BLUMEA 28 (1983) 231–270

THE ASCIDIFORM EARLY DEVELOPMENT OF FREE CARPELS, A S.E.M.-INVESTIGATION

W. A. VAN HEEL

Rijksherbarium, Leiden, The Netherlands

SUMMARY

Carpels develop centripetally as oblique slightly ascidiform structures provided with a seat-like support. The terminal mouth of the ascidiform primordium becomes the lateral cleft of the carpel. Solitary terminal carpels develop as lateral structures. The sections *Tasmannia* and *Drimys* of the genus *Drimys* differ by the varying degree of ascidiform development. *Austrobaileya* is like *Drimys*. The structure of the carpel margins with submarginal placentation may have evolved from a slit like that in Winteraceae. Allometric development of an oblique ascidiform structure may have formed a large basal ovary, and may thus have moved the stigmatic part apically. A possible cupular origin of carpels is discussed.

INTRODUCTION

In my first paper (1981) the early development of the carpels of 20 species belonging to 8 apocarpous families was investigated with the scanning electron microscope. I took up this investigation stirred by the work of Rohweder (1967) on the carpels of Ranunculaceae. In the present paper results on 25 species are added, extending the number of families with free carpels to 16, including the Winteraceae.

In my first paper it was concluded that on the floral apex a meristem develops into an obliquely ascidiform primordium by unequal growth of its periphery. This primordium develops into a young carpel by further unequal growth. The terminal mouth of a cup becomes the lateral cleft of a carpel. The varying degree of development of the adaxial region of the meristem causes the different forms of young carpels of different species. In the present paper the early development is further investigated. The initial convex bulge proves to be the abaxial beginning of the ascidiform primordium. This feature was not made quite clear in my first paper. Furthermore, attention is drawn to the development of the basal part of each carpel, especially of its inside shape (bottom).

In the discussion on conduplicate versus peltate (ascidiform) carpel theory the structure of the carpels of the Winteraceae is of prime importance, as explained in my first paper. Therefore, a few species of that family are incorporated now. This primitive family may serve as a starting point for morphological comparisons.

The photographs are reproduced in such a way that the magnifications of the early stages for each species are the same. The magnifications of the older stages are given in proportion. This procedure, though time-consuming, is adopted because it will lead to a better comparison. The stages are as it were 'seen to grow'. However, it should be remembered that all stages pictured are from different objects.

MATERIAL, METHODS, AND PHOTOGRAPHS

The following species were investigated: *Knema tomentella, Horsfieldia iryaghedi, Amherstia nobilis*, from the Kebun Raya at Bogor*; *Michelia montana*, from the Kebun Raya at Cibodas*; *Ailanthus altissima, Alchemilla monticola, Cimicifuga racemosa, Thalictrum aquilegiifolium, Geum urbanum*, from the Botanic Garden at Leiden; *Akebia quinata, Decaisnea fargesii, Drimys winteri, Zanthoxylum simulans*, from the Botanic Gardens at Amsterdam; *Alisma plantago-aquatica, Butomus umbellatus, Quassia amara*, from the Botanic Garden at Groningen; *Adenanthera microsperma, Bauhinia purpurea, Caesalpinia sapan, Pithecellobium dulce*, from the Botanic Garden at Singapore; *Rubus* spec. from natural habitat at Leiden; *Bubbia* spec., McKee 29168, and *B. pancheri*, McKee 39723, both from New Caledonia; *Drimys piperita*, Vink 17159 from East New Guinea; *Austrobaileya scandens*, Vink s.n., from Queensland. I wish to express my gratitude to the directors and staff of the botanic gardens concerned. The material was either fixed in F.A.A. and washed in alcohol 50%, or in C.R.A.F. and washed in demineralized water. All material was stored in alcohol 50%.

After preparation the primordia were quickly transferred into aceton, and critical-point dried in freon, using a Polaron-equipment. After gold-sputtering in a Polaron apparatus, the objects were studied with a Jeol-35 scanning electron microscope. All scales at the photographs represent 0.1 mm.

RESULTS

Remark on terminology. – Topographic terms such as apical and basal, above and below, upper and lower, abaxial and adaxial, all relate to an, imaginary vertical, central floral axis. Mostly these terms also reflect the way of development. However, the terms proximal and distal pertain to the original lower and upper regions of a developing carpel, whatever be its changing position. The latter terms are used in the descriptions of the rise of a cup-shaped organ into a vertical position during carpel development. The distal part forms a lateral, adaxial, cleft. However, once this is established a distinction of the original proximal and distal regions is no longer practical.

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* My visit to Bogor in 1969 was subsidized by the 'Stichting voor Wetenschappelijk Onderzoek van de Tropen' (WOTRO), the 'Maatschappij voor Wetenschappelijk Onderzoek in de Tropen' (Treub Maatschappij), the 'Greshoff's Rumphius Fonds', and the 'Van Leersumfonds'.

1. Drimys winteri (Winteraceae). — **Photos 1–10**

The beginning of a carpel is a convex bulge on the periphery of the floral apex (1 on top; the other bulges are stamen primordia). This primordium grows strongly, especially on its abaxial side. It gives rise to a peripheral ring-shaped margin which grows upwards. At first this ring arises abaxially, then, as the primordium is larger and wider at the base, also adaxially. Finally the primordium is delimited from the residual apex adaxially by this process (2, 3). The terminal depression which is caused by the growth of the ring-shaped margin is bowl-shaped at first, but later becomes oval as the primordium continues to grow in length mainly (4, 5). Moreover, as the abaxial growth is stronger than the adaxial, the mouth, which is morphologically distal gradually becomes lateral on the adaxial side. In this way an obliquely ascidiform organ is formed (6) provided with a tapering seat-like support. In addition the lateral margins of the mouth appear somewhat thicker than the upper and lower regions. As the carpel primordium enlarges, the margin of the mouth grows in centripetal direction, so that the primordium hangs over the residual apex (7). At the same time the opening becomes slit-like and the ovule primordia are initiated on the border between the slit and the beginning locule. Finally the ascidiform carpel primordium enlarges in its morphologically proximal regions considerably (8, 9). Through continued extra enlargement below and above, a space is created in which the ovules may develop further. The later ovule primordia are initiated towards the base and the top; together they form a long ellipse, the raphes facing. However, the exact ends of the ellipse are not occupied. As a result of this unequal growth of the proximal regions of the obliquely ascidiform young carpel, the distal region, which lags behind, is situated subapically, forming the stigmatic slit, tapering toward the outside (10).

Tucker (1959) described how the carpel of *Drimys winteri* grows as a cylinder by means of a continuous meristematic rim. The great part of the carpel is peltate in ontogeny; the subterminal part has 'conduplicate' margins, and forms the stigmatic crest. No fusion of the margins is involved. Similarly no fusion was found to occur during the ontogeny of the carpels of *Pseudowintera axillaris* by Sampson (1963). Moreover, Sampson and Kaplan (1970) reported that these carpels arise laterally, abaxial side first. Leinfellner (1966) clearly described – from mature flowers – the tapering of the slit of *Drimys winteri*.

2. Drimys piperita (Winteraceae). — **Photos 11–19**

In the female flowers all primordia arising after the two lateral petal primordia are carpel primordia. They arise laterally on the slopes of an asymmetrical floral apex in two successive quartets, the first diagonally, the second alternating and higher up. In addition the abaxial organs precede the adaxial ones (Vink, 1970). At first the primordia are low convex bulges (11), then they broaden and thicken especially above, fitting tightly between the calyptral calyx and the apex (12, 13). A thick peripheral margin is formed by almost the entire primordium on the abaxial side. However, as the primordium enlarges, the peripheral margin arises also in adaxial direction (14, 15), and progressively occupies the adaxial side. The wall grows upwards and in centripetal direction, and by the prominent longitudinal growth of the primordium, the enclosed depression from almost circular becomes upright oval and slit-like. At this stage the median adaxial part of the primordium develops less strongly, but is clearly present (15, 16). In some carpels, especially the upper ones, the slit may be closed by a larger median adaxial part of the margin (17). Mostly, however, the lateral parts of the peripheral margin of more advanced carpels just seem to touch, and to close the meristematic ring in that position, without a median adaxial margin of appreciable extension being formed (18). The closed base of the ascidiform primordium is raised on a small adaxially rounded stalk (19). In this stage practically the whole carpellary space is slit-like, except proximally ('dorsally' according to the classic theory). The primordial ovules are located on the inner edge of the slit. In longitudinal sections of carpels at this age or older, frequently a short sterile part of the locule can be detected below.

According to Leinfellner (1965) the carpels of the *Tasmannia* section of *Drimys* have a small basal ascidiform part. Tucker and Gifford (1966b) have found that the solitary carpel of *Drimys lanceolata* is initiated terminally, passes a tilted-cup stage and grows up as a tube .... by the activity of an encircling row of initials. They added that the adaxial activity is weak. These results were obtained with serial sectioning.

3. Bubbia spec. (Winteraceae). — Photos 20–24

The carpel primordia arise as large bulges on the side of the apex. Their irregular surface, caused by contacts with the perianth parts, prevents definition of their precise shape (20). Somewhat later the carpel primordia are organs with a bowl-shaped apical region (21). Later again the mouth of the primordium is oblique and oval in form, the abaxial region growing faster than the adaxial region (22). This primordium enlarges and grows upwards. Its mouth is narrow, and lined by lateral slightly flaring margins (23).

A much older stage, shown in longitudinal section, is taken from another species, *Bubbia pancheri*. Like in *Drimys winteri*, the mouth has given rise to a stigmatic slit, which tapers outwards. As the slit is very narrow and not straight a longitudinal section cannot sever two halves precisely (24). The ovule primordia are situated along the inner edge of the slit forming an elongated ellipse, as may be judged from the way the raphes are facing each other.

4. Austrobaileya scandens (Austrobaileyaceae). — Photos 25–26

The development of the distinctly ascidiform carpels (Endress, 1980) could not be investigated. Longitudinal sections of young carpels (25) show that the mouth has grown into a prolonged narrow tube. This is proved by the upward bending configuration of the cells (26) on the inside surface of the tube, which can be observed before these cells become glandular. The inner edge of the tubular slit carries the young ovules in an elliptic formation, their raphes facing each other. Thus there is correlation in the orientation of the ovule insertion and the tubular slit. The outer edge is much shorter and can be found at the base of the two lateral lobes that terminate the tube. In this way the carpel structure may be compared with that of *Drimys winteri*.

The inside surface of the slit of that species shows the same upward bending rows of cells (9). A similar structure is most probably present in *Zygogynum* (Vink, 1977, fig. 8e).

5. Michelia montana (Magnoliaceae). — **Photos 27–30**

This species is unusual in Magnoliaceae by having two to four carpels which are stalked. Figs. 27, 28, and 29 show one of two opposite carpels. The locules are sterile at the very base. Unfortunately primordia could not be investigated. Young carpels, with a vertical adaxial cleft, show their ascidiform character by the inward bending of the apical part and the presence of a median adaxial part of the margin at the base (27). Subapical growth may result in a transverse position of the apical part of the young carpel (28). When the carpel is about twice as large an apical slit bisects the top of the stigmatic distal part of the carpel (29). Also the margins along the cleft start to fuse below. Sometimes the floral apex produces a single carpel (30). The precise investigation of the carpels of Magnoliaceae is long overdue. Canright's paper (1960) is not ontogenetic.

Leinfellner (1967) reported that in full-grown flowers of *Michelia kingii* the carpels have a small ascidiform base of which the upper part is free from the axis. This species is closely related to *M. montana.*

6. Knema tomentella (Myristicaceae). — **Photos 31–37**

A shallow depression appears on the floral apex. The growth of the peripheral margin starts on one side and is strongest there. It gradually decreases in strength toward the other side, while medianly on the low side it is minimal. In this way an obliquely ascidiform primordium is constituted with an upright oval mouth (32). A demarcation of the primordium and the floral apex is not possible. In a later stage a differentiation takes place into two parts of the long mouth, an upper part forming the stigma, and a lower part forming the 'ventral' part of the carpel. Firstly the greater part of the margins below form two lateral lobes (33), secondly the lowest parts of these margins increase in size by the addition of transverse segments of cells layers (34). As a result of the latter the main part of the lobes is shifted upwards in a horizontal position, giving the stigma part its 'wrapped around' appearance. Moreover, the lowest part of the lobes forms the vertical 'ventral' part of the carpel and its suture (35). When older a kind of socle differentiates at the base of the young carpel (36), which is covered with hairs. A similar structure in *Horsfieldia iryaghedi* shows a protuberance on the adaxial side (37), which might represent a residual apex. A collar of tissue occurs below the solitary carpel of *Drimys lanceolata* (Tucker & Gifford, 1966b, and Vink, 1970). However, it is not clear whether this collar is comparable with that in *Knema tomentella.* It is possible that the single (sub)basal ovule arises within the young carpel in the median plane on the minimal adaxial part of the peripheral carpellary margin (cf. Leinfellner, 1969). The stigma becomes bilobed later.

7. Akebia quinata (Lardizabalaceae). — **Photos 38–44**

At first the carpel primordia are approximately convex bulges on the side of the floral apex, slightly compressed by contacts with the stamens (38). They grow upwards faster on the abaxial side, so that a flat surface results on the inside. Then this surface is seen to change into a depression caused by the development of the peripheral carpellary margin. While the primordia enlarge the margin circles inwards, but it does not reach the median adaxial region (39). Thus the primary convex bulges represent the abaxial parts of the carpel primordia on which the peripheral margin appears first (40). The ascidiform structure shows much later, after the carpels have grown in length considerably by the inward bending of the apical parts of the young carpels (41). However, later the hooded form is changed by the formation of two subapical lateral lobes (42), so that the distal carpellary part is displaced horizontally. In this way the stigma is formed, and the upper part of the cleft now forms the stigmatic slit. I discovered a flower with a central carpel which was stalked and ascidiform at the base (44).

The primary development of *Decaisnea fargesii* was similar (45–47).

