

# Early floral developmental studies in *Annonaceae*

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**Abstract:** In the *Annonaceae* the perianth mostly consists of three trimerous whorls, with a slight tendency to a spiral sequence of their members. The androecium and the gynoecium are variable in the number of their organs (high polymery to low, fixed numbers). In this study the early development of polymerous androecia is investigated in *Ariabotrys hexapetalus* and *Annona montana*. In these species the androecia begin their development with six stamens in the corners of a hexagonal floral apex. This early developmental pattern resembles that in some *Aristolochiaceae* and *Alismatales*. Not only in this respect but also because of other important features the *Annonaceae* may be regarded as closely related to these two groups, but as more archaic.

The carpels in the mostly choricarpous gynoecia are conduplicate (not peltate) or very rarely (*Cananga*) slightly peltate. The gynoecium of *Monodora* consists of a single, clearly peltate carpel with a very peculiar laminal placentation (the ovules are inserted in seven double rows). This unusual condition can be interpreted as the expression of two sequential genetical programs during development: the program for a single carpel and that for a pluricarpellate gynoecium (simulation of a syncarpous gynoecium).

## Introduction - Morphology of the adult flowers

The family *Annonaceae*, with about 130 genera and 2300 species by far the largest family of the *Magnoliales*, makes up about three-fourths of the order (CRONQUIST 1981). As regards the floral construction, most of the members of the family are characterized by a cyclic perianth of three trimerous whorls, an androecium of numerous stamens, and a gynoecium of more or less numerous free carpels on a flat or conic receptacle.

Nevertheless, the *Annonaceae* show a high variability in the number of their floral parts. In the following we refer to the data of FRIES (1959). The trimerous perianth structure is relatively stable. In a few cases one of the three whorls can be absent. In species of *Annona* and in the genera *Dasymaschalon* and *Dennettia* the inner whorl is reduced or totally lacking. In the genus *Enantia* the middle whorl is wanting. On the other hand, FRIES (l.c.) reported that *Feneriva* has 15 perianth members and *Tetrameranthus* has 12 (4+4+4). Like in *Tetrameranthus*, non-trimerous whorls are also found in *Disepalum* (6, 8 or 10 perianth members, with two in an outer whorl) and *Tetrapetalum* (two members in an outer whorl are followed by four further perianth members in two whorls).

Commonly the members of the outer perianth whorl are called sepals. In the adult flower they are usually small and shorter than the members of the two following whorls (petals). The petals (the members of the middle and

inner perianth whorl) differ in size, shape and consistence. Seldom the members of the outer petal whorl are much shorter than the inner three and more or less sepal-like (*Miliusa*, FRIES l.c.). More frequently the three inner petals are smaller than the three outer ones and of a different shape. The three inner perianth members can remain closed or curved over the flower centre, thus covering the reproductive organs and forming a so-called floral or pollination chamber (see GOTTSBERGER 1970, 1989).

The usually numerous stamens are firmly packed together, forming a  $\pm$  hemispherical mass, with the carpel tips standing out in the centre. The stamens have short filaments, and their connectives are mostly notably prolonged and expanded over the anther to form connective shields, which are either more or less truncate (e.g. *Artabotrys*: Fig. 17, *Monodora*: Fig. 62) or prolonged into a tip (*Cananga*: Fig. 46). Rarely the stamen number is lower, and then the arrangement is thought to be cyclic (e.g., *Mezzettia* with 9-12 stamens in 2 series, *Orophea* with 6-18 stamens in 1-3 series, *Exellia* with 12-15 stamens in 2 series, *Hornschuchia* with 6 stamens in 2 series, all after FRIES l.c.). Outer or inner androecial organs can become staminodes.

In most genera of *Annonaceae* the more or less numerous carpels are distinct and conduplicate (not peltate). Six genera are characterized by a single carpel (*Dasoclema*, *Dielsiothamnus*, *Kingstonia*, *Mezzettia*, *Monocarpia*, *Tridimeris*) and some others can have only one carpel (*Alphonsea* 1-several, *Cyathocalyx* 1-several, *Deeringothamnus* 1-6, *Onychopetalum* 1-2, *Oxandra* 1-4-13, *Trigynaea* 1-6, *Xylopia* 1 or usually several, *Uvaria combretifolia* 1, FRIES l.c.). The carpels have numerous or two ovules or only one ovule. The gynoecium of the african genera *Monodora* and *Isolona* is somewhat peculiar (unilocular with several double rows of ovules). Recently the *Monodora* gynoecium has come into debate (syncarpous versus monocarpellate; LEINS & ERBAR 1980, 1982, GUÉDÈS & LE THOMAS 1981, DEROIN 1985, ENDRESS 1990a).

Despite the wide interest in this important family, information on floral ontogeny is poor (*Monodora crispata*: LEINS & ERBAR 1980, 1982; *Annona montana*, *Cananga odorata*, *Polyalthia glauca*, young carpel development only: van HEEL 1981; *Artabotrys hexapetalus*, androecium only: ENDRESS 1986, 1987; *Annona cherimolia*, androecium only: ENDRESS 1990b; *Popowia whitei* = *Monanthotaxis whytei*: RONSE DECRAENE & SMETS 1990).

In this study, the present ontogenetical knowledge is summarized and supplemented by new information, esp. by early developmental stages of the androecium.

The following material has been studied: *Annona cherimolia* MILL. (leg. P. LEINS, 20.5.1977, Botanical Garden of the Institute of Agricultural Botany, Bonn); *Annona montana* MACF. (leg. W. MORAWETZ, April 1990, Botanical Garden Vienna); *Annona muricata* L. (leg. P. LEINS, Botanical Garden Münster); *Artabotrys hexapetalus* (L. fil.) BHANDARI (leg. W. MORAWETZ, April 1990, Botanical Garden Vienna); *Asimina triloba* (L.) DUN. (leg. P. LEINS, Botanical Garden Bonn); *Cananga odorata* (LAM.) HOOK. f. & THOMS. (leg. W. MORAWETZ, 111-29187, Papua New Guinea); *Monodora crispata* ENGL. & DIELS (leg. P. LEINS, 23.2.1978, Botanical Garden Bonn); *Polyalthia suberosa* (ROXB.) BENTH. & HOOK. f. (leg. W. MORAWETZ, April 1990, Botanical Garden Vienna).

The material was fixed in FAA. For SEM technique, flower buds were transferred to 70 % ethanol, dehydrated in dimethoxymethane, critical point-dried using liquid CO<sub>2</sub>, mounted with colloidal graphite on aluminium stubs, coated with gold and studied in a Cambridge (Stereoscan S-4) or Leitz (AMR 1200 B) scanning electron microscope. For serial sections, the flower buds were dehydrated in an alcohol series, embedded in paraplast, dissected with a rotary microtome (6 µm thickness) and stained with Delafield's hematoxylin.

## Observations and conclusions

### Perianth

Only a few young flower buds were available from *Artabotrys hexapetalus*, *Annona montana* and *Monodora crispata* for studying the development of the perianth. In these species, like in most other *Annonaceae*, the perianth consists of three alternating trimerous whorls (3+3+3). In none of the species investigated the members of a whorl arise simultaneously. In *Artabotrys*, the primordia of the outer perianth whorl are initiated successively in a rapid sequence, judged from the size differences of the primordia in a young flower bud (Fig. 1). In *Monodora*, it seems that after the inception of the first perianth member, the next two arise more or less simultaneously (Fig. 49). In somewhat older buds, however, the aestivation of the outer perianth members seems to reflect a successive origin of all three members (Fig. 50). Occasionally, we could also observe a contorted aestivation in the outer perianth whorl of *Monodora*. Judged from the size of their members, the two inner perianth whorls of *Monodora* seem to have the same sequence of inception as in the outer whorl (Fig. 51; see also LEINS & ERBAR 1980). In *Artabotrys*, we can presume from the flower buds shown in Figs. 2 and 3 that the members of the middle and inner perianth whorls arise successively, but in a very rapid sequence like in

the outer whorl (see numbering). A successive formation of the members of the middle perianth whorl also can be inferred in *Annona montana* (Fig. 20). Relevant information about the initiation of the outer perianth whorl cannot be given for lack of suitable flower buds of this species. Fig. 21 shows the inception of the inner perianth whorl of *Annona montana*. Two larger primordia (7 in Fig. 21) are situated on both sides of the smallest member of the middle perianth whorl. A size difference between these two primordia is not recognizable. They seem to have arisen simultaneously, followed by the third primordium of this whorl.

The non-simultaneous initiation of the perianth members within a whorl is to be interpreted as a reminiscence of a spiral perianth with a variable number of organs (compare with *Magnolia*, ERBAR & LEINS 1981, 1983, ERBAR 1988). The whorled arrangement comes about by the rhythmisation of a spiral sequence, i.e., the intercalation of a longer plastochron after three shorter ones.

### **The form of the floral apex after perianth inception**

After the inception of all nine perianth members the floral apex is hexagonal in outline. The length of the sides in front of the members of the second and the third perianth whorl can be different. In *Annona montana*, the longer sides of the hexagonal floral apex are in front of the leaves of the second perianth whorl (Fig. 21). This is correlated with a lateral expansion of the insertion area of the middle perianth members. In *Artabotrys hexapetalus*, the longer sides of the hexagonal apex are in front of the members of the third, i.e., the inner perianth whorl (Figs. 3, 4). This is correlated with a rapid lateral expansion of the insertion area of the inner perianth members. In *Monodora crispata*, the outline of the floral apex is more regularly hexagonal after the inception of the perianth members (Figs. 51, 52). In *Annona cherimolia*, it is circular at least at the developmental stage shown in Fig. 26. The members of the inner perianth whorl are very small in this species.

### **Androecium**

Our results refer only to androecia with a high and variable number of stamens (*Artabotrys hexapetalus*: about 80 stamens, *Polyalthia suberosa*: close to 100 stamens, *Annona cherimolia*, *Asimina triloba* and *Monodora crispata*: about 200 stamens, *Annona muricata*: about 900 stamens, *Annona montana*: about 2000 stamens). We could study the earliest developmental stages of the androecium only in *Artabotrys hexapetalus* and *Annona montana*.

