

## FLORAL MORPHOLOGY OF STEMONACEAE AND PENTASTEMONACEAE

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### SUMMARY

The early development of the stamens in *Stemona* and *Stichoneuron* is similar, in spite of significant differences in the adult stages. Moreover, as the peculiar gynoecia in both genera are chiefly similar, their mutual affinity seems substantiated. It is concluded that *Stichoneuron* is very close to *Croomia*, so that these genera can be merged. However, *Pentastemona* is different. In its androecium it shows a corona-like development of the basal staminal region (like *Peliosanthes*, Convallariaceae). Therefore, the removal of *Pentastemona* from the Stemonaceae is corroborated. The late differentiation of its stamens into extensions that contact the stigma, as well as the inferior position of the ovary, suggest a relationship with *Trichopus* (Trichopodaceae) and *Stenomeris* (Stenomeridaceae).

### INTRODUCTION

This paper is mainly based on specimens that were collected after Van Steenis (1982) described *Pentastemona* and placed the new genus in the Stemonaceae. The new material made observation of developmental stages in the scanning electron microscope possible. The new data are compared with the report by Van Steenis, and the affinity of *Pentastemona* with Stemonaceae or other taxa within Liliales or Dioscoreales is discussed. Dahlgren et al. (1985) and Takhtajan (1987) inserted the Stemonaceae and *Pentastemona* in the Dioscoreales, the former authors adding that *Pentastemona* should deserve family rank. Finally, Duyfjes established the Pentastemonaceae (1991). The Stemonaceae represent monocotyledons with tetramerous (dimerous) flowers in its three genera, *Stemona*, *Stichoneuron*, and *Croomia*. *Pentastemona* has pentamerous flowers. However, the gynoecia are oligomerous in all genera. *Croomia* will not be described in this paper. *Croomia pauciflora* has been investigated by Tomlinson & Ayensu (1968), and a comparison with *Stemona* and *Stichoneuron* was presented by Rogers (1982). The present report accompanies the treatment of Stemonaceae and Pentastemonaceae for Flora Malesiana (Duyfjes, 1992).

### MATERIAL

*Dioscorea hirtiflora* Kunth: Zenker 1890 (L).

*Peliosanthes teta* Andr. subsp. *humilis* (Andr.) Jessop: Kerr 17977 (L); cult. Bot. Garden L (unknown provenance).

*Pentastemona egregia* (Schott) Steen.: *Bogner 1724*, cult. Bot. Garden L and M. — *P. sumatrana* Steen.: *de Wilde & de Wilde-Duyffjes 20311* (L), *21399* (L).

*Stemona australiana* (Benth.) C.H. Wright: *Wightman 1063* (DNA). — *S. collinsae* Craib: *Maxwell 75-94* (AAU). — *S. javanica* (Kunth) Engler: *de Wilde & de Wilde-Duyffjes 21410*, cult. Bot. Garden Bogor. — *S. kerrii* Craib: *Umnat 93* (BKF 32037). — *S. tuberosa* Lour. var. *ternatensis* Duyffjes: *de Wilde & de Wilde-Duyffjes 21411* (L). — *S. tuberosa* Lour. var. *tuberosa*: cult. Bot. Garden Bogor. — *S. wardii* J.J. Smith: *Delavay 1835* (L).

*Stenomeris borneensis* Oliver: *Rahmat si Toroes 3175* (L).

*Stichoneuron caudatum* Ridley: *Bogner 1789*, cult. Bot. Garden M.

*Tacca spec.*: cult. Bot. Garden Zürich.

#### DESCRIPTIVE PART

##### *Stemona tuberosa*

The four tepals are arranged into two pairs; the lower outer one develops earlier than the upper inner one. In addition, one tepal of each pair is slightly larger than the other. The larger pair of tepals and the stamens in front of these are located on the far sides of the bilaterally symmetrical flower primordium (figs. 2, 5).

The stamen primordia are ellipsoid bodies that are slightly folded inwards. Their rate of development is about equal. The residual floral apex between them is very small, which might indicate protandry. The stamens originate as separate simple organs, showing at first no trace of the two kinds of later extension (fig. 2). A young flower bud in longitudinal section (fig. 3) shows the stamens separately and knuckle-shaped at the top, sterile on the outside, and with two bisporangiate thecae laterally on the inside. The young stamens are provided with two median extensions, a sterile apex both on the out- and on the inside. The latter originates from a median apical connection that bridges the two primordial thecae transversely (figs. 3, 4).

Two halves of flowers in older stages of development show that the stamens are connected basally by a low ring-shaped meristem (figs. 1, 4). Epibasally, the stamens are for a short distance less broadened laterally; these parts may be considered as filaments. As to the fertile part the stamens are lanceolate, sterile abaxially, and with a synangium on the adaxial side. The synangium is composed of two bisporangiate protruding thecae that upwards are sterile and are transversally connected in the median line (figs. 1, 4, 6). Later on, at anthesis, the intercalary development of this thecal connection gives rise to the adaxial sterile synangial peaks that grow freely upwards and are not connected to the outward parts of the stamen. Moreover, the four peaks of a single flower, growing slightly inwards, become connected at their apices, thus building a bridge over the floral axis with four piers (fig. 1). The apices on the outside of the stamen primordia have grown into four large outward extensions. Each stamen has one unbranched vascular bundle running upwards into the outward peaks. Thus, the lateral broadening of the stamens does not give rise to vascular bundles. Also the synangial peaks are without vascular bundles (cf. Swamy, 1964).

At later stages the four stamens broaden considerably in lateral-abaxial direction so that the stamens touch each other laterally at the fertile level. Moreover, a median

sterile longitudinal ridge originates between the thecae of each stamen (figs. 1, 6). The resulting four median inward longitudinal ridges may finally touch each other in the floral axis. In this way, four lengthwise spaces arise between the stamens in which the thecae of two neighbouring stamens are located (Lachner-Sandoval, 1892: 'Längscanäle'). When the pollen sacs open, the pollen are kept in these spaces, presumably awaiting pollen collectors. Entrance to these spaces is given by way of the four 'windows' between the synangial peaks above. According to Lachner-Sandoval there is no entrance to the 'Längscanäle', but I disagree with him.

Young stages of the gynoecium (figs. 7, 8) show the rise of an elliptic meristematic wall in the axis of the outer tepals and surrounding the floral apex. This wall is on one end higher than on the other (the 'dorsal' and 'ventral' end, respectively). This primordial gynoecium grows upwards, overarching the apex, especially so on the dorsal end so that the dorsal half is closed and the ventral one remains open through a slit. Later on, around the uppermost region of this slit dermal cells start differentiation into stigmatic hairs. In the lower region of the slit the margins of the gynoecium are both slightly extended in a young stage. Thus, the impression is given of two more members building up the gynoecium together with the 'dorsal' member. The further upward growth of the terminal part of the young gynoecium is so much advanced that the greater part of the slit is shifted on the slope of the gynoecium toward one side (the 'ventral' side). Lachner-Sandoval also noticed the beginning of the gynoecium wall on one end from which he concluded that the flower has but one carpel.

