

A S.E.M.-INVESTIGATION ON THE DEVELOPMENT OF FREE CARPELS

W. A. VAN HEEL

Rijksherbarium, Leiden, The Netherlands

SUMMARY

The early development (ontogeny) of the carpels of 20 species belonging to 8 apocarpous families was investigated with the scanning electron microscope. The results indicate that on the floral apex a circular or a convex meristem develops into an obliquely ascidiate primordium by unequal growth of its periphery. By further unequal growth it develops into a young carpel. The terminal mouth of a cup becomes the lateral cleft of a carpel. The different forms of the young carpels in different species are defined by the varying degree of development of the adaxial region of the initial meristem and/or its margin on the side of the floral apex. This hypothesis is theoretically evaluated.

INTRODUCTION

Carpels characterize the Angiosperms. They carry the ovules, conduct the pollen tubes, and lodge and liberate the seeds. The knowledge of the basic structure of carpels is important for the understanding of the systematics and the descent of Angiosperm families and genera. The fundamental morphology of carpels has been disputed for more than a century. Unfortunately no fossils have been found and recognized as yet to bring a conclusion in the same way as for the fertile scales of Conifers.

The theories on carpel structure can roughly be divided into two categories. According to the classical theory, mainly following topographic and teratological criteria, the carpels are leafy structures and should preferably be compared with foliage leaves. In some other theories the carpels are considered as combinations of leafy and axial structures, chiefly on arguments derived from the pattern of vascular bundles.

Although the classical theory is most widely accepted, its adherents are separated by two modifications. According to American authors as Bailey (1951), Eames (1961), and Stebbins (1974), the carpels are conduplicate leaflets that are fused at the margins. However, according to Leinfellner (1950) the carpels are peltate leaflets, that is they are ascidiate at the base and plicate above. Most European authors follow Leinfellner. In view of this controversy the present investigation has been initiated. Gynoecia with free carpels were selected first, and are the subject of this paper.

The development of carpels has hitherto been studied by means of light microscopy of microtome sections of which the orientation is inevitably uncertain. The spatial reconstruction is obtained by comparing sections. With the S.E.M., on the other hand, the spatial images are presented directly, and microtome sections can be made afterwards, the orientation of which can be defined more reliably. Moreover, scanning of free-hand sections of primordia may give direct information which otherwise can be reached only by laborious microtoming.

MATERIAL, METHODS, AND PHOTOGRAPHS

The following species were investigated: *Annona montana* Macf., *Cananga odorata* Hk.f. & Th., *Polyalthia glauca* (Hassk.) Boerl., *Nectandra angustifolia* Nees., *Calliandra tetragona* B. & H., *Albizia* spec., and *Cassia* spec., from the Kebun Raja at Bogor*; *Clematis montana* DC., *Delphinium elatum* L., *Helleborus foetidus* L., *Myosurus mininus* L., *Magnolia stellata* (Sieb. et Zucc.) Maxim., *Rosa* spec., *Erythrina crista-galli* L., and *Lupinus albus* L., from the Botanic garden at Leiden; *Magnolia thompsoniana* (G. Don) Steud. from the Botanic Garden at Amsterdam; *Aquilegia vulgaris* L. from the Botanic Garden at Haren; *Delphinium ajacis* L. from my home-garden; *Ranunculus acris* L. and *R. sceleratus* L. from natural habitats near Leiden. I wish to express my gratitude to the directors and staff of the botanic gardens concerned. The material was either fixated in F.A.A. and washed in alcohol 50% (the Bogor material), 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 acetone, 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, unless indicated otherwise.

RESULTS

1. *Delphinium ajacis* (Ranunculaceae). — Photos 1-7

Each flower has one single terminal carpel. After the last stamen is formed, the floral apex becomes bowl-shaped by the development of its peripheral margin. A little later the carpel primordium is obliquely cup-shaped, and a lower and a higher part of its margin can be distinguished. The lower part is on the side of the last formed stamen, the higher part on the opposite side of the floral apex. There the peripheral growth possibly starts earlier, or is stronger at once. Growth occurs predominantly at the higher part, and at the same time growth in length is more important than growth in width. As a result the mouth of the cup, at first round and horizontal, becomes narrow and vertical. When a carpel primordium is about half a millimeter in length (photo 5), its cleft still betrays its derivation from the mouth of a cup by the fact that its ends are rounded by the margins of the cup. However, later this is lost by the persistent unequal growth, especially below. Then the lower part of the cup is no longer distinct, and the young carpel, at a length of more than one mm, looks like a folded leaflet with contiguous margins. However, it is evident that the young carpel, originating as a cup-shaped organ, changes into a 'folded leaflet' by unequal growth; the apical mouth of the cup changes into the 'ventral' cleft. This change is shown by a series of figures on the same scale in plate 3.

The question whether a carpel can be terminal has often been asked. For a recent discussion see Endress (1972). My photographs do not show any remaining parts of the floral apex in any of the species investigated. The question is important for morphologists who wish to categorize carpels as either leafy (lateral) or axial (terminal) structures. Originally this was decided by studying mature plants. In a developmental study, however, a rigid distinction between axis and leaf (carpel) is impossible because of the lack of qualitative criteria to distinguish between apex and appendage.

* 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'.

2. *Delphinium elatum* (Ranunculaceae). — Photos 8–12

This species has three carpels. Three primordia arise on the rim of a flat apex, which are elliptic in outline as seen from above. They grow faster on the outside margin than on the inside. As the growth on the outside, as well as the growth in length, is dominant, the young carpels become horseshoe-shaped. The primordia resemble primordia of *D. ajacis* that would not grow further on the inside. They look like mountains with a broadly elliptic base and with increasingly steeper slopes. At first the base of the carpel primordia can be well demarcated from the floral apex, but later the inside region of the primordia cannot be demonstrated any more, because it is entirely surpassed by the extreme growth of the young carpels from the outside region of the primordia. In contrast with *D. ajacis*, in *D. elatum* the development of the carpellary meristematic field lags behind on the inside. Later on a beginning of syncarpy can be noticed at the base of the young carpels.

3. *Clematis montana* (Ranunculaceae). — Photos 13–18

Many hemispherical primordia originate upon a convex floral apex. They grow faster on the outside, and are flattened on the inside below the top. In addition they become narrow at the base. The flat region is depressed, so that the whole carpel primordium is obliquely cup-shaped and slightly stalked. The growth of this primordium is now chiefly located on the outside, and also the growth in length is more prominent than the growth in width. Because of this unequal growth, the mouth of the cup first becomes lengthwise elliptic to narrowly triangular, and then is shaped as a vertical slit. This is the 'ventral' cleft of the carpel. Also in later stages the cleft remains discernable as the deformed mouth of the cup, as no further unequal growth is disturbing its position (as opposed to that in *Delphinium ajacis*). As the cleft is closed by contiguous parts of the margins first, the origin of the ovules cannot be observed by external view. One ovule develops in median low position, and some develop along the cleft, but only the former will develop into a seed. As such *Clematis* ranks between Ranunculaceae with follicles and those with achenes. The development is shown by a series of figures on the same scale in plate 3.

4. *Ranunculus acris* (Ranunculaceae). — Photos 19–24***R. sceleratus*. — Photos 25–30**

Many hemispherical primordia originate on the floral apex. When about 0.1 millimeter high (photos 21 and 26), they have developed into obliquely cup-shaped lateral organs which are slightly tapering toward the base. The margin of the cup is higher on the outside than on the inside and encloses an elliptic to triangular mouth. Then the inside margin becomes thicker medianly where the ovule originates and at the same time the outside margin develops into a cap. Ultimately the ovule primordium is enclosed in the cap. Thus the origin of the ovule can be observed on the lower margin of the cup prior to the closure of the ovary (as opposed to the situation in *Clematis*). A low edge develops secondarily along the inside margin as well as partly upwards along the outside margin. Later on the lateral margins of the cap meet and form a medium carpellary cleft which closes basipetally, presumably by a secondary marginal division process (the secondary edge). Consequently also in *Ranunculus* the cleft of the carpel is derived from the mouth of an obliquely cup-shaped primordium by unequal growth of the margins. The final development into an achene is characterized by the deepening of the ovary.

5. *Myosurus minimus* (Ranunculaceae). — Photos 31–36

The development is very much like that in *Ranunculus*. However, the hemispherical primordia originate on the side of a floral apex which strongly grows in length. Cup-shaped organs are formed which grow much stronger on the outside. The adaxial (upper) region of the lateral hemispherical primordium develops into the inside margin of the cup. On this margin a median ovule develops in a very early stage. The edge on the margin, which is formed secondarily, is very low.

6. *Aquilegia vulgaris* (Ranunculaceae). — Photos 37–41

Rows of six stamen primordia originate in front of the sepals and the petals. Moreover the antesepalous rows are each terminated by one carpel primordium. These primordia are situated on the rim of a broad, slightly convex, floral apex, partly fitting in between the uppermost stamen primordia. They are hemispherical to broadly ellipsoid, but they can hardly or not be demarcated from the floral apex on the inside. On the outside the margin grows upwards as a horseshoe-shaped wall. The development of the inside regions lags behind and these regions cannot be detected any more later on. Finally a beginning of syncarpy occurs at the base of the young carpels.

7. *Helleborus foetidus* (Ranunculaceae). — Photos 42–45

Three large carpel primordia develop latero-apically on the floral apex. Their basal outline is circular or broadly elliptic, but is faintly demarcated from the apex on the inside. A half-circular upgrowth of the outside region starts early, so that at first the primordia are flat above. Whereas the outside region forms the horseshoe-shaped carpellary wall, the inside region is enclosed and becomes unrecognizable. Consequently the development of a lower inside margin does not occur. As in *Aquilegia*, the ascidiate base of the carpels is caused by the latero-apical location of the original carpellary meristematic fields on the floral apex. Part of the discrepancies in earlier investigations can be solved by the proper understanding of this position (cf. Rohweder, 1967).