In *Artabotrys hexapetalus* (see also ENDRESS 1987, who used the synonym *Artabotrys uncinatus*) and *Annona montana*, the androecial development

starts with six primordia in the corners of the hexagonal floral apex (Figs. 5, 6, 22, 23). This is presumably also the case in *Polyalthia suberosa* (Fig. 31) and *Monodora crispata* (Fig. 53), and the same has been reported for *Popowia whitei* (RONSE DECRAENE & SMETS 1990; now named *Monanthotaxis whytei*). For the last three species, however, the initial stage of androecial development, with only the first six stamen primordia, has not been documented.

In *Artabotrys hexapetalus*, the next step in the development of the androecium is the formation of further stamen primordia along the sides of the hexagonal floral apex (in front of the middle and inner perianth members). As a rule, one (to two) primordia are formed in front of the middle perianth members, and three to five in front of the inner ones (Figs. 7, 8). Further stamen primordia originate on the floral apex centripetally in a relatively rapid succession (Figs. 9, 10, 11). We could never observe a regular spiral sequence of stamen primordia, but in some areas there are more or less distinct parastichies (e.g. Figs. 10b-d). An acyclic, acropetal sequence of stamen primordia and their partial arrangement in parastichies have been found in all species investigated (*Annona montana*: Fig. 25, *Annona cherimolia*: Fig. 26, *Annona muricata*: Fig. 27, *Polyalthia suberosa*: Fig. 31, *Monodora crispata*: Figs. 54-55, *Cananga odorata*). The young androecium in *Asimina triloba* (Fig. 38) seems to be most irregular.

We can assume that there are morphogenetical correlations between the irregularities in the stamen arrangement and the small size of stamen primordia relative to the entire floral apex, the short plastochrones as well as the large gaps between the perianth members (see ERBAR & LEINS 1981, 1983, ERBAR 1988, ENDRESS 1987, 1990a).

In *Annona montana* the number of stamens is very high (about 2000). The high number is correlated with an immense enlargement of the floral apex during early androecial development. In Fig. 24 there are two (or three) strikingly large primordia in front of the middle perianth whorl. Unfortunately, no flower buds were available from a developmental stage between those shown in Figs. 23 and 24. Still we have no doubt that six of the large primordia are the first androecial organs, which originally were situated in the corners of the hexagonal floral apex. We assume that horizontal growth in the apex, in the areas between the middle and the inner perianth members (marked by arrows in Fig. 24) as well as the rapid enlargement of the first androecial primordia are responsible for the "new" arrangement. The enlarged primordia seem to develop into staminodes, and some other basal primordia also can become staminodial.

The very high degree of polymery in the androecium, as observed in *Annona montana* (Fig. 25) and *Annona muricata* (Fig. 27), can be regarded as advanced within the family. On the other hand, the androecia with a relatively low and fixed stamen number (e.g., in *Mezettia*) are presumably also advanced in the family. Both types may have developed from androecia with a moderately high and unfixed number of stamens.

### Related and roecial patterns

In recent papers (LEINS & ERBAR 1985, 1991a, b, ERBAR 1988, ERBAR & LEINS 1994) we compared the early androecial pattern of the *Annonaceae* with those of *Aristolochiaceae* and *Alismatales*. We could show that the androecial development in *Artabotrys* and *Annona* as well as in *Asarum* (*Aristolochiaceae*) and in the monocotyledonous *Alismatales* starts with six stamen primordia, situated on both sides of the three inner perianth members (petals). Additional stamens arise either collateral-centrifugally (e.g. in *Asarum caudatum*, *Aristolochiaceae*) or collaterally (*Echinodorus*, *Alismataceae*) or centrifugally (*Hydrocleis*, *Limnocharitaceae*) or centripetally (*Sagittaria*, *Alismataceae*; *Annonaceae*). If we have a look at species of *Annonaceae* with a small and fixed number of stamens, like in *Popowia buchananii* and *Mezzettia umbellata*<sup>1</sup> their androecia easily could be ranged among those of the *Aristolochiaceae* and *Alismatales* as regards number and arrangement of the stamens.

In *Alismatales*, the mode of intercalation of additional stamens depends on the way in which the floral apex enlarges (LEINS & STADLER 1973, LEINS 1975). In this context we refer to the fact that in *Annona montana* the high number of stamens (about 2000) is correlated with an immense enlargement of the floral apex after the inception of the first six androecial organs.

On the basis of the androecial patterns and other features<sup>2</sup> we can perhaps assume that *Annonaceae*-like Dicotyledons had been the ancestors of the *Aristolochiaceae* as well as of the *Alismatales*, which have specialized early

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1 The flowers of these two species could only be studied in herbarium material from the Botanische Staatssammlung Munich (M): *Popowia buchananii* (ENGL.) ENGL. & DIELS (leg. TORRE & CORREIA 14.422), *Mezzettia umbellata* BECC. (leg. SINCLAIR & KADIM BIN TASSIM 10417).

2 Occurrence of the monocotyledonous p-type of sieve-tube plastids (BEHNKE 1971a, b, 1977), adaxial prophylls, trimerous perianth whorls, successive type of microsporogenesis, and monoaperturate pollen grains (in *Aristolochiaceae* in the genus *Saruma*; ERDTMAN 1966).

in different ways (LEINS & ERBAR 1985, ERBAR 1988). The androecium of the *Annonaceae* ultimately can be derived from spiral androecia of the *Magnoliales* (ERBAR & LEINS 1981, 1983, 1994, ERBAR 1988, LEINS & ERBAR 1991a, b).

## Gynoecium

### The choricarpous gynoecium

The number of organs in the gynoecium is highly variable in *Annonaceae* (*Annona muricata*: almost 500 carpels, *Annona montana*: about 300 carpels, *Annona cherimolia*: about 55 carpels, *Artabotrys hexapetalus*: 14-20 carpels, *Polyalthia suberosa*: 15-19 carpels, *Cananga odorata*: about 14 carpels, *Asimina triloba*: 2-6 carpels).

Like the stamens the carpels mostly do not follow an undisturbed spiral sequence. But the more the floral apex becomes symmetrical (circular in outline), the more a spiral pattern can be observed in the apical part (see also ENDRESS 1987). In the flower bud of *Artabotrys hexapetalus*, which is shown in Fig. 10a, we can number the last six carpels in a spiral sequence. Fig. 29 shows a flower bud of *Annona muricata* with 21 regular parastichies in the upper part of the gynoecium, which become irregular only on the top of the floral apex (see also Fig. 30).

A single carpel usually develops from a more or less hemispherical primordium. Then the primordium becomes horseshoe-shaped, i.e., lateral flanks are formed by plication. Only plication (no peltation) occurs in the carpels of *Artabotrys hexapetalus* (Fig. 19), *Annona montana*, *Annona cherimolia*, *Annona muricata* (Figs. 27-30), *Polyalthia suberosa* (Figs. 31b, 33), *Asimina triloba* (Figs. 39-40), and *Polyalthia glauca* (van HEEL 1981).

In an earlier study (LEINS & ERBAR 1982) we have reported that in *Cananga odorata* (leg. D. ROTH in Sumatra) the innermost carpel has a low cross zone ("Querzone"; see Fig. 16 in LEINS & ERBAR 1982) in contrast to the other, epeltate carpels. In the *Cananga* material used in this study all carpels, which are stalked (Fig. 47), seem to be somewhat peltate (Fig. 48).

Numerous members of the *Magnoliidae* with apocarpous gynoecia (especially many *Annonaceae*) partly compensate for the lack of the advantages of syncarpy by forming an "external compitum" ("extragynoecial compitum", ENDRESS 1982, 1986). We can demonstrate a beautiful example in *Cananga odorata*. In adult flowers the apices of all carpels are in very close contact and covered by a secretion, on which pollen grains may stick (Figs. 43, 45). In younger buds the apices of the single carpels are still discernible

(Fig. 41). Cross-sections through the carpel apices at this developmental stage (Fig. 42) reveal that the carpel tips are in close contact by their epidermal cells, which are smaller and richer in plasma than the other cells. In adult flowers the carpel tips separate, and their ventral slits are wide open. The epidermis of both the outer carpel flanks and the inner surface becomes long papillate (Fig. 44). The space among and within the carpel tips is filled with the above mentioned secretion. By this, the carpels share a common space allowing a regular distribution of the pollen tubes to all carpels and ovules like in syncarpous gynoecia.

GOTTSBERGER (1970, 1989) has reported that in several *Annonaceae* the stigmata become covered by a viscid liquid in self-pollinated as well as in cross-pollinated flowers, and that cross-pollinated species are strongly protogynous and shed their "stigmatic head" (stigmata of the individual carpels connected by the hardened fluid) from the carpels at the beginning of the male phase. This behaviour also can be confirmed from our fixed material of *Artabotrys hexapetalus*. In *Artabotrys* the stigmata, which are distinct from the lower (fertile) part of the carpels (Figs. 13, 14), possess a long-papillate stigmatic tissue on their whole surface (Figs. 15, 18, 19). In the transition area to the fertile carpel part the papillae become restricted to the area of the ventral slit (Figs. 16, 19c) and then continue via the carpel margins (Figs. 19d-f) down to the funiculi (Fig. 19g) of the two ovules (pollen tube transmitting tissue). Because the stigmata stand relatively close together it seems possible that the tubes of deposited pollen can reach all ovaries. The whole of the stigmata can be regarded as a compitum (in our cultivated material a pollination drop was not observed).

Only immature stages of carpel development were available from *Polyalthia suberosa*. Again the young carpels are conduplicate (Fig. 33). In later stages the carpels bear long hairs at their tips and their bases (Figs. 34-36). Presumably, these hairs have nothing to do with the stigmatic tissue, but perhaps they have the function of retaining a pollination drop. Note that there are globular papillae in the upper part of the carpel (Fig. 37).