Later on the bottom of the gynoecium is manifestly convex and is covered by young ovules which are anatropous and have their micropylae directed towards the outside. Arillar tissue starts to develop around the ovule bases, from the funicle as well as from the distal part of the outer integument. It develops into vesicular hairs. Finally, the seeds hang from the tough base of the two-valved fruit.

### *Stemona australiana*

The stamens resemble those of *S. tuberosa*, but are less broad (figs. 9, 10). The thecae are located proximally and laterally. A stamen consists largely of a slender subulate sterile extension of the proximal fertile region. This extension is rounded triangular in transverse section and does not look winged. The connective between the thecae develops into an inward rim that may also spread to the basal part of the stamen. The stamens are connate at the base.

The main difference in stamen structure with *S. tuberosa* is the absence of the upward sterile extension of the synangium. However, one of the few stamina investigated showed a small sterile synangial continuation, in which the transverse connection between both bisporangiate thecae was manifest (fig. 10).

The gynoecium is identical to that of *S. tuberosa* (fig. 11).

### *Stemona collinsae*

The large lanceolate stamens (fig. 12) have two adaxial submarginal thecae along most of their length. A transverse section of the stamen on the level of the thecae is similar to that in *S. tuberosa*. The stamens, too, have a short filamental part that is not laterally broadened, but at their bases they are connate. The stamen, including the

syngangium, tapers toward the apex; the thecae are sterile there (fig. 13). The part of the connective between the thecae is provided with a prominent adaxial ridge which reaches up to half the height of the stamen. At that level the thecae continue upwards as two lines of thickened sterile tissue that give evidence at some places of being composed of two sterile pollen sacs (fig. 14). At the distal tapering region of the syngangium the sterile tissue of the two thecae is continuous in the median line, but does not project freely upwards like in *S. tuberosa*. Also on the basal narrow part of the stamen a median ridge is present. Thus, the main difference with the stamens of *S. tuberosa* is the absence of the large, free, outer extensions of the stamen and the free extensions of the syngangial parts.

One older flower had a gynoecium much like that of *S. tuberosa*, but it showed a somewhat four-lobed stigmatic part.

### *Stichoneuron caudatum*

The dimery of the tepals and stamens is rather distinct, and can be shown in ontogeny by the difference in time of origin, in insertion, and in size of the primordia (figs. 15, 16). In flower buds the tepals are sharply bent inwards; over the large thecae they reach the young gynoecium with their tips. Presumably, the flowers are also protandrous. At anthesis some tepals are lifted up just a bit and the anthers open. A mass of pollen may be enclosed, sticking together by the pollen tubes.

The stamens appear to be of the usual form, composed of anther and filament, thus being different from the special stamens of *Stemona*. Yet, there is similarity in detail. Four short and variously broad stamens are inserted on the hypanthium of the perigynous flower (fig. 17). They narrow downwards and remain free. Two reniform thecae are attached on the inside of the broader, apical, sometimes bilobed part of the stamen. The thecae are protruding (figs. 22, 23). On the salient outside of the apical part of the stamen there is a field marked by one- or two-celled epidermal papillae. This is the location of the outward extension of the stamens of *Stemona*. Developmental stages (figs. 18–21) show that this region originates from the proximal part of the connective. It is also shown that on the base of the young stamens short filamental parts develop later. In *Stichoneuron caudatum* filaments and tepals are covered with numerous uniseriate multicellular hairs. After anthesis the anthers hang downwards by means of the vascular bundle of the filament. The tissue around this bundle deteriorates (observations in FAA).

The gynoecium resembles that in *Stemona*, but it is half inferior, and the placentation is not basal. The primordium (figs. 24–26) grows upwards as a conical wall, of which one radius is the apical slit. The opposite radius is closed and later on grooved on the outside. Possibly, this groove opens during fructification. The upper region of the slit is surrounded by primordial hairs which are the beginnings of the uniseriate stigmatic hairs of much later stages. The middle part of the slit is occluded by dermal papillae. The sides of the lower part close later, presumably by epidermal fusion. The insertion of the primordial ovules is submarginal along the middle part of the slit (fig. 25); their distance from the margins is relatively large, as the slit is deep in young stages. Later on, as the space for the developing ovules becomes much larger (the ovary s.s.), the placentation appears 'apical'. There are two ovules on either side of the slit, and a third one on one side which does not develop further.

The ovules are anatropous; their micropylae are directed toward the wall of the ovary. At anthesis the stylar-stigmatic region is filled with dermal hairs terminating into a tuft of uniseriate hairs which also become stigmatic. Downwards the hairs are continuous with similar hairs inside the upper part of the ovary along the 'dorsal' side, and at that level they meet such hairs derived from the funicles of the ovules.

### *Pentastemona egregia*

The five stamen primordia originate on the inside of the rim of a concave floral apex (fig. 30). They are separate trapezoid organs of unequal size, and are located in front of the tepals which are also of different size. Tepals and stamens seem to originate in one 2/5 spiral.

Later on, when primordial pollen sacs can be distinguished, the primordial anthers are raised on a pentagonal 'androecial zone' (fig. 31). The earlier, higher parts of this zone are the staminal regions. They bear five protruding pairs of thecae on their margins and are connected to one another by the later developing, lower parts of the androecial zone. The staminal regions grow upwards on the outside and the synangia bend slightly inwards (figs. 32, 41). These extensions seem comparable with the young outward peaks of the stamens in *Stemona tuberosa*. However, in *Stemona* these extensions are prolongations of the 'connectives', whereas in *Pentastemona* they grow from the 'staminal region' below the anther. It is difficult to correlate mature areas with earlier stages. In a later stage the upward extension curves inwards, covering the top of the connective between the thecae which has become wide (figs. 33, 34). Also, the connective forms an adaxial ridge of sterile tissue, like in *Stemona* but shorter. These median protuberances contact the stigma on its upper side. Strikingly, the upward extensions do not only curve inwards, but they continue also their growth downward, to fuse finally with the stigma by epidermal fusion (figs. 34, 35). A similar fusion was noticed in *Stenomeris borneensis*, but here the apical stamen extensions are very slender and their origin is unknown.

As a result the androecium is subdivided into five staminal regions and five interstaminal spaces (figs. 29, 35). These spaces are bordered on their lateral sides by the median inward ridges of the connectives contacting the stigma, and on the outside by the lower regions of the androecial zone. The spaces are in open connection with each other below the anthers. When, by the lifting of some tepals, the flowers open, the thecae open up into the interstaminal spaces. The flowers seem protandrous. Just opened flowers with empty pollen sacs, or with pollen sticking only along the wall, were seen.