The paper by Payne and Seago (1968) is not ontogenetic. They adduce a developmental hypothesis in conformity with that of Bailey to explain their results.

8. Thalictrum aquilegiifolium (Ranunculaceae). — Photos 48–56

In photograph 48 in the carpel primordium on the right side the exact phase is shown in which the peripheral carpel margin, subsequent to its abaxial origin, arises in adaxial direction. As a result the lower part of the margin and the apical-adaxial bowl-shaped depression of the carpel primordium is formed. The primordium is demarcated from the residual apex by a distinct basal part, and takes the shape of an obliquely ascidiform organ (49 right). By continued growth in length, mainly on its abaxial side, the primordium is raised in a more upright position; its base is tapering (50). The adaxial part of the carpellary margin remains broad and gets thicker, and overhangs the floral apex. Next the high part of the margin grows hood-shaped, making the mouth triangular. A median adaxial ovule develops on the low part of the margin and grows into the cap (51). When the carpel primordium is about twice as large, the mouth has changed into a vertical cleft. The margin of the cleft differentiates into two halves, the upper half is increasingly thick upwards, the lower half is slightly lobed and less thick (52, 53). The upper part forms the stigma, and the lower part the glandular open part of the cleft (54, 55) which does not catch pollen. As there is no additional bending of the apical part in abaxial direction, the hooded, ascidiform, aspect of the carpel is retained. The lower open part of the cleft remains present below the stigma also in the fruiting stage. Then the basal ascidiform part has formed a large ovary which contains the young seed (56). Later there may be a small additional stalk below the carpel (53, 54).

9. Cimicifuga racemosa (Ranunculaceae). — Photos 57–63

The first signs of carpel development are some low convex bulges on the flanks of the floral apex. These change into lateral primordia with a flat upper surface or with a faint border (57). When they enlarge further the peripheral margin circles inwards and arises also adaxially. In some carpels this is more distinct than in others. In this way the primordium is raised from the residual floral apex. At the same time a shallow apical-lateral depression becomes evident (58). The result is an obliquely ascidiform primordium, of which the adaxial part of the margin does not develop further, but remains visible as a low ridge for some time (59). On enlarging the primordium is not raised by marked abaxial growth. Whereas the lateral parts of the ring-shaped margin get slightly thicker and are flaring, the median adaxial part is somewhat delayed (59). Subsequently the primordium is elevated by the piling of obliquely transverse cell layers in its proximal part (60). The mouth of the primordium becomes a cleft which closes later on (61). A distal stylar part is formed by subapical intercalary growth. This part becomes stigmatic and flaring (63). The presence of a delayed adaxial part of the carpellary peripheral margin makes possible the formation of a very long stalk by renewed growth later on (62, 63).

Baum (1953) noticed that the Querzone does not necessarily coincide with the border of the ovary and the stalk of the carpel in *Cimicifuga americana* and *Eranthis hiemalis*. My descriptions of the development do not correspond with hers.

10. Alchemilla monticola (Rosaceae). — Photos 64–69

The carpel shown by photograph 64 is a small hemispherical primordium with a tapering base and a weak subapical depression. When slightly larger the primordium is ellipsoid, with a tapering base and top, and it has thicker sides (65). Photograph 66 shows an upright ascidiform primordium with a tapering base and top, and two small lobes at the sides of the oval depression. Photograph 67 shows that the lower half of the mouth of the primordium is closed by the expansion of the lateral lobes. However, at the same time the upper half of the mouth remains open. The basal and apical parts grow in length and taper. Then the ovary starts to widen and the stalk and style become evident (68). The style and also the stigma are developed from the apical part of the carpellary margin only without participation of the depression (locule). The result is a solid style without a canal. The later growth of the ovule is strongly one-sided. The single ovule is probably initiated basal-laterally, not medianly.

11. Rubus spec. (Rosaceae). — Photos 70–77

The carpel primordia originate on the large dome-shaped floral apex in upward and centripetal direction. At first they are convex bulges, then grow faster below and abaxially, with the result that they appear flat above (70, 71). In fact this marks the beginning of the peripheral carpellary margin, and at the same time the base of the carpel primordium on the abaxial side. When the primordium is larger, and especially longer, the peripheral margin is more clearly visible on the abaxial side, and subsequently also toward the adaxial side. A boat-shaped primordium is the result (72). Finally the peripheral margin reaches the median adaxial region, and the base of the carpel starts its development also there (73). At that stage the carpel primordium is an obliquely ascidiform primordium with a tapering base and oval mouth. Next the carpel primordium is subdivided into an ovary part and a stylar part, mainly by growth in length of the upper half. The apical part is 'thrown backwards' by special subapical growth, giving a fluted style and stigma. An ovary can be distinguished at the base of the ascidiform carpel (76) that encloses a single basally lateral ovule. The slit between ovary and style is bordered by two reduced lobes. After extensive longitudinal growth of the style and stigma their margins fuse, the suture remaining visible on the outside (77). The ultimate development of the parts of the pistil is very unequal as compared with the primordium development.

12. Geum urbanum (Rosaceae). — Photos 78–82

The development of the carpel is similar to that of *Rubus* spec. Also in *Geum* the development of the carpellary margin in the adaxial region is late as compared to the rest of the primordium (81).

Payer (1857) draws a small median adaxial margin in the carpel primordia of *Alchemilla* and *Rubus*, and a distinct one in *Geum*. Schaeppi and Steindl (1950) found a peltate carpel in *Filipendula*, and the same was found by Kania (1973) in three more Rosoideae. These investigations are based on microtome slides. All authors agree that there is one ovule that is inserted basal-laterally (in some cases two basal lateral ovules are initiated of which one aborts). Only *Dryas* is reported to have peltate carpels with a long stalk and one basal median ovule. However, *Dryas* has not yet been investigated developmentally. Sattler (1973) shows that in *Fragaria* continued growth of the margins toward the adaxial side leads to the closure of the developing pistil. His study is founded on direct observations of the primordia.

13. Pithecellobium dulce (Mimosaceae). — Photos 83–92

The carpel starts to develop in the centre of the floral apex after the first stamens, leaving enough space for the later stamens (83). On one side the floral apex rises less strongly. An obliquely bowl-shaped primordium becomes visible, with a broad high margin on the side where the carpel development began, and a low margin on the opposite side. The height and thickness of the carpellary ring-shaped margin diminish gradually in adaxial direction (84, 85). Possibly a small part of the floral apex remains unoccupied on the low side of the carpel primordium and below it. During the further development of the carpel primordium the lower part of the margin lags behind the higher part (86). This higher part grows upwards strongly and at the same time the bowl-shaped mouth of the carpel changes into a cleft. Then the primordia differentiate into three parts, an upper stylar part, a middle ovary, and a beginning basal stalk (87, 88). Whereas the margins of the cleft in the ovary part start to close and fuse, the cleft in the upper part remains open and is surrounded by margins that are forming a stigmatic surface (87). The stigmatic part is 'thrown backwards' by the growth of two subapical marginal regions (88). These regions fuse subsequently and enclose the stigmatic cleft (89). A very long style is formed by intercalary growth of the subdistal part of the carpel primordium; the suture on it remains visible (90–92). Finally the carpellary base is extended into a very long stalk (89–92).

14. Adenanthera microsperma (Mimosaceae). — **Photos 93–99**

The floral apex changes into a carpel primordium with irregular faces that are caused by pressure of the perianth parts and stamens (93). Photograph 94 shows an oblique stalked primordium with two prominent flanks and a tip that is slightly backwards directed. Photographs 95 and 96 show lengthening ascidiform carpel primordia, slightly stalked, and provided with a narrow mouth and a small margin on the low side. The proximal part of the primordium enlarges strongly to give rise to the ovary, the margins of which start to fuse (97). The distal part lags behind and encloses the uppermost part of the space of the carpel primordium, forming the incipient stylar and stigma canal. The basal part of the ascidiform carpel seems rather distinct (97). Later a constricted stylar part elongates considerably. The base of the carpel tapers into a short stalk below.

15. Bauhinia purpurea (Caesalpiniaceae). — **Photos 100–108**

A carpel primordium is situated on the floral apex centrally when the second whorl of stamens is not yet visible (100–102, the outer primordia in these photographs represent petals). It is a crescent-shaped wall, high and thick on the abaxial side and gradually lower and narrower toward the opposite side. Although the primordium gets larger, its margin does not develop on the median adaxial side. On that location there is a triangular, slightly convex region which at first runs into the surrounding floral apex (100), but later is demarcated at the base of the carpel (101, 102). By the upward growth of the carpel wall, especially on the abaxial side, the at first adaxially open shallow space of the primordium changes into a vertical slit (103). In this stage the triangular unused apex may be observed at the base of the hooded young carpel, as judged by the different character of the cells (103). In this phase there is no adaxial carpellary margin. When the carpel enlarges the margins fuse except at the base and the top. The appearance of a stalked carpel in this phase is due to contacts with the stamens (105, 106). By subapical lobing the apical part is bent backwards, and in this way the stigmatic cleft is formed. The stalk of the carpel is formed by the basal region of the carpel primordium where it originated on the apex of the flower without the sharing of a carpel margin median adaxially (107, 108).

16. Caesalpinia sapan (Caesalpiniaceae). — **Photos 109–113**

The primordium of the carpel starts as a mound on the floral apex, which is situated slightly on the abaxial side of the centre. When higher the mound is crescent-shaped, sloping on its inside in adaxial direction (109–110). The floral apex is higher there than on the abaxial side. Then by prolonged mainly abaxial growth the primordium changes into a broadly based oblique organ with a crescent-shaped margin that does not reach down to the adaxial side (111). An about triangular region remains at the primordium base on the adaxial side. Later growth is similar to that of *Bauhinia purpurea*, except for the fact that no carpellary stalk develops. Photograph 112 shows a young carpel with its stigmatic upper part 'thrown backwards'. The margins of the cleft fuse, a basal gap being saved. Also in this phase a region at the adaxial base seems to remain unoccupied.

Payer wrote that in Papilionaceae there is a crescent-shaped protuberance of which the extremities tend to approach each other. His drawings of a species of *Lathyrus* and of *Trifolium* show very clearly how an at first obliquely circular primordium changes into an oblique bowl-shaped primordium. The photographs by Sattler (1973) show the absence of an adaxial carpellary margin in *Albizzia lophanta* and in *Pisum sativum.* The investigations of Leinfellner (1969, 1970) are on sections of open flowers or advanced bud stages. Most species in 25 genera of Papilionaceae studied by him are considered epeltate. However, *Amorpha, Glycyrrhiza, Trifolium* and *Lupinus* are said to be peltate, but not to have ovules in adaxial position. Occasionally Leinfellner found peltate and epeltate flowers on one plant in *Erythrina* and *Sophora.* Also in some Mimosaceae and Caesalpiniaceae he found epeltate, as well as peltate carpels. Generally in Leguminosae the development of the carpels in their median adaxial region is weak. The only developmental study, using microtome slides, is that by Newman (1936) on *Acacia.* According to Newman the apex is displaced and overtopped by the developing carpel primordium, so that later the apex has the appearance of being merely a part of the surface of the stipe. However, he also wrote that the apex is clasped by the base of the lamina of the legume. On balance his photographs are difficult to interpret.

17. Amherstia nobilis (Caesalpiniaceae). — Photos 114–119

All stages shown are derived from one inflorescence. Evidently the primary development of the carpel is similar to that of the two species of Caesalpiniaceae described above (114, 115). In all cases an additional, non-functional, carpel arises on the adaxial side of the first carpel, and in the sagittal plane. Photograph 115 possibly shows the beginning, and photograph 116 the next stage. The margins of the two carpels seem to arise fused. The triangular region at the base of the cleft shown by photograph 117 seems similar to that described in some normally developing carpels in several species of Leguminosae. As the development has progressed rather far in this case, it is not likely that further development would have given an additional carpel. A second non-functional carpel was found once (119). Also Sattler (1973) pictured an additional carpel facing the first one, this time in *Albizzia lophanta.* The phenomenon is of frequent occurrence. Sampson and Kaplan (1970) reported that if two carpels arise in *Pseudowintera traversii* they arise fused and facing.

18. Zanthoxylum simulans (Rutaceae). — Photos 120–125

The female flowers of this species have three to five carpels. When mature the carpels are arranged in a whorl. However, they originate successively and centripetally. The last formed carpel primordia abort. The approximately convex initial bulges (120) grow in width and thickness more than in height (121), the whole floral apex increasing in size during this process. Then, during the upward growth of the abaxial parts of these primordia the inside is at first flat, then changes into a vertical mouth (122) by the upward and inward growth of a peripheral margin. The peripheral margin does not extend fully along the floral apex into median adaxial direction. During the further enlarging of the carpel primordium the mouth changes into a cleft of which the margins start to fuse apically (123). A stigma is formed by the backward bending of the apical region. Later the stigma is elevated on a style (124, 125). On the style the suture remains visible for some time, especially below. The carpels are not really stalked, they are inserted abaxially lower than adaxially, and they widen epibasally. There are two epibasal lateral ovules, and two ovule primordia above which abort.

Gut (1966) contributed a study on floral morphology in Rutaceae, but little of it is based on ontogeny. According to him Rutaceae have latently peltate and epeltate carpels.

19. Quassia amara (Simaroubaceae). — **Photos 126–134**

A hemispherical floral apex is surrounded by an obdiplostemonous androecium (126). The carpel primordia originate on it as apical-lateral convex bulges in petal radii (127). They show an upward bending growth (128). They enlarge and broaden, becoming flat on the inside. Possibly this marks the beginning of the carpellary peripheral margin (129). When the carpel primordium gets larger, its margin becomes clearly visible, its top and flanks below growing inwards (130, 131). It should be noted that the margin differentiates rather late, on already large upright primordia. Shortly afterwards the peripheral carpellary margin is raised also in the median adaxial region high upon the floral apex. An ascidiform carpel with a round mouth is thus formed (132). The massive distal part represents the future stigma-stylar part. Further growth is marked by growth in length, so that the mouth becomes a cleft. The basal part of the ascidiform carpel is rather large (133). The massive styles fuse with one another. The free ovaries enlarge greatly, in each there is one ovule inserted on the inside of the adaxial margin. The base of the cleft remains open for a long time (134).