In *Polyalthia* we studied a floral type characterized by "growth as open buds" (MORAWETZ 1988). This behaviour seems to be not rare in the family, and has been described by MORAWETZ (l.c.) for several species of *Tetrameranthus*, *Artabotrys*, *Cleistopholis*, *Crematosperma*, *Guatterrella*, *Malmee*, and *Polyalthia*: The young flower buds are at first closed, then open and the "open flower buds" grow considerably, and only shortly before anthesis the perianth closes partly again, forming a "pollination chamber" (sensu GOTTSBERGER 1970). The same behaviour has already been described by GOTTSBERGER (1970) for species of *Guatteria*. GOTTSBERGER (l.c.) has



reported that in *Gutteria curvinervia* the period of open but still growing buds may last more than one month. The stages of *Polyalthia suberosa* shown in Figs. 31-35 are from young, still closed flower buds, whereas Figs. 36-37 are from an open, immature flower bud.

### The *Monodora* gynoecium

The *Monodora* gynoecium consists of a unilocular ovary with a closed longitudinal slit, extending downwards for about three-fourths of the ovary length. Many ovules are arranged in seven distinct double rows distributed over the whole inner surface (Fig. 63). The ovary bears a lobed stigma head (Fig. 62). The interpretation of the gynoecium of *Monodora* is still controversial. It is thought to be either a syncarpous, pluricarpellate gynoecium (e.g., BAILLON 1868, BUCHHEIM 1964, LEINFELLNER 1969, GUÉDÈS & LE THOMAS 1981, DEROIN 1985) or a monocarpellate one (LINDLEY 1853, LEINS & ERBAR 1980, 1982). We believe that there are enough important ontogenetical features to regard the *Monodora* gynoecium as monocarpellate with an unusual placentation. The main steps of the development of the *Monodora* gynoecium are:

1. The gynoecium develops from a single primordium which arises in the centre of the flower bud (Figs. 56-57).
2. The gynoecial primordium passes through a sloping cup-like (chair-like) stage (Fig. 58), as has been demonstrated in several *Magnoliidae* with free peltate carpels (ERBAR 1983).
3. During further development (Figs. 59-60) the gynoecial primordium becomes tube-like (with a lower ascidiate and an upper plicate zone; for terminology see LEINFELLNER 1950). The elongated ventral slit closes by interlocking of the epidermal cells.
4. The marginal areas differentiate as it is usual in single carpels (ERBAR 1983). The cells of the inner ridges of the marginal area remain rich in plasma, whereas the cells in the outer ridges of the marginal area become vacuolized. In the subepidermal layer of the outer ridges periclinal cell divisions occur (compare with the carpels in *Magnolia*, *Liriodendron*, *Calycanthus*, *Drimys* and *Illicium* (ERBAR 1983).

There is no evidence from early floral ontogeny for a pluricarpellate condition of the gynoecium in *Monodora* (for the discussion of vascularization see LEINS & ERBAR 1982). Also the development of the lobed stigma head (Figs. 61-62) does not give a hint. The stigma lobes do not correspond with the placentae.

Only the arrangement and orientation of the ovules (Fig. 63) may lead to the opinion that the ovary of *Monodora* consisted of several (seven) carpels. We can explain this unusual placentation at best by the overlapping of different genetic programs: At the beginning of the gynoecial development the genetic program of a single carpel is expressed; later on this program is overlapped by a program of a pluricarpellate gynoecium, of which only the placentae are expressed (simulation of a syncarpous gynoecium, LEINS & ERBAR 1982, LEINS 1983). This kind of view approaches to the opinion of ENDRESS (1990a), who speaks of "internal doubling" or "multiplication" of an originally single carpel. In any case, the *Monodora* carpel (or gynoecium) can be understood as advantageous in terms of floral economy: the advantages of a syncarpous gynoecium (with internal compitum) are attained with the low expense for a single carpel.