After flowering, the interstaminal spaces appear as gaps (Van Steenis: pouches) as seen from above. This is due to late growth processes. The androecial zone, after late broadening of the hypanthium, changes into a broad ring covered with papillate cells (fig. 35) between the tepals and stamens. Similar cells cover the whole inside of the flower. Possibly, these structures may have an attractive function in pollination. The existence of a similar zone in *Peliosanthes* (Convallariaceae) is figured by Larsen (1966), and reproduced by Dahlgren et al. (1985). I noticed that the cuticle has an exuding function. Burkill (1960) reported the existence of New World *Dioscoreas* with "the torus spread flat about the flower centre as a rather thick food furnishing area for visiting insects."

The concave floral apex develops into a funnel-shaped hypanthium forming an inferior ovary in the centre (figs. 27, 28). The young ovary has parietal rows of ovules, and three or four apical lobes which later on fuse into a rather large stigma. If there are three lobes one of them may be larger than the other two. The rows of ovule primordia are placed submarginally of ovarian regions that may be delimited in the ovary below the stigmas. Downwards in the ovary the rows may become mixed up. Later on, the larger ovules lose their place in a row.

#### *Pentastemona sumatrana*

The differences in inflorescence and flower structure are presented by Van Steenis (1982).

As in *P. egregia* the stamen primordia develop on an 'androecial zone' on the rim of a concave apex (fig. 36) close to the young tepals, and they are followed by the primordial gynoeceum. This zone grows upwards into five staminal regions carrying the anther primordia (fig. 37). Later on, the staminal regions are connected laterally by growth of the interstaminal regions (fig. 38). The staminal regions enlarge and increase in thickness outwards (fig. 38), then produce apical extensions that grow farther upwards, overtopping the synangia, and curve towards the stigma (fig. 39). Finally the extensions fuse epidermally with the stigma (figs. 40, 41). By later hypanthial growth the androecial zone becomes broad and covered with papillose cells as in *P. egregia*.

*De Wilde & de Wilde-Duyfjes 21399* bears fully developed inflorescences, in which the last few flowers seem to be male. The structure of these male flowers is the same as that of the earlier flowers, also as regards the pollen; only the hypanthial gynoeceum is reduced. Concerning the inflorescence structure and polygamy, see Duyfjes (1991).

### COMPARISON AND DISCUSSION

#### *Androecium in Stemona*

*Stemona* species share a peculiar structure of their stamens which, however, differs in detail. A short proximal part may be considered the filament. At the very base of it there is usually an irregular lateral connection to the adjacent filaments. The stamens may have two kinds of apical extensions, which is rare in flowering plants. Two extensions as in *S. tuberosa* occur also in *S. japonica*, *S. javanica*, *S. prostrata*, and *S. wardii*. It suggests a duality in stamen structure. Arguments for the singleness of these stamens are the origin as one primordium, found in *S. tuberosa*, and the presence of one unbranched vascular bundle. Ontogeny shows that the inward extension is due to the transverse connection of apically sterile thecae of a very young protruded synangium followed by all-over elongation. I think Swamy (1964) was wrong in negating the thecal origin by lack of ontogenetic data.

The outward elongation should represent the prolongation of the connective tissue of a stamen with a protruded synangium. Similar outward extensions, foliar in appearance, are recognized in *Costus* (Zingiberaceae; Leinfellner, 1956), in which the stamens also have protruded synangia. In *Costus igneus*, as in *S. tuberosa*, these

stamen extensions originate early in ontogeny. In *S. collinsae* the slender thecae have sterile extensions in the same way, being thickened above but remaining attached to the winged connective. The same occurs in *S. kerrii*, but here the very long sterile prolongation of the thecae gives rise to a thick elliptic part above that is free from, but close to the leaf-like connective. As such, the stamens of *S. kerrii* are intermediate. Thus, the stamens of all *Stemona* species have thick, broadened and extended connectives, median adaxial ridges, and protruded thecae with sterile parts that extend into free or connate special bodies. However, mutual proportions differ strikingly.

Late in ontogeny the stamens of *S. tuberosa* broaden considerably, and median ridges are larger in the fertile region of the thecae. These tangential and median wings of the four stamens in one flower close up and touch, so that lengthwise interstaminal spaces develop in which the pollen of two neighbouring thecae are shed. In addition, the flowers become a kind of window-flowers by the terminal fusion of the inward apical extensions of the stamens. The pollen shed in the interstaminal spaces would be accessible via these windows. Possibly, the inward extensions separate in a later stage. However, as yet nothing is known of the floral biology of *Stemona*, particularly about a special function of the stamen extensions. An interesting detail is the presence of bulbous epidermal cells on the rims of the lateral margins and on the median ridge in the stamens of *S. kerrii*. The reader is referred to Duyfjes (1991) for more data on colour and odour of the flowers.

#### *Androecium of Stichoneuron caudatum*

A comparison shows that the bidirectional development as in *Stemona tuberosa* (figs. 1–4) is reverse in *Stichoneuron caudatum* (figs. 18–23). In the latter the synangial part overtops the external stamen extension. This extension is represented by a bulge of tissue covered with special hairs, as described. A transverse section of that region in full-grown stamens is much like figure 35c, given by Schaeppi (1939) for the anther of *Dioscorea sativa*. The top of the anthers of *Stichoneuron caudatum* shows bulges that may be compared with a minor form of the synangial inward extensions in *Stemona* (figs. 18, 19).

#### *Androecium of Pentastemona*

The five interstaminal spaces lodging the thecae of two adjacent stamens are comparable with those in *Stemona tuberosa*, but they develop in different ways.

The apical outward extensions of the staminal regions grow toward the stigma and fuse there. In *Stemona* such extensions flare outwards. By this feature and by the inferior ovary the flower of *Pentastemona* differs clearly from that of *Stemona*. It is not known whether pollen are shed, exposed, or sheltered in the interstaminal spaces, but some free pollen was found there in fixated flowers. Actually, nothing is known on floral biology as yet.

In *Pentastemona* the basal lateral connections of the stamens originate early, in *Stemona* late. Later on this androecial tissue is circular, cushion-like, and with papillose cells. It suggests an attraction zone at the bottom of the campanulate flower. A similar ring-shaped zone was noticed in *Peliosanthes*, as described above, but here it is more clear, like a corona, possibly because the hypanthium is shallow.