8. *Magnolia stellata* (Magnoliaceae). — Photos 50–54

The carpel primordia originate laterally on a high convex floral apex. Mostly they are circular in outline. For the greater part each develops into the outside margin of a lateral cupuliform organ. The development begins with the widening of the lower half of the hemispherical primordium, after which a thick margin grows outwards and also upwards. The upper (adaxial) region of the initial primordium develops into the inside margin of the cup. Sometimes the primordia do not seem to be exactly circular in outline, they appear slightly flattened above from the start. But also in these cases the adaxial margin develops later on, after the outside margin has reached some size. A similar late development of the inside margin has been described in *Pseudowintera axillaris* by Sampson & Kaplan (1970). In any case the adaxial inside margin, although less well developed, is distinct as well as the obliquely cup-shaped lateral development of the carpel as a whole. However, later this adaxial region cannot be distinguished any more from the floral axis. On the side of the floral axis the cup is deepened secondarily, and two ovules originate in it laterally on the inside of the margin quite close to the floral axis, when an ovary and a style have

not yet differentiated. Later on such a distinction is evident, as the margins have closed then. The margins are provided with curious protuberances which are more or less alternating (photos 53 and 54). Carpels of *Magnolia thompsoniana* (photo 55) do not show adaxial margins at all, only the uppermost may show some traces.

9. *Annona montana* (Annonaceae). — Photo 46

The floral apex is rather flat and is covered by numerous carpel primordia. The primordia have a circular base and are convex. The formation of a semicircular wall starts very early and quickly on the outside of these primordia. The inside region is lagging behind and soon plays no role any more. As a result young carpels develop without an inside margin. A similar development was observed in *Cananga odorata* and *Polyalthia glauca*.

10. *Nectandra angustifolia* (Lauraceae). — Photos 47, 48 and 56–60

The earliest stage observed is a rather high convex floral apex which is slightly flat on one side. The top of the floral apex and the region all around the flat part develop into a peripheral margin on which a cap-shaped part and a lower part on the opposite side can be distinguished. In this way the floral apex as a whole develops into one obliquely cup-shaped carpel primordium. Then the entire low margin develops into a massive ovule primordium. The carpel primordium as a whole is now tapering at the base. The ovule primordium bends into the cap, and at the same time the cap grows over the young ovule. There is a prominent development of a secondary lobed edge around the base of the ovule. This edge is continuous with a similar formation on the margins of the cap. It seems that by this growth the cleft of the carpel is closed. On the whole the development is like that in lateral carpels of *Ranunculus*. Endress (1972) published S.E.M. – photographs of *Laurus nobilis*, and schemes of *Cinnamomum camphora*, which indicate an exactly similar development.

11. *Rosa spec.* (Rosaceae). — Photos 61–63

Hemispherical primordia move to the periphery of a low convex floral apex, as younger ones originate in the centre. In the meantime they grow more strongly on the outside than on the inside. Then a cap-shaped upper margin originates on the outside, whereas on the inside no margin is formed. In this way each hemispherical primordium differentiates into a young horseshoe-shaped carpel on a stipe. In each carpel one ovule originates at the base of one of the lateral margins (not illustrated). Also the ovary is formed by the elaboration of the proximal parts of the lateral margins. Thus a fully cup-shaped structure is not basic to this carpel, as no lower margin develops.

12. *Albizia spec.* (Mimosaceae). — Photos 64–67

The youngest stage available shows the floral axis changed into a shallow oblique bowl-shaped primordium. The higher margin is thicker than the lower margin. The primordium as a whole slightly tapers towards the base, and is well demarcated from the floral apex. When the carpel primordium is about three times larger it has a prominent, but variable, obliquely cup-shaped form, tapering toward the base. The latero-apical direction of growth of the margins is suggested by the pattern of the epidermal cells. The

elliptic mouth of the cup changes into a latero-apical cleft. When again the young carpel is about three times larger, the entire proximal part appears surpassed and lost, and the cleft is lateral and extends toward the base. The change in aspect from cup-shaped to 'folded leaflet', is brought about by the suddenly dominant growth of the higher margin. It is the same process as in *Delphinium ajacis*.

13. *Calliandra tetragona* (Mimosaceae). — Photos 68–75

The floral apex develops into one single carpel. A circular space is left between the raised centre of the apex and the developing androecium. At first the low convex dome is constricted at the base and shallowly depressed at the top. A higher and a lower part of a broad peripheral margin is formed. The carpel primordium is obliquely bowl-shaped now. Whereas the further growth of the higher margin is strong, the growth of the lower margin is weak and variable. At best an oblique but distinctly cup-shaped carpel primordium results, which has an elliptic upright mouth and a small tapering base. The mouth will become the lateral cleft of the young carpel. However, at the time the margins of the cleft fuse, the originally slight lower margin cannot be detected any more because of the dominant latero-apical growth of the higher margin. The cleft is not closed apically; a stylar part is formed there that elongates considerably. At the base a tapering stalk is formed, which is derived from the outside region only (the higher margin) of the at first cup-shaped carpel primordium. Therefore the closed cleft can be observed to run down the stalk.

14. *Cassia spec.* (Caesalpinaceae). — Photos 76–80

A single carpel arises on one side of the floral apex. The primordium is broadly elliptic and slightly flattened at the inside base. As it grows a lateral thick margin becomes evident along the inside surface. Then the young vertical carpel is half cup-shaped, and horseshoe-shaped in cross-section. The young carpel considerably grows in length, and also width, so that its mouth becomes a cleft. The growth of the remaining part of the floral apex does not keep up with the dominant growth of the carpel, which basally is pursued around the apex to the opposite side, at a slow rate as compared with the predominant longitudinal growth of the carpel wall. Finally the whole floral apex has developed into the carpel. However, an adaxial rim is not formed. The margins of the cleft fuse except at the very base where an entrance to the ovary remains visible for some time.

15. *Erythrina crista-galli* (Papilionaceae). — Photos 81–82

The floral apex as a whole develops into a carpel primordium in its centre, prior to the development of the inner whorl of stamens (for which, as it seems, enough space is saved). The centre of the floral apex becomes hemispherical and slightly higher on the abaxial side. In this way a thick outside margin of the carpel primordium arises, which is followed later by a low inside adaxial margin (near to the first stamen of the second whorl). At this stage the primordium as a whole is faintly cup-shaped, rather oblique, and tapering toward the base. The further growth of the outside margin is dominant.

16. *Lupinus albus.* (Papilionaceae) — Photos 83–85

At the time the floral apex changes into the carpel primordium, the development of the inner stamen whorl has not yet begun. The apex takes the shape of a round mountain with

a high crest (a high margin) on one side, and a gradual slope on the other. There may be just a shade of depression in the centre of the slope, indicating a potentially cup-shaped development. However, on the opposite side a low margin does not actually develop. If the carpel primordium is about one tenth of a millimetre high, it consists entirely of a thick high margin, which represents the half of a cup-shaped, vertical, structure. However, its basal field remains circular, and its inside adaxial part can be detected at the base of the lateral margins of the young carpel as a cross connection. The whole functional carpel, and its cleft, is formed by the high margin only.

DISCUSSION

The present limited investigations permit some suggestions for lines of further research. A provisional hypothesis may be as follows. The meristematic field of origin of the carpels on the floral apex is circular in outline. In this regard a special case is when the entire floral apex changes into a single carpel. In the next developmental stage the border of the primordium is raised as an oblique margin, forming an obliquely cup-shaped organ. However, the meristematic field may first form a convex dome, which then differentiates into a basal stalk-like part and an upper cup-shaped part. By continuing predominant growth of the higher part of the margin and by predominant growth in length, the cup is raised in a vertical position and its mouth becomes a vertical slit which forms the future cleft of the carpel. The growth of the lower part of the margin may be variable according to the species and so may be the cup-like shape of the young carpel. The lower margin may not be formed at all. Moreover it may be that the carpellary field is not formed on the side of the floral apex, the basal outline of the primordium becoming broadly elliptic. As a consequence the lower margin cannot develop on the inside and on the outside only the higher margin gives rise to a carpel primordium which is horseshoe-shaped in cross-section. It should be investigated if there is any correlation between these different grades of development and carpel type. For instance if many-ovulate lateral carpels mostly have no lower margin, or if terminal carpels as well as few to mono-ovulate carpels tend to show a stronger cup-shaped development. It should be remarked that even if there is some – or even considerable – growth of the lower margin, the entire basal region may be surpassed by the extreme dominant growth of the higher margin later on, so that the actual cup-shaped development at the base is no longer traceable. The distribution over the Angiosperm taxa of these gradually different developmental possibilities should be studied.

In this view the carpel is developing like a cup-shaped or partly cup-shaped organ, depending on the degree of the development of the inside part of the initial meristematic field. Mostly the appearance of a 'folded leaflet' is reached at stages above one millimetre. However, sometimes the obliquely cup-shaped form persists in the fully grown carpels.

Evidently the result of this investigation fits better with the theory of Leinfellner (1950), and the conclusions of Rohweder on Ranunculaceae (1967), and those of Endress on Laurales (1972), than with the theory of the American authors cited above.

However, some differences with Leinfellner's theory do exist. In the first place I think

that there is no sharp limit between a basal ascidiate part and an upper plicate part of a carpel, for it is the carpel as a whole which grows as an obliquely ascidiate organ. Apical growth of the periphery (margin) changes gradually into more lateral growth. Probably the division of a carpel in the sense of Leinfellner is the consequence of the method of comparing cross-sections. In the second place a comparison with peltate foliage leaves turns out negatively. In this respect Leinfellner based his opinions on Troll's investigations on peltate leaves (1932), which were reached by the comparison of fully grown leaves and the deduction of developmental changes. However, after the actual developmental and meristematic research done by Roth (1952), the ideas of Troll had to be dropped. According to Roth peltate leaves always originate as bifacial primordia on which later a thickening 'ventral' meristem develops. At the relevant site this adaxial meristem, or Querzone, is activated (incorporated: Hagemann 1970) by the adjacent abaxial marginal meristem of the primordial leaf, so that a continuous marginal meristem is formed, which gives rise to the peltate leaf blade. As such a 'ventral' meristem does not occur the early development of carpels only superficially resembles that of peltate foliage leaves. Because they are based on the incorrect comparison with foliage leaves, Leinfellner's terms peltate, latently peltate, and epeltate, describing the gradually different ways of development, should be replaced by better terms. Possibly ascidiate, or ascidiform, or cup-shaped may serve as a more neutral term for the time being.