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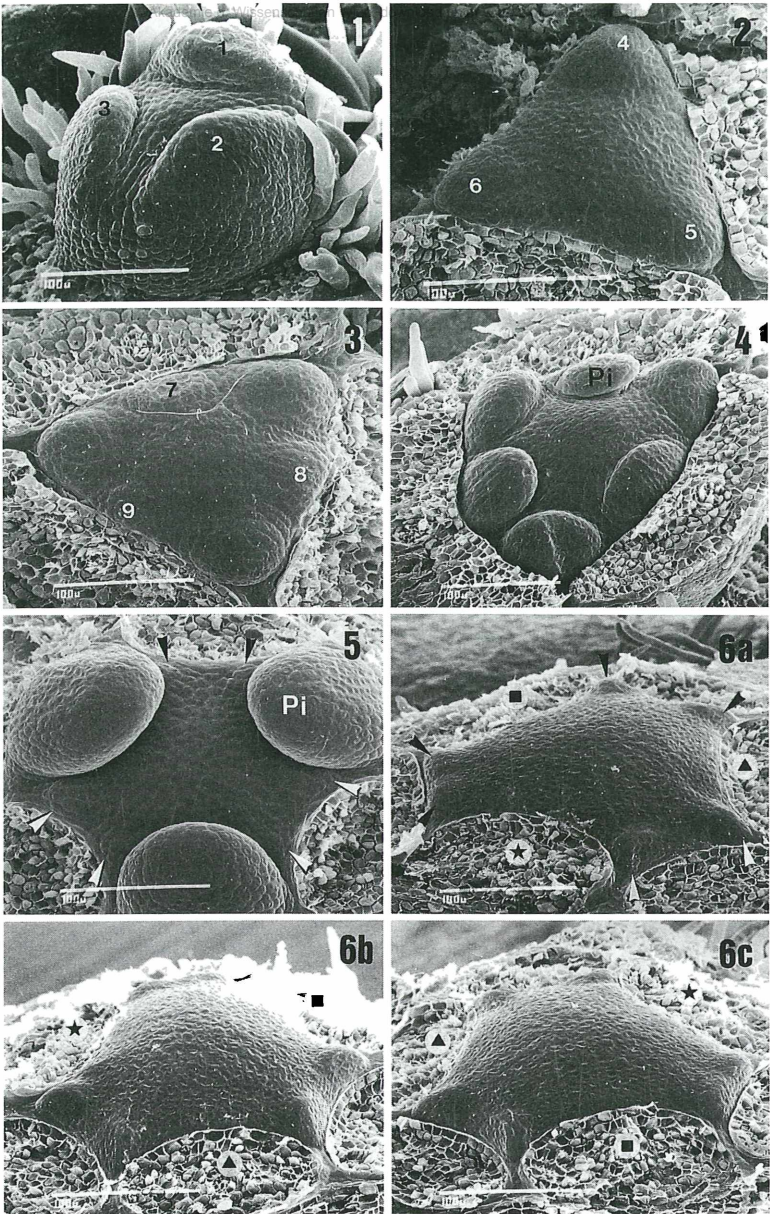
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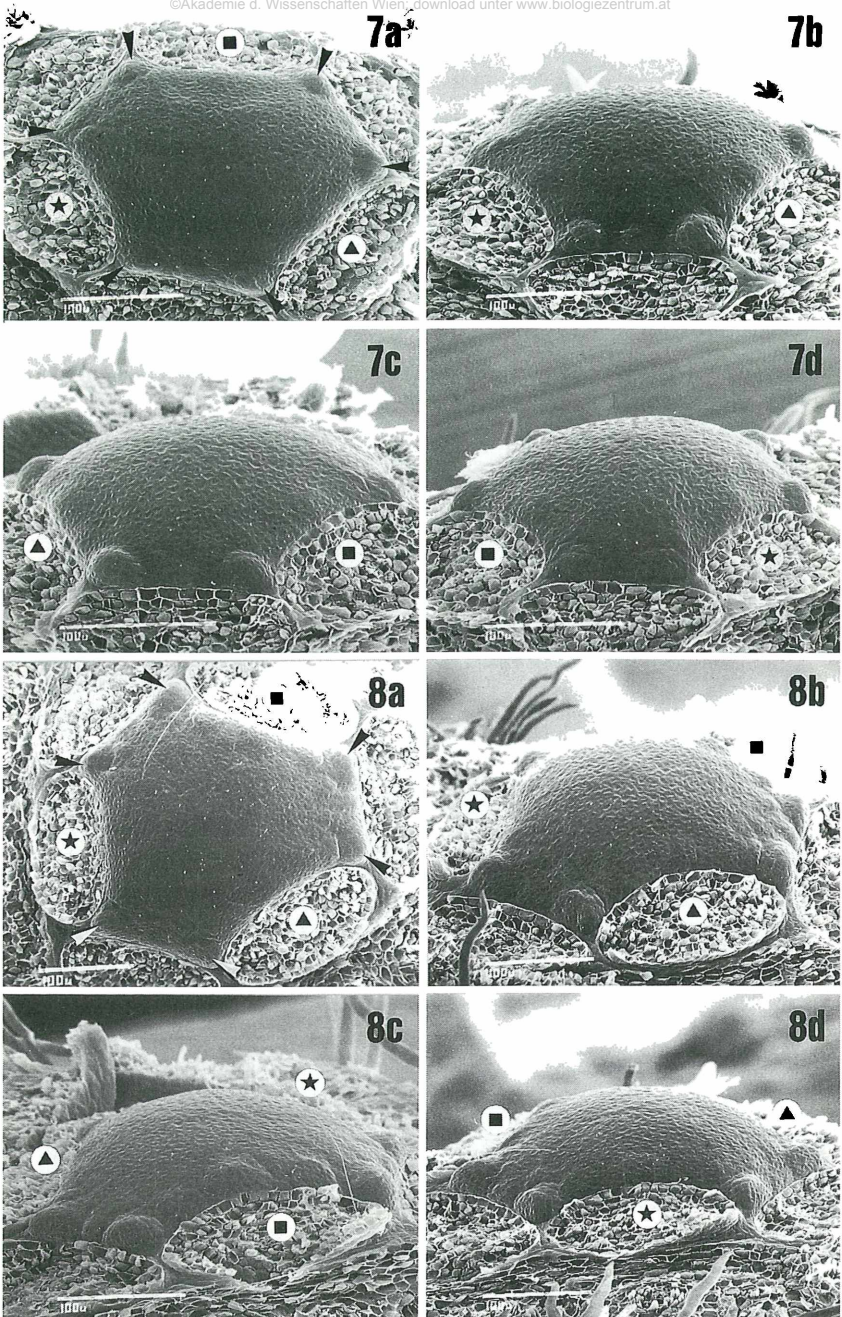
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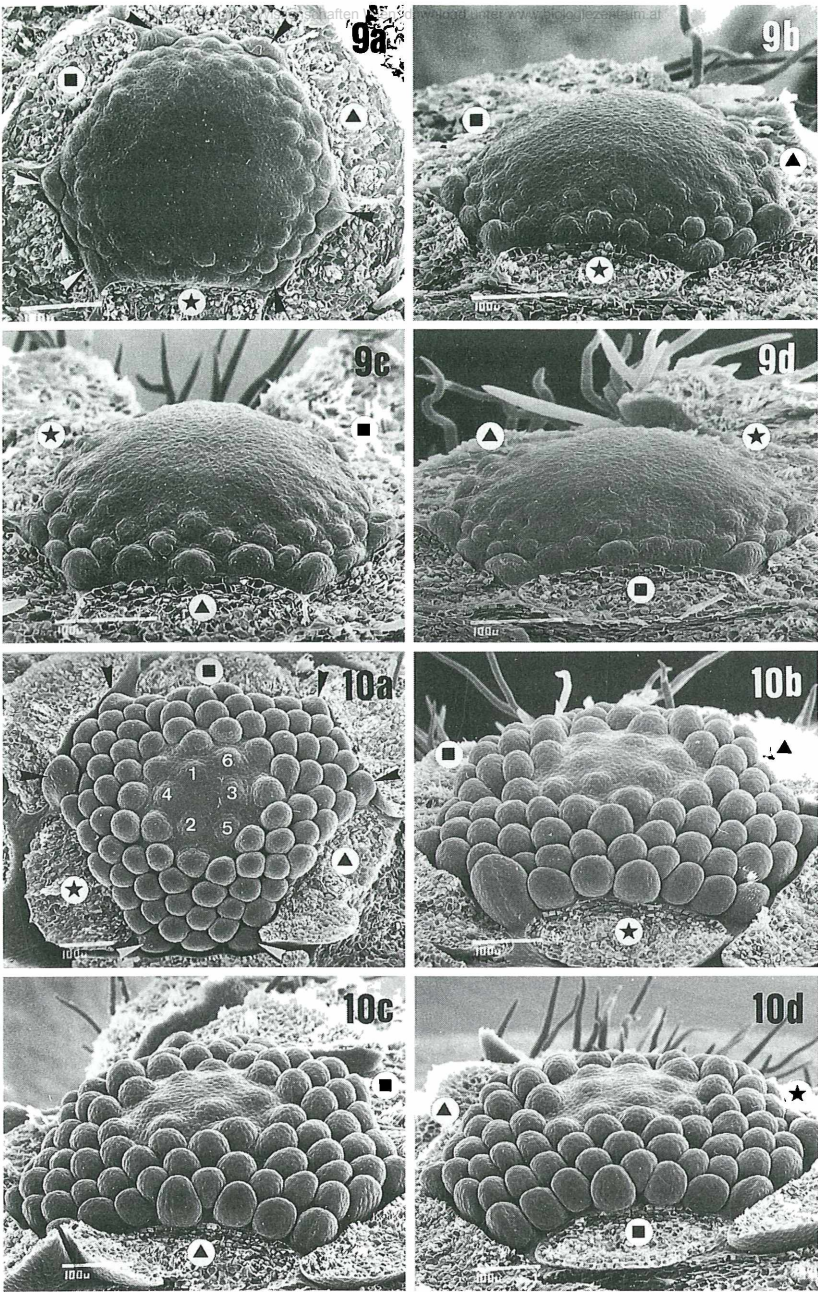
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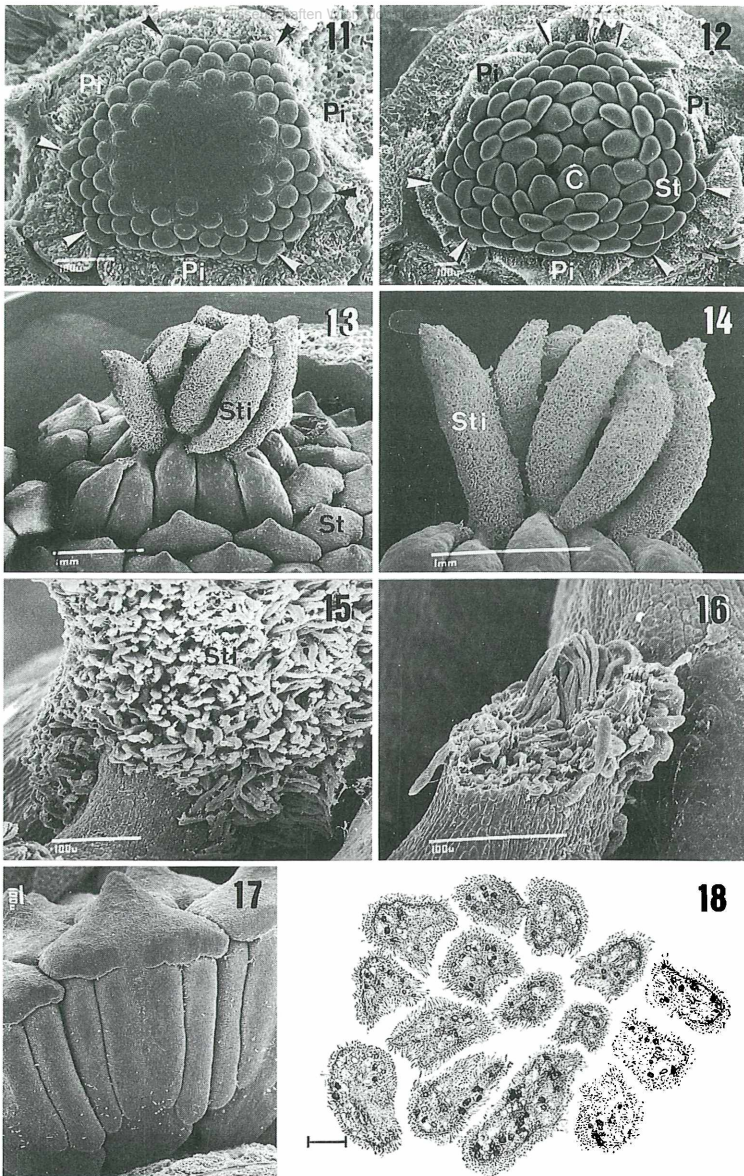
Figs. 1-6. *Artabotrys hexapetalus*. 1, Inception of the three outer perianth members (1-3, calyx). 2, Inception of the second whorl of perianth members (4-6, calyx removed). 3, Inception of the third perianth whorl (7-9, calyx removed). 4, Floral apex before androecial development (calyx removed). 5, The first six stamens begin to arise in the corners of the hexagonal floral apex (arrows), outer and middle perianth whorl removed. 6, The first six stamen primordia are more prominent; a-c different profile views of the same flower bud. In each case the symbols mark the same scar of an inner perianth member. - Pi = inner perianth member. - Bars: 100  $\mu$ m.



Figs. 7-8. *Artabotrys hexapetalus*. After the formation of the first six stamen primordia (arrows) a few additional stamen primordia begin to arise. Top view (7a + 8a) and three profile views (7b-d, 8b-d) of two flower buds, nearly in the same stage. In each case the symbols mark the same scar of an inner perianth member. - Pi = inner perianth member. - Bars: 100  $\mu$ m.



Figs. 9-10. *Artabotrys hexapetalus*. Top view (a) and three profile views (b-d). In each case the symbols mark the same scar of an inner perianth member. 9, Non-spiral, centripetal inception of stamens. Arrows indicate the six androecial "corner" primordia. 10, The last six carpels are numbered according to their presumed spiral sequence (1 = youngest carpel primordium). - Bars: 100  $\mu$ m.



Figs. 11-18. *Artabotrys hexapetalus*. 11, Floral bud with centripetally initiated stamens before carpel formation. 12, Floral bud with stamen (St) and carpel (C) primordia. In 11 and 12 the androecial "corner" primordia are marked by arrows. 13, Stigmata (Sti) which are distinct from the fertile part of the carpel. 14-16, Part of the gynoecium shown in 13. 14, Close-up of the stigmata (Sti). 15, Transition area between the stigmatic and the fertile part of the carpel. 16, Scar left by a stigma that has broken off. 17, Stamens with connective shields. 18, Cross-section through the stigmata of a gynoecium. - Bars: 11-12, 15-18: 100  $\mu$ m, 13-14: 1mm.