### Gynoecium

The gynoecia of *Stemona* and *Stichoneuron* are similar except for the position of the ovules. The form of the gynoecium is unusual. Its structure may be compared with the model of a one-carpelled gynoecium by considering that the dominance of the dorsal side is limited. As a result the 'dorsal' side is not overtopping the 'ventral' side, the structure being conical with the 'ventral' slit in one radius (in a plane bisecting the flower). The slit is the opening of the gynoecium, which is not completely shifted toward the ventral side. Style-stigma elongation of this structure is also limited. Dermal hairs border the slit of the gynoecium; in the apical part they become stigmatic, forming a tuft of hairs that changes into a fluid drop later.

The different position of the ovules, basal in *Stemona* and apical (submarginal) in *Stichoneuron*, is not understood. It might be helpful if the ontogeny of the placentation in *Stemona* species with few ovules were investigated.

The primary development of the gynoecium of *Stemona tuberosa* starts in the form of a single, oblique, low, elliptic wall. This structure shows two 'lateral' loci of preferred growth, one on either side of the slit. This observation suggests a transition from trimery to monomery, which is known to occur in gynoecia of Restionaceae and Gramineae (Philipson, 1985; Kircher, 1986), and also in Araceae (Eyde et al., 1967; Barabé et al., 1987). However, comparative ontogenetic data are scarce.

### Systematics

A comparison of our data with those given by Tomlinson & Ayensu (1968) leads to the conclusion that the floral morphology of *Stichoneuron caudatum* and *Croomia pauciflora* is very similar. On this ground the genera can be merged.

*Croomia/Stichoneuron* and *Stemona* share an unusual type of gynoecium, apart from the insertion of the ovules. Stemonaceae have no common character in aril structure, formed by vesicular hairs as described by Van Steenis (1982). The aril consists of uniseriate hairs in both *Stichoneuron* and *Croomia*. Only *Stemona* has vesicular hairs. The stamens are characterized by short filaments, protruding thecae, and lateral broadening, mainly of the anther region. The broadening may pass into various outward extensions at the connective, and into median ridges. Various adult stamen structure can be traced back to similar ways of development. For that reason there is a basis for affinity between *Stemona* and *Croomia/Stichoneuron* also on the ground of the androecium structure. Presumably, the various adult structures are associated with special floral biologies which are hitherto unknown. As to floral biology, the curious 'interstaminal spaces' in *Stemona* and *Pentastemona* draw special attention. They might lead pollinators to interior space below in which pollen is present.

*Pentastemona* differs from *Stemona* and from *Croomia/Stichoneuron* in its inferior ovary, the prominent stigmatic lobes, and the extensions of the stamens which curve inwards and fuse with the stigmatic lobes. These extensions originate from the broadening of the proximal staminal regions (not from the connectives as in Stemonaceae) in a 'corona'-like fashion (figs. 38, 39). These three peculiar structures corroborate the position of *Pentastemona* in Pentastemonaceae. The floral characters of Stemonaceae and *Pentastemona* are summarised in table 1. Data on pollen, ovules, and seeds are included.

Table 1. Summary of floral characters in Stemonaceae and *Pentastemona*.

	<i>Stemona</i> spp. div.	<i>Stichoneuron caudatum</i> ( <i>Croomia pauciflora</i> )	<i>Pentastemona</i> 2 spp.
Perianth	4 tepals	4 tepals	5 tepals
Gynoecium	superior	half inferior	inferior
carpels	3-1, 1 cell	1, 1 cell	3, 1 cell
stigma	hairs	hairs	lobes
placenta	basal	submarginal → apical	submarginal → parietal
Stamens	4, basally connate	4, free	5, basally connate
connective	broad, winged	broad, not winged	broad, not winged
extension	large extension of connective not contacting stigma	small extension not contacting stigma	extension of basal stami- nal part contacting stigma
syngonium	extension evident / reduced	extension reduced	extension absent
ridge	median adaxial	absent	median adaxial
spaces	interstaminal	absent	interstaminal
Pollen <sup>1</sup>	average 28.0 µm	average 26.6 (29.4) µm	average 16.1 µm
aperture	monosulcate	inaperturate (monosulcate)	inaperturate
sexine	tectate	tectate	intectate
infractectum	columellate / granular	columellate	indistinguishable
ornamentation	diverse	microreticulate (reticulate)	scabrate
Ovules	extended chalaza	normal chalaza	normal chalaza
Seeds <sup>2</sup>	outer epidermis of outer integument tanniferous	unknown	transparent
ridges	by cell division of inner epiderm of outer integument	unknown	by cell enlargement of inner epiderm of outer integument
aril	vesicular hairs	uniseriate hairs	vesicular collar

1) From Van der Ham (1991).

2) From Bouman &amp; Deventer (1992, this issue).

Some remarks should be added on a possible affinity of *Pentastemona* with genera outside the Stemonaceae. Firstly, the Ophiopogoneae should be considered. The systematic position of this group in the Convallariaceae (Liliales) is disputed (Stützel et al., 1991). *Peliosanthes* flowers have a violet corona-like ring with exuding function. The ontogeny of this ring is similar to that of the androecium of *Pentastemona*. I also discovered rings with six lobes in staminal radii in one *Peliosanthes* species. However, apical extensions and fusions with the stigma do not occur in *Peliosanthes*, and the gynoecium is also different. Therefore, this similarity in androecium

structure could be based on convergence. Secondly, some genera placed near the Dioscoreaceae (Dioscoreales) draw attention. The flowers of *Stenomeris borneensis* have a multiovulate inferior ovary passing into a tubular androecial hypanthium above. Apart from tepals the latter has six stamens on its rim, separated by areas with hairs. Also a large stigma is enclosed below in the tube. The thick and broad stamens are curved downwards with outwardly directed (adaxial) thecae. The stamens terminate into linear extensions which reach downwards toward the stigma and fuse there with it. The ontogeny is unknown. Also the genus *Trichopus* should be investigated fully. The anthers join edge to edge, making a roof over a chamber into which pollinating insects should enter (Burkill, 1951). This has been confirmed by Sivarajan et al. (1990). Nagarajo Rao (1955) figured a transverse section of the anther, which shows the lateral broadening of the outward connective tissue as well as the median inwards outgrowth of the connective. Burkill mentioned that "the filament is prolonged into a process which projects forwards between the stigmas." A transverse section given by Kale & Pai (1979) corroborates that observation. These descriptions are reminiscent of *Pentastemona*. In *Tacca spec.*, by incurving, thickening and broadening but not extension of the connective, the stamens become contiguous with the stigma, between the stigma lobes. Thus, six separate interstaminal entrances are created leading downwards to a circular hypanthial space around the style-stigma which is provided with a light-coloured bottom. Also within Dioscoreaceae special flowers occur, as in *Dioscorea hirtiflora* (Burkill, 1960). I found that, if one of the external tepals is removed, an elliptic opening is disclosed between two inner tepals. Through that gap a stamen is seen having an adaxial protruding anther, an apical extension, and another outward abaxial extension (or curve?) halfway up. The flower morphology of Dioscoreaceae is poorly known.