20. Ailanthus altissima (Simaroubaceae). — **Photos 135–140**

Five carpel primordia arise as apical-lateral convex bulges on the floral apex. The apex is surrounded by an obdiplostemonous androecium, and the carpels are in the petal radii (135). The top of the bulges grows slightly upwards and inwards. The primordia broaden and its lateral parts grow upwards (136). In this way the abaxial part of the carpel primordium is formed, with its base and the peripheral margin. The abaxial regions thicken considerably (137). As the floral apex grows upwards, the peripheral carpellary margin grows inwards and is narrower there. Then the carpel primordium is also formed on the inside, and the margin also occupies the median adaxial region (138). This part of the margin becomes rather thick. The result is an ascidiform primordium with a broad oval mouth, based low on the flanks of the floral apex abaxially, and high adaxially. A solid and thick apical part of the primordium marks the young stigma-stylar part. By predominate growth in length the mouth of the locule becomes a cleft and the resulting locule is greatly enlarged below (139). This ovary has one median ovule on the inside of the adaxial rim. Later the style elongates and a stigma broadens on top. Between ovary and style the cleft remains open at the base for some time (140).

My results resemble the drawings by Payer (1857) very much. It is not reported in the text where the ovule develops. Payer wrote (translated): 'the protuberances, at first semi-globular, soon take the form of a horse-shoe, of which the bend is in the highest part, and of which the branches, instead of remaining parallel, converge to each other and tend to unite. This union is effectuated later .... '. Payer also described *Xanthoxylum fraxineus* as very similar to *Ailanthus*, but with two ovules. I have not seen that Rutaceous species.

21. Butomus umbellatus (Butomaceae). — **Photos 141–149**

Six carpels arise in two successive alternating whorls, the one above the other. The second whorl is situated in the same radii as the inner tepals of the flower. Photographs 141 and 142 show how the stamens originate in three pairs that are followed by three stamens in petal radii higher up. The carpel primordia quickly get broader, and their lateral parts grow upwards and centripetally, the median parts lagging behind (143, 144). During the enlargement of the carpels the floral apex widens below (145, 146). As a result the flanks of the carpel primordia can develop inwards strongly. The median apical parts remain bent backwards (147). There is no çarpel margin on the adaxial side at all. The distal part of the young carpel elongates upwards into a style-stigma region that is covered by glandular cells along its margin on the inside, especially above (149). Many ovules develop scattered on the large flanks of the carpel, the stylar area and the stigmatic margin excepted. Also the median abaxial region of the carpel is free from ovule primordia. The carpels are not stalked.

The drawings of Payer (1857) indicate that the origin of the stamen and carpel primordia is in two whorls, as described above. My results correspond with those of Singh and Sattler (1974). The developmental stage given in my photograph 141 is not young enough to verify their hypothesis that three bulges arise on the floral apex, from each of which originates one inner tepal, one pair of stamens in front, and one inner stamen.

22. Alisma plantago-aquatica (Alismataceae). — **Photos 150–162**

The floral apex on which the carpel primordia originate is a low convex dome, faintly triangular in outline below and on the angles slightly lower than on the sides (150, 151). This shape, especially the difference in height, persists when the floral apex becomes larger during the development of the carpels (156, 158). The carpels arise laterally on the floral apex as approximately ellipsoid primordia the one next to the other. They start to arise on the angles and then as the floral apex widens, they proceed to arise on the sides (150, 153). During the whole further development the lead of the earlier carpels, those near the angles, is maintained. An apical depression is formed on the carpel primordia, presumably in relation with the formation of a peripheral carpellary wall immediately around it. The peripheral wall and the basal attenuation of the primordium on the adaxial side is defined more clearly in the later formed carpels, those on the sides (156, 157). Thus the carpels originate as obliquely ascidiform organs, tapering at the base. Later development is marked by extension of the flanks, and the concommittant change of the bowl-shaped mouth of the primordium into the narrow locule of the young carpel. The carpel grows upwards together with the residual floral apex so that the locule is extended in height (158). It is seen that at the same time, on the enlargement of the carpel, the adaxial margin, at first evident, plays no role any more. Then the carpel primordia grow over the floral apex cap-shaped (159). Finally the distal part elongates into a style (160), and the apical part grows backwards giving a stigma (161). Outward expansion of the ovary part creates a space for the single ovule, which is inserted on the bottom of the carpel in the middle (162).

Singh and Sattler (1972) report for *Alisma trivale* the same sequence of formation of the carpel primordia. However, each three first-formed primordia are grouped in common bulges originally. These primary gynoecial bulges would alternate with three primary corolla-androecium bulges. I have not investigated such young stages. Singh and Sattler also mentioned the cup-shaped development of the carpel primordia. According to them the ovule originates on the Querzone. Leins and Stadler (1973) report a similar sequence in development in *Alisma plantago-aquatica*. However, they do not indicate common bulges neither for petal-stamen pairs and nor for the first-formed carpels. These primordia originate separately as space and time permit.

COMPARISON AND DISCUSSION

1. The common form of the carpel primordium. – The carpels of all species pass the form of an oblique ascidiform primordium, with a margin, and a seat-like base; it may be incomplete on the adaxial side. This primordium develops on the slope of a floral apex which increases in size. As a consequence the adaxial regions of the carpel primordia develop later than the abaxial ones, as the growth of the apex proceeds. Thus not only the separate primordia, but also the parts of the primordia develop centripetally. This process is also well demonstrated in the convex stamen primordia of *Drimys winteri* (1), the abaxial parts of which originate earlier than the adaxial ones.

2. The development of the carpel primordia. – The carpel primordia become first visible as convex bulges which, as seen by the broadening above, soon differentiate into the median abaxial parts of the margin and the base of the ascidiform primordium, with the restriction that a sharp delimitation of these parts is not possible. This process is well shown by the photographs of *Akebia, Rubus, Geum,* and *Magnolia* (1981). When these primordia increase in size they do so in all directions, also in a radial direction. As the primordia get higher on the abaxial side, they are also elevated more and more in centripetal direction. At the same time the peripheral margin, as well as the base of the primordium, originate in radial centripetal direction, and as a result the seat-like bottom of the organ is formed. Finally the peripheral margin and the base of the primordium may be formed also adaxially in their median plane, so that the seat-like bottom of the ascidiform organ is completed. This sequence in the development is well shown in the photographs of *Drimys win-*

teri, Thalictrum, Caesalpinia, Ailanthus, and *Delphinium elatum* (1981). The initiation field of a carpel is circular or elliptic, and its activity is generated in centripetal direction. The bottom of a carpel is described by Tucker and Gifford (1966a) for the terminal carpels of *Drimys lanceolata.*

The fact that the development of a carpel is latest on the adaxial side means that there the development may cease, or be minimal, and that it may be variable there, as for instance in Leguminosae. The adaxial margin is developed strongly in Winteraceae (not in all), most probably also in *Austrobaileya,* and in cases where one, mostly median, ovule is formed. A suppression of the adaxial margin occurs in *Akebia, Zanthoxylum, Butomus,* and in *Caesalpinia, Cassia,* and *Bauhinia.* In these cases the development of a peripheral margin proceeds into the direction of the median adaxial plane, but it does not reach till there. In the Leguminosae mentioned it seems that the peripheral ring-shaped meristem approaching the median adaxial plane grows very late – as compared with the abaxial parts – and that there no margin is formed subsequently. These carpels are called epeltate in the works of Baum and Leinfellner (cf. Weberling, 1981). In many species studied the development of the adaxial margin is slight but distinct. This is called latently peltate, or subpeltate, by the authors just mentioned. The adaxial part of the meristem completes the seat-like bottom and the base of the primordium on that side. This was found in *Drimys piperita, Magnolia stellata, Cimicifuga, Pithecellobium, Adenanthera,* and *Alisma.*

A possible minimal adaxial development of the carpel primordium, including a radial extension of the bottom of the carpel, may be of importance for the interpretation of syncarpous gynoecia in which single ovules are placed axillary to the carpels.

As regards a possible variation it should be noted that sometimes there is a distinct adaxial formation in the upper carpels of a flower, whereas this is less so in lower carpels. This was observed in *Drimys piperita* (the upper carpels are normally stronger developed according to Vink, 1970), *Magnolia thompsoniana* (1981), *Akebia quinata, Cimicifuga* and *Alisma.* It is mentioned for *Helleborus* by Baum (1952) from a study of young flowers.

Possible correlations should be investigated between the degree of development of the preceding abaxial part and the time of initiation and subsequent development of the adaxial part of the peripheral margin.

3. The insertion of the low ovules. – In Anemoneae and in Lauraceae (1981) the development of an adaxial margin is evident. It is also early as compared with the abaxial margin. In *Ailanthus,* and in *Quassia* the adaxial margin is also evident, but does not seem to arise early. All these cases have median adaxial ovules. In *Rubus* and *Geum* the adaxial margin is evident but narrow; the one functional ovule is basal-lateral. In this connection it is important to realize that the ascidiform primordium changes into an organ with a slit when it gets larger. As a consequence there is no room any more for an ovule to develop median adaxially, so that it is restricted to one of the lateral margins. A median ovule can develop only when the adaxial margin is still broad, as it is in the early bowl-shaped stage of the carpel primordium, or in a cap-shaped stage a little later. Presumably there are transition stages precisely in

those groups in which the exact position of the ovule – whether median or basal-lateral – is debated, as for instance in Rosaceae and in Myristicaceae. In *Magnolia stellata* two ovules are developed on the inside of the margins when the carpel primordium is in the bowl-shaped stage. In *Drimys winteri* ovules can originate quite close to the sagittal plane, but they do not develop further (cf. Leinfellner, 1966; Tucker, 1975).

4. The stalk of the carpels. – The stalk of a carpel originates from the enlargement of the carpel base. This is most clear in the prominent ascidiform carpels of *Drimys winteri, Bubbia* spec., Anemoneae, *Rubus, Geum*, and *Austrobaileya*. Also in weakly ascidiform carpels the growth of a stalk can be considerable, as in *Michelia montana, Cimicifuga*, and *Pithecellobium*. An additional late intercalary extension occurs in *Alchemilla* and in *Thalictrum*. Incompletely ascidiform carpels like those of *Akebia* and *Butomus* appear sessile. However, this may not mean that these carpels are entirely without a base and a bottom. In *Zanthoxylum* the base grows into a short stalk on the abaxial side only. In *Cassia* and *Bauhinia* it is the large base of the carpel which grows into the stalk, the residual apex has no share in it. It follows that the formation of a stalk is related with the development of the carpellary meristem and the carpel base in adaxial direction, but not with the consequent degree of the development of the margin in that region.

5. Remark on the growth of the wall. – The development of the wall of the carpel primordium is the resultant of upward and centripetal growth. This is well shown by my photographs of *Cimicifuga* (61), *Adenanthera* (96), *Delphinium grandiflorum* (4, in 1981), *Ranunculus sceleratus* (28, in 1981), *Albizzia* spec. (65, in 1981), *Calliandra tetragona* (71, in 1981). Tucker (1959) wrote on *Drimys winteri*: 'the total growth is a combination of .... apical and marginal growth. This early development differs considerably from the marginal growth occurring later, which parallels marginal growth of bracteoles and vegetative leaves'. This means that microtome sections of these early stages, which are – as usual – made transversally on the flower axis, in reality are oblique. This may have caused errors in investigations which have been carried out in order to define the margins of the carpel by tracing the division of meristematic cells. The 'real' margin, according to the –involute – classic theory, carries the ovules, and it is in a way overtopped by a 'secondary' margin. On S.E.M.-study a difference, or a time-lapse between a primary and a secondary margin is not observed, except perhaps in some Lauraceae. The carpel margins enclose a slit, and the ovules are initiated sooner or later at some distance of the outer edge of the slit. Swamy (1949) wrote on *Degeneria*: '.... the ovule-bearing region of a *Degeneria* carpel does not represent the margin of a carpel .... the flared-out regions of the sporophyll are the true margins'. Swamy was an adherent to the conduplicate version of the classic carpel theory. It is necessary that future research on the meristems and tissue is accompanied by S.E.M.-information in order to be sure on the correct orientation of microtome sections.

6. Remark on the terminal solitary carpel. – In all species studied the carpels start their development laterally on the apex, but soon occupy almost the entire apex. In *Delphinium ajacis* possibly a residual apex is present, showing in photograph 3 (1981) below left. In some Leguminosae studied an unused small portion of the apex appeared to be present in young stages of carpel development, on which the adaxial meristem of the carpel may not develop, not even later on. It should be realized that then, during the later stages of development, a possible residual part of the apex is no longer detectable because the base of the carpel has enlarged considerably in the formation of a stalk. Newman (1936) described this feature for *Acacia.* If in other Leguminosae a low adaxial carpel margin is formed early, it seems that a small portion of the apex remains visible below in the beginning. The frequent occurrence in Leguminosae of a second, reduced carpel is well known. Here it is photographed in *Amherstia* (114–118). The second carpel appears opposite to the first one. This corresponds with the locality of the residual apex at the base of the cleft of the first carpel. Vink (1970) doubts the validity of Tucker and Gifford's assumption that the carpel of *Drimys lanceolata* is terminal. Vink found that 'if a second carpel happens to occur, this is opposite to .... the first carpel. Both are oriented as lateral appendages'. Vink suggested that the solitary carpel is adaxial to the activity centre which terminates its activity and is lost in the abaxial side of the torus.

The salient point is that both a terminal carpel and a lateral carpel of a polycarpellate flower develop as a slightly ascidiform organ on a circular basis. In the case of a terminal carpel this basis comprises almost the whole apex. Whether – in bordercases – a terminal carpel may start to grow as a ring-shaped meristem at once, or may occupy the entire apex, is of less importance and cannot be ascertained.

