BLUMEA 33 (1988) 357–370

NOTE ON THE FLORAL DEVELOPMENT OF THOTTEA (ARISTOLOCHIACEAE)

P. LEINS*, C. ERBAR* & W.A. VAN HEEL**

SUMMARY

The occurrence of four placentae is a constant character in *Thottea*. The species can be distinguished by differences in the androecium. The androecial pattern is relatively variable and its rather high plasticity in the genus is suggested to be a derived feature within the family. The gynoecial structure is most remarkable, as the stylar organs do not correspond with the placentae in number nor in position. It is assumed that these organs do not belong to the gynoecium morphologically. They may represent independent, phylogenetically secondary organs, which may function in the capturing of pollen.

INTRODUCTION

The floral morphology and development of the genus *Thottea* in the Aristolochiaceae have received no attention until recently. We were fortunate to be able to investigate some material of several species of this genus, which occurs in Malesia and India. The Malesian Aristolochiaceae have been published in Flora Malesiana by Ding Hou (1984).

MATERIAL AND METHODS

Investigated were flower buds, either fixated in FAA or preserved in ethanol, belonging to the following collections: *Thottea tomentosa* (Blume) Ding Hou, *van Balgooy 5159*, Bogor Botanic Gardens; *T. siliquosa* (Lam.) Ding Hou, *L.L. Narayana & V.S. Raju s.n.*, Tamil Nadu; *T. spec.*, sent as *Bragantia dalzellii* Hook.f., *Swarupanandan & Sujith 296*, this collection was annotated as *T. siliquosa* by Ding Hou, Wynad, Kerala; *T. dinghoui* Swarup., *Swarupanandan s.n.*, Kerala; *T. tricornis* Maingay ex Hook.f., *van Balgooy 2627*, Malaya. Voucher specimens of most of these collections are at Leiden.

The procedures for S.E.M. are according to Gerstberger & Leins (1978).

* Institut für Systematische Botanik und Pflanzengeographie der Universität Heidelberg, F.R.G.
** Rijksherbarium, Leiden, The Netherlands.

ACKNOWLEDGEMENTS

The authors are very grateful to Prof. L.L. Narayana (Warangal), Dr. K. Swarupanandan and Dr. C. Renuka (Peechi, Kerala), Dr. Ding Hou and Dr. M.M.J. van Balgooy (Leiden) for providing material. To Dr. Ding Hou we are much indebted for fruitful discussions.