Comparative morphology which includes development – if applied to the genera mentioned above and allied genera – may reveal a series of different but comparable specializations in the androecium that are related to special floral functions. A possible close resemblance of *Pentastemona* to those rare genera that are considered to be satellites of the Dioscoreaceae (*Trichopus*, *Stenomeris*) should be investigated (cf. Huber, 1991: 104).

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## EXPLANATION OF THE PLATES

(Figures 1–41; white scale bars are 1 mm; black bars are 0.1 mm)

Plate 1. *Stemona tuberosa*. – 1: Two stamens with basal connation, short filament, broad apically extended connective, median ridge, apical synangial extension, dehiscent thecae on one side of the ridge. – 2: Four stamen primordia on floral apex, tepals removed. – 3: Androeceum of halved flower older than in 2, young stamens showing outward extension of connective, synangial part with apical cross-connection of thecae. – 4: Androeceum of halved flower older than in 3, broadening stamens with apical extension; apical synangial connection of sterile thecae develops into inward apical extension. Primordial gynoeceum at the base.

- Plate 2. 5–8: *Stemona tuberosa*. – 5: Two pairs of primordial tepals. – 6: Transverse section of anther in stage of photo 1, indicating the ‘interstaminal spaces’ at the sides. Vascular bundle in the middle. – 7 & 8: Two successive stages of primordial gynoecia with excentric opening and possibly trace of trimery in 8 (7 is partly cut off).  
9–10: *Stemona australiana*. – 9: Halved young flower. Stamens connected at base. Undulating median adaxial ridge. Small apical synangial extension at left stamen. Large apical outward extensions. Young gynoecium at the base. – 10: Detail of 9.
- Plate 3. 11: *Stemona australiana*. – Top of gynoecium with tuft of stigmatic hairs (cf. photo 9).  
12–14: *Stemona collinsae*. – 12: Stamen with large winged anther part and median ridge, thecae prolonged into sterile part. – 13 & 14: Details of 12. 13: Apical thecal connection; 14: transition of fertile and sterile synangial region.  
15–17: *Stichoneuron caudatum*. – 15: Four stamen primordia (one severed). – 16: Halved bud. Dimery of tepals and stamens. Gynoecium in the middle. – 17: Halved pre-anthesis stage, perigynous half-inferior ovary. One theca of right stamen removed. Subapical extension with bulging hairs, narrow filament. Ovules related to excentric slit (the slit not precisely sectioned).
- Plate 4. 18–23: *Stichoneuron caudatum*, successive stages of stamen development. – 18: Primordial filament at base. Apical extension at each theca. – 19: Primordial outward extension of connective, apical part of synangium. – 20 & 21: Origin of the difference between extension of connective and filament. – 22: The regions last mentioned get different epidermal hairs. This anther is clearly bilobed. – 23: Anthesis stage with pollen germinating in situ.
- Plate 5. 24–26: *Stichoneuron caudatum*, stages of gynoecium development. – 24: Surface view with excentric slit. – 25: Primordium like 24, not precisely sectioned through the whole slit. Submarginal ovule primordia. – 26: Surface view of older stage. Tuft of stigmatic hairs culminating the slit. Epidermal fusion of the slit.  
27–29: *Pentastemona egregia*. – 27: Young bud halved. ‘Interstaminal space’ on the right. Near staminal radius on the left. Inferior gynoecium. – 28: Transverse section of ovary. – 29: Base of tepal tube at anthesis. Interstaminal (dark) spaces. Three stigmatic lobes in the middle. Androecial zone with bulging epidermal cells, its extensions fusing with stigmatic lobes.
- Plate 6. 30–35: *Pentastemona egregia*, stages of androecium. – 30: Five primordial stamens on the rim of hypanthial apex, the androecial zone. – 31: By development of the androecial zone the young stamens are laterally connected. – 32: Outward extensions of the staminal parts of the androecial zone bent inwards, covering median ridges on the anthers. – 33: Detail. The androecial zone has become a hypanthial region with bulging epidermal cells. Stigma lobes in the middle. – 34: The extensions reach the stigma. Interstaminal space. – 35: Halved flower. Attractive field at the base of campanulate tepals, interstaminal spaces, stigma, and dehisced thecae.
- Plate 7. 36–41: *Pentastemona sumatrana*, developmental stages. – 36: Tepal and stamen primordia on a convex apex, probably in one quincuncial spiral. – 37: Young stamens (synangia + staminal base) on rim of hypanthium between tepals and primordial stigmatic parts (the androecial zone). – 38: The androecial zone (staminal + interstaminal) enlarges. Its staminal regions start extension upwards. Stigma lobes in the middle. – 39: Connective broadens, the extensions grow over them. The stigma lobes close. – 40: The extensions are adjacent to the stigma lobes. Their fusion. – 41: Halved bud; interstaminal space at left, extension touching stigma at right. Inferior ovary and parietal bitegmic ovules.