7. On the carpel development in Drimys. – The carpels of the primitive Winteraceae, devoid of normal styles, have drawn much attention. In *Drimys* the section *Tasmannia* has carpels with a stigmatic crest as long as the carpel, the section *Drimys* on the other hand has carpels with a short subapical crest. Bailey and Nast (1943) have based the conduplicate version of the classic theory on the *Tasmannia* carpels. According to this theory the Angiosperm carpels are megasporophylls with the ovules inserted submarginally. The carpels of section *Drimys* are derived from those of *Tasmannia* by assuming a fusion of the carpel margins leading to the restriction of the stigmatic cleft to a subapical region. The fact that also *Tasmannia* carpels exhibit an incipient fusion of their margins during their development was used as an argument. As a result of this comparison the subapical style-stigma projection of *Drimys* carpels can be seen as a remnant of the long adaxial stigmatic crest of the *Tasmannia* megasporophyll. The view of Bailey and Nast was based on the investigation of full-grown carpels.

Tucker (1959), investigating cell divisions of the meristems forming the carpels of *Drimys winteri* (section *Drimys*), found that: 'the carpel grows upwards as a cup-shaped or peltate structure, never open except in the region which will form the crest. Hence no closure can occur. The development of an enclosed locule has occurred through modification of ontogenetic processes different from those hypothesized by Bailey & Nast'. And she added: 'the carpel is peltate rather than conduplicate and the lower part undergoes no fusion of its margins'. Guédès (1966) criticized the argument of Tucker because he considered that the fusion, which is 'postgenital' in *Drimys piperita* (section *Tasmannia*), occurs 'congenital' in *Drimys winteri.* Guédès lucidly added that the congenital fusion is the ontogenetic process employed by evolution to realize the 'fusion'. As to the nature of this process Guédès, on theoretical grounds, adheres to the assumptions made by Bailey and Nast. Essentially, it is a matter of investigating, by means of the comparison of the development of recent carpels, how the evolution, by changing the ontogenetic pathways, may have worked. As to this my results indicate that a more or less strong ascidiform development is concerned, not the occurrences of fusion processes. The S.E.M.-photographs corroborate the statement made by Tucker and Gifford (1966b): '.... early differences in initial activity .... of the components of the meristematic ring .... are critical in determining carpel form'.

In this context the transitional forms between *Tasmannia* and *Drimys* carpellary forms are of interest. Leinfellner (1965) mentioned *Drimys vickeriana.* Vink (1970) in his description of *Tasmannia* carpels states that: 'a longitudinal slit extends over the apex and the ventral side but often does not reach the base of the carpel c.q. the apex of the stipe'. This variation may occur in one flower (Vink, pers. comm.) and also applies to *Drimys piperita* entity *xerophila* (which is *Drimys vickeriana*). In other words the *Tasmannia* carpels have stigmatic crests of varying length, and the part below the crest is a part of an ascidiform carpel, which equally varies in length. A carpel rim on the adaxial side is always there, be it low. Thus the carpels of the genus *Drimys* vary from strongly to weakly ascidiform, the two extremes being rather frequent. However, the one extreme of the *Tasmannia* section, has become stereotyped in connection with the conduplicate carpel theory. In the genus *Drimys* the whole space of the ascidiform carpels ushers into a style-stigma slit that is enclosed by the marginal parts of the carpels in their entirety. This is clearly proved by the upward bending course of the cell rows as shown by photograph 9 of *Drimys winteri.*

8. Note on Austrobaileya. – It is in the same way as in *Drimys* that the carpel of *Austrobaileya* must be understood. This distinctly ascidiform carpel has been compared with *Drimys* by several authors. Bailey and Swamy (1949, 1951) explain both in the same way, namely as having evolved by concrescence of the stigmatic ventral surface of the conduplicate megasporophyll. According to them this closure is complete on the outside, but incomplete on the inside, as evidenced by the structure of the cleft in the carpellary wall. A space shows conspicuously on cross-sections of the carpellary wall on the adaxial side, because in later stages of development, it has papillate conductive cells. This space is called the 'ventral niche' by Endress (1980). Endress adds that this ventral niche cannot be seen as preserved evidence of the ventral suture, as was surmised by Bailey and Swamy, at least not in an ontogenetical sense (because there is no trace of a fusion of cells). Rather it is the transition region between the ovary and the stylar canal. This is corroborated by my photo-

graphs. But nevertheless Endress is lead to consider that the extreme ascidiform condition has evolved from a plicate ancestral structure, on the ground of the fact that there are two rows of ovules deeply seated in the ascidiform part of the carpel, as if flanking the two margins of a plicate ovary. However, in my opinion the two rows of ovules in this distinctly ascidiform carpel are placed exactly where they are placed in the carpels of *Drimys winteri*, namely along the inside edge of the style-stigma slit. The difference is that in *Austrobaileya*, immediately above the inside edge, the space of the slit narrows down dramatically and continues obliquely upwards. The slit has its outside edge on the base of the two lateral apical lobes of the carpel. I base this conclusion on a comparison of photographs 9 of *Drimys winteri* and 26 of *Austrobaileya*. Both show the upwards bending course of the rows of cells in the proximal part of the slit, but in *Austrobaileya* it is extreme. The 'ventral niche' or 'the unfused inside part of the ventral margin' represents the proximal region of a trunk-like slit of an oblique ascidiform carpel. Leinfellner (1966) rejected the derived plicate explanation for the position of the rows of ovules in *Drimys winteri*, but he remained puzzled by the structure of *Austrobaileya.*

The *Tasmannia* carpel – with a slit almost the length of the carpel – but not deep, and the *Austrobaileya* carpel – with a trunk-like slit – represent two extremes of ascidiform carpel development, as regards the form of the style-stigma part. Possibly the former has a closer affinity with the carpels in other groups of Angiosperms than the latter. Possibly a not deep style-stigma slit is the explanation for the 'submarginal' placentation in most Angiosperms. There may transitions be discovered in the carpels of Magnoliales. The, according to the classic theory, 'primary' (real or true) margin, which bears the ovules, and the 'secondary' margin may represent the inner and the outer edges, respectively, of a style-stigma slit of an ascidiform carpel that is not deep. The frequent insertion of an ovule on the inside edge of the median adaxial carpel margin (Querzone) may be explained in the same way.

9. The trends of specialization. – Bailey and Swamy (1951) have presented a well-known scheme of specialization leading to the carpels of other Angiosperm groups, in which the supposedly original conduplicate *Tasmannia* type of carpel with extensive crest, is taken as a starting point. The main operating processes are closure of the carpel and the restriction of the paired stigmatic crests. The crests progress upwards to form the terminal stigma. Of course the authors are led to this idea by comparison with the carpel form of the *Drimys* section of Winteraceae. However, although the process of style-stigma terminalization seems evident, in my opinion the process of fusion of margins, as advanced by Bailey and Swamy, has possibly played no role in achieving this terminalization, no more than it has in the forming of the carpel of the *Drimys* section. In the following I will tentatively bring forward some details of my photographs which suggest that modifications during the later development stages might have worked otherwise.

As the photographs show the margins of the mouth of the carpel primordium of *Drimys winteri*, when it has changed into a slit-like opening, are slightly bilobed, especially in the proximal half. There is also a notch below. The same configuration occurs in the *Bubbia* species which was studied. A similar notch was described in *Degeneria* by Swamy (1949). Bailey and Nast stated that the terminal parts of the *Bubbia* carpels are homologous with the ventral parts of the primitive carpels. However, my results suggest that the terminalization of the stigma has been caused by the advancing development of an ovary part, originating from the lower portion of an oblique ascidiform carpel. The beginning of this allometric evolutionary development can still be seen in the carpel ontogeny as photographed in *Knema tomentella*. At first there are two lateral proximal lobes, as in *Drimys winteri*. Then, they extend strongly, especially below, to form the ovarian cleft ('ventral'). At the same time the at first round distal part is bent backwards to form the style-stigma. In *Thalictrum* the differentiation of the margin into two portions is still evident during ontogeny. But here the proximal part, which undergoes a slight lateral growth, remains without ovules, as described. The same is observed in *Rubus*. Also during the ontogeny of *Alchemilla* and *Adenanthera* the differentiation of the original carpel into two functionally different parts can be observed. In *Cimicifuga racemosa* the style-stigma character of the carpel develops rather strongly at first, but then the ovary part soon becomes the largest part. In *Akebia* the ovary part develops strongly from the start, later a distal style-stigma part is bent backwards by the formation of two subapical lobes. The same occurs in *Pithecellobium*, in which the round mouth of the carpel primordium is for some time maintained distally. This has not been observed in the other Leguminosae studied. In *Magnolia* the persistence of a large part of the original margin as the style-stigma part is well-known. In *Zanthoxylum* the development of a style-stigma is long postponed.

10. The cupular origin. – Generally it seems that evolution moves away from the ascidiform structure which nevertheless is latently present in all instances. The weakly ascidiform carpel development is prevalent. However, it is not certain if the strongly or the weakly ascidiform carpels are closer to the ancestral – oldest – Angiosperms. Some clues as to this may be discovered if the development of many Winteraceae carpels could be compared in detail (cf. Melville, 1969, and Sampson & Tucker, 1978).

The fundamental ascidiform development may indicate a relation of the carpels with cupules of Angiosperm forerunners. The evolution may have been from cupular to 'conduplicate'. Theoretically free carpels of intermediate structure may be expected to occur in Angiosperm taxa, in which the evolution of dorsiventrality and one – median – plane of symmetry, and the evolution of a carpellary cleft and the connection of the ovules to it, has not reached the typical state. As to this, carpels that show a markedly ascidiform development must be considered, and they should be further investigated.

CONCLUSIONS

Carpel primordia develop in adaxial direction as oblique bowl-shaped to ascidiform organs provided with a basal support. Mostly the ascidiform development is slight on the adaxial side; then the carpels have a basal support like the seat of a chair. It is strong in many Winteraceae, and in carpels that have one ovule.

By predominant oblique abaxial and longitudinal growth the distal mouth of an ascidiform primordium becomes the lateral cleft of a carpel. The position of the ovules is related to the cleft. Carpels are less oblique in Winteraceae.

The stalk of a carpel develops by the extension of its base.

Solitary terminal carpels possibly all are initiated laterally, but then occupy almost the whole floral apex. Also in Leguminosae the carpels originate as lateral organs. Their early development is essentially the same as that in polycarpellate flowers. The development of the adaxial region is mostly slight, or very late, or non-existent. The residual apex is not detectable later.

The difference of carpel structure between section *Tasmannia* and section *Drimys* of the genus *Drimys* (Winteraceae) is the result of a different degree of ascidiform development, not of fusion processes. It leads to variously long and deep style-stigma parts.

In *Austrobaileya* the carpel is distinctly ascidiform with a very deep and oblique trunk-like slit. The structure is fully comparable with that of *Drimys* section *Drimys*.

The structure of the margins of most Angiosperm carpels, showing 'submarginal' placentation, may be understood by comparison with a style-stigma slit of Winteraceae that is not deep.

A main evolutionary event leading to Angiosperm carpels may have been the allometric development of an oblique ascidiform structure, that gave a large ovary at the base and left the stigmatic part apically.

REFERENCES

BAILEY, I.W. & C.G. NAST. 1943. The comparative morphology of the Winteraceae. II. Carpels. J. Arnold Arb. 24: 472–481.

—— & B.G.L. SWAMY. 1951. The conduplicate carpel of dicotyledons and its initial trends of specialization. Amer. J. Bot. 38: 373–379.

BAUM, H. 1952. Die Querzonenverhältnisse der Karpelle von Helleborus foetidus und ihre Bedeutung für die Beurteilung der epeltaten Karpelle. Österr. Bot. Zs. 99: 402–404.

—— 1953. Die Karpelle von Eranthis hiemalis und Cimicifuga americana als weitere Verbindungsglieder zwischen peltaten und epeltaten Karpellen. Österr. Bot. Zs. 100: 353–357.

CANRIGHT, J.E. 1960. The comparative morphology and relationships of the Magnoliaceae. III. Carpels. Amer. J. Bot. 47: 145–155.

ENDRESS, P.K. 1980. The reproductive structures and systematic position of the Austrobaileyaceae. Bot. Jahrb. Syst. 101: 393–433.

GUÉDÈS, M. 1966. Réflexions sur la notion de carpelle pelté. Beitr. Biol. Pflanzen 42: 393–423.

GUT, B.J. 1966. Beiträge zur Morphologie des Gynoeceum und der Blütenachse einiger Rutaceen. Bot. Jahrb. Syst. 85: 151–247.

HEEL, W.A. VAN. 1981. A S.E.M.-Investigation on the development of free carpels. Blumea 27: 499–522.

KANIA, W. 1973. Entwicklungsgeschichtliche Untersuchungen an Rosaceenblüten. Bot. Jahrb. Syst. 93: 175–246.

LEINFELLNER, W. 1965. Wie sind die Winteraceen-Karpelle tatsächlich gebaut? I. Die Karpelle von Drimys, Sektion Tasmannia. Österr. Bot. Zs. 112: 554–575.

—— 1966. Ibidem. II. Über das Vorkommen einer ringförmigen Plazenta in den Karpellen von Drimys, Sektion Wintera. Österr. Bot. Zs. 113: 84–95.

—— 1967. Über die Karpelle verschiedener Magnoliales. IV. Magnolia und Michelia (Magnoliaceae). Österr. Bot. Zs. 114: 73–83.

—— 1969. Zur Kenntnis der Karpelle der Leguminosen. I. Papilionaceae. Österr. Bot. Zs. 117: 332–347.

—— 1970. Ibidem. II. Caesalpiniaceae und Mimosaceae. Österr. Bot. Zs. 118: 108–120.

LEINS, P. & P. STADLER. 1973. Entwicklungsgeschichtliche Untersuchungen am Androecium der Alismatales. Österr. Bot. Zs. 121: 51–63.