RESULTS

Thottea tomentosa

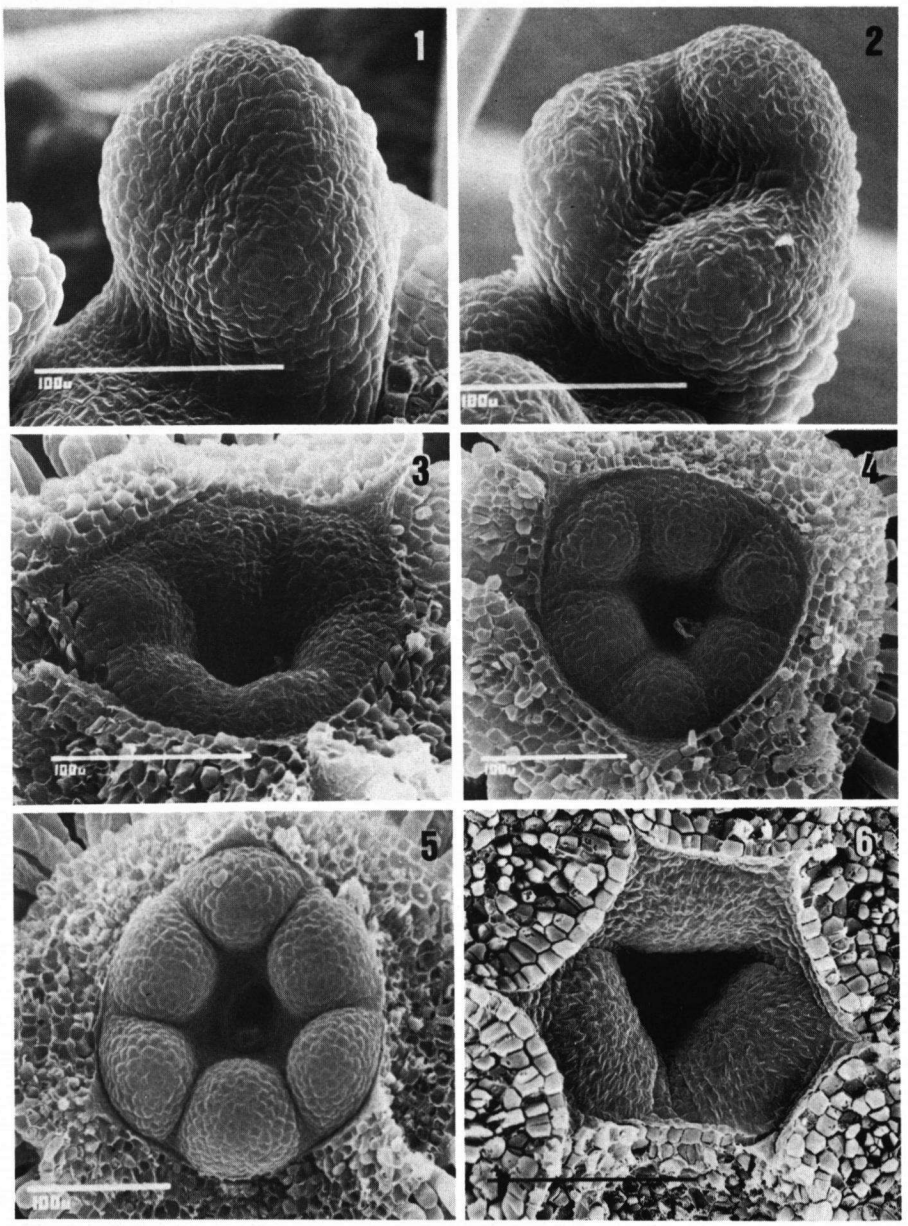
The youngest flower buds we have studied are dorsiventral and bent towards the axis. They show three primordial perianth parts on an oblique pedestal. The sequence of origin could not be determined, and it was also difficult to determine whether any of the three primordia is larger than the others (figs. 1, 2).

The triangular floral apex between the three perianth primordia becomes crateriform. Six stamen primordia arise on its margin following the perianth primordia. Probably those in the corners are slightly earlier in development (fig. 3), but later those on the sides reach more toward the centre (figs. 4, 5). The floral apex becomes hexagonal on its rim and gives rise to three primordia from which stylar structures will develop (fig. 6). The space surrounded by these primordia is triangular in outline, alternating with the perianth parts. Lower down the hypanthium is quadrangular at least in later stages. Sometimes one of the stylar primordia is larger than the others: it looks as if it consists of two protuberances, one larger than the other (fig. 7). The stylar primordia grow as subulate organs, and later grow up fused together at the base (fig. 8). On their tips grow hairs (fig. 9), that later become hooked (fig. 10). Below the stylar organs the gynoecial tube is provided with four long parietal placentae. In transverse sections we could observe that, whereas on two locations one placenta is situated in the radii between two stylar organs, on a third location two placentae are situated between two stylar organs. The ovule primordia originate in bidirectional sequence on the base of the flanks of the placentae (fig. 11). The placentae are triangular in cross section, and protuberant cells develop on their edges centrally (fig. 12). Later the placentae fuse dermally in the centre, so that the ovary is four-chambered (fig. 13).