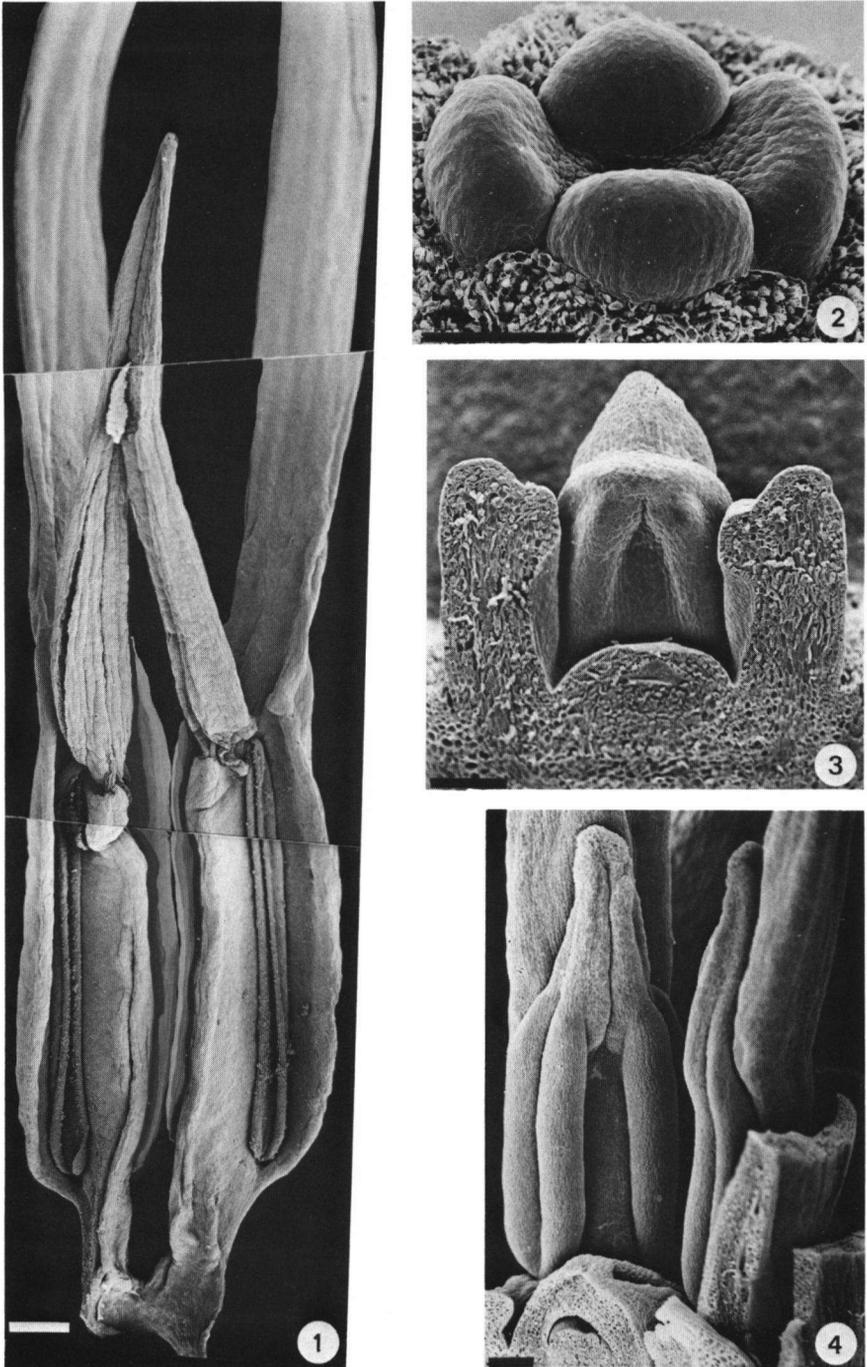


Plate 1 (figs. 1-4; legend on page 491)

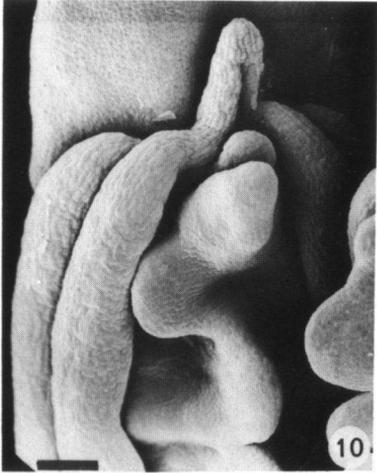
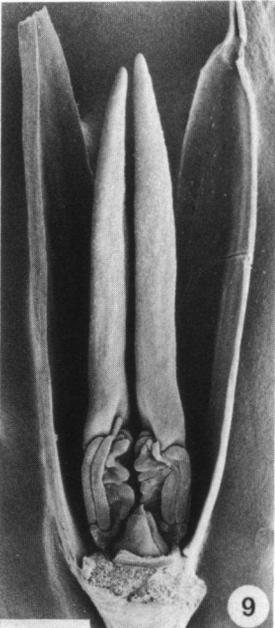
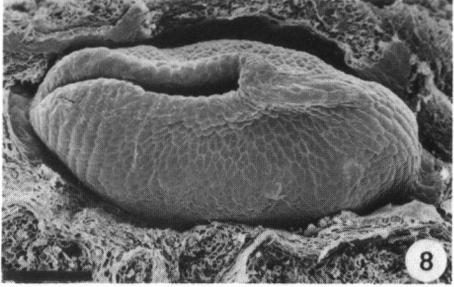
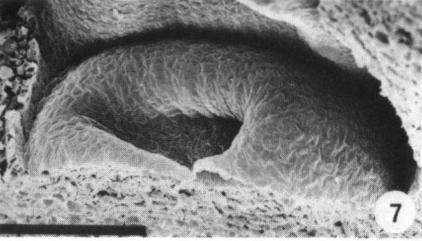
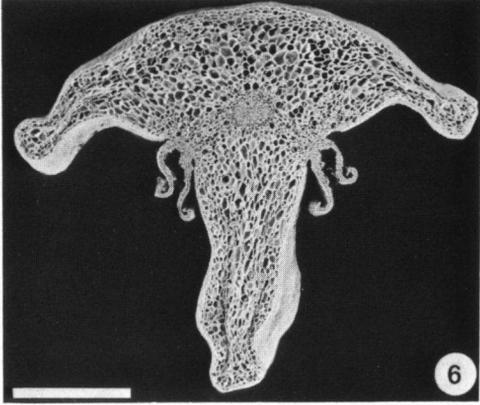
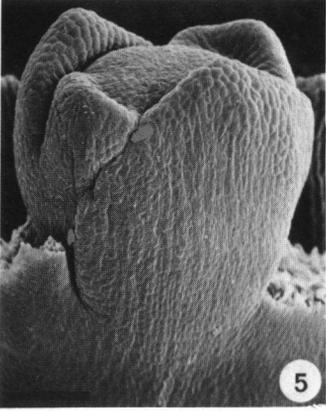


Plate 2 (figs. 5-8; legend on page 492)