MELVILLE, R. 1969. Studies in floral structure and evolution. I. The Magnoliales. Kew Bull. 23: 133–180.

NEWMAN, I.V. 1936. Studies in the Australian Acacias. VI. Proc. Linn. Soc. N.S.W. 61: 56–88.

PAYER, J.-B. 1857. Traité d'organogénie comparée de la fleur. Paris.

PAYNE, W. & J.L. SEAGO. 1968. The open conduplicate carpel of Akebia quinata (Berberidales: Lardizabalaceae). Amer. J. Bot. 55: 575–581.

ROHWEDER, O. 1967. Karpellbau und Synkarpie bei Ranunculaceen. Ber. Schweiz. Bot. Ges. 77: 376–432.

SAMPSON, F.B. 1963. The floral morphology of Pseudowintera, the New Zealand member of the vesselless Winteraceae. Phytomorphology 13: 403–423.

—— & D.R. KAPLAN. 1970. Origin and development of the terminal carpel in Pseudowintera traversii. Amer. J. Bot. 57: 1185–1197.

—— & S.C. TUCKER. 1978. Placentation in Exospermum stipitatum (Winteraceae). Bot. Gaz. 139: 215–222.

SATTLER, R. 1973. Organogenesis of flowers. A photographic text-atlas. Univ. of Toronto Press.

SCHAEPPI, H. & F. STEINDL. 1950. Vergleichend-morphologische Untersuchungen am Gynoeceum der Rosoideen. Ber. Schweiz. Bot. Ges. 60: 15–52.

SINGH, V. & R. SATTLER. 1972. Floral development of Alisma triviale. Canad. J. Bot. 50: 619–627.

—— & —— 1974. Floral development of Butomus umbellatus. Canad. J. Bot. 52: 223–230.

SWAMY, B.G.L. 1949. Further contributions to the morphology of the Degeneriaceae. J. Arnold Arb. 30: 10–38.

TUCKER, S. 1959. Ontogeny of the inflorescence and the flower in Drimys winteri var. chilensis. Univ. Calif. Publ. Bot. 30: 257–336.

—— 1975. Carpellary vasculature and the ovular vascular supply in Drimys. Amer. J. Bot. 62: 191–197.

—— & E.M. GIFFORD Jr. 1966a. Organogenesis in the carpellate flower of Drimys lanceolata. Amer. J. Bot. 53: 433–442.

—— & —— 1966b. Carpel development in Drimys lanceolata. Amer. J. Bot. 53: 671–678.

VINK, W. 1970. The Winteraceae of the Old World. I. Pseudowintera and Drimys. Morphology and Taxonomy. Leiden.

—— 1977. The Winteraceae of the Old World. II. Zygogynum. Morphology and Taxonomy. Blumea 23: 219–250.

WEBERLING, F. 1981. Morphologie der Blüten und der Blütenstände. Ulmer, Stuttgart.

EXPLANATION OF PLATES

Plate 1. — *Drimys winteri.*

Plate 2. — 8. *Drimys winteri*; 11–16. *Drimys piperita.*

Plate 3. — 17–19. *Drimys piperita*; 20–22. *Bubbia* spec.; 24. *Bubbia pancheri.*

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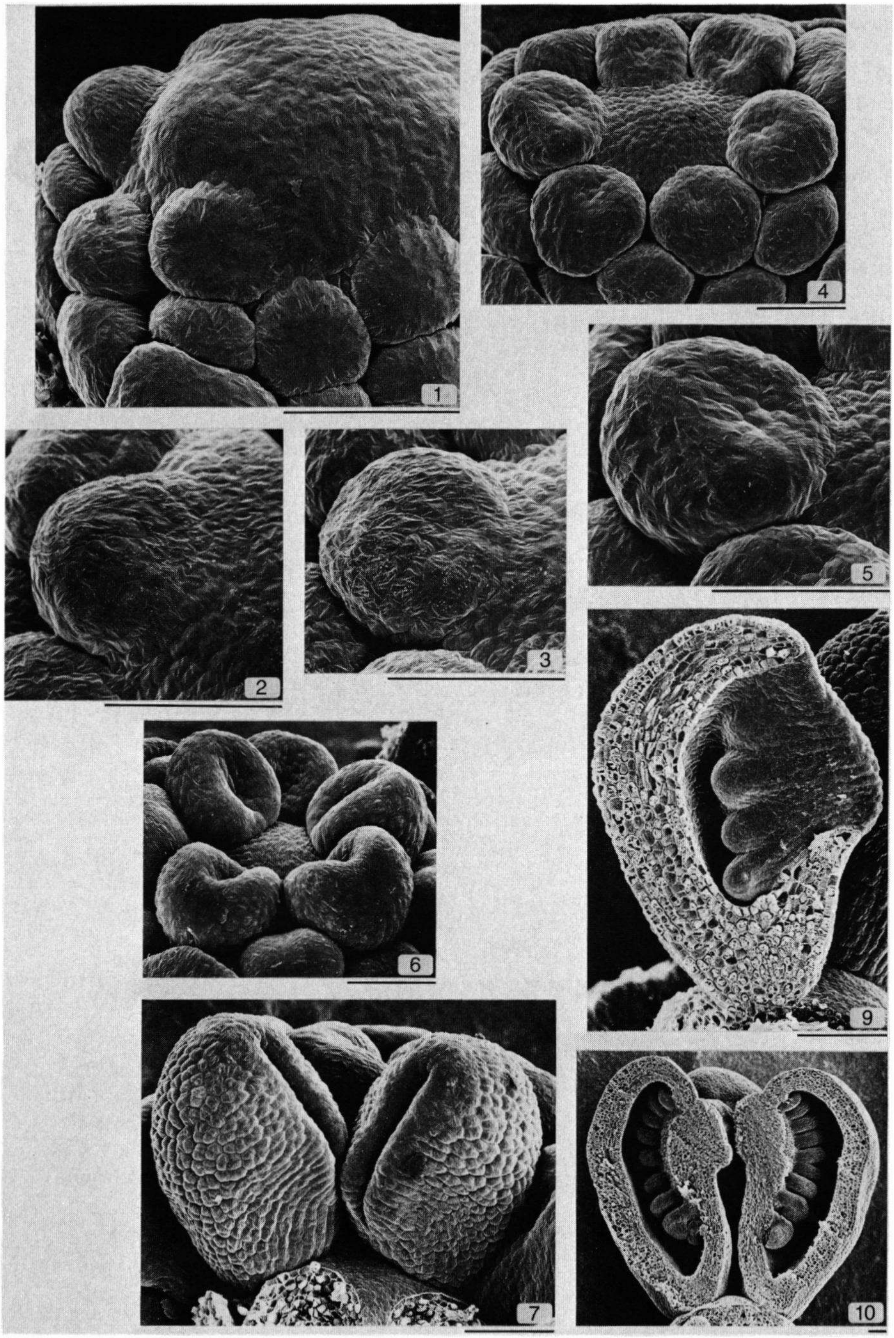
Plate 16. — 135–140. *Ailanthus altissima*; 141, 142. *Butomus umbellatus.*

Plate 17. — 143–149. *Butomus umbellatus*; 150–153. *Alisma plantago-aquatica.*

Plate 18. — 154–162. *Alisma plantago-aquatica.*



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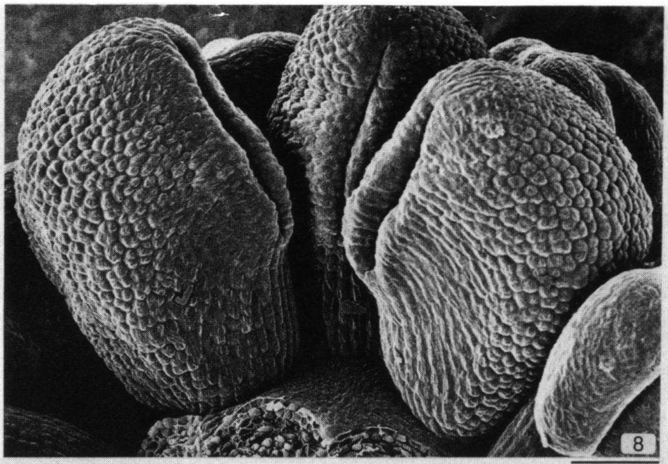

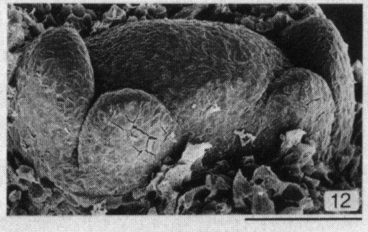

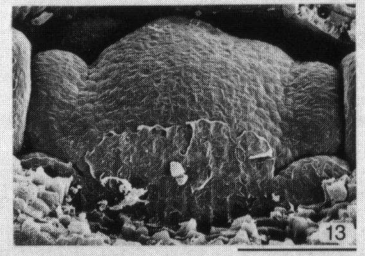

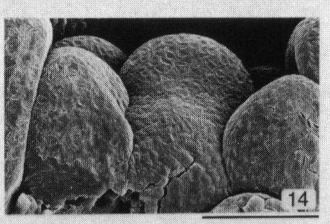

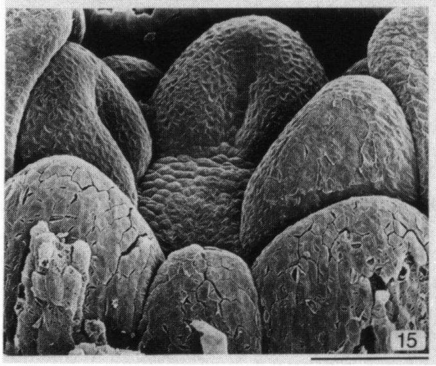

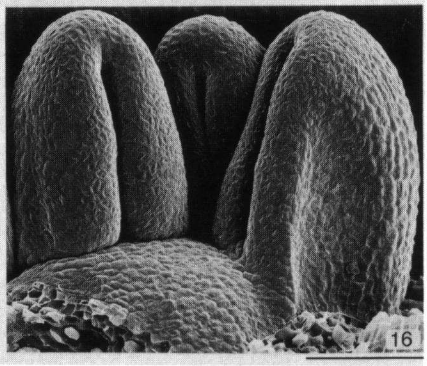

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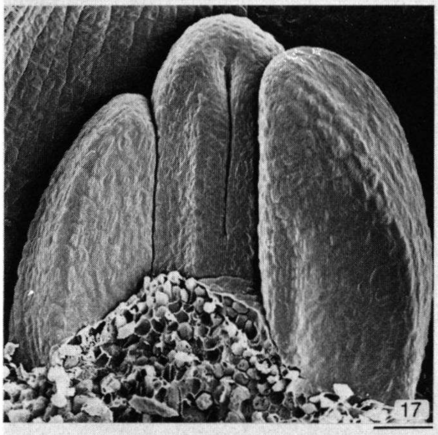
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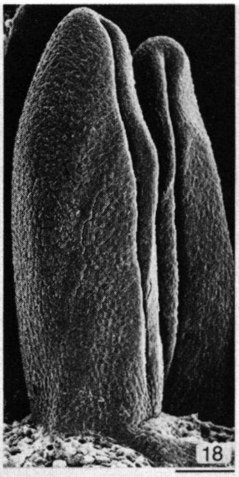
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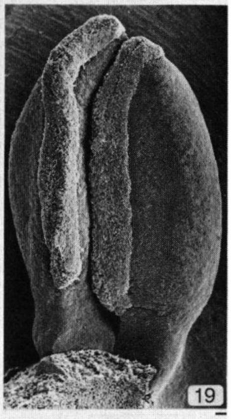
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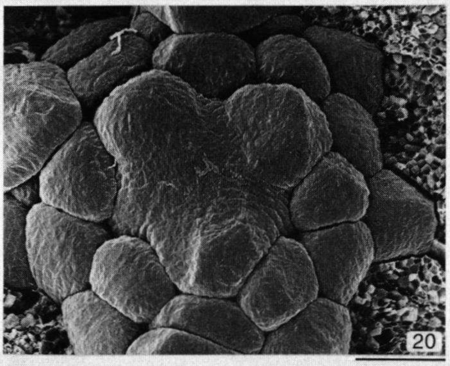
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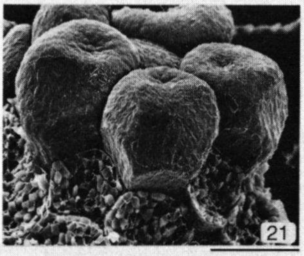
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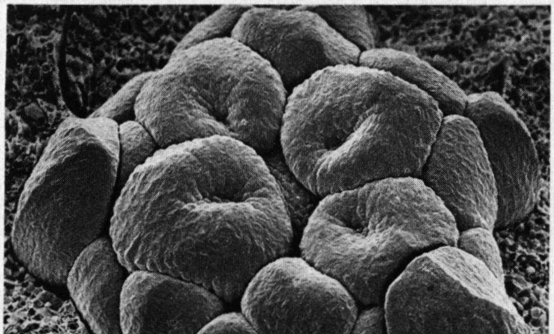
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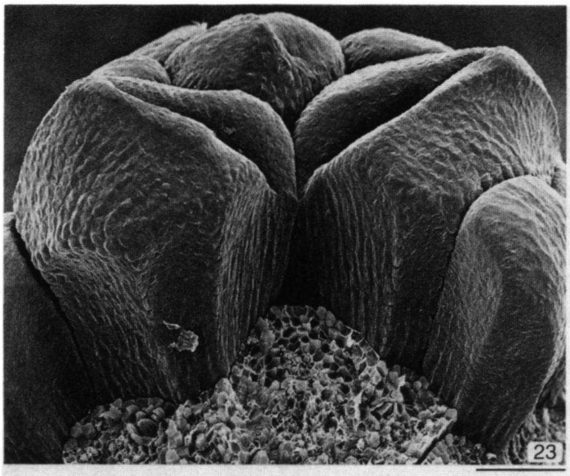