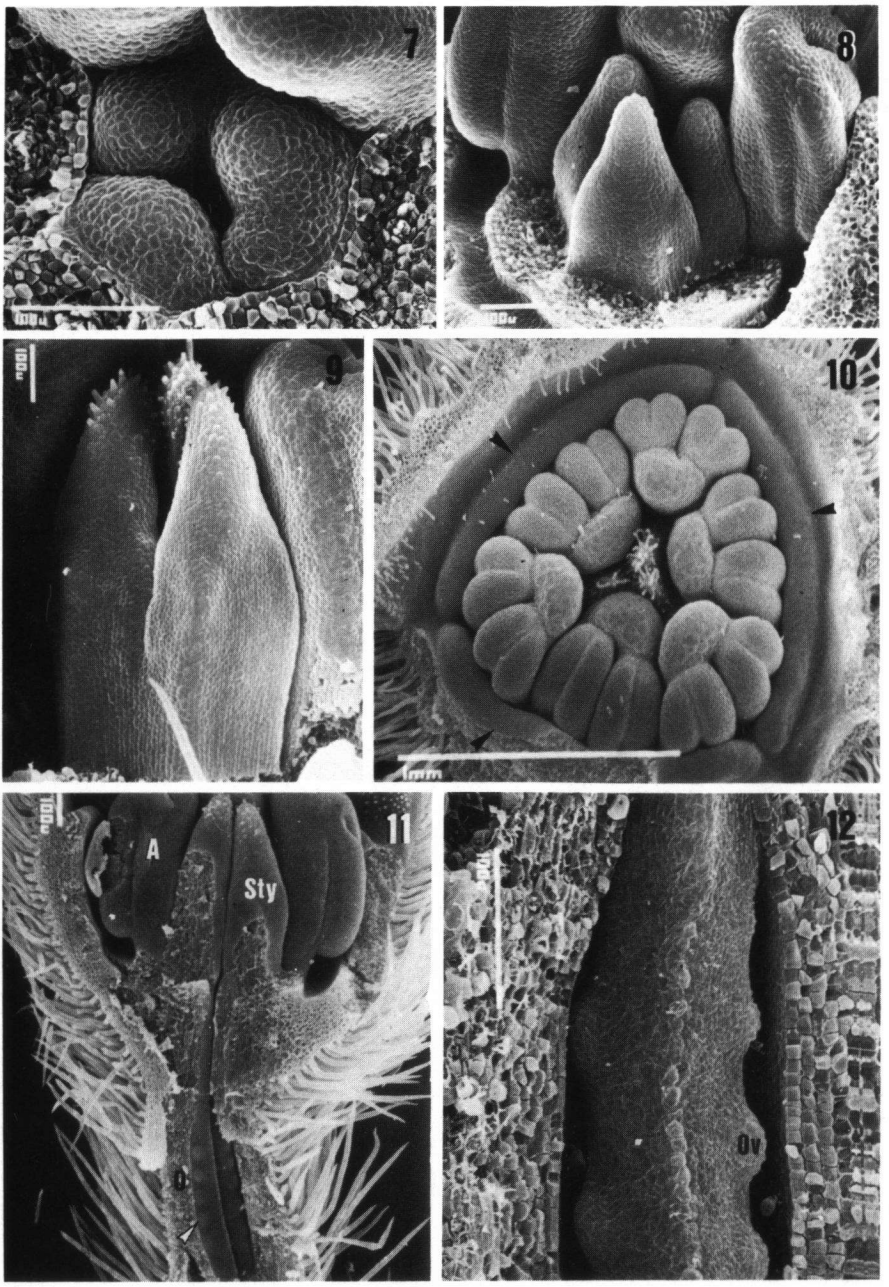
Thottea siliquosa

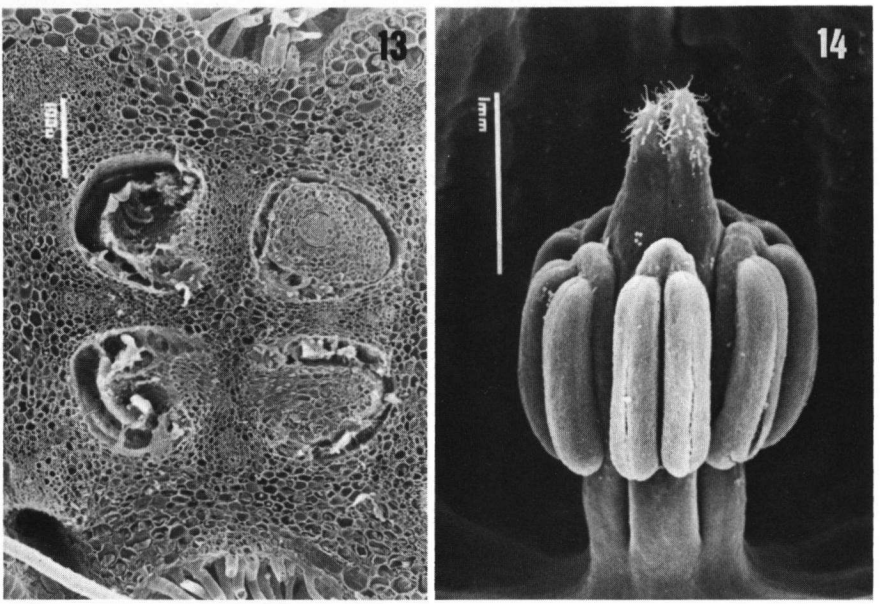
The very early stage of the flowers is similar to the corresponding stage in *T. tomentosa*. However, the initiation of the androecium differs considerably, despite the fact that also six stamens may originate. The primordia are situated pairwise in front of the three perianth parts (fig. 15). Sometimes there are three stamen primordia in front of one or two of the perianth members (fig. 16). The three corner regions of the floral apex, which alternate with the stamen pairs, remain either without primordia, or one, two, or all three of them may have one primordium (fig. 17). These primordia will develop into subulate sterile organs (fig. 21).