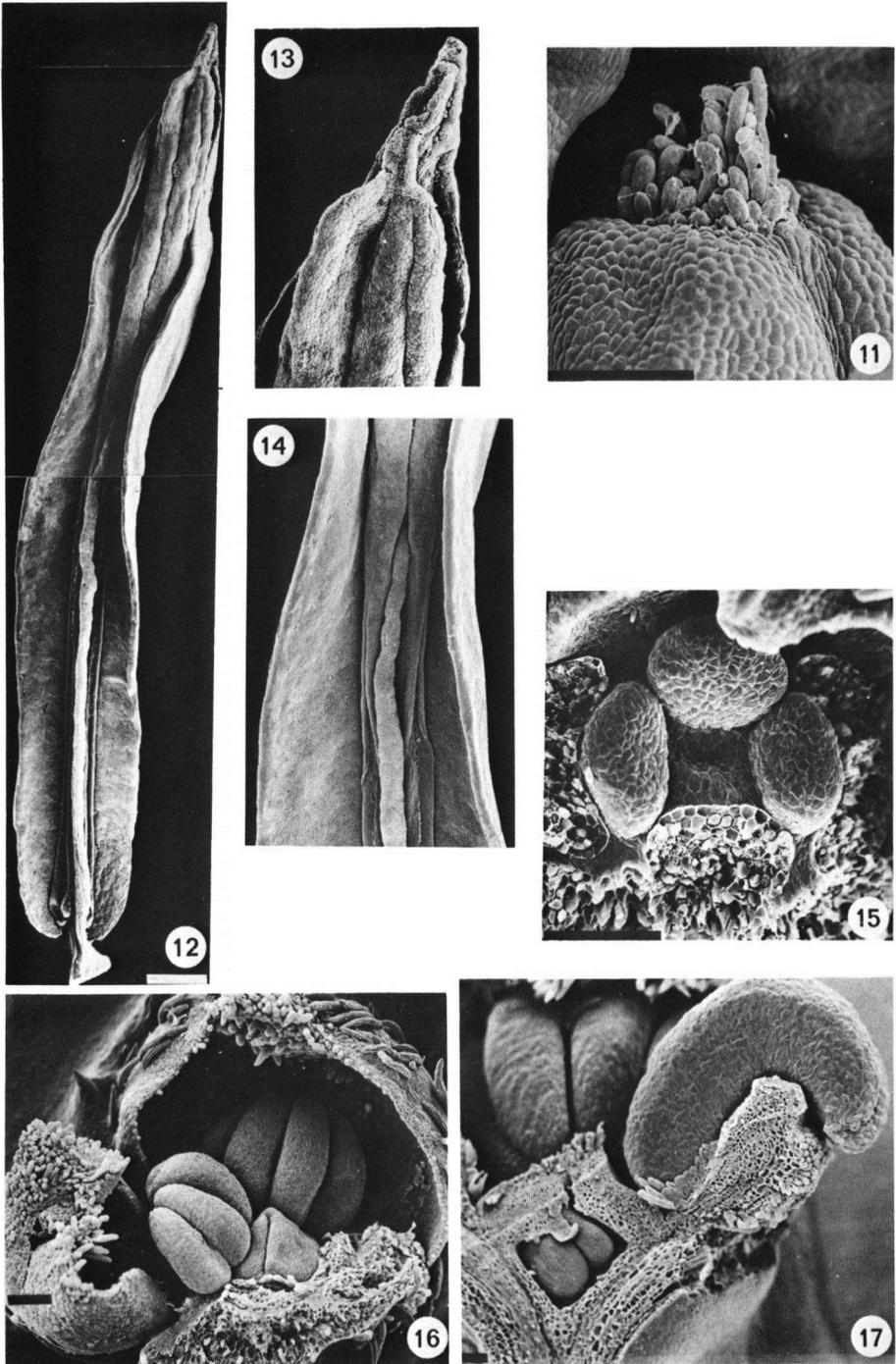


Plate 3 (figs. 11–17; legend on page 492)

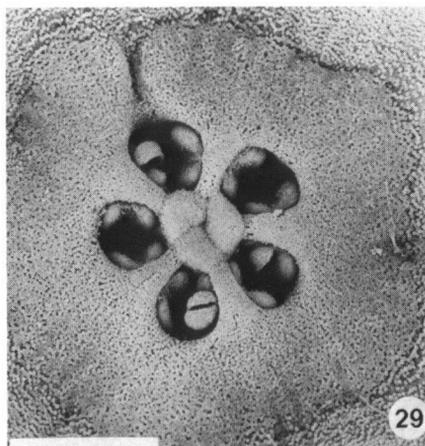
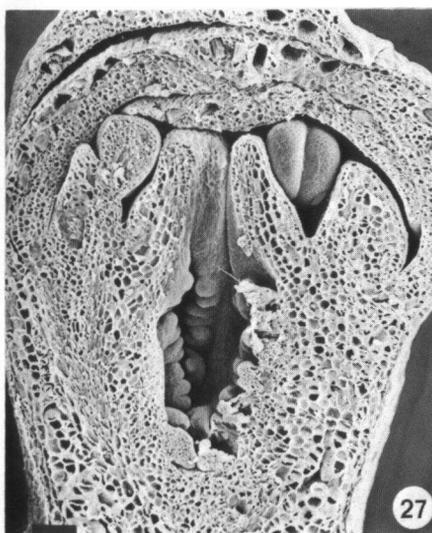
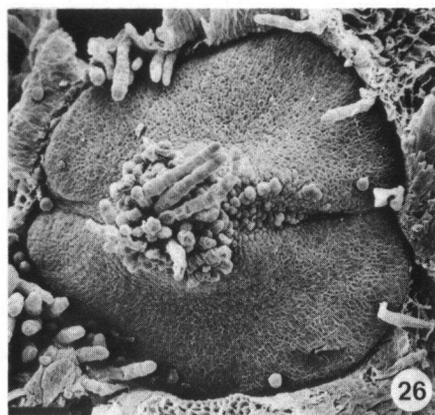
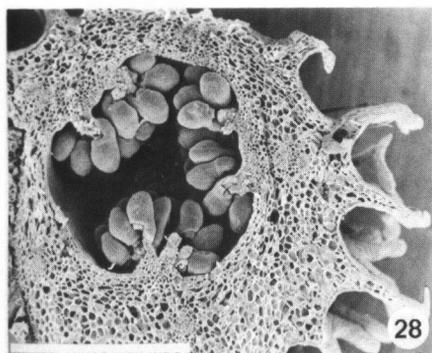
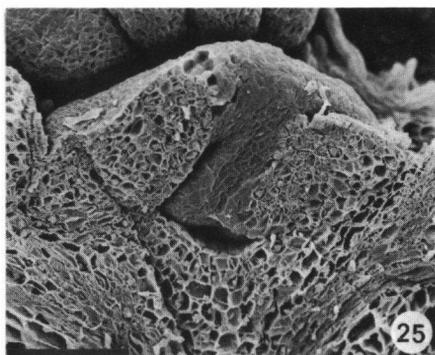
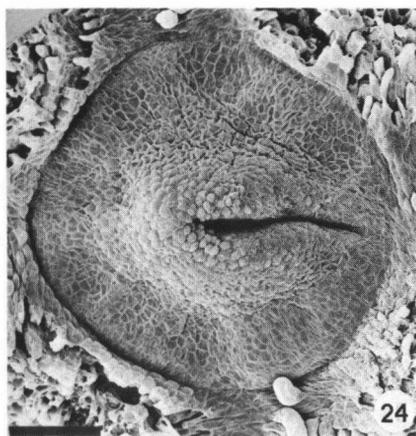


Plate 4 (figs. 18–23; legend on page 492)