According to Eames (1961) an at first crescent-shaped primordium becomes ring-shaped at the base by lateral extension of the basal meristem on the receptacle. However, it is not clear on which observation this opinion was based, nor does it seem that this approach was pushed any further. His interpretation is that in the case of peltate carpels the margins of the conduplicate carpel arise fused proximally (are congenitally concrescent). Eames maintained that such is an advanced condition and that therefore the peltate theory reads the series in carpel form in the wrong direction, namely from peltate to epeltate. In this regard attention was focussed on the genus *Drimys* of the primitive Winteraceae which, in its section *Tasmannia*, is supposed to have ideal conduplicate carpels with unfused margins. However, investigations of Leinfellner (1965), and of Tucker and Gifford (1966), showed that the carpels in the section *Tasmannia* are weakly ascidiate during early development. Therefore Tucker and Gifford criticize the conduplicate carpel theory. Moreover, the *Wintera* section of the genus *Drimys* has cup-shaped carpels even when mature. Also the exemplary conduplicate carpels of *Degeneria*, doubtless a primitive genus of Angiosperms, develop from a cup-shaped primordium according to Swamy (1949). Systematists like Cronquist (1968) and Takhtajan (1969, 1980) tend to disregard the wide-spread occurrence of the peltate (obliquely cup-shaped) development of the carpels, as well as its presence in *Degeneria* and other Angiosperms considered primitive by them. They select one end-stage of development, in which carpels look like folded leaflets, instead of considering the whole development.

Ascidial or cupulate structure of the carpels is claimed to occur in *Nypa* by Uhl (1972), and in *Peperomia* by Tucker (1980). Long (1977), as a paleobotanist, tries to relate the structure of pteridospermous cupules to that of Angiospermous carpels.

In the search for Angiosperm fossils the thesis of an obliquely elongated more or less ascidiform way of development of the carpels might be of interest, especially as cupulate fertile structures are frequent in paleozoic and in mesozoic Pteridosperms which, by

many paleobotanists, are considered as a possible cradle of Angiosperms. The present primary development may indicate that the carpels historically were cupular prior to becoming 'conduplicate'.

REFERENCES

- BAILEY, I. W. & B. G. L. SWAMY. 1951. The conduplicate carpel of Dicotyledons and its initial trends of specialization. *Am. J. Bot.* 38: 373-379.
- CRONQUIST, A. 1968. The evolution and classification of flowering plants.
- EAMES, A. J. 1961. Morphology of the Angiosperms.
- ENDRESS, P. K. 1972. Zur vergleichenden Entwicklungsmorphologie, Embryologie und Systematik bei Laurales. *Bot. Jb. Syst.* 92 (2/3): 331-428.
- 1972. Aspekte der Karpellontogenese. *Verh. Schweiz. Naturf. Ges.* 152: 126-130.
- HAGEMANN, W. 1970. Studien zur Entwicklungsgeschichte der Angiospermenblätter. *Bot. Jb.* 90 (3): 297-413.
- LEINFELLNER, W. 1950. Der Bauplan des synkarpn Gynözeums. *Österr. Bot. Zs.* 97 (3-5): 403-436.
- 1965. Wie sind die Winteraceen-Karpelle tatsächlich gebaut? I. Die Karpelle von *Drimys*, Sektion *Tasmania*. *Österr. Bot. Zs.* 112 (4): 554-575.
- LONG, A. G. 1977. Lower carboniferous pteridosperm cupules and the origin of Angiosperms. *Transactions Royal Soc. Edinburgh* 70: 13-35.
- ROHWEDER, O. 1967. Karpellbau und Synkarpie bei Ranunculaceen. *Ber. Schweiz. Bot. Ges.* 77: 376-432.
- ROTH, I. 1952. Beiträge zur Entwicklungsgeschichte der Schildblätter. *Planta* 40: 350-376.
- SAMPSON, F. B. & D. R. KAPLAN. 1970. Origin and development of the terminal carpel in *Pseudowintera traversii*. *Am. J. Bot.* 57 (10): 1185-1196.
- STEBBINS, G. L. 1974. Flowering plants. Evolution above the species level.
- SWAMY, B. G. L. 1949. Further contributions to the morphology of the *Degeneriaceae*. *J. Arnold Arb.* XXX: 10-38.
- TAKHTAJAN, A. L. 1969. Flowering plants. Origin and dispersal.
- , 1980. Outline of the classification of flowering plants (Magnoliophyta). *The Bot. Rev.* 46 (3): 225-359.
- TROLL, W. 1932. Morphologie der schildförmigen Blätter. *Planta* 17: 153-314.
- TUCKER, S. 1980. Inflorescence and flower development in *Piperaceae*. I. *Peperomia*. *Am. J. Bot.* 67 (5): 686-702.
- TUCKER, S. & E. M. GIFFORD JR. 1966. Carpel development in *Drimys lanceolata*. *Am. J. Bot.* 53 (7): 671-678.
- UHL, N. W. 1972. Inflorescence and flower structure in *Nypa fruticans* (Palmae). *Am. J. Bot.* 59 (7): 729-743.

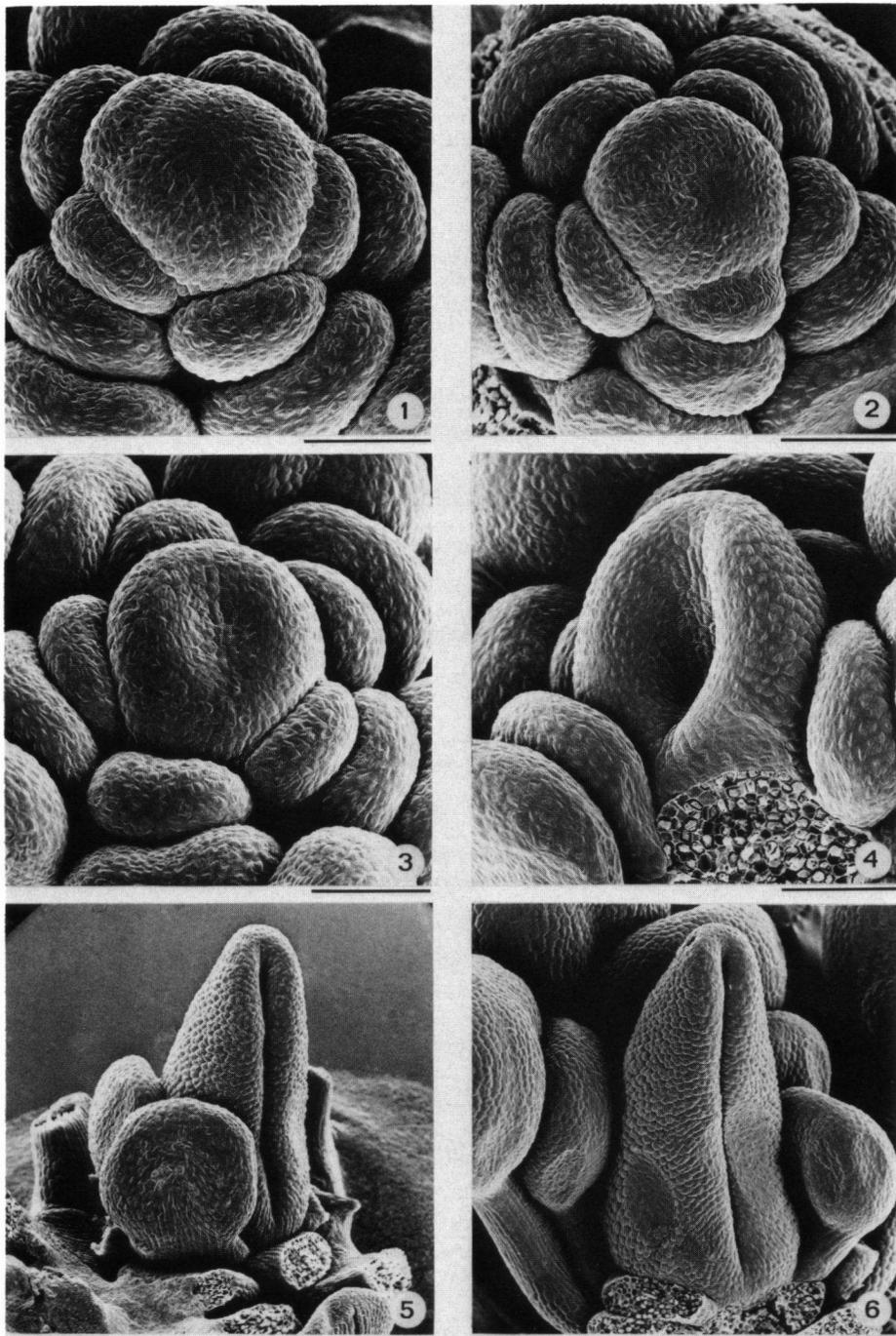


Plate 1. — *Delphinium ajacis*.