The floral apex is clearly crater-like when the stylar primordia originate on its rim (fig. 18). The number of these primordia varies from four to six, but in some cases some of these appear to be double or even subdivided into three parts (fig. 22). The



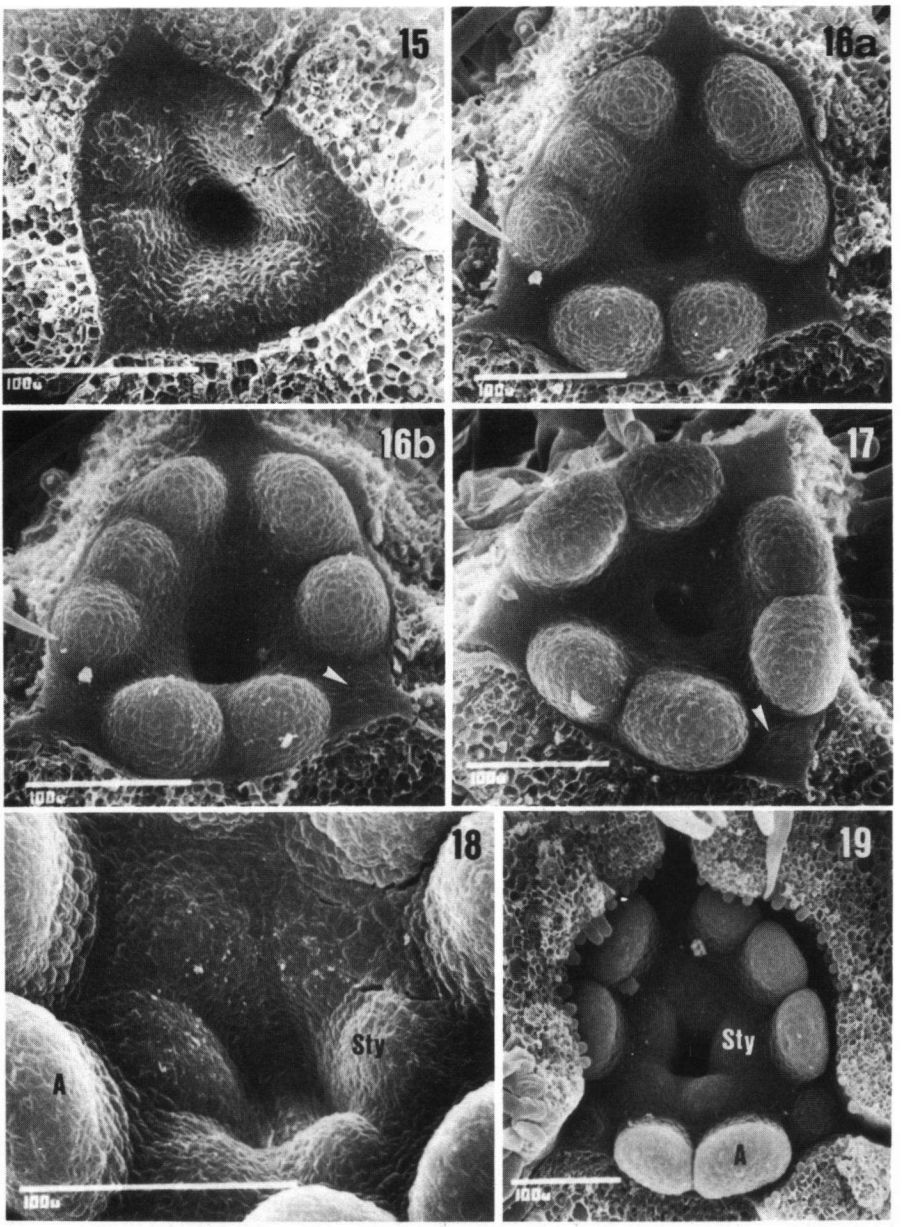
Figs. 1–6. *Thottea tomentosa.* — 1 & 2. Inception of the three perianth parts. — 3–5. Development of the six stamen primordia; perianth members removed. — 6. Inception of three stylar organs; stamen primordia removed, bar = 100 µm.


