his transfer primarily on floral biological grounds (see also paragraph 6.2). In a subsequent palynological study, Robbrecht (1982) largely confirmed Puff's (1982) redelimitation of the Anthospermeae and Paederieae but noted that *Mitchella* is an exception in that it is palynologically inconsistent with all other Paederieae. Johansson (1987a, b) maintained *Damnacanthus* in the Morindeae. Recent local floristic accounts of *Damnacanthus* (Lo, 1979; Yamazaki, 1987b) did not deal with the position of the genus.

5.5. *The species of Mitchella and Damnacanthus*

Both *Mitchella* and *Damnacanthus* were originally described as monotypic genera. The only taxon ever added to the North American type species *Mitchella repens* is the E Asian *M. undulata*. The two species are very close to one another, and the latter is sometimes reduced to infraspecific rank, *M. repens* L. var. *undulata* (Sieb. & Zucc.) Makino. On the contrary, more and more *Damnacanthus* species became known. It was e.g. recently found that two Chinese species, originally described in *Canthium* and later transferred to *Prismatomeris,* in fact belong to *Damnacanthus* (Lo, 1979; palynological confirmation of generic position: Johansson, 1987a). *Damnacanthus* is by now in need of revision; it seems that there are less then ten species.

6. THE TAXONOMIC POSITION OF DAMNACANTHUS AND MITCHELLA

and the circumscription of the Morindeae

6.1. *Damnacanthus and Mitchella are sister genera*

Chapter 4 of the present study impressively corroborates Baillon's (1879, 1880) opinion that *Damnacanthus* and *Mitchella* are very closely allied. The two genera agree in many characters (see also table 2):

- inflorescence position and morphology (paired flowers in *Damnacanthus,* fused flower pairs in *Mitchella*);
- flowers (including details of placentation, and campylotropous ovules which, at least according to our present state of knowledge, are otherwise unknown in Rubiaceae);
- red drupaceous fruits;
- pyrenes (in the two genera without preformed germination slits and with remarkably pitted endocarp);
- seeds, seed-coat, oily endosperm and minute embryos;
- colporate pollen;
- chromosomes (2n = 22).

Chorological data are also not in contradiction to the close affinity between the two, since the distribution of *Mitchella* (E Asia and North to Central America) is virtually vicariant of that of *Damnacanthus* (India through Southeast Asia to Japan).

Baillon's wide generic concept, i.e. his proposal to reduce *Damnacanthus* to a section of *Mitchella,* should not be followed, however. Differences in various important character states support and justify a separation at generic level (see table 2: life form, branching, thorns, heterophylly, heterostyly, flower fusion by ovaries).

6.2. *Does Mitchella belong to the Anthospermeae ?*

It is clear that *Mitchella* has been associated with the Anthospermeae primarily because of the erroneous interpretation of its placentation, its herbaceous habit and some superficial similarities with *Nertera.* Hooker (1873) described the ovules as "in loculis solitaria, e basi erecta, anatropa"; Schumann's (1891) generic description does not mention the ovules, but he implicitly accepted placentation and ovule position to agree with the ovules of the Anthospermeae, "1 vom Grunde aufsteigenden ... in jedem Fache." The two authors of the classical system of the Rubiaceae were clearly misled by the inferior embryo radicle orientation of *Mitchella.* Their conclusion must have been that inferior radicle position in a seed is deducible from a basally attached, anatropous ovule in flowering stage (a situation that is, in fact, the rule; see paragraph 4.4.2). They probably never dissected ovaries of *Mitchella* so that the true situation remained unknown to them.

Puff (1982) accepted their description of the placentation and the ovules and thus left *Mitchella* in the group of tribes with solitary, erect, anatropous ovules but transferred the genus to the Paederieae, a tribe closely allied to the Anthospermeae.

Thus, only two alternatives for the position of *Mitchella* and *Damnacanthus* need consideration, viz. the Morindeae and Baillon's "série des Chiococca." Before doing so (paragraph 6.4), we first need to discuss delimitation problems of the Morindeae.