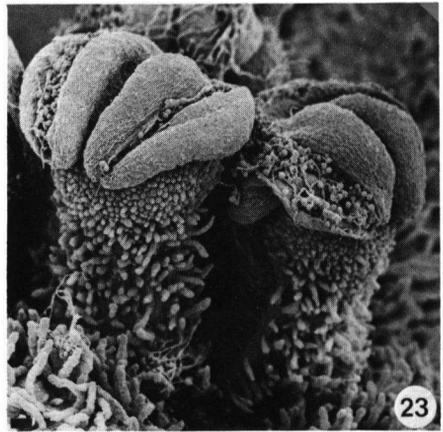
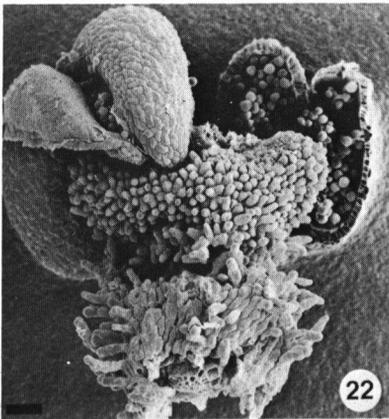
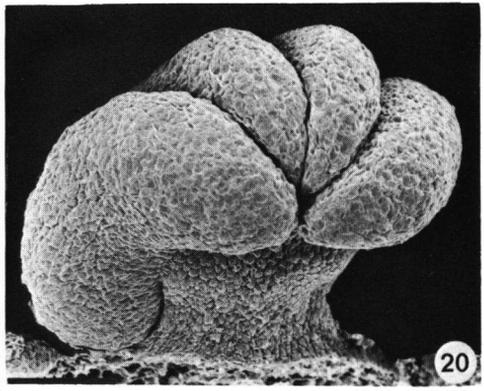
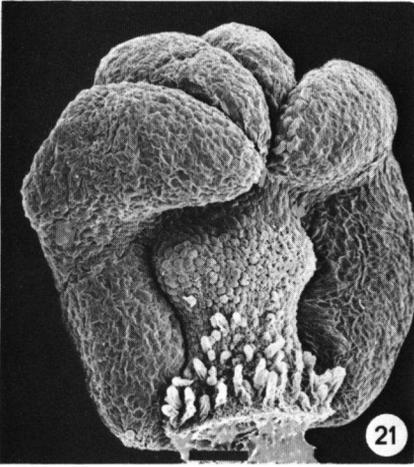
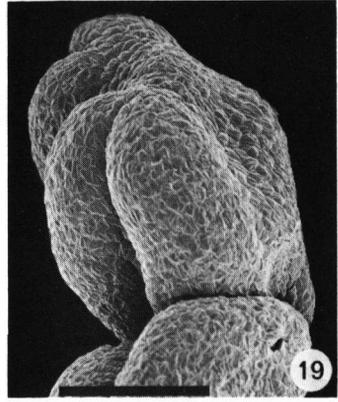
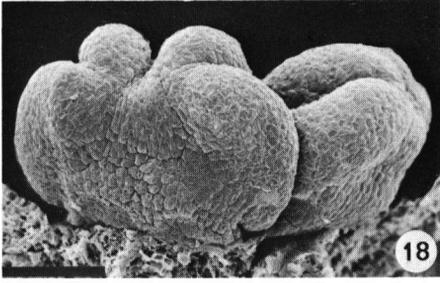


Plate 5 (figs. 24–29; legend on page 492)

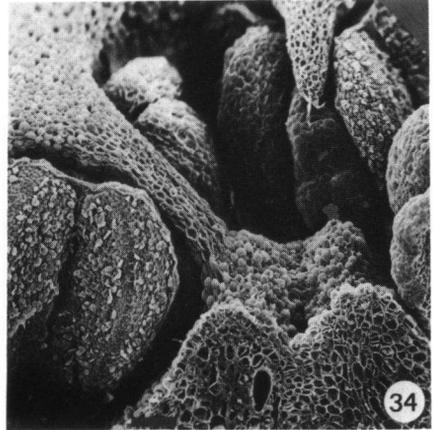
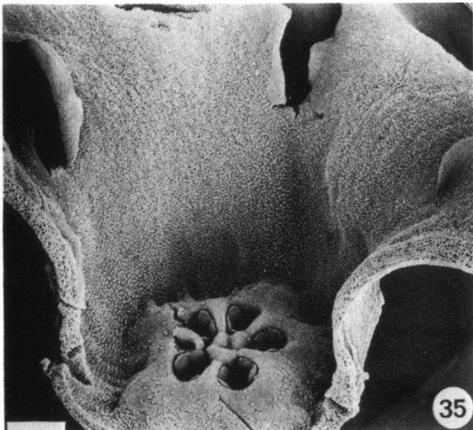
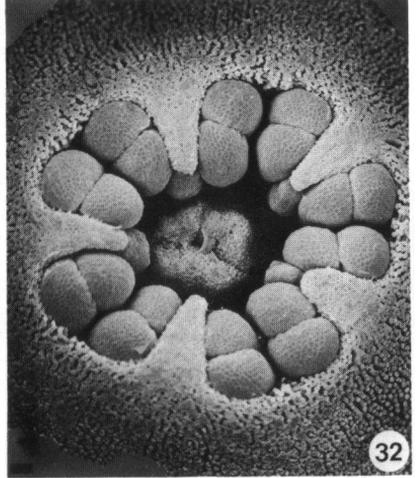
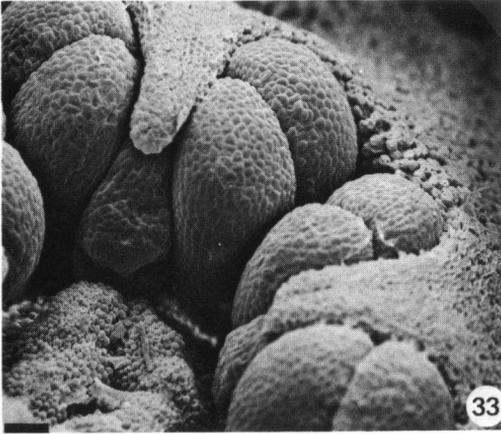
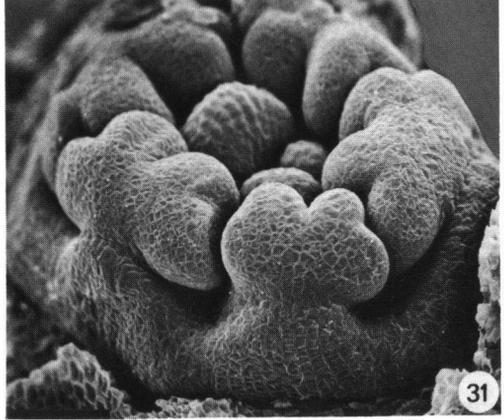
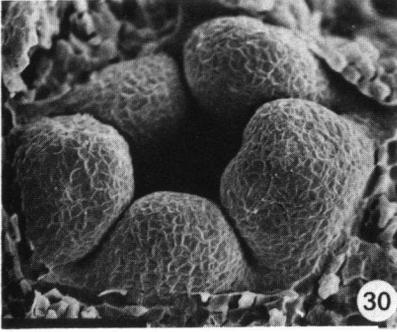


Plate 6 (figs. 30–35; legend on page 492)