7
8
9
10
11
A
Sty
12
Ov

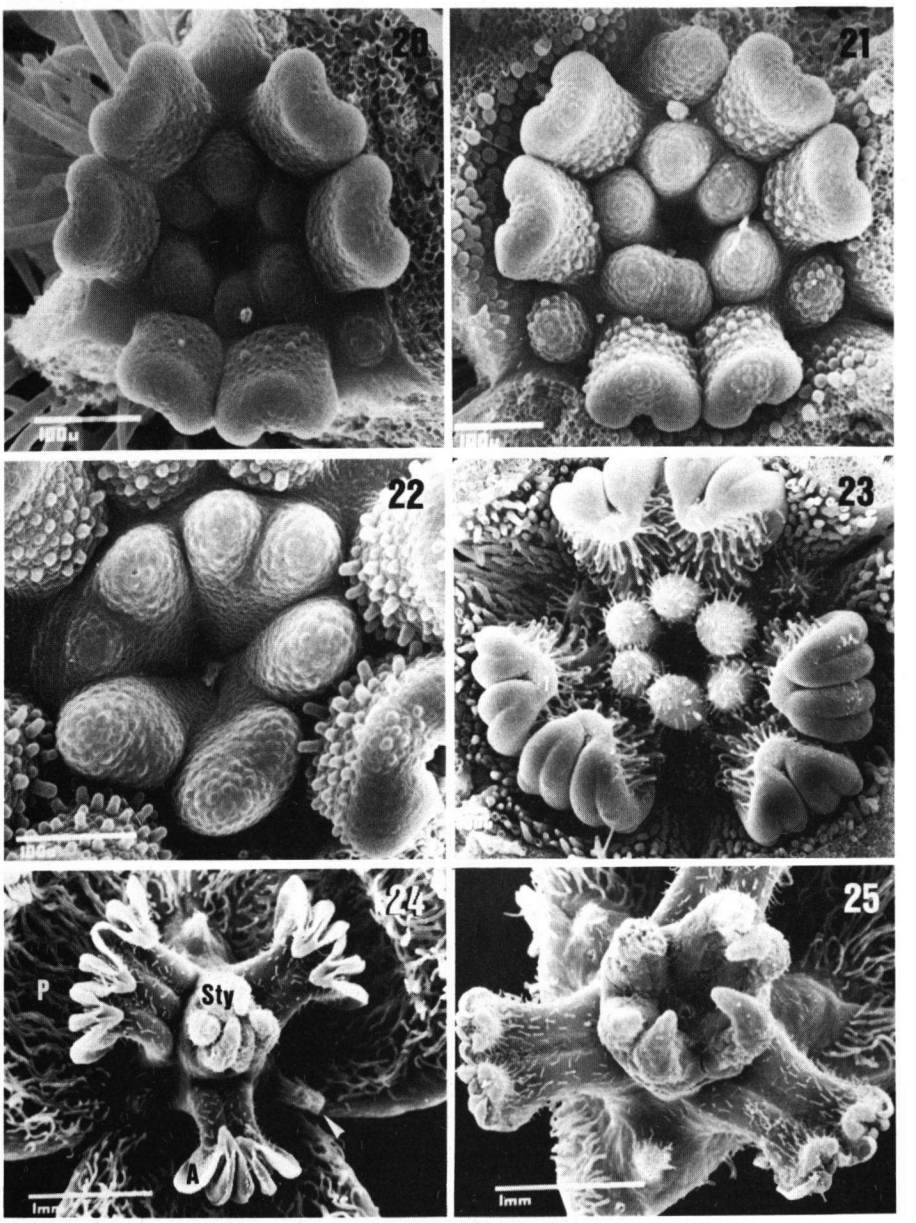


Figs. 13–14. *Thottea tomentosa.* — 13. Cross section through the ovary with four fused septa. — 14. Six stamens surround the three stylar organs, anthers just opened.