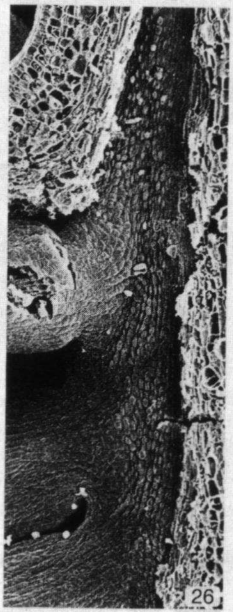

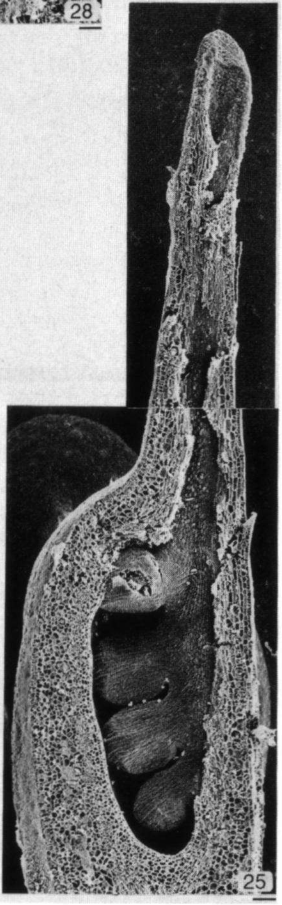

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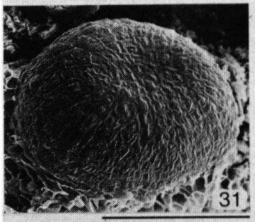
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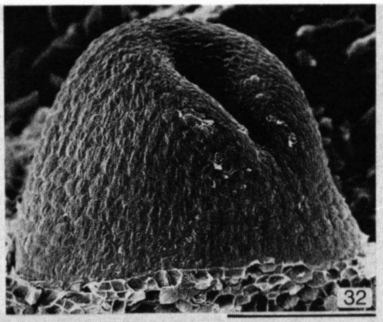
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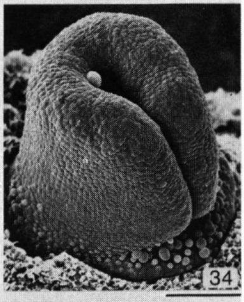
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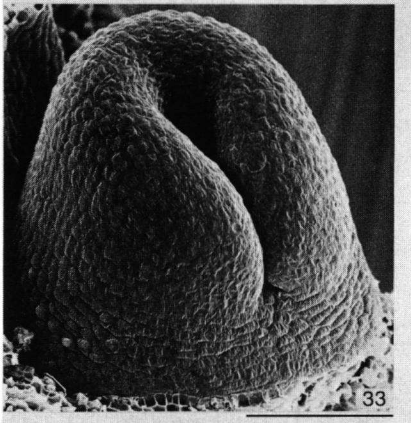
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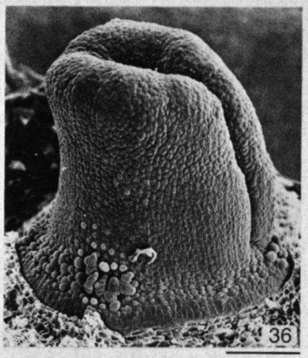
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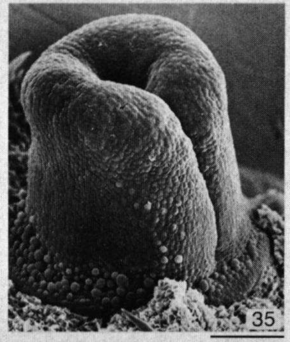
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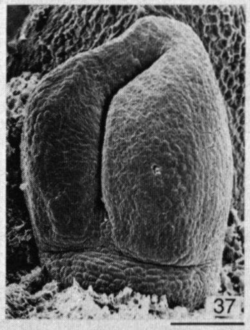
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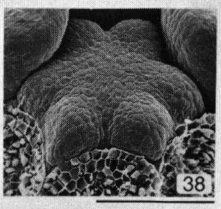
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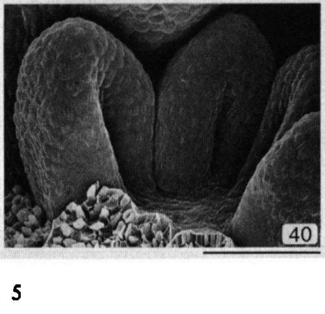
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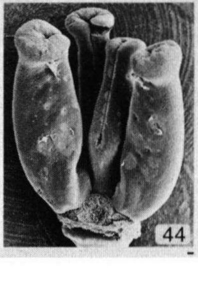
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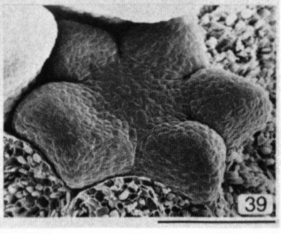
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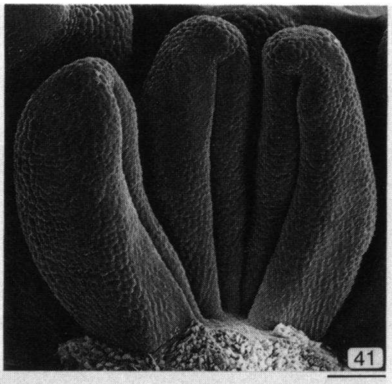
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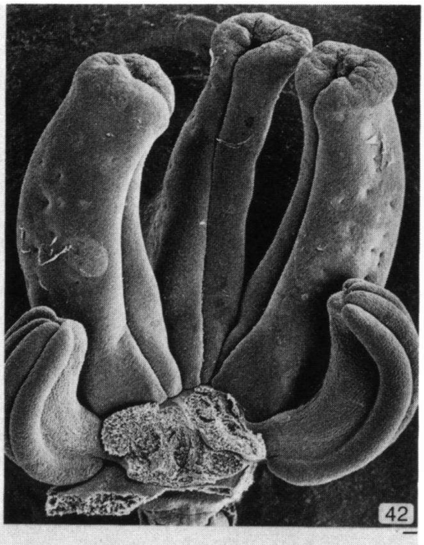
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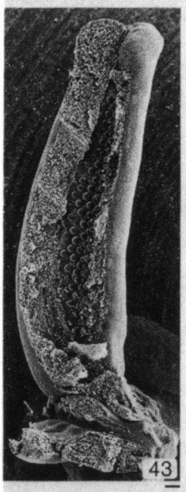
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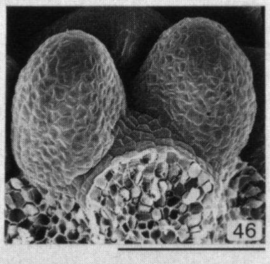
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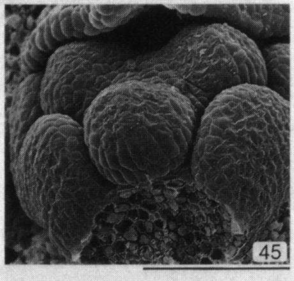
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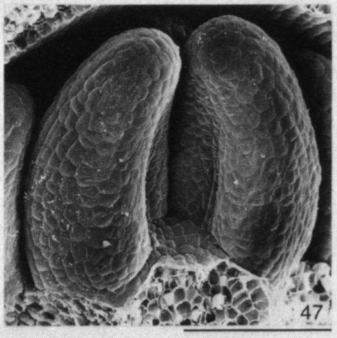
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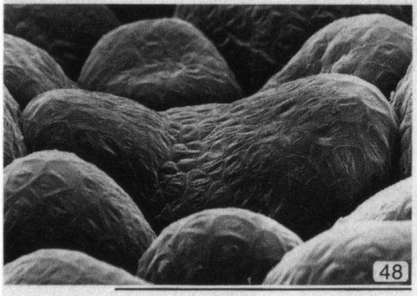
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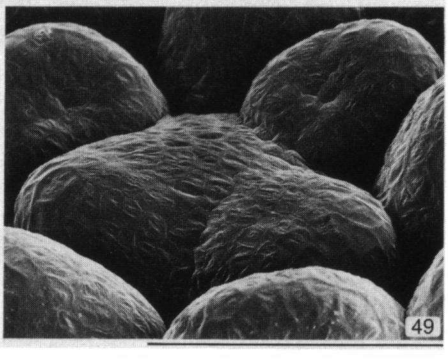
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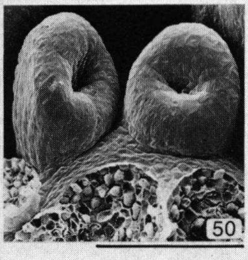

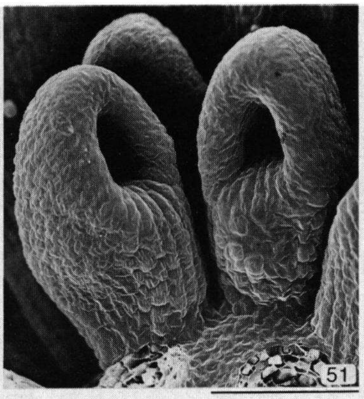

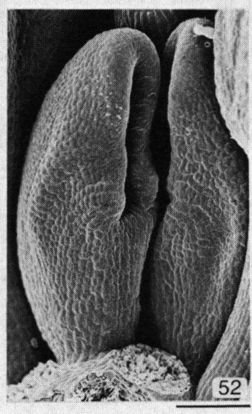

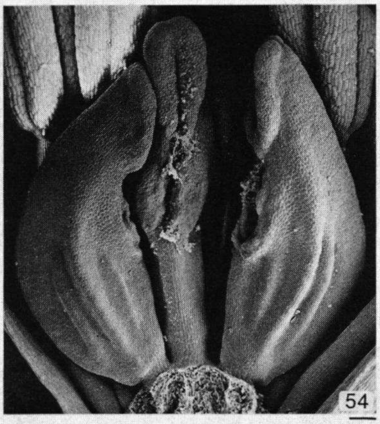

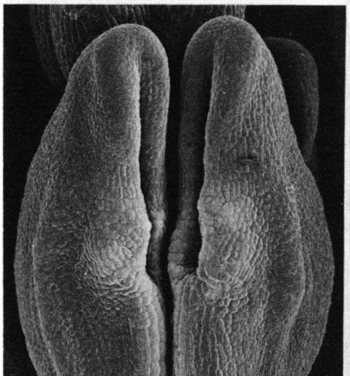

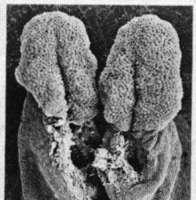

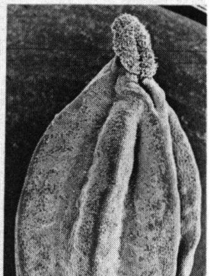

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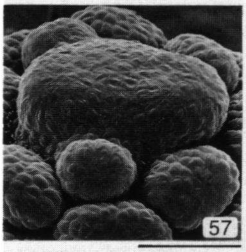

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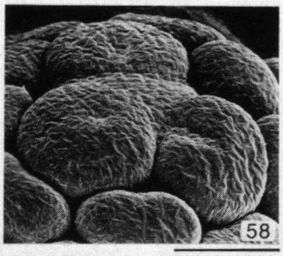

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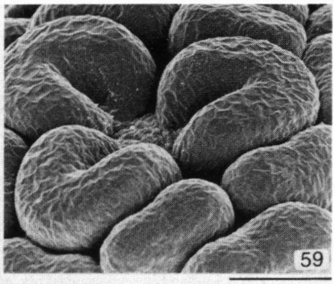

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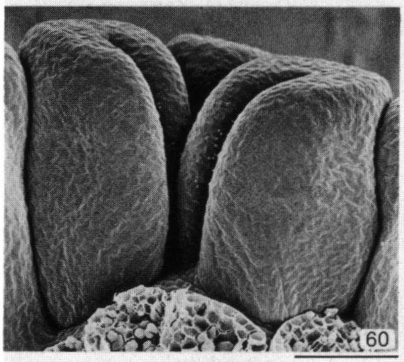

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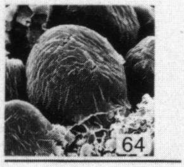

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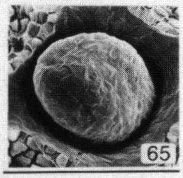

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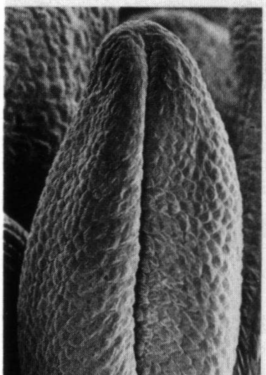

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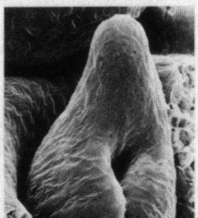

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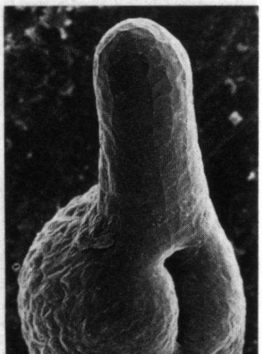

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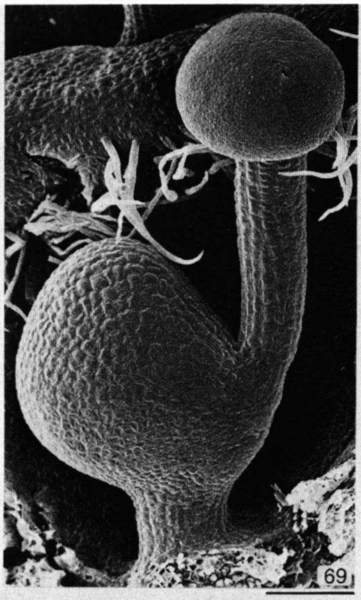