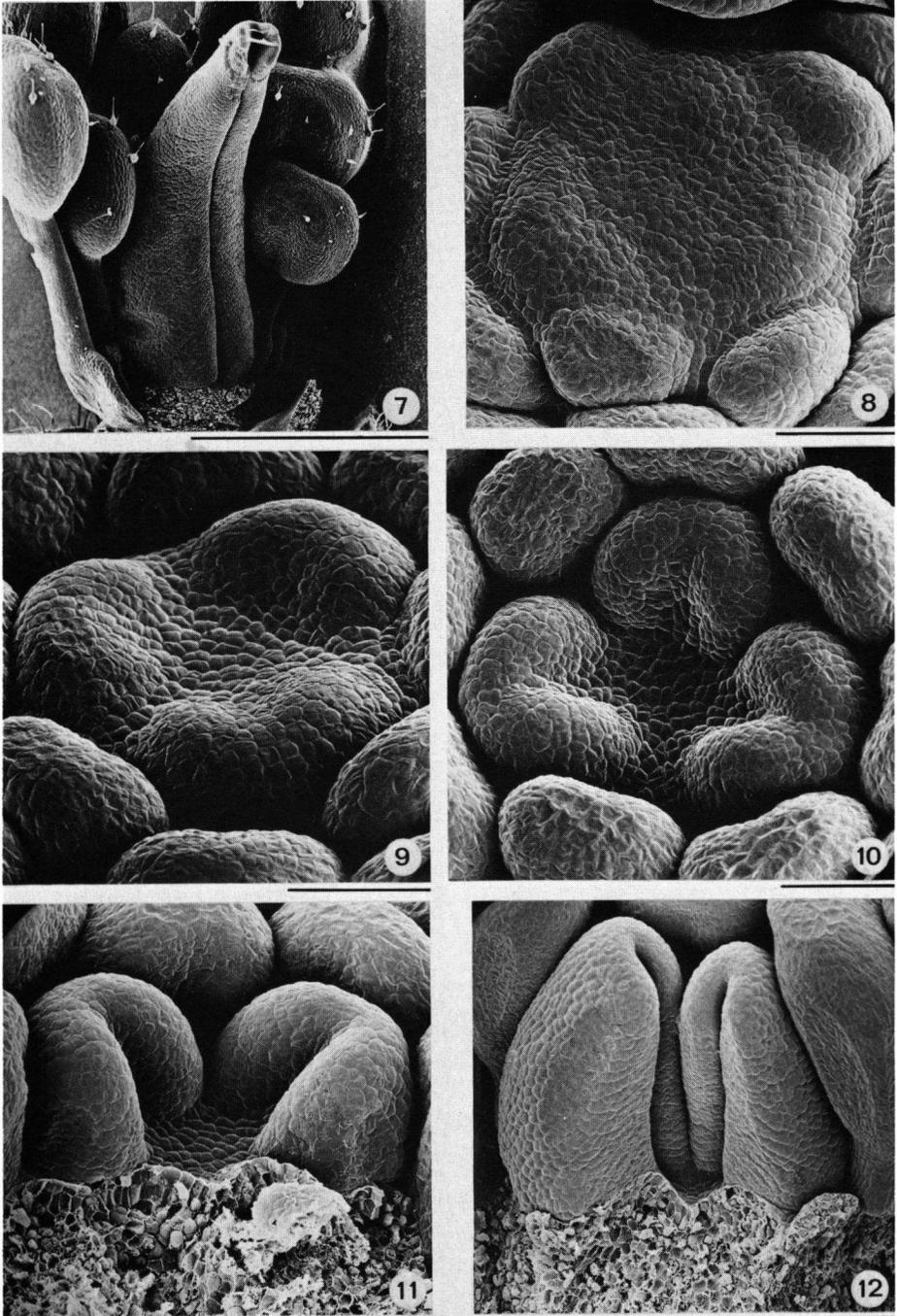
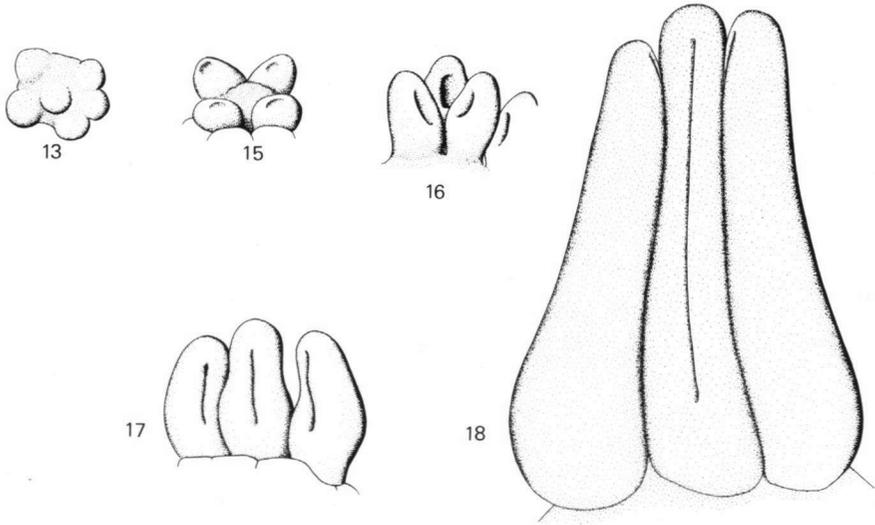
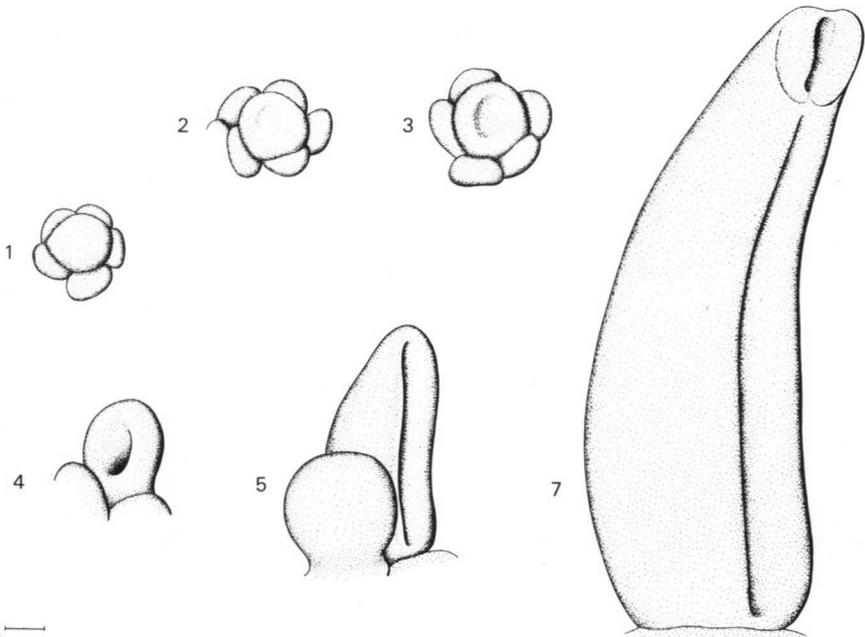


Plate 2. — 7. *Delphinium ajacis*. Scale is 1 mm; 8–12. *Delphinium elatum*.



1/10 mm



1/10 mm

Plate 3. — 1-5.7. *Delphinium ajacis*; 13. 15-18. *Clematis montana*. Scale at all figures is 0.1. mm.

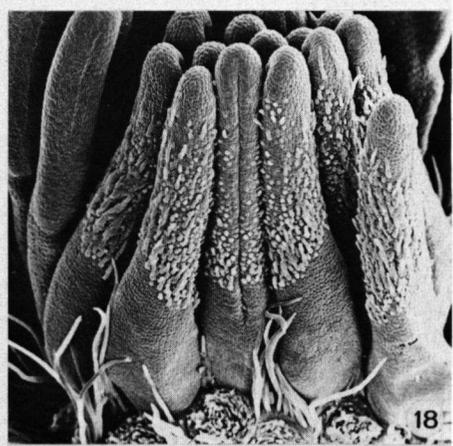
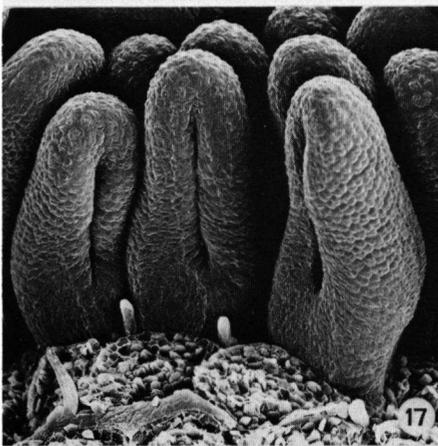
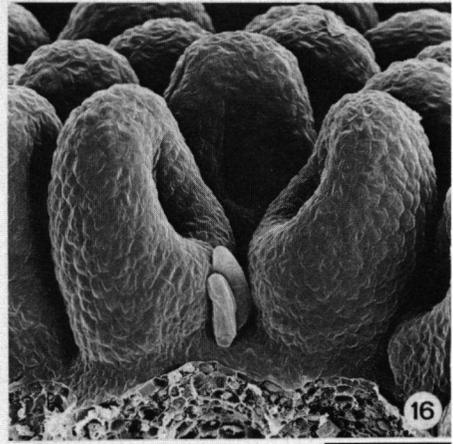
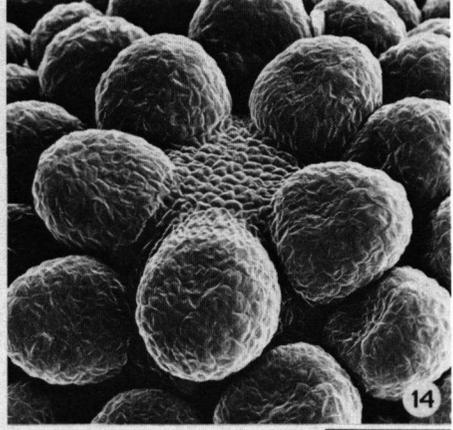
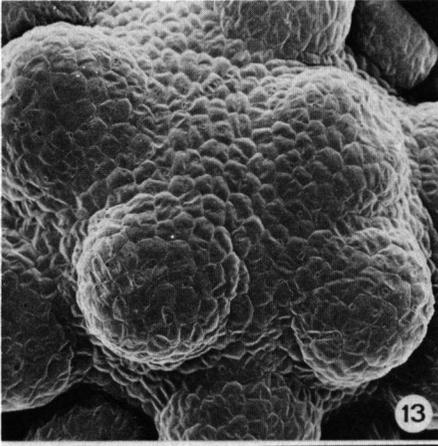


Plate 4. — *Clematis montana*. Scale at 18 is 1 mm.