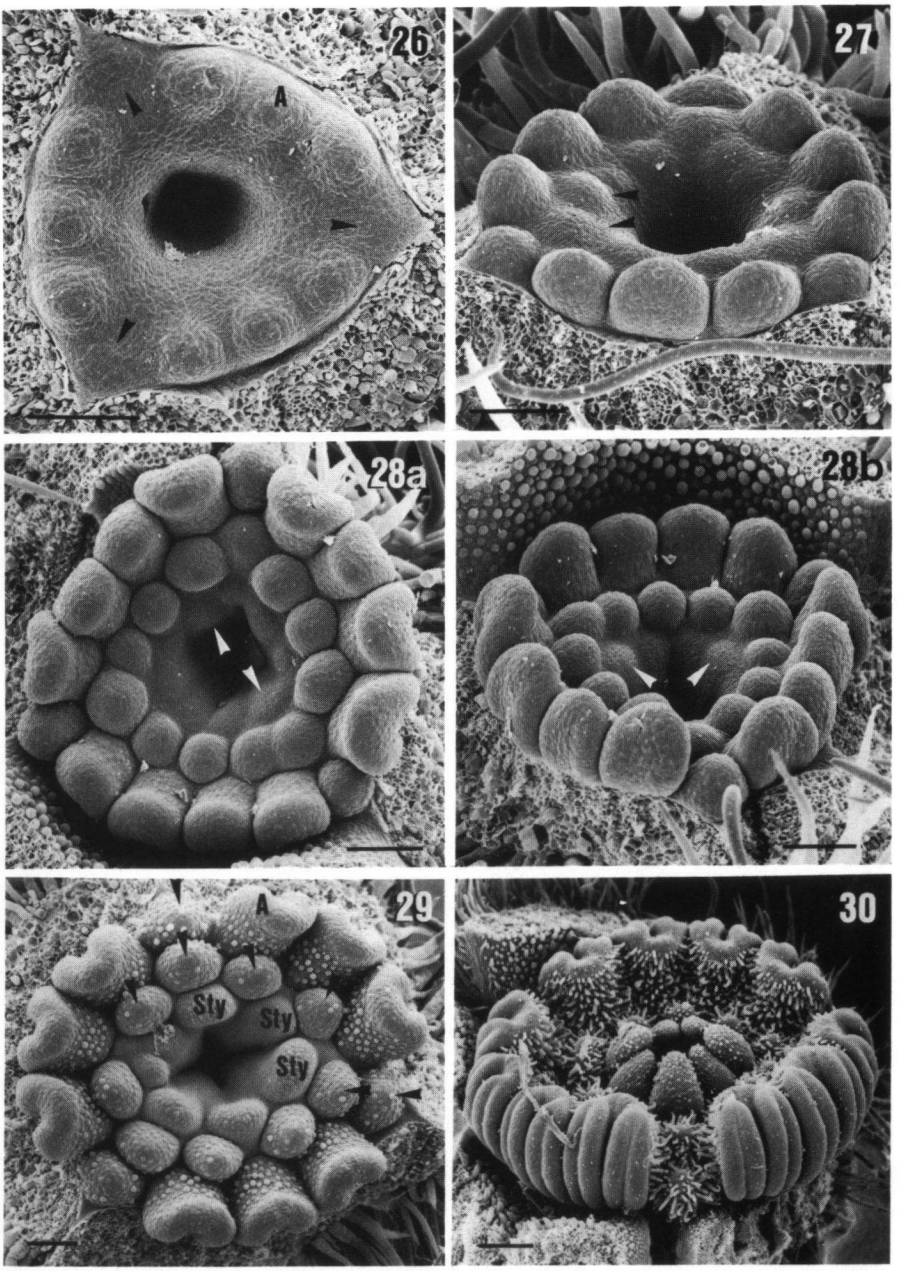
Figs. 7–12. *Thottea tomentosa.* — 7–9. Development of the stylar organs; stamens partly removed. — 10. Flower bud from above with six stamens and the tips of the three stylar arms with hooked hairs. The three perianth members cut off, each showing one young appendage (arrows). — 11. Longitudinal section through flower bud with stamens (A), stylar organs (Sty) and ovarium (O) showing initiation of ovules (arrow). — 12. Placenta viewed from the centre of the ovary; Ov = ovule.