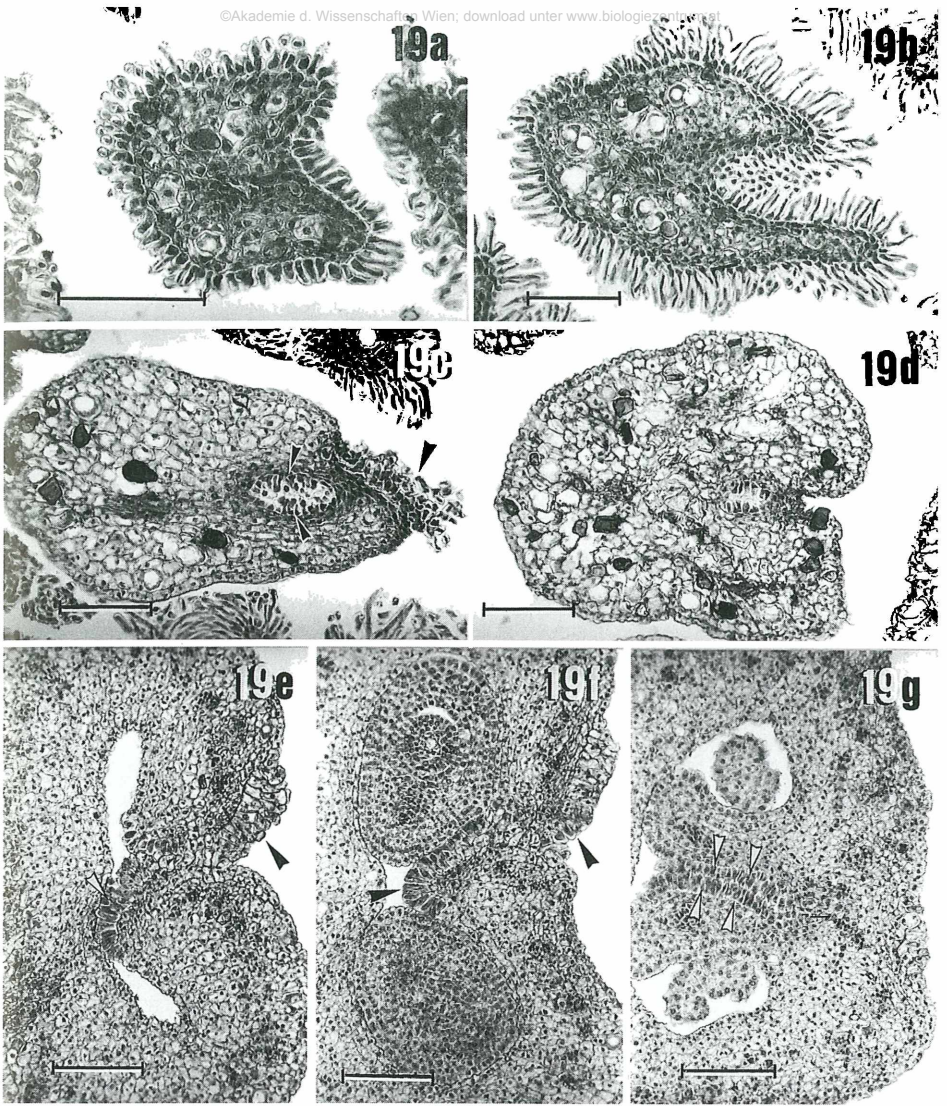
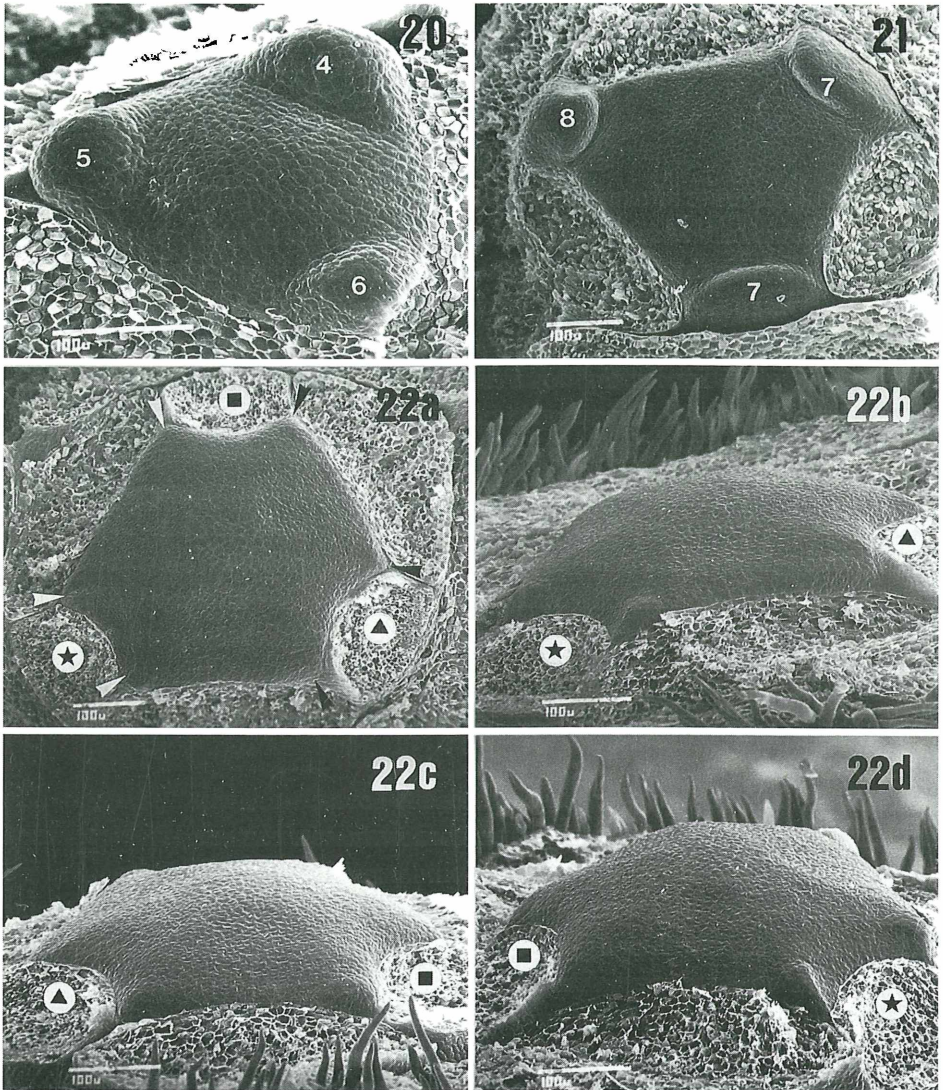
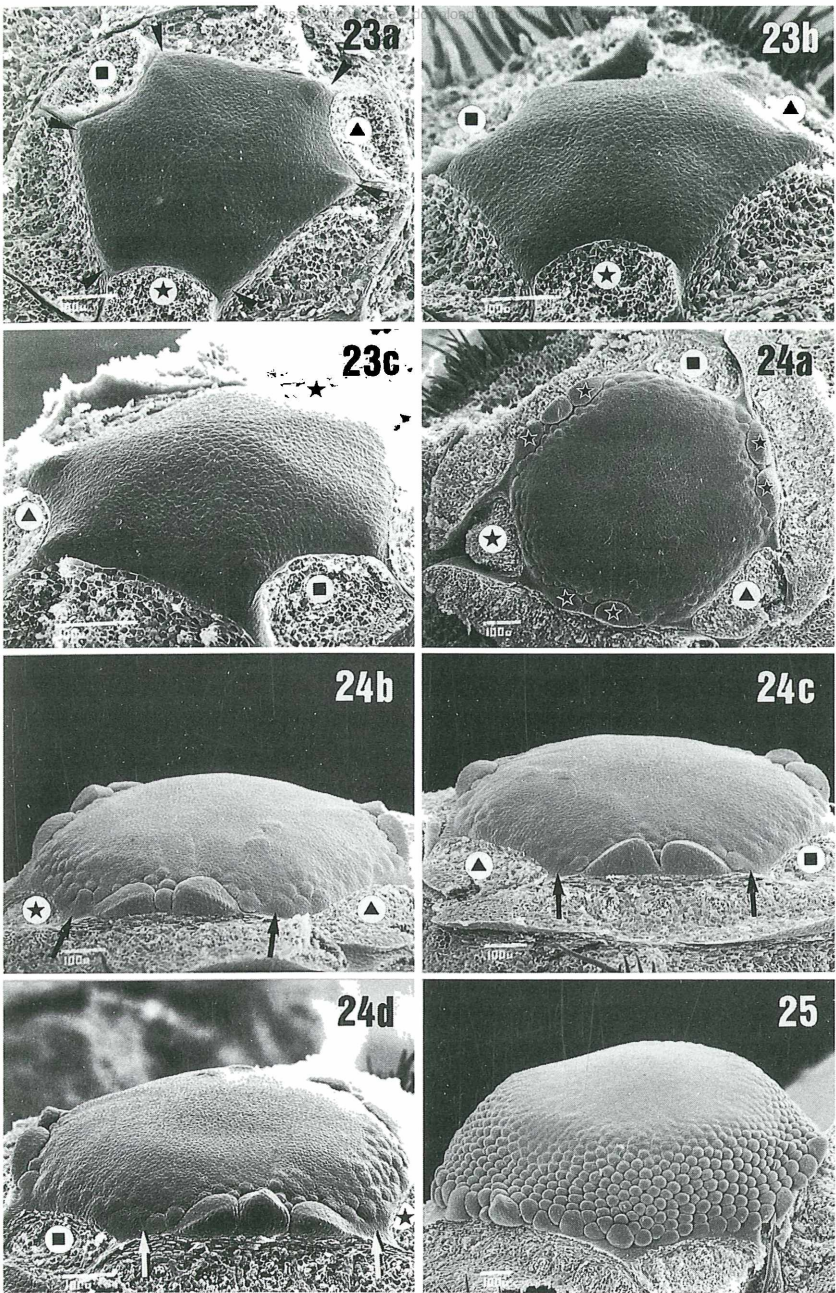


Fig. 19. *Artabotrys hexapetalus*. Cross-sections through different zones of a carpel from the stigmatic tip (a) down to the fertile ovary (g) with the two ovules. The stigma has long papillae on its whole surface (a, b); in the transition zone to the fertile carpel part they become restricted to the area of the ventral slit (c, arrows) and then continue via the carpel margins (d-f, arrows) down to the funiculi (g, arrows). - Bars: 100 μm.