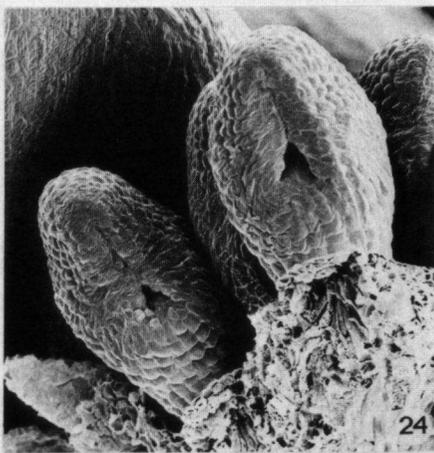
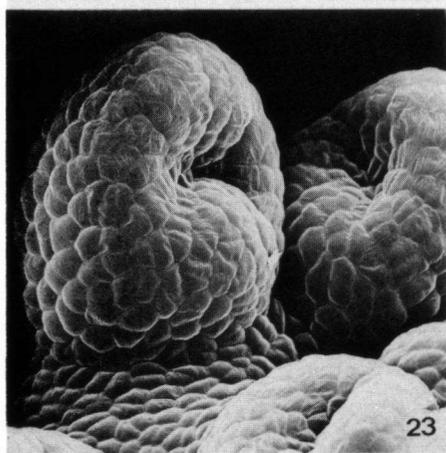
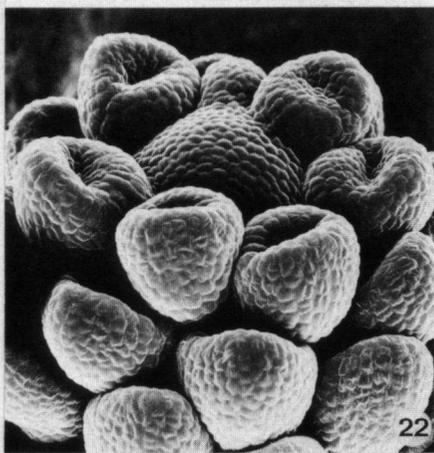
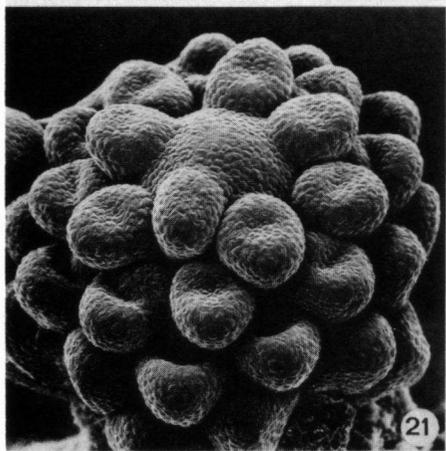
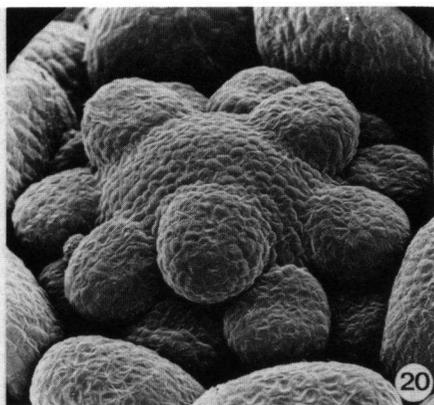
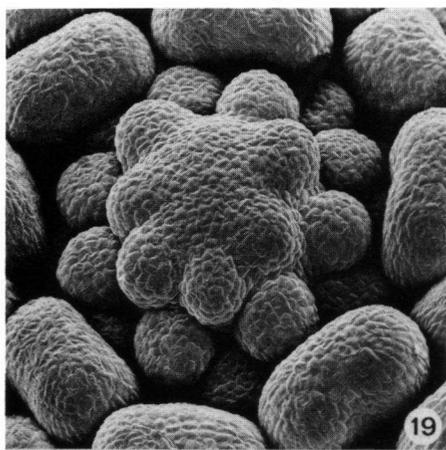


Plate 5. — *Ranunculus acris*.

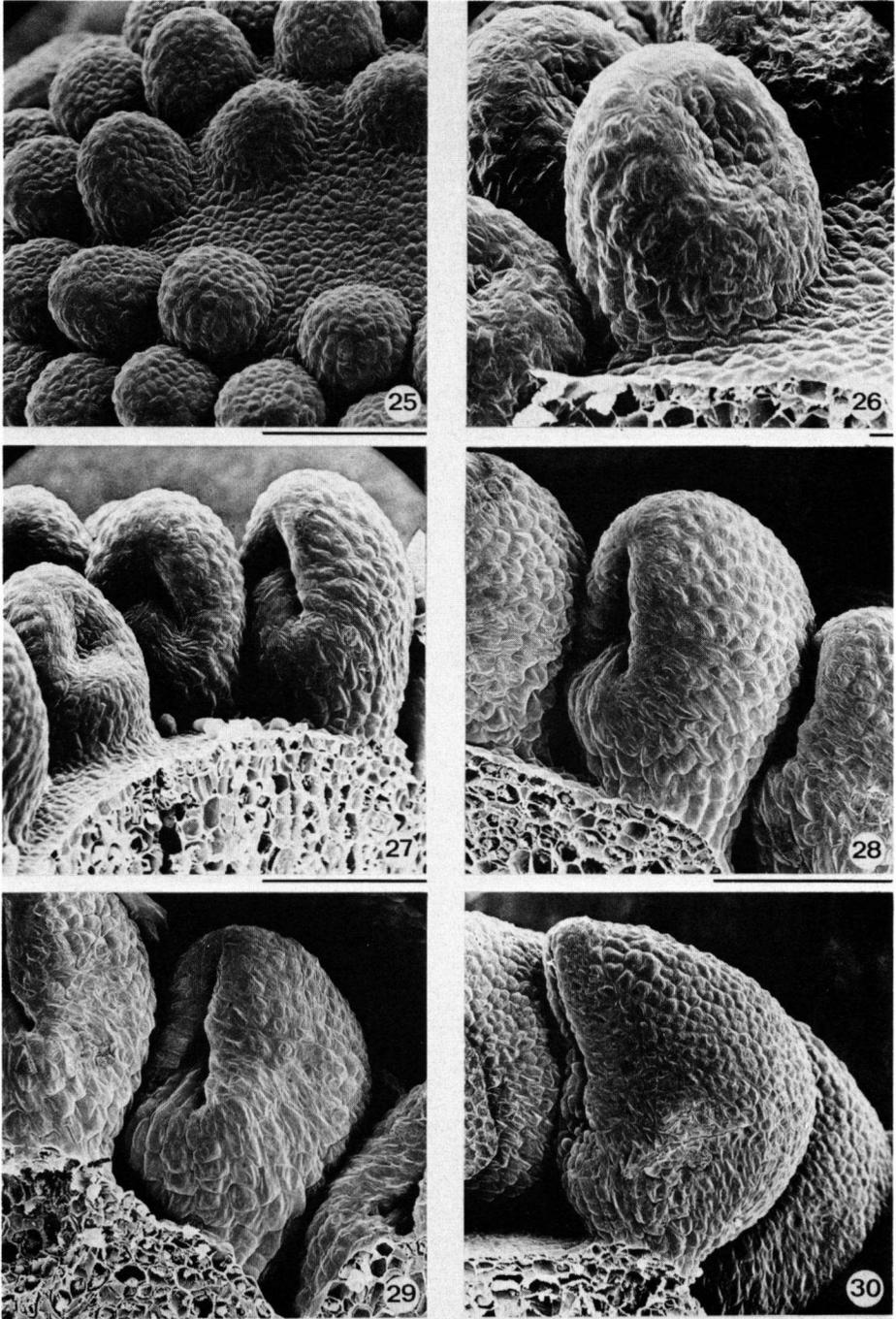


Plate 6. — *Ranunculus sceleratus*. Scale at 26 is 0.01 mm.

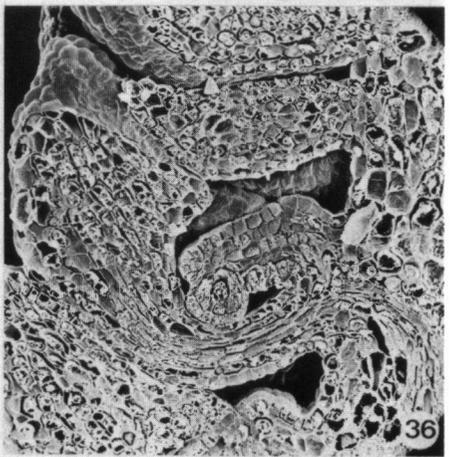
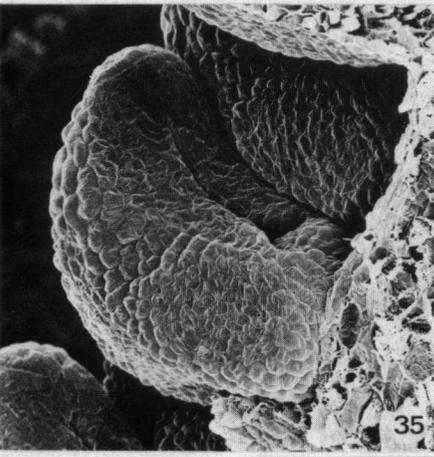
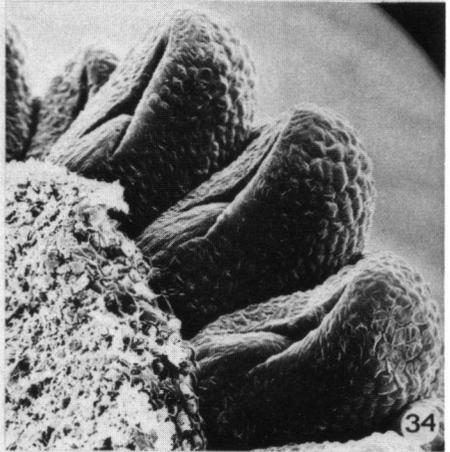
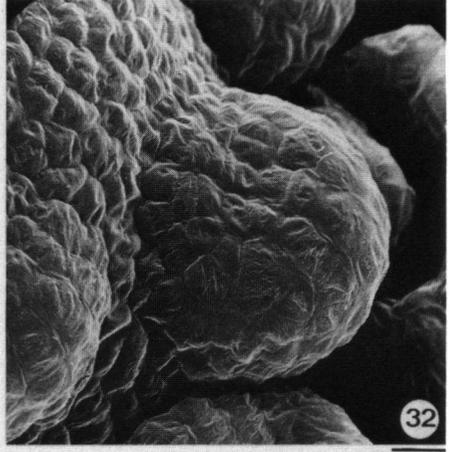
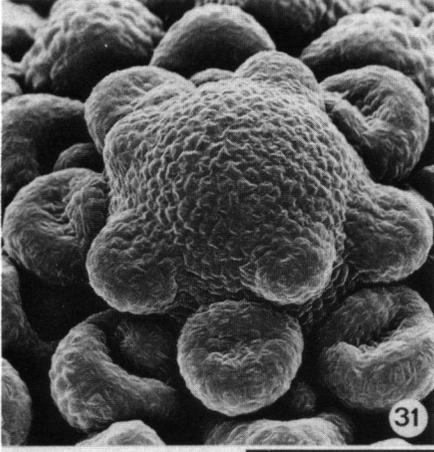


Plate 7. — *Myosurus minimus*.