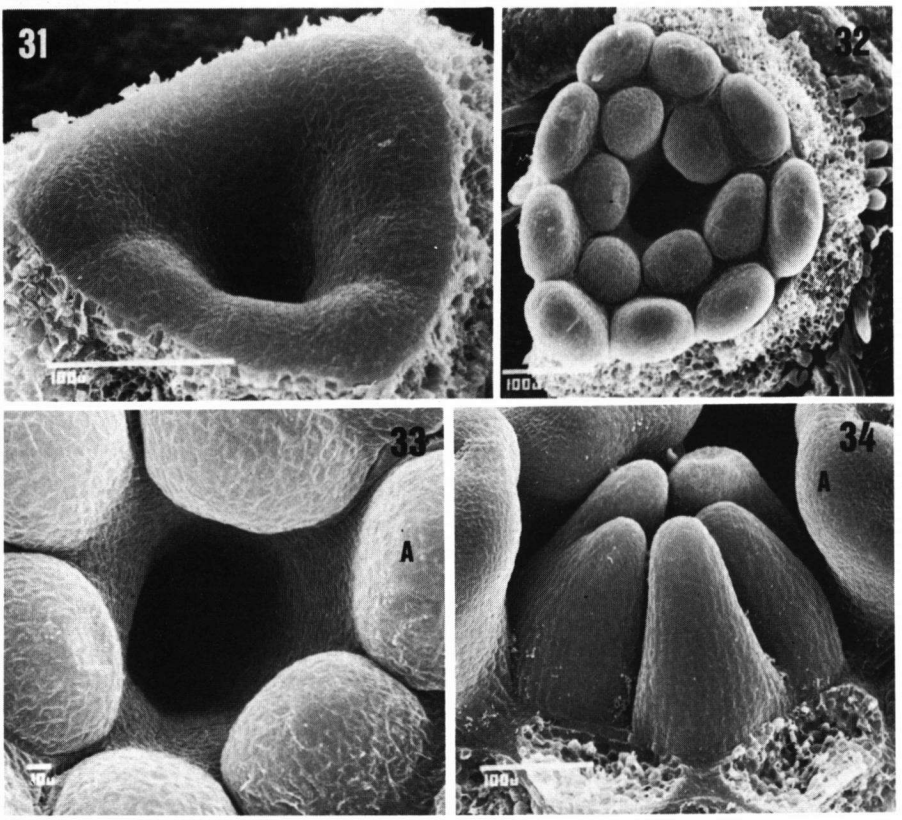


Figs. 15–19. *Thottea siliquosa*. — 15. Initiation of paired stamens in front of the three removed perianth members. — 16. Young stage of androecium, in front of one of the three perianth parts three stamens have arisen. Like in 17 low primordia are visible in the corners between perianth parts (arrows). — 18 & 19. Inception of six or five stylar organs, entrance of floral tube quadrangular. — A = stamen, Sty = stylar organ.



Figs. 20–25. *Thottea siliquosa*. — Later stages of floral development (20–23), adult flower (24) and flower in post-anthesis (25). P = perianth, A = anther, Sty = stylar organ, arrow shows at one of the three sterile appendages between the perianth parts.


26
A
27
28a
28b
29
A
Sty
Sty
Sty
30



Figs. 31–34. *Thottea dinghoui.* — 31. Inception of the outer whorl of (nine) stamens at the rim of the crateriform floral apex; perianth removed. — 32. The two whorls of the androecium, the inner one consists of six stamens. — 33. Entrance to the floral tube surrounded by stamens (A). — 34. Five stylar organs in the centre of the flower; A = stamen.