Figs. 20-22. *Annona montana*. 20, Inception of the second perianth whorl (4-6, calyx removed). 21, Inception of the third perianth whorl (7, 8; numbering according to the presumed sequence), first and second perianth whorl removed. 22, Hexagonal floral apex after the inception of the perianth, with the first six stamen primordia in the corners of the floral apex (arrows). Top view (a) and three profile views (b-d). In each case the symbols mark the same scar of an inner perianth member. - Bars: 100  $\mu\text{m}$ .



Figs. 23-25. *Annona montana*. 23a-c, Floral bud in nearly the same stage as shown in 22. 24a-d, Inception of further stamens in a rapid acropetal succession. Six of the larger stamen primordia (marked by \* in the top view: a) are presumably the first six androecial "corner" primordia. The arrows in the profile views (b-d) point to the enlargement area of the floral apex (see text). 25, Acropetal, but somewhat chaotic initiation of stamens. - Bars: 100 µm.

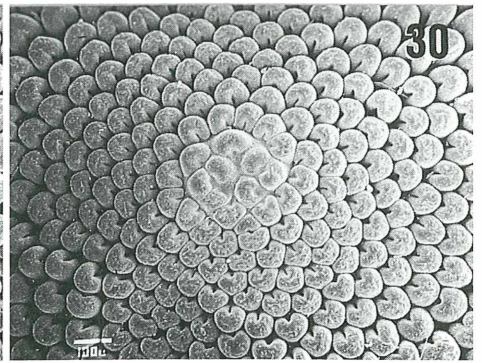
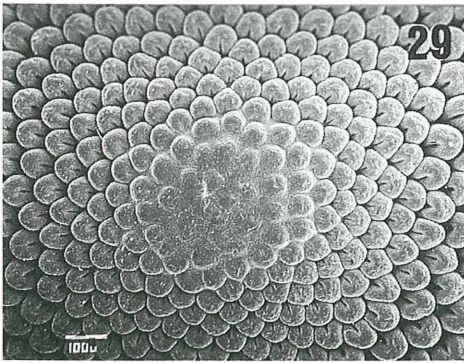
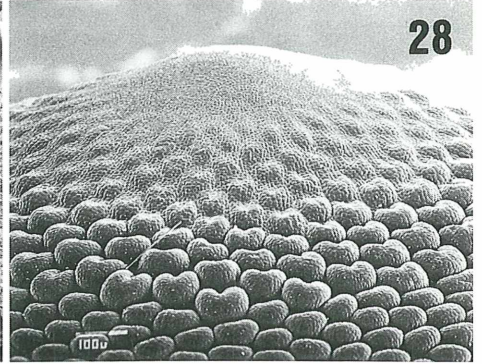
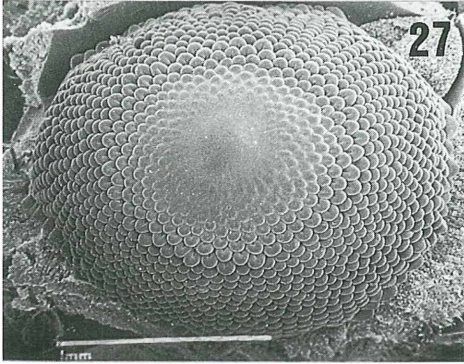
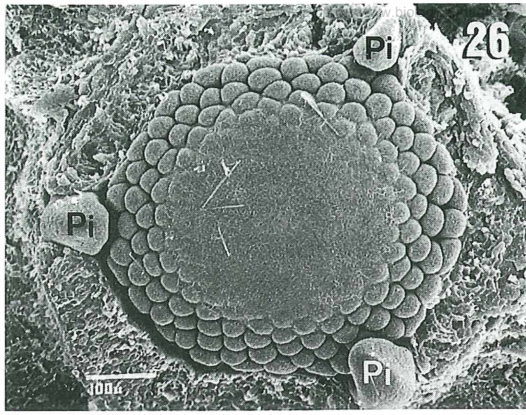
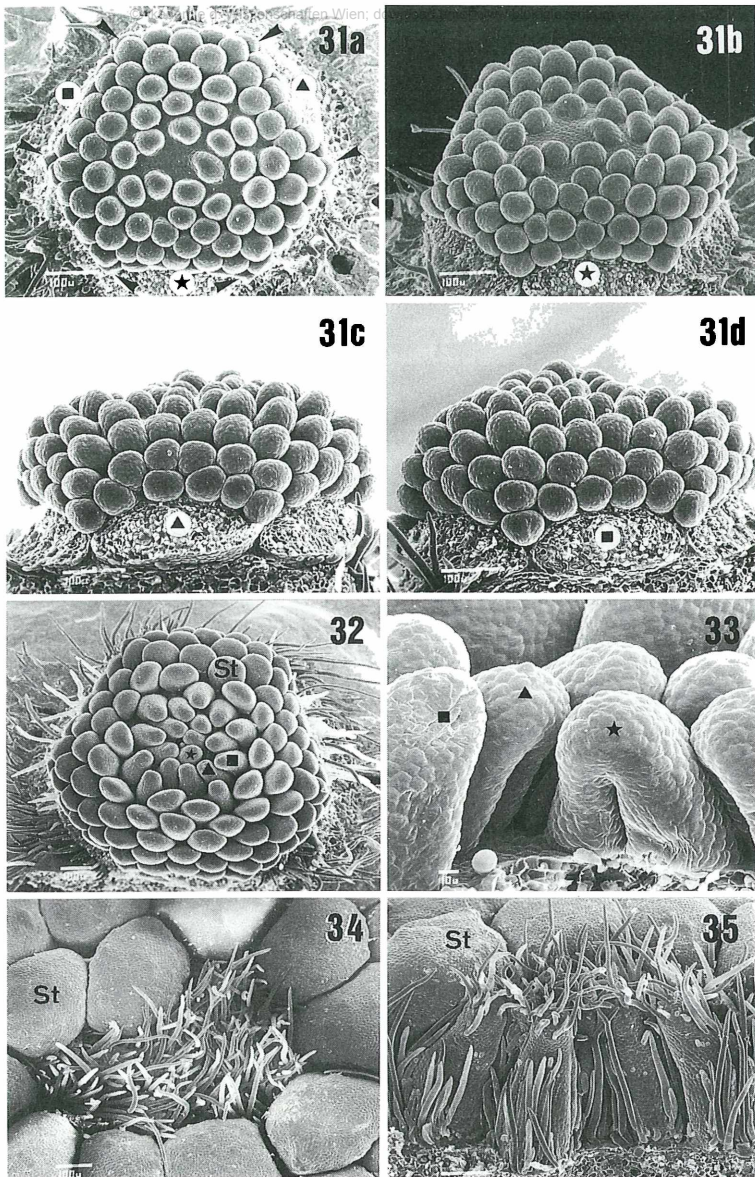
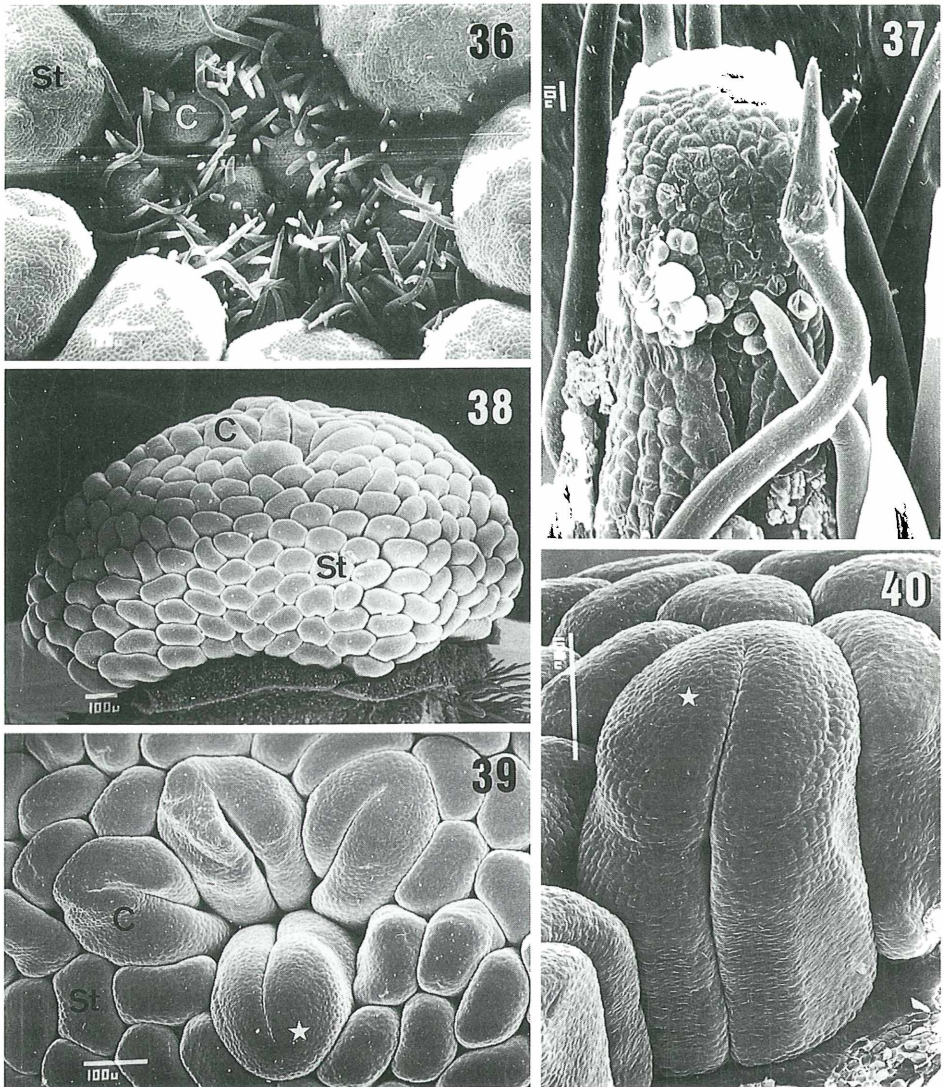


Fig. 26. *Annona cherimolia*. Initiation of stamens on a rounded floral apex, top view, first and second perianth whorl removed. Note the very small inner perianth members (Pi). - Bar: 100  $\mu$ m.