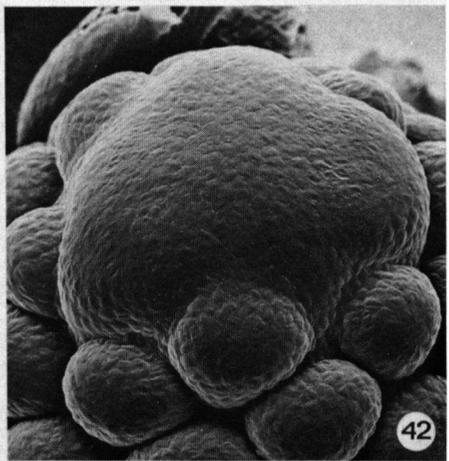
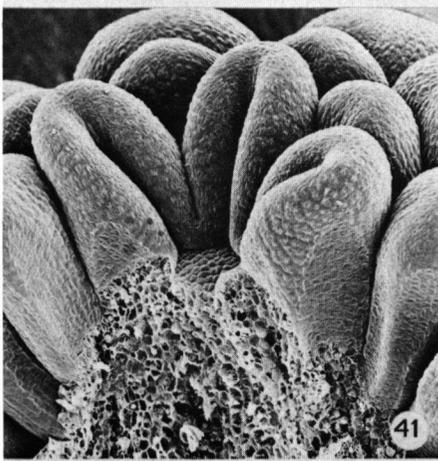
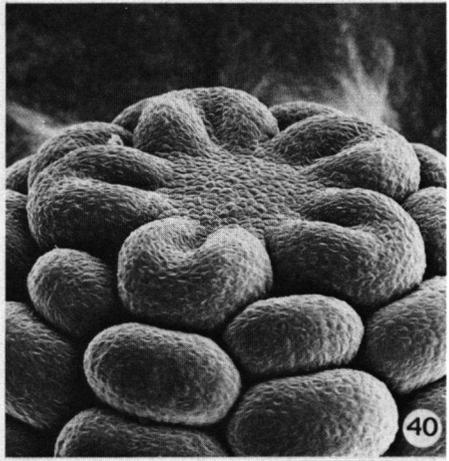
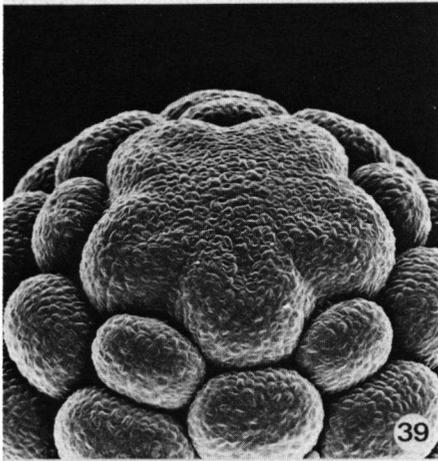
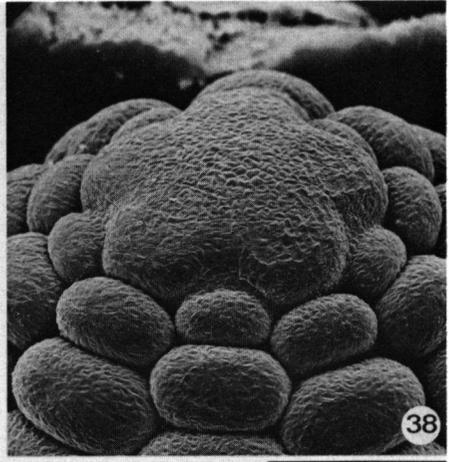
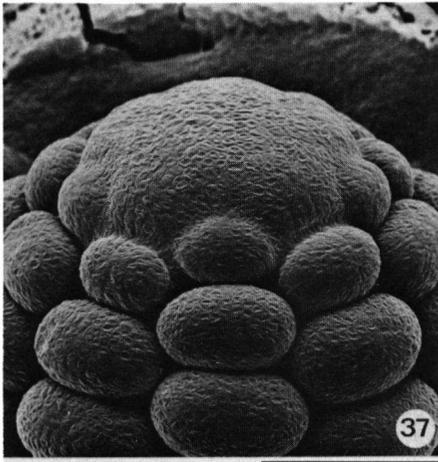


Plate 8. — 37–41. *Aquilegia vulgaris*; 42. *Helleborus foetidus*.

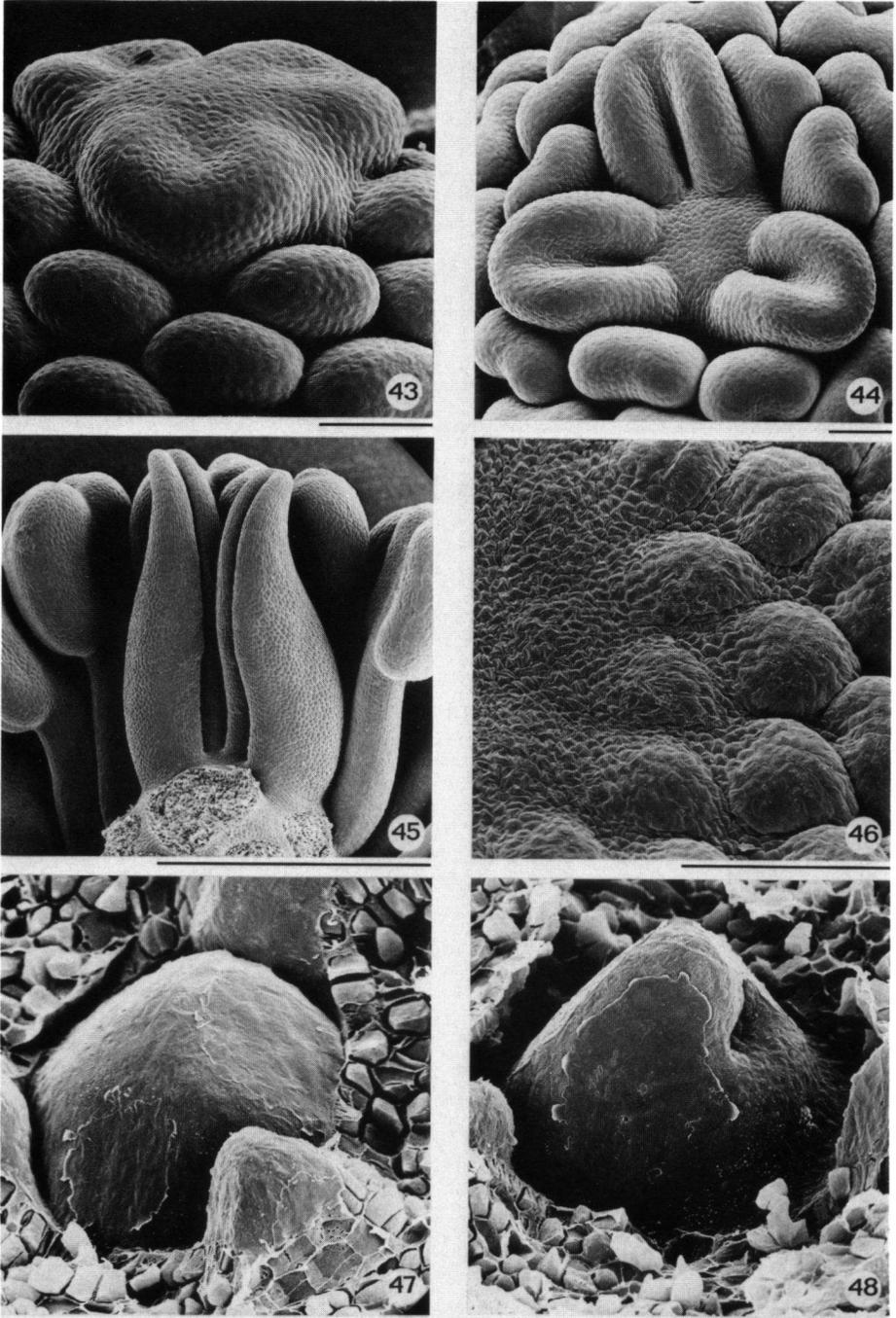


Plate 9. — 43–45. *Helleborus foetidus*. Scale at 45 is 1 mm.; 46 *Annona montana*
47–48. *Nectandra angustifolia*. Scale at 47 is 0.01 mm.