Figs. 26–30. *Thottea spec. (Swarupanandan & Sujith, Ecol. 296).* — 26. Inception of the stamens (A, three in front of each perianth part in this flower bud) and of three sterile corner primordia (arrows). — 27. Initiation of an inner whorl of sterile organs (arrows). — 28a & b. The stylar organs originate at the rim of the quadrangular floral tube (arrows). In this flower bud there are four stamens in front of the perianth parts. — 29. A later stage of floral development; perianth removed, A = stamen, arrows show at some of the sterile organs, Sty = stylar organs. — 30. Almost adult flower; perianth removed. — Bar = 100 µm in 26–29, 200 µm in 30.

base of the crater is quadrangular in cross section in this stage (figs. 18, 19), and probably even before the initiation of any stylar primordia on its rim (fig. 16a). If there are six stylar primordia, as frequently occurs, three of them are situated in the corner regions between the pairs of stamen primordia, and three in front of them (fig. 20). The flanks of the quadrangular crateriform tube develop as four placentae, triangular in cross section, in the lower part where they later will fuse dermally in the centre. The rows of ovules develop on the base of the flanks of the placentae. For a clear comprehension of the positions of the four placentae in relation to the six stylar primordia we start from two perpendicular planes passing through the grooves between the placentae. One of these planes connects two opposite stylar organs, the other runs between two stylar organs on each side (fig. 20, five cases studied). The first plane passes through one stylar organ placed in front of one of the corners between the perianth parts. Like in *T. tomentosa* hooked hairs occur on the stylar primordia, not only on the tips but all over. Similar hairs cover the filaments and the anthers on the inside as well as the subulate organs alternating with the perianth parts (fig. 23). The mature flowers have the stylar lobes clawed together when the extrorse anthers have opened by slits, but later the lobes spread apart (figs. 24, 25).

Thottea spec. (cf. *Bragantia dalzellii*)

The present material, of which the adult flowers were also studied by Renuka & Swarupanandan (1986), was identified by Swarupanandan as *Bragantia dalzellii* Hook.f. This species has been included in *Thottea siliquosa* by Ding Hou (1981). However, in our opinion the present material differs from *T. siliquosa* in important floral characters.

The earliest stage which we have examined (fig. 26) shows a series of three collateral stamen primordia in front of each of three perianth parts. Three lower primordia occur in the corners alternating with the perianth parts (arrows in fig. 26), which will develop into sterile subulate appendages. In this young stage the crateriform floral apex already shows a quadrangular opening seen from above. Next a second whorl of primordia develops most of which alternate with the stamen primordia. This means that three of them are opposite to the corner primordia (fig. 27). All these primordia will develop into similar sterile appendages like the corner primordia. The constancy of alternating primordia is especially evident in a flower bud shown in fig. 28. In this flower series of four stamens occur in front of the perianth parts, separated by the three sterile corner organs. As a consequence the next set of primordia consists of twelve organs, all exactly alternating. Also in this stage the floral apex betrays a quadrangular central shape. Stylar primordia are observed to originate on its rim, which reach down into the crater (fig. 28b). As to the position of the four placentae in relation to the stylar primordia it may be remarked that one of the two perpendicular planes (see above) between the placentae intersects with two opposite stylar primordia, like in *T. siliquosa* (fig. 29). This plane most probably lies in the symmetry plane of the flower. In the same bud two or three stylar primordia occur to the right or the left of this plane respectively. In fig. 30 a flower bud shortly before anthesis shows hooked hairs covering all sterile appendages as well as the stamens on their inside. Unlike in *T. siliquosa* the stylar primordia only have short papillae.

Thottea dinghoui

The initiation of the three perianth parts on the young flower bud is as described in *T. tomentosa*. The crateriform apex which is surrounded by the primordial perianth parts gives rise to nine stamen primordia on its upper rim. As this rim is roughly triangular in shape, three stamen primordia arise in the corners and three pairs of stamen primordia arise along the sides. It seems that along one of the sides the primordia arise slightly later than along the other two sides (fig. 31). Next a second whorl of stamen primordia arises. This consists of three primordia in the corners, and three alternating ones on the sides (fig. 32). In this stage the central part of the crater-like apex is not yet quadrangular in shape (fig. 33), in contrast to the condition in *T. siliquosa* and *T. spec.* as described above. We could not investigate the initiation of the stylar primordia. In older stages we discovered five or six subulate, basally