6.3. *Problems regarding the circumscription of the Morindeae*

The circumscription and delimitation of the Morindeae is problematic and was frequently discussed (Petit, 1963; Bremekamp, 1966; Darwin, 1979). Johansson, after having carried out a pollen morphological investigation (1987a) of most and taxonomic revisions of certain morindeous genera, concluded (1987b: 21) that "the delimitation and relationship of the Morindeae are still uncertain. The included genera differ from each other in many important respects, and it is possible that the tribe is polyphyletic." In Robbrecht's (1988: 174, 193) survey of the classification of the Rubiaceae, no attempt has been made to clarify the delimitation of the Morindeae, and "the problem of how to define the tribes in the Psychotrieae/Morindeae/Coussareeae aggregate' is indicated as one of the major gaps in our rubiaceous knowledge. Since then, Johansson published new views, remarking that in the Morindeae at least two major groups may be distinguished. In 1989, he indicated that a smaller group (*Prismatomeris* and its allies *Gentingia, Motleya,* and *Rennellia*; see also Johansson & Wong, 1988) is characterized by a combination of characters absent in the core of the Morindeae, comprised of genera related to *Morinda.* The globose to hemispherical seeds with an adaxial hollow and corneous endosperm are the most striking of these characters. Robbrecht's (1988: 193) diagnosis of the Morindeae is hardly applicable to *Prismatomeris* and its allies, but rather describes the group of genera related to *Morinda.*

Table 2. Selected character states of *Damnacanthus* and *Mitchella*, compared with those known for the Morindeae s. str. (after Robbrecht, 1988) and the Prismatomerideae (after Johansson, 1989). [ ]: information added here.

Character	*Damnacanthus*	*Mitchella*	Morindeae s. str.	Prismatomerideae
life form	shrubs	perennial herbs	shrubs, trees, lianas	shrubs, trees
branching sympodial	+	+	[probably –]	[probably –]
sympodial branching units with 3 internodes	+	–	[–]	[–]
thorns	+, ±, –	–	[–]	[–]
leaves evergreen	+	+	[+]	[+]
heterophylly	+	–	[probably –]	[probably –]
stipules	bilobed or entire	entire	entire or bilobed	bilobed or ± entire
raphides	+	+	+	+
flowers per smallest inflorescence unit	2 (1)	2 (1; rarely 3, 4)	[2–many]	[1–many]
inflorescence terminal (t) or axillary (a)	t	t	t; a and paired	t
flowers: -merous	4	4	4 – 6	4 – 5 (–6)
base of corolla	+	+	+ (*Caelospermum*)	[–]
corolla lobes valvate	+	+	+	+
corolla tube hairy inside (at least above)	+	+	[+]	–
heterostyly	–	+	frequently +	frequently +
flowers fused by ovaries; fruits fused	–	+ (2)	+ (many); –	+ (3); –

(Table 2 continued)

Character	*Damnacanthus*	*Mitchella*	Morindeae s. str.	Prismatomerideae
number of carpels	4	4	2–12	2
placenta insertion above the middle of septum	+	+	– (base of locule; ovules erect	– (at middle of septum)
ovule: massive obturator	+	+	[–]	[+]
ovule curved (± campylotropous), micropyle slightly pointing upwards	+	+	[–; anatropous?]	[–; anatropous?]
fruit	drupaceous	drupaceous	drupaceous	berry-like
endocarp	pyrenes without	pyrenes without preformed germination slits	pyrenes with lateral preformed germination slits	membranous preformed germination slits sometimes forming lid
seed	± ellipsoidal	± ellipsoidal	± ellipsoidal, frequently winged at base	globose to hemispherical, with adaxial excavation
exotestal cells with thickening along radial and outer tangential walls	+	+	–; ?parenchyma-like	–; very reduced exotesta ± crushed
endosperm	soft, oily, white	soft, oily, white	soft, oily, white	corneous, frequently dark blue
embryo small, with minute cotyledons	+	+	–	±
radicle ± pointing downwards	+	+	[+]	+
colporate pollen, number of apertures	3–6	3	3(–6)	3(–5)
chromosomes (2n =)	22	22	[22, 44, 88]	[?]
distribution	E & SE Asia	E Asia and North	pantropical to Central America	tropical Asia

A short survey of the Morindeae convinced us of the naturalness of Johansson's group of genera related to *Prismatomeris*. To his diagnostic characters we add:

- the typical placentation (placenta attached to middle of septum; ovules sessile, basally surrounded by a massive, possibly placental tissue);
- the berry-like drupes with poorly developed membranous endocarp;
- the large seeds with frequently dark blue endosperm and excavation filled with parenchyma-like possibly placental tissue; and
- the pellicle-like seed-coat with very thin parenchyma-like exotesta.

Incidentally, Ruan (1988) recently proposed the new monogeneric tribe Prismatomerideae (as 'Prismatomereae'). In his diagnosis, only the description of the placentation ("ovula supra medium septi subpeltatim affixa") reflects the characters Johansson and we believe to characterize the *Prismatomeris* group.