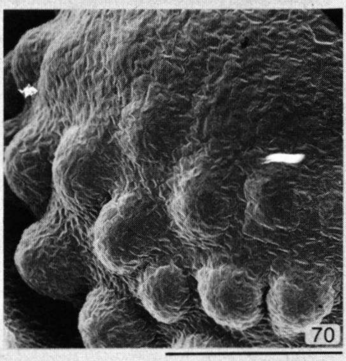

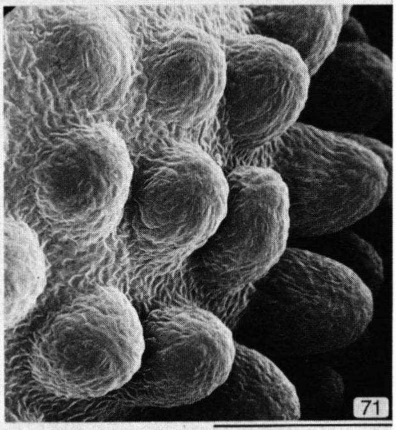

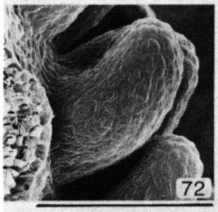

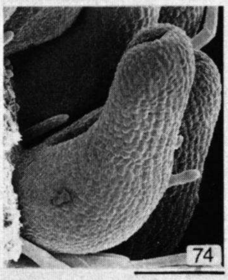

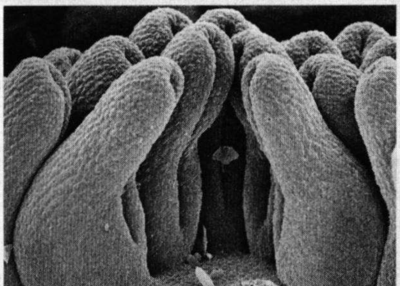

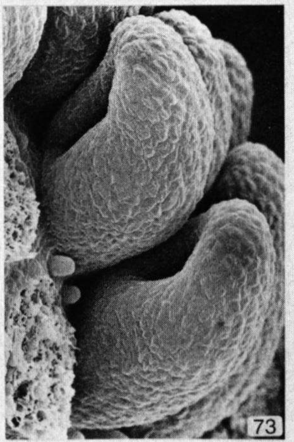

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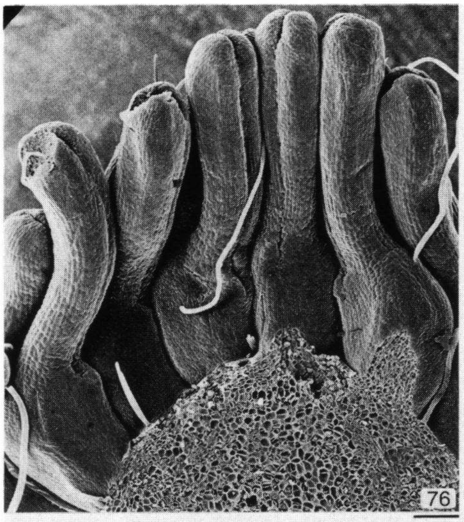
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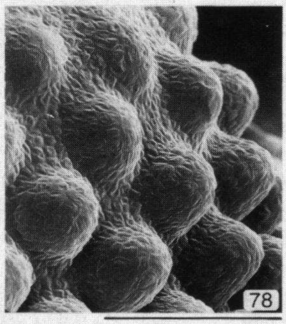
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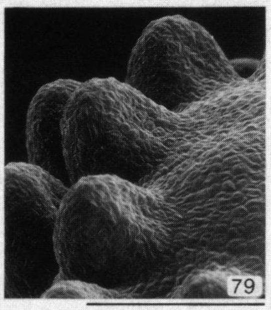
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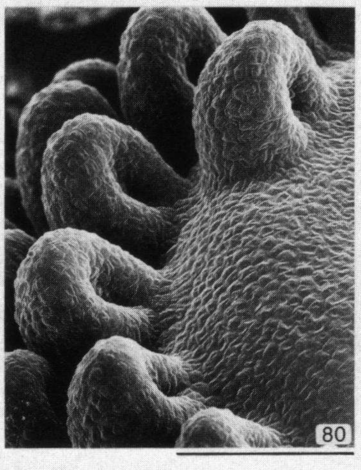
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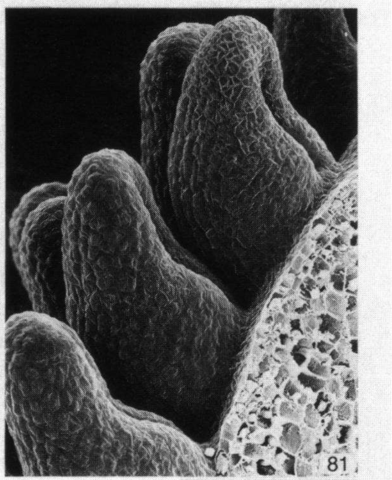
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PLATE 10


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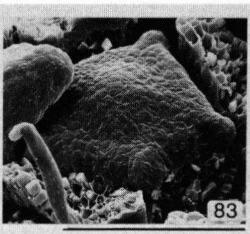
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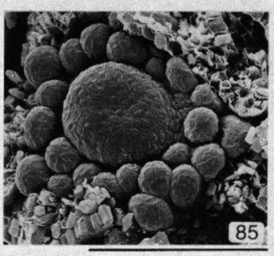
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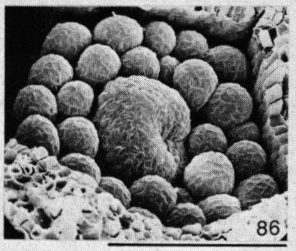
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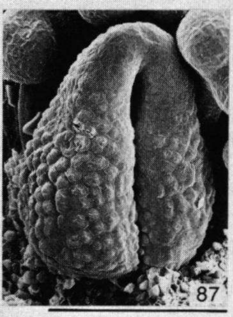
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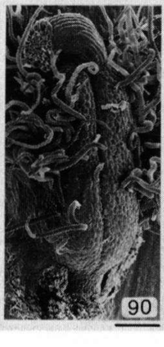
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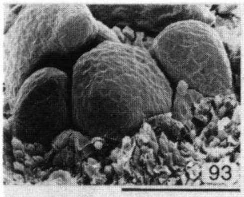
PLATE 11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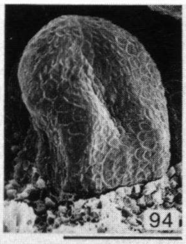
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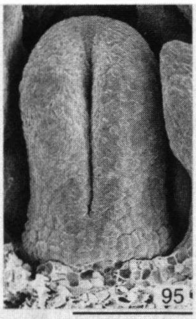
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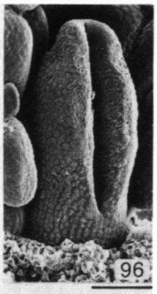
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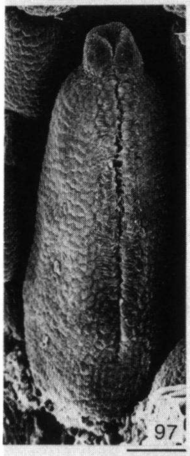
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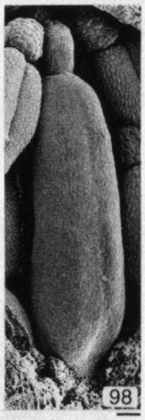
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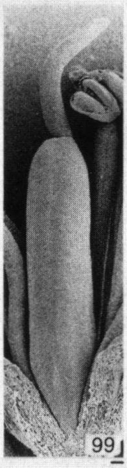
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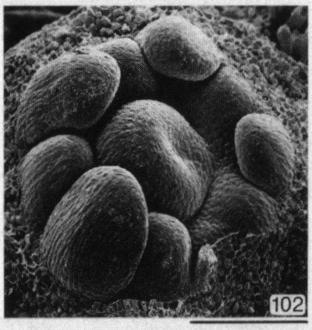
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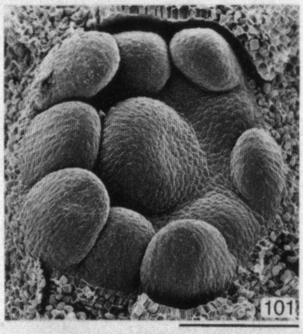
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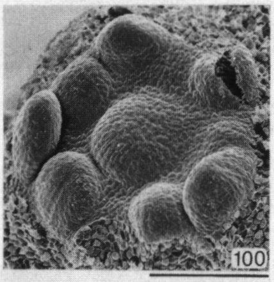
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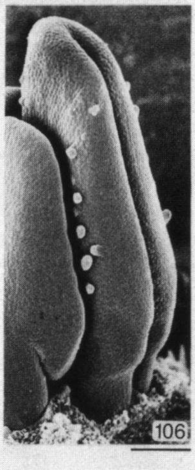
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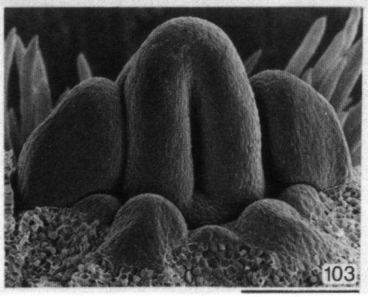
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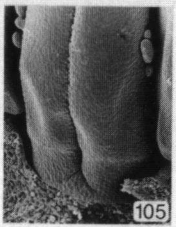
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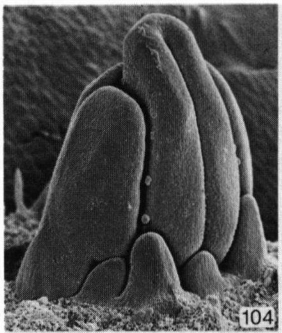
PLATE 12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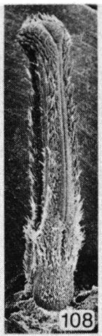
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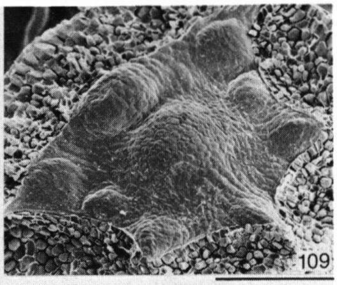
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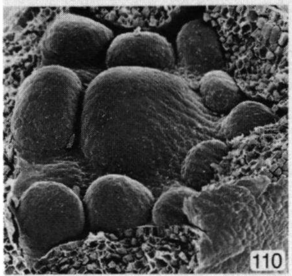
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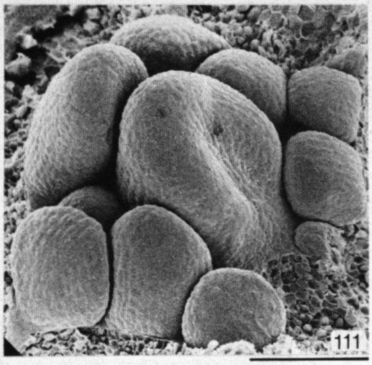
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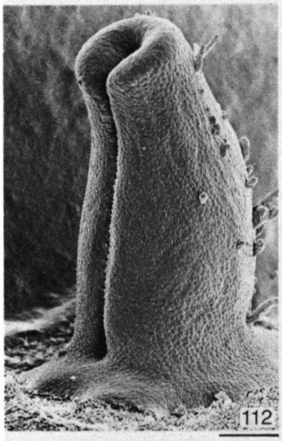
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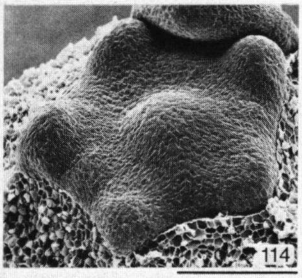
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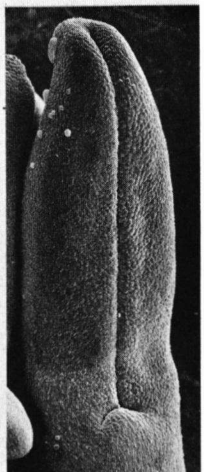
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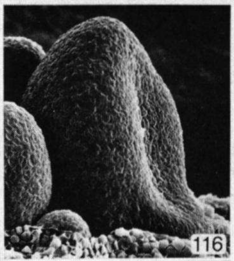
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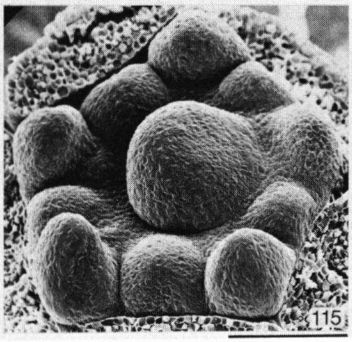
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PLATE 13