Figs. 27-30. *Annona muricata*. Inception of very numerous stamen and carpel primordia in acropetal succession. In 28 and 29 parastichies are obvious, in 30 the pattern of inception of the innermost carpel primordia is irregular. - Bars: 27: 1mm, 28-30: 100  $\mu$ m.

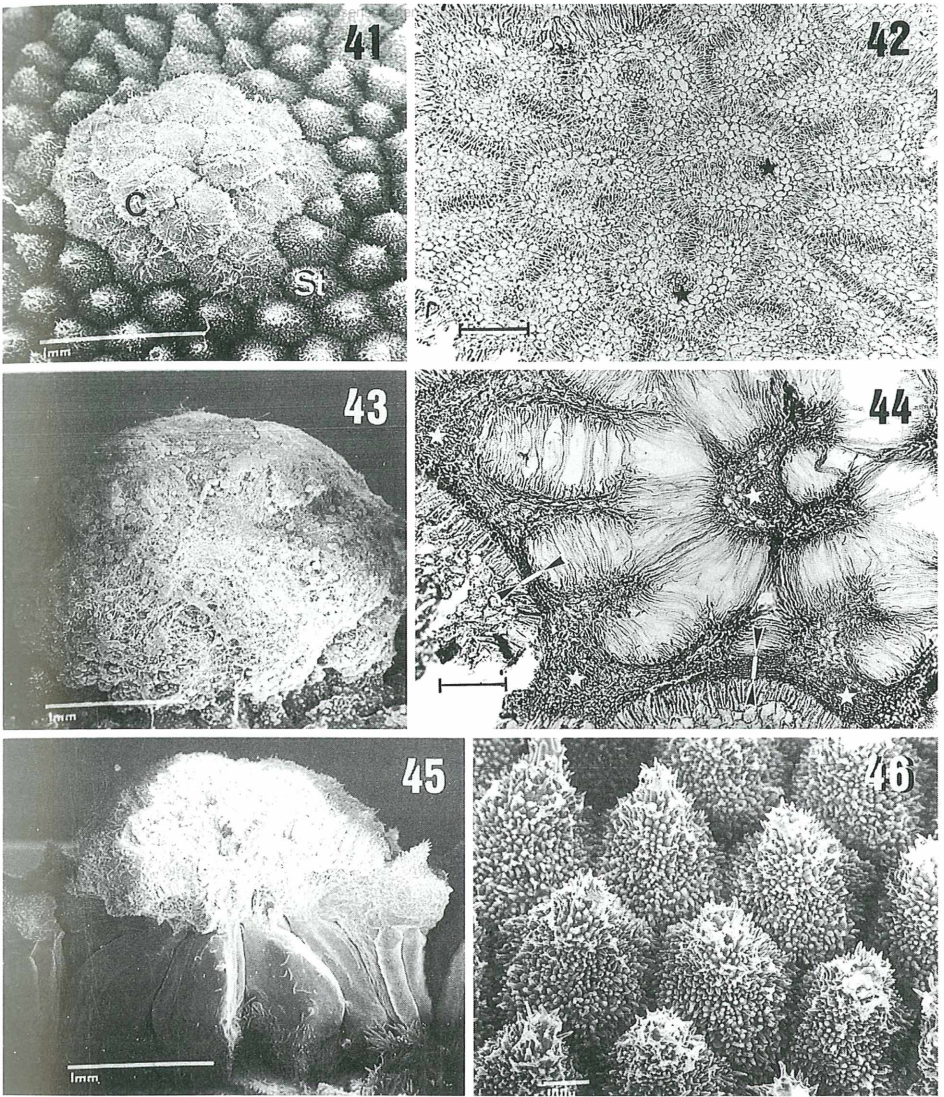


Figs. 31-35. *Polyalthia suberosa*. 31, Inception of stamen and carpel primordia on a hexagonal floral apex. The first six stamen primordia in the corners are marked by arrows. Top view (a) and three profile views (b-d). In each case the symbols mark the same scar of an inner perianth member. 32, Flower bud with numerous stamens and 19 carpels. 33, Same flower bud as in 32, in longisecton, showing the conduplicate carpels (the same carpels are marked in 32 and 33). 34, Top view of the gynoecium in a still closed flower bud just before opening. 35, Same flower bud as in 34, in longisecton, showing the carpels. - St = stamen. - Bars: 31-32, 34-35: 100  $\mu\text{m}$ , 33: 10  $\mu\text{m}$ .

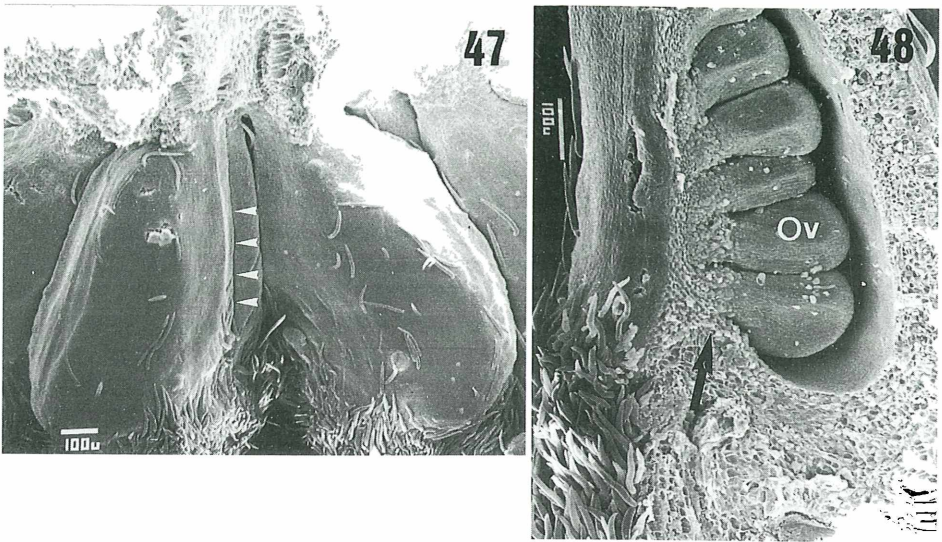


Figs. 36-37. *Polyalthia suberosa*. 36, Top view of the gynoecium of an open, immature floral bud. C = carpel, St = stamen. 37, Tip of an immature carpel (dissected from the bud shown in 36). - Bars: 36: 100 µm, 37: 10 µm.

Figs. 38-40. *Asimina triloba*. 38, Profile view of an older stage of flower bud with stamens (St) and carpels (C). 39, Top view of the gynoecium (same bud as in 38). 40, One conduplicate carpel of the gynoecium shown in 39 (marked by \*). - Bars: 100 µm.

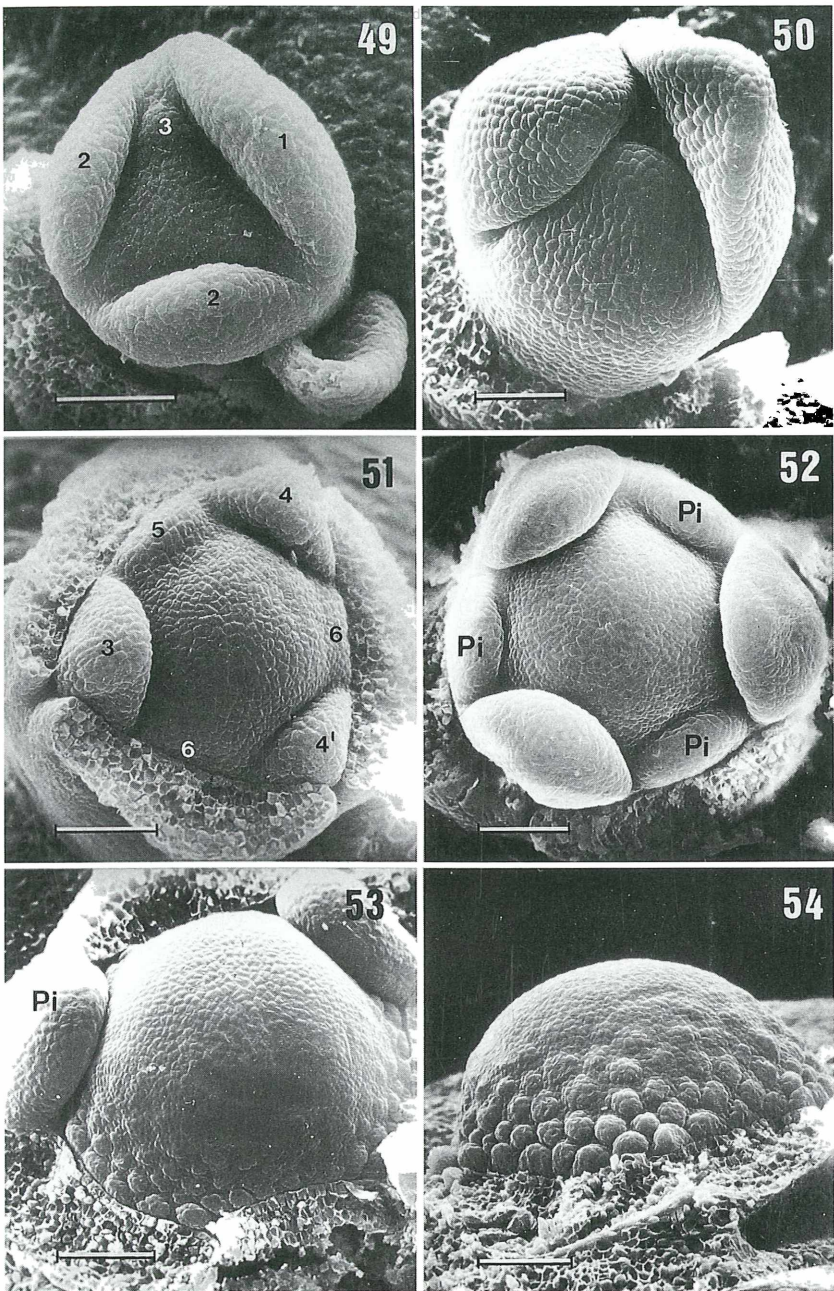


Figs. 41-46. *Cananga odorata*. 41, Top view of a gynoecium before anthesis. C = carpel, St = stamen. 42, Cross-section through the carpel tips, stage comparable to that shown in 41. \* = dorsal vascular bundle of a single carpel. 43, Common stigma head of the choricarpous gynoecium, covered by a secretion. 44, Cross-section through the carpel tips, stage comparable to that shown in 43. Carpel boundaries marked by arrows (see text). \* = dorsal vascular bundle of a single carpel. 45, Profile view of a gynoecium of an adult flower, a few carpels removed. 46, Top view of the connective shields. - Bars in 42 and 44: 100  $\mu$ m. - Bars: 41, 43, 45: 1 mm, 42, 44, 46: 100  $\mu$ m.