Detailed anatomical examinations of the placentation and ovules is urgently needed to help clarify the relationships in the Psychotrieae/Morindeae/Coussareeae aggregate. Untill such work is available, we provisionnally propose:

- to restrict the Morindeae to the group of genera related to *Morinda* (e.g. *Trichostachys, Lasianthus, Caelospermum*);
- to emend Ruan's monogeneric Prismatomerideae to Johansson's group of genera related to *Prismatomeris* (*Rennellia, Gentingia, Motleya*).

Table 2 gives a survey of the differences of the Morindeae s.s. and the Prismatomerideae.

6.4. *The taxonomic position of the genus pair*

The majority of previous authors had placed *Damnacanthus* in the Morindeae s.l., while only a few present-day authors referred *Mitchella* to this tribe (see table 1). Hayden (1968), for example, concluded that there is a strong morphological agreement between the fruits of *Morinda* and those of *Mitchella*; this is at least overrated, and was primarily based on exotesta similarities which were perhaps not fully understood (see paragraph 4.4). She moreover stated that "a natural relationship [between these two genera] is strengthened by the double nature of the fruits and flowers of *Mitchella*" but there is no doubt that parallel evolution leads to ovary fusion in several not necessarily closely allied lines of Rubiaceae (see Robbrecht, 1988: 90).

The characters of the genus pair *Damnacanthus*/*Mitchella* are compared to those of the Morindeae s.s. and the Prismatomerideae in table 2. The two genera can clearly not be accommodated in one of these two groups, as the placentation differences alone immediately indicate. *Damnacanthus* and *Mitchella* are very distant from the *Prismatomeris* group (see especially the fruit and seed differences), and show some minor resemblances with the *Morinda* group (drupes with pyrenes in common, those of the Morindeae s.s. provided with preformed germination slits, however).

Is Baillon's (1880) "série des Chiococca" more appropriate for the position of the genus pair? This concept is much wider than the actual definition of the (neotropical) Chiococceae, and more or less agrees with Robbrecht's (1988) subfamily Antirheoideae. In their placentation *Mitchella* and *Damnacanthus* come indeed close to this subfamily. But in the Antirheoideae, the occurrence of idioblasts with raphides and heterostyly is only known from the Craterispermeae and the Knoxieae. Each of these two tribes (recently well-documented, Robbrecht, 1988 and Puff & Robbrecht, 1989 resp.) is characterized by highly advanced features and differs in many respects from *Damnacanthus* and *Mitchella.* The Knoxieae represent a paleotropical herbaceous lineage with generally dry fruits splitting into mericarps. The woody Craterispermeae seem a somewhat more plausible candidate for alliance, but inflorescence position (axillary and paired at nodes), fruit and seed differences, and geography (the monogeneric tribe is African-Madagascan) enfeeble this hypothesis.

The chromosome numbers of *Mitchella* and *Damnacanthus* ($n = 11$, $2n = 22$, the most common number in the Rubiaceae), cannot provide conclusive supplementary support for the taxonomic position of the genus pair. According to our present state of knowledge, the Morindeae are predominantly diploid (base number: $x = n = 11$). The majority of the counted species of *Morinda* are diploid, but tetraploidy is also known in the genus. From *Lasianthus,* the only other chromosomally known genus in the tribe, so far only a single octoploid species is recorded. The Prismatomerideae remain unknown as regards their chromosomes. Chromosome numbers of members of the subfamily Antirheoideae in Robbrecht's (1988) delimitation, roughly corresponding to Baillon's (1880) "série des *Chiococca*", are not of much value for the evaluation of possible relationships: the base number of 11 is most common, and there is a predominance of tetraploids in most chromosomally investigated tribes. The derived base number of $x = 10$ is, however, also known from the subfamily. The three known counts of *Chiococca* species (tribe Chiococceae) are somewhat puzzling in that each has a different base number, i.e. $x = 11$, $x = 12$, and $x = 14$ (compilation of chromosome numbers based on data in Kiehn, 1986).

In conclusion it can be said that, while the close affinity between *Mitchella* and *Damnacanthus* is well proven, the placement of the genus pair in the system of the Rubiaceae remains doubtful. It seems to stand quite isolated and is to be excluded both from the Anthospermeae and the Morindeae. Because of their placentation, the two genera may be referred to the Antirheoideae, but their campylotropous ovules cast considerable doubt on such a transfer. Campylotropous ovules are, at present, neither known to occur in the Antirheoideae nor in any other subfamily of Rubiaceae. It seems that only a large-scale comparative anatomical examination of the placentation and the ovules of Rubiaceae with raphides and solitary ovules could shed new light on the alliances of *Mitchella* and *Damnacanthus.*

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