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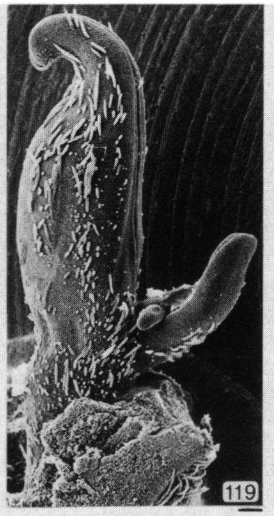
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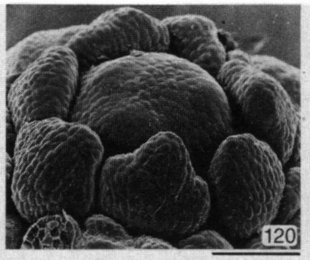
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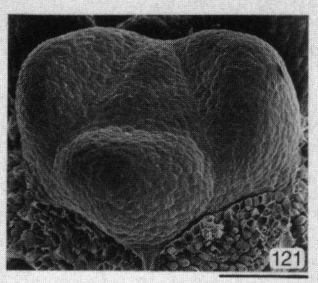
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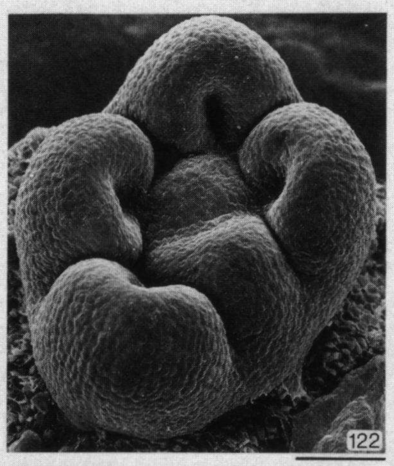
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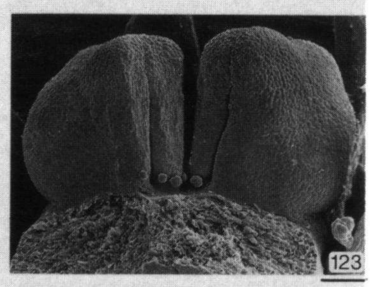
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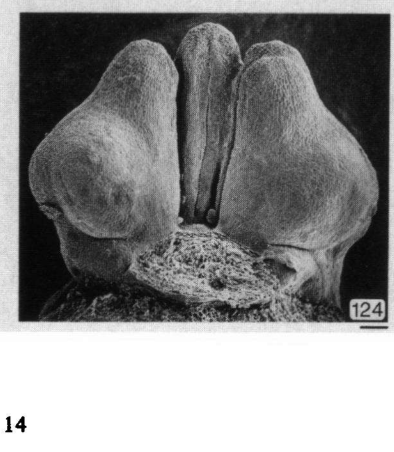
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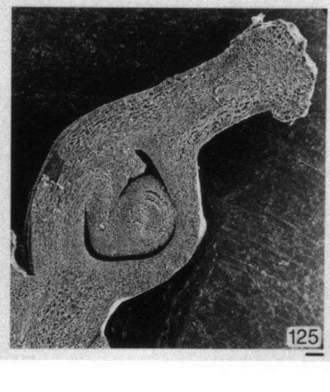
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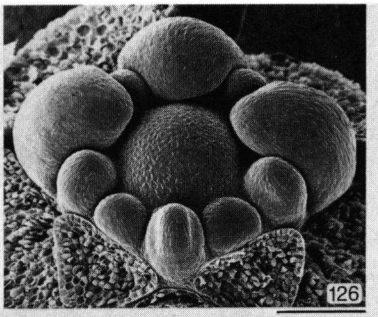
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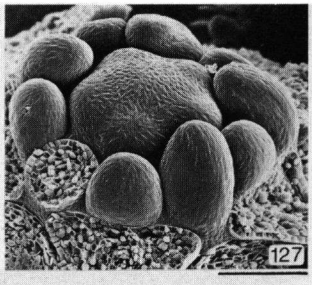
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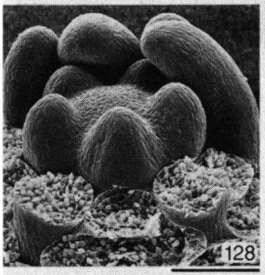
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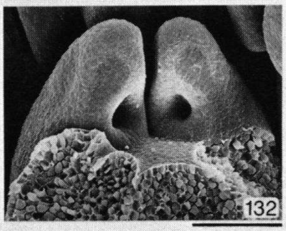
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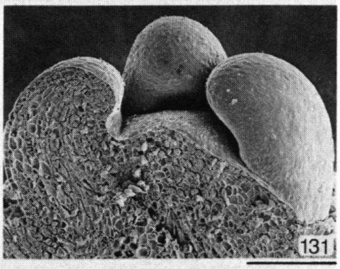
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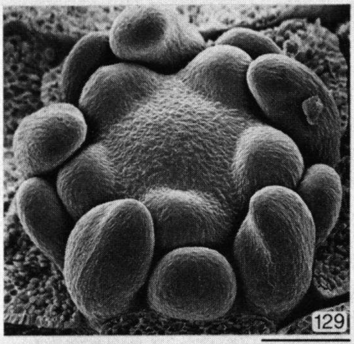
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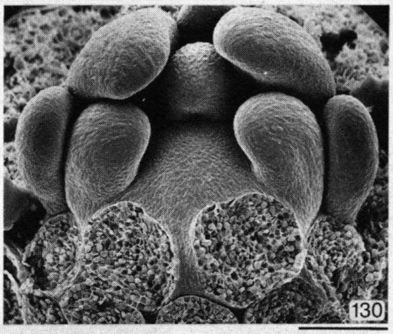
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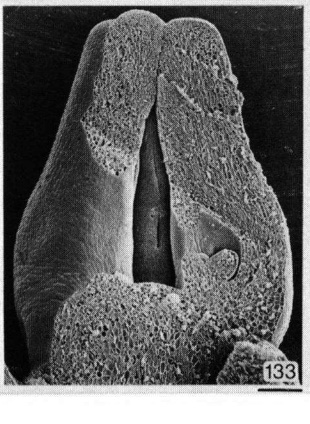
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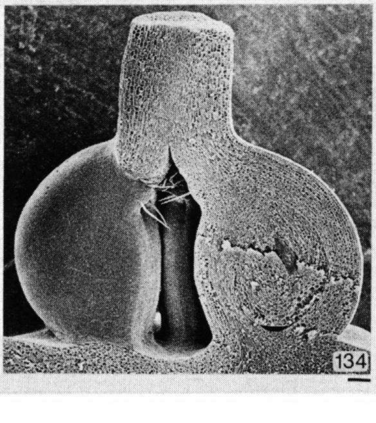
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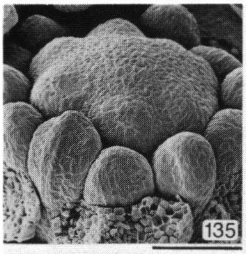
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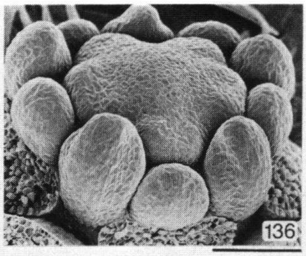
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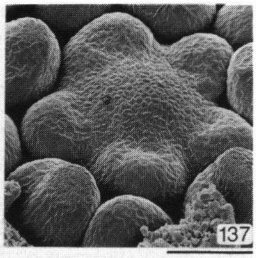
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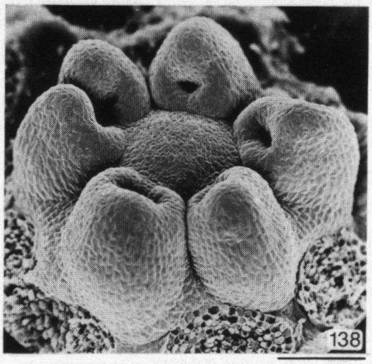
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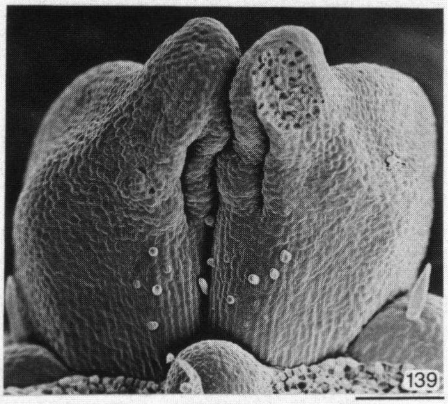
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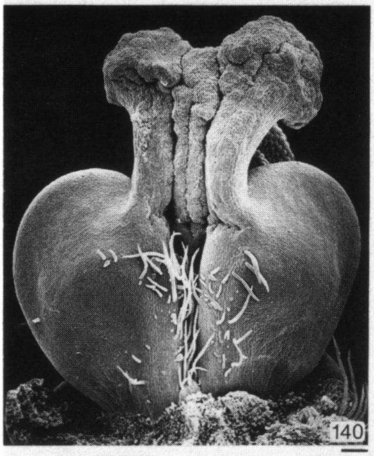
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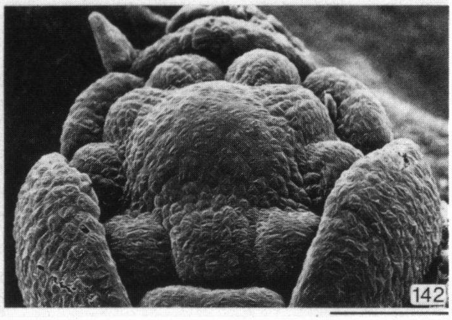
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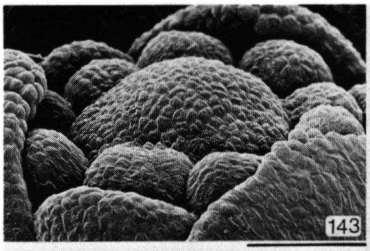
PLATE 16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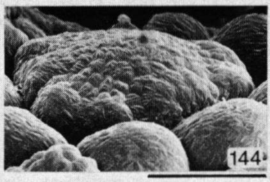
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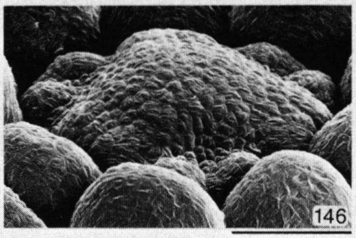
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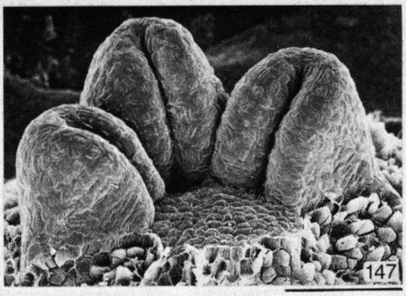
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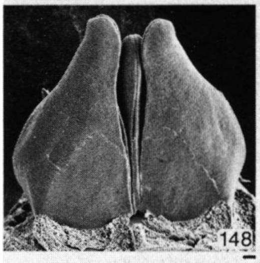
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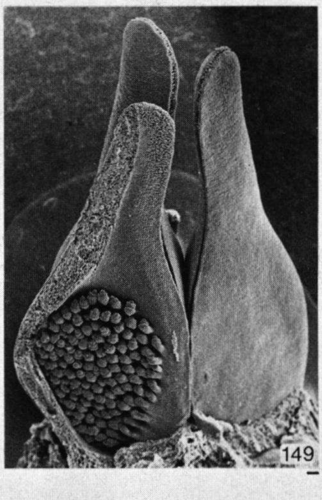
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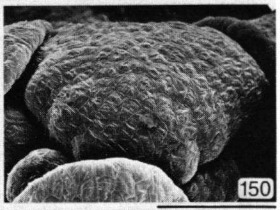
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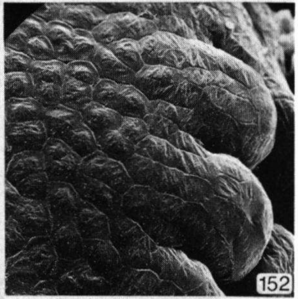
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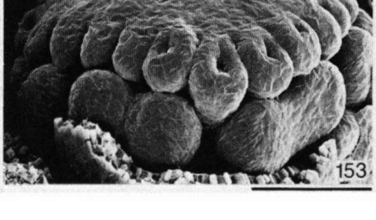
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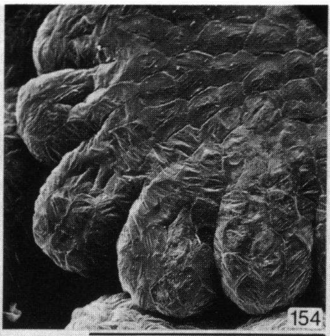
PLATE 17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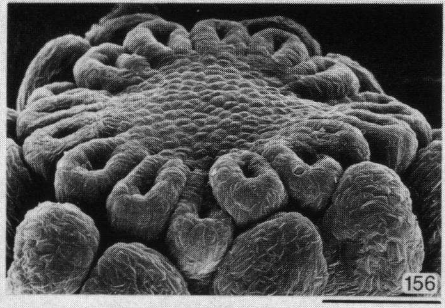
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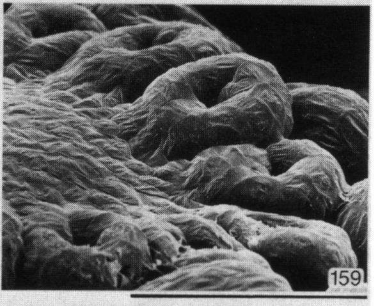
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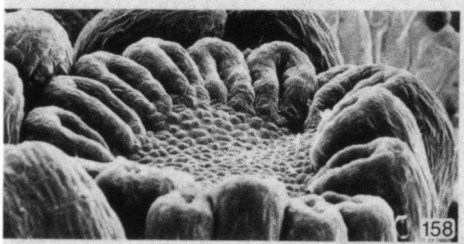
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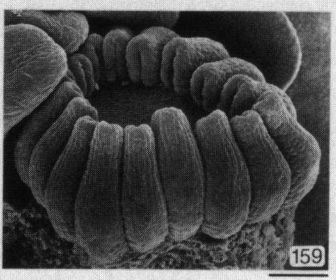
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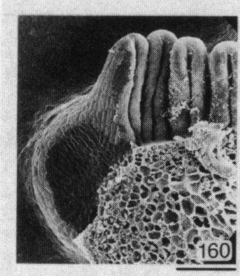
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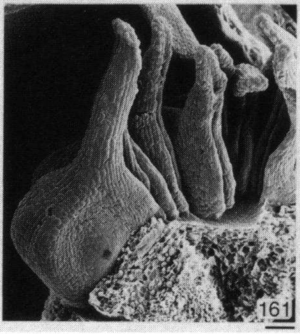
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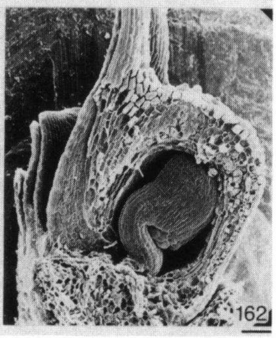
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PLATE 18