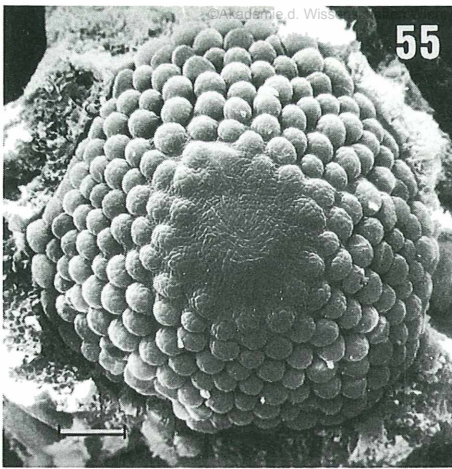


Figs. 47-48. *Cananga odorata*. 47, Stalked carpels in profile view (close-up of the gynoecium shown in 46). Ventral slit marked by arrows. 48, Young carpel in longisection with ovules (Ov) and a low cross-zone (arrow). - Bars: 100  $\mu\text{m}$ .

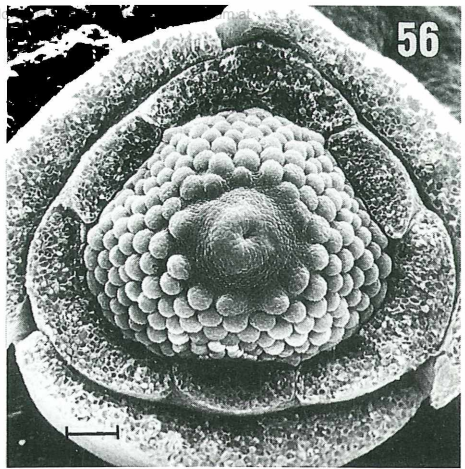




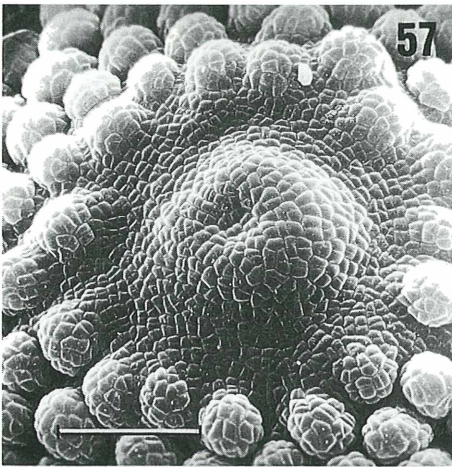
Figs. 49-54. *Monodora crispata*. 49, Inception of the outer perianth whorl (1, 2) and first member of the second whorl (3). 50, Aestivation of the outer perianth whorl (calyx). 51, Inception of the second (3, 4, 4') and third perianth whorl (5, 6), calyx removed. 52, Hexagonal floral apex after the inception of all perianth members, just before the formation of the first stamen primordia. 53-54, Acropetal initiation of the stamens. - Pi = inner perianth member. - Bars: 100  $\mu$ m.



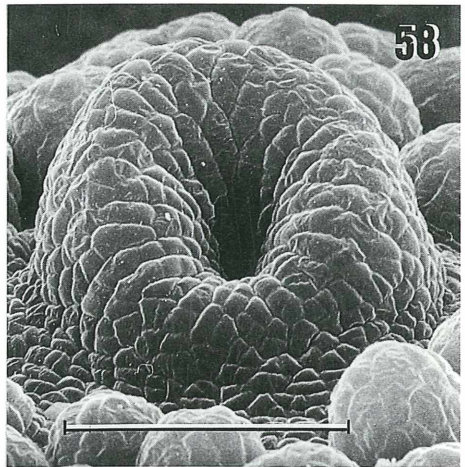
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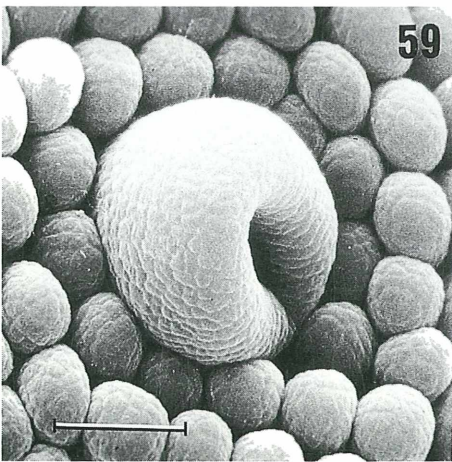
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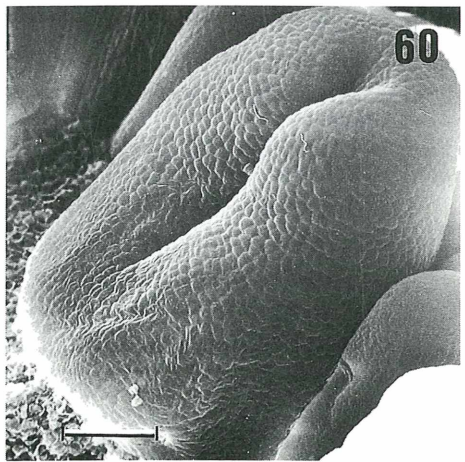
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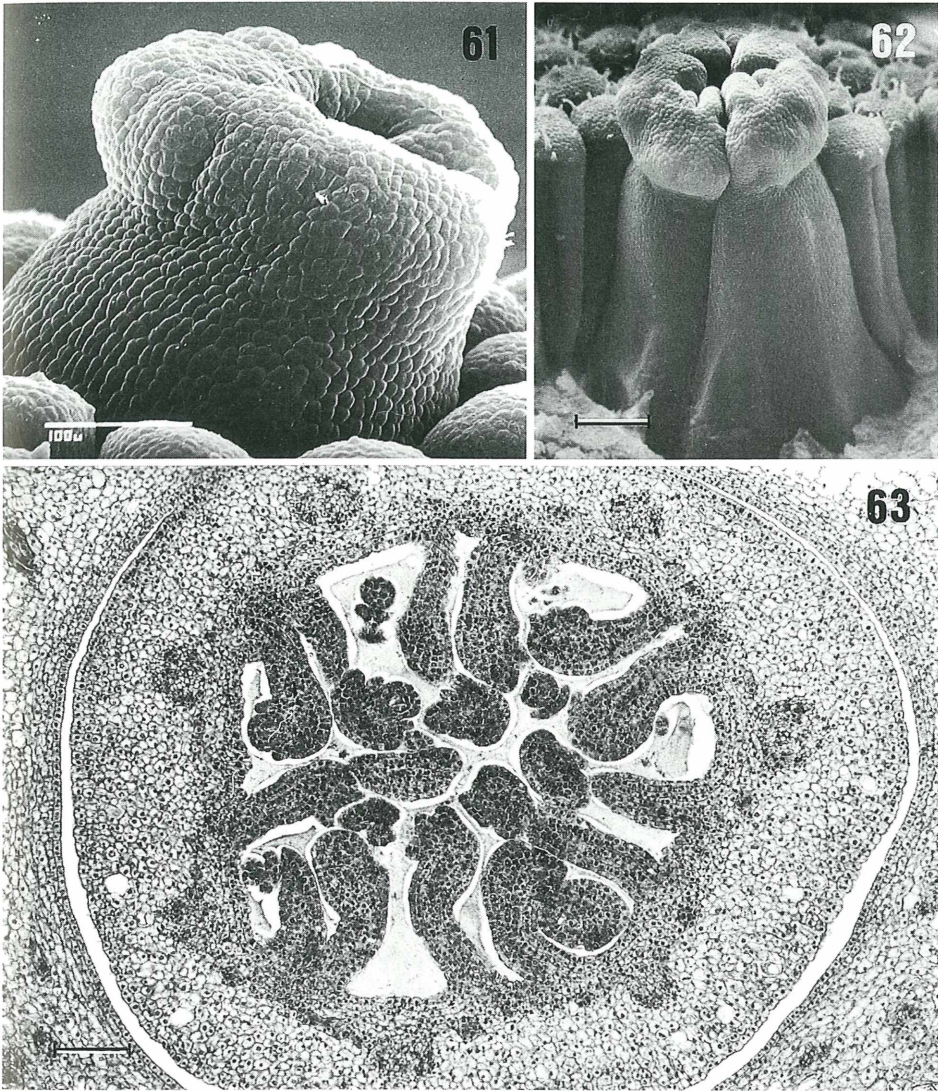


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Figs. 55-60. *Monodora crispata*. 55, Acropetal, but somewhat chaotic initiation of stamens, top view. 56, Older flower bud with young gynoecial primordium. 57-60. Development of the gynoecium. - Bars: 100  $\mu$ m.



Figs. 61-63. *Monodora crispata*. 61, Formation of the lobed stigma head. 62, Older gynoeceium with ventral slit and stigma head. 63, Cross-section through the ovary with the ovules arranged in seven double rows. - Bars: 100  $\mu$ m.



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