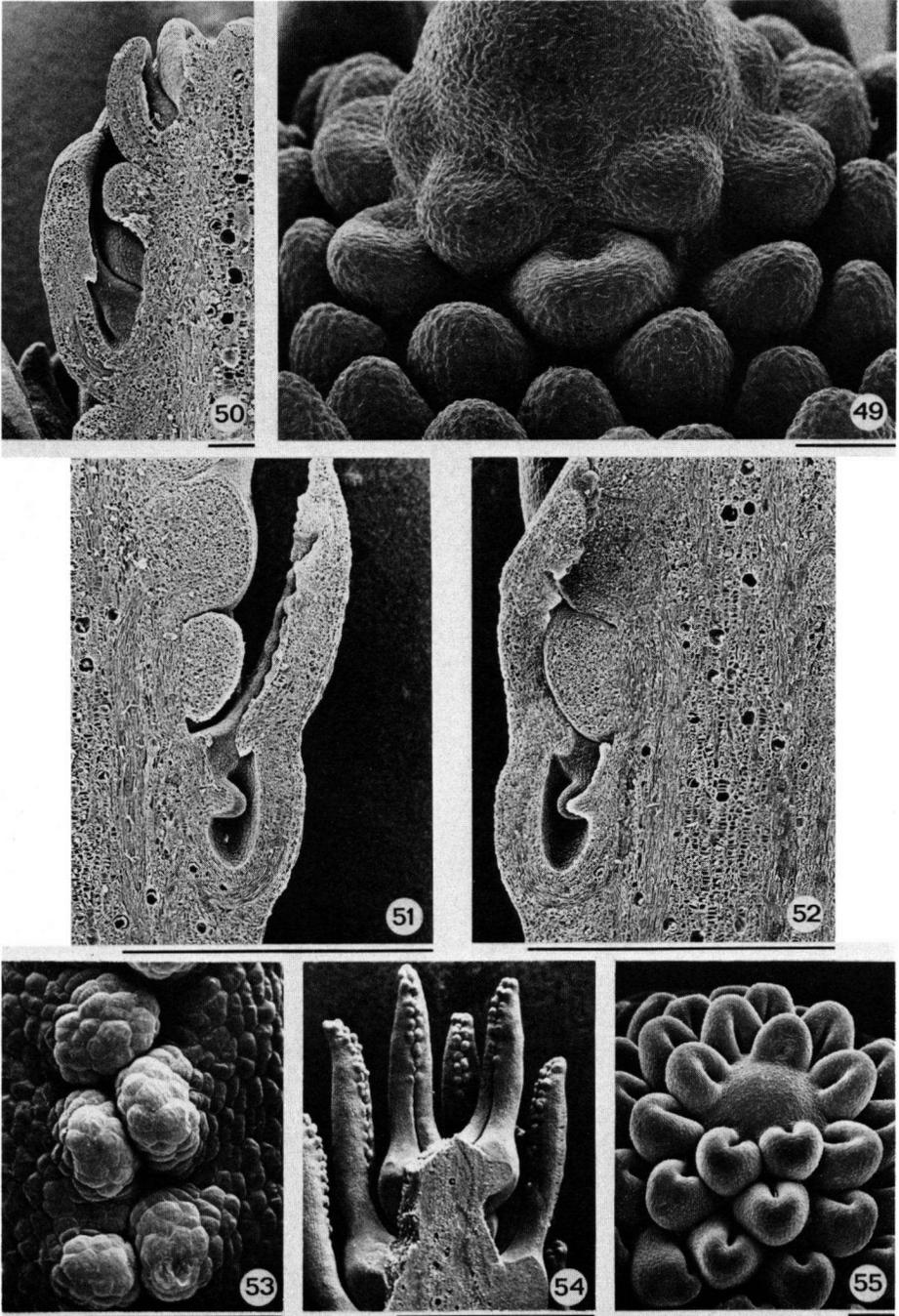


Plate 10. — 49–54. *Magnolia stellata*. Scale at 51–52 is 1 mm.; 55. *M. thompsoniana*.

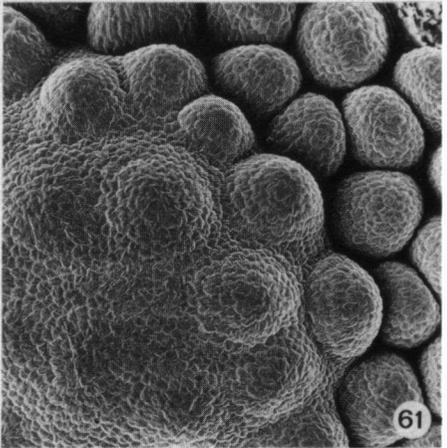
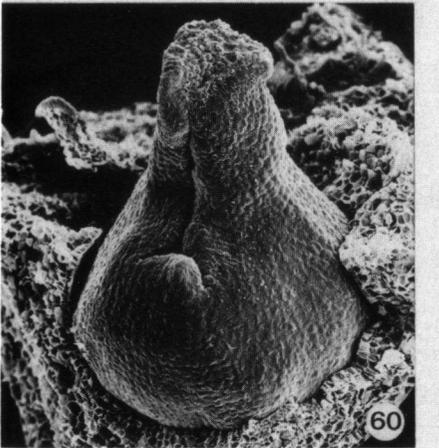
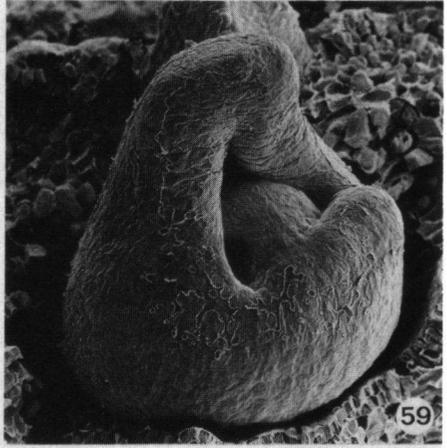
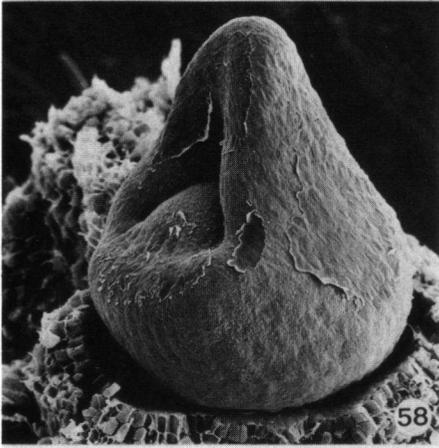
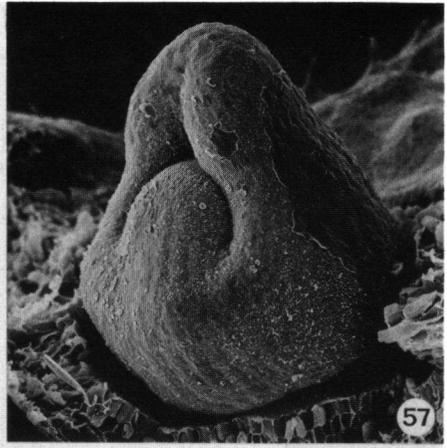
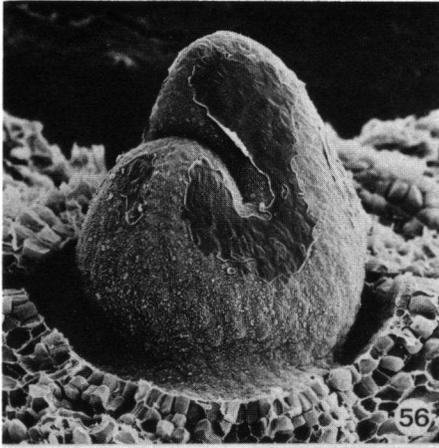


Plate 11. — 56–60. *Nectandra angustifolia*; 61. *Rosa* spec.

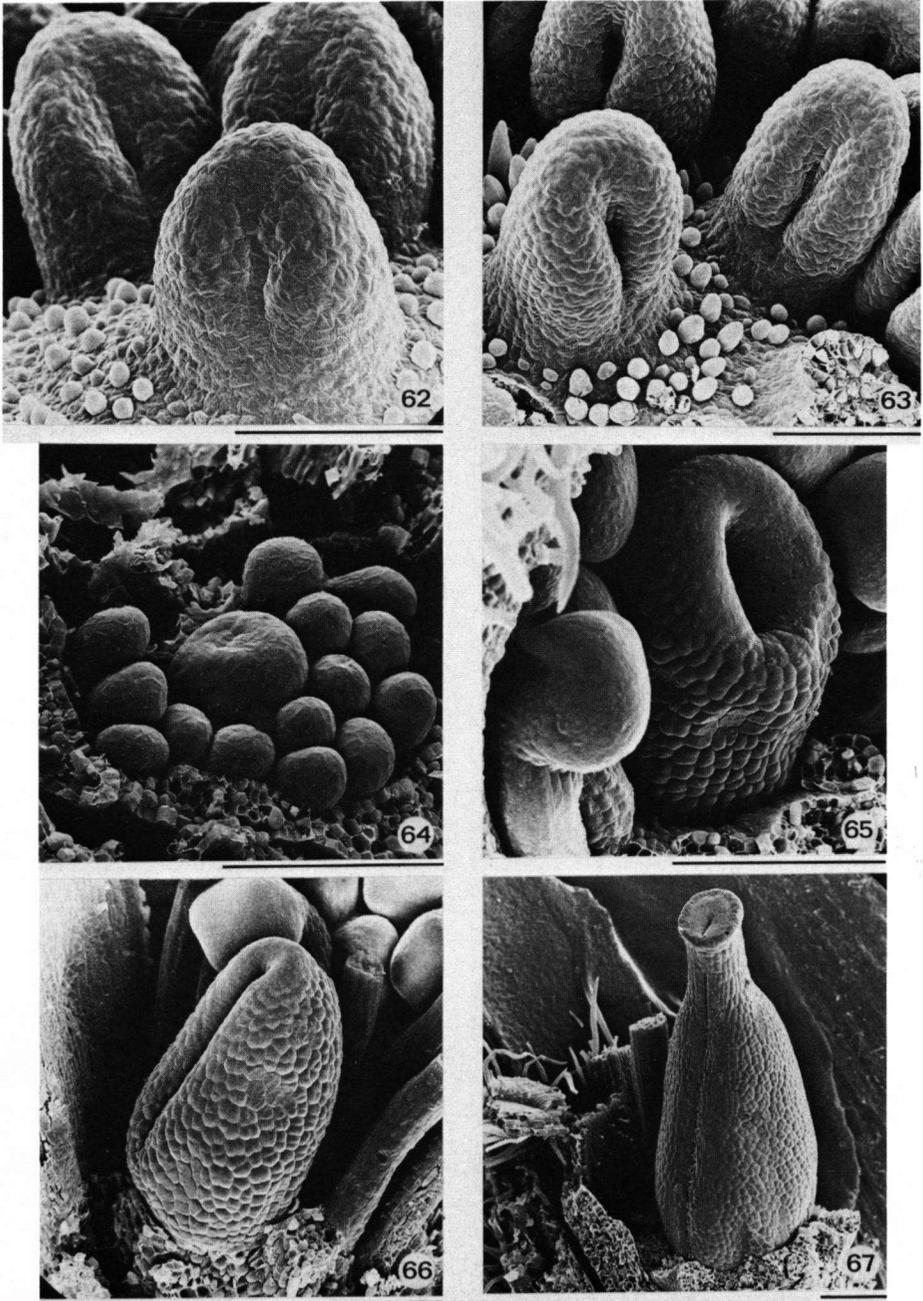


Plate 12. — 62-63. *Rosa spec.*; 64-67. *Albizzia spec.*

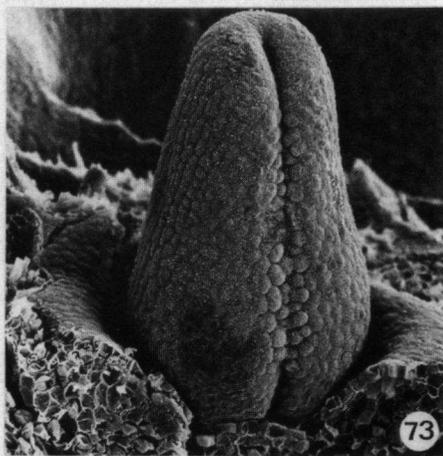
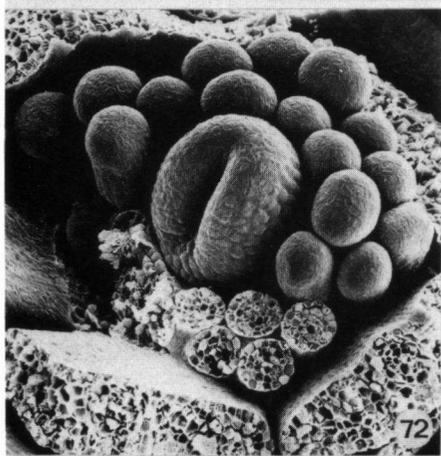
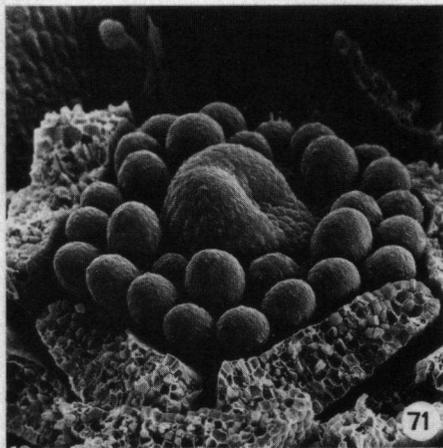
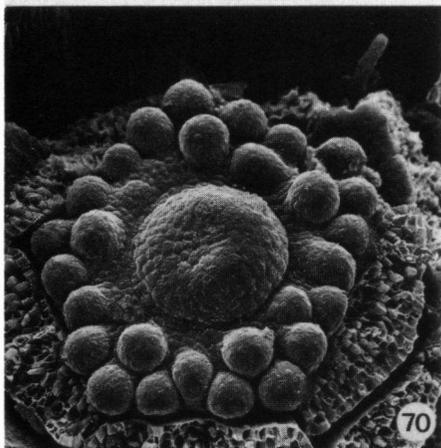
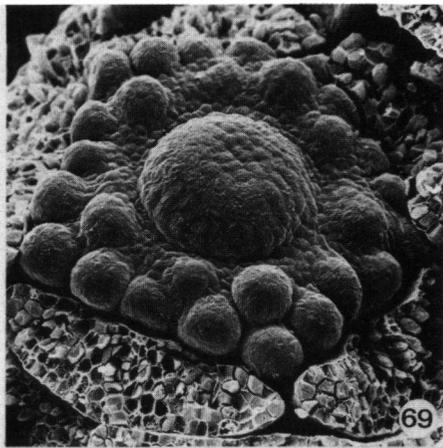
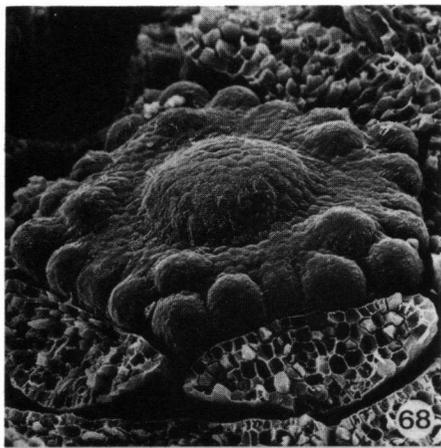


Plate 13. — *Calliandra tetragona*.

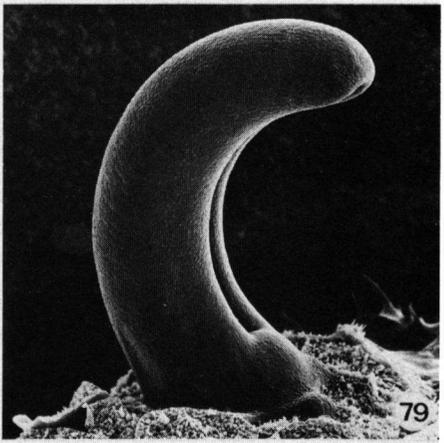
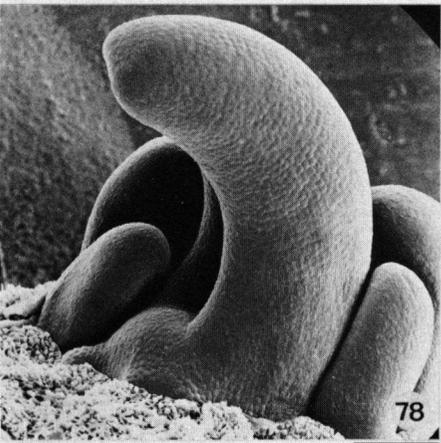
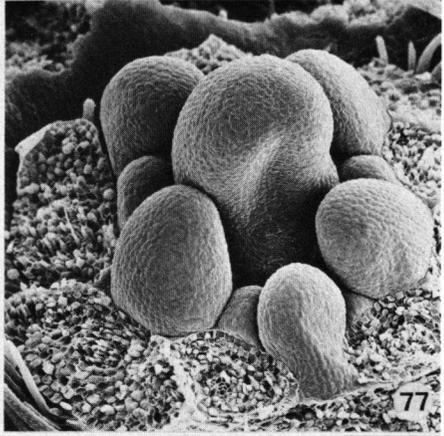
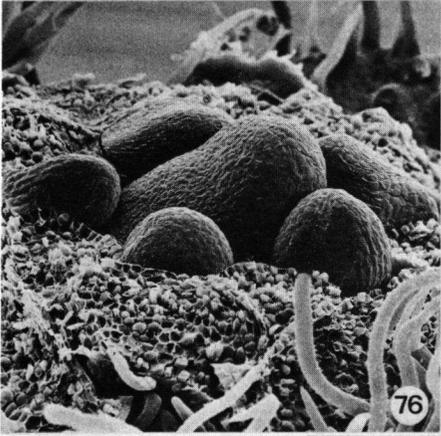
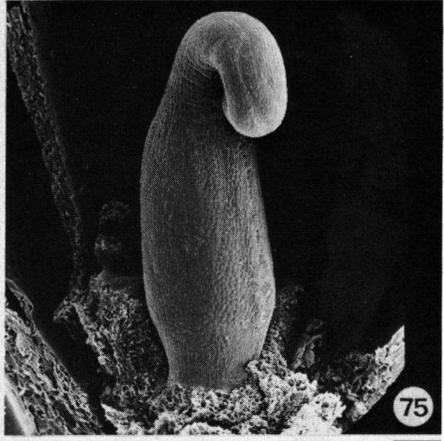
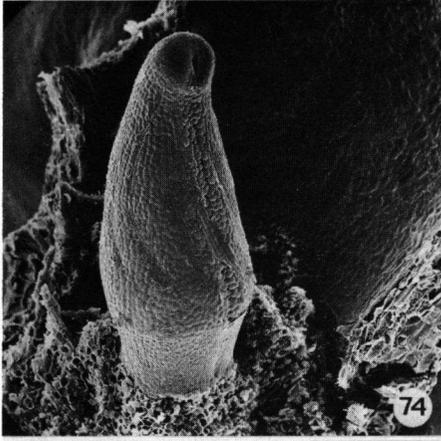
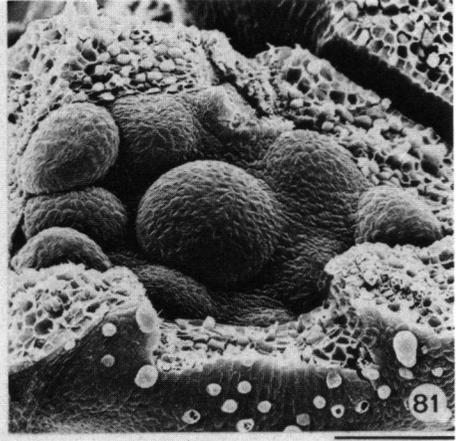


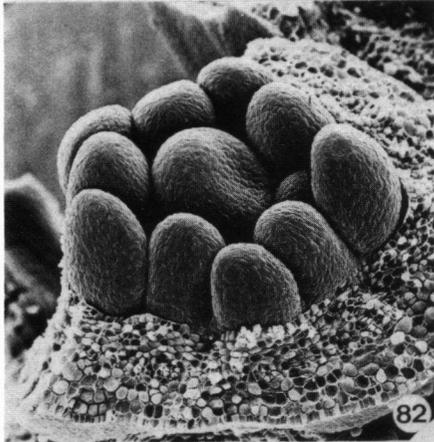
Plate 14. — 74–75. *Calliandra tetragona*; 76–79. *Cassia spec.*



80



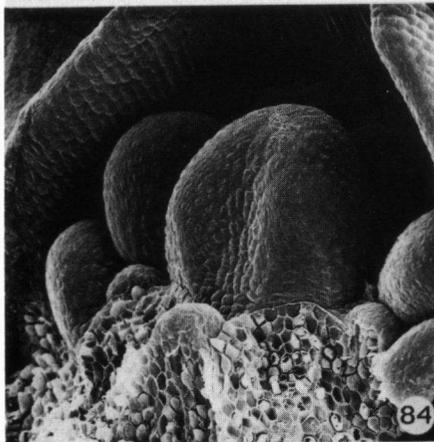
81



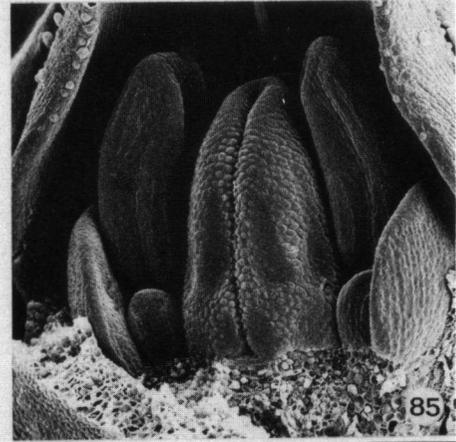
82



83



84



85

Plate 15. — 80. *Cassia* spec. Scale is 1 mm.; 81–82. *Erythrina crista-galli*; 83–85. *Lupinus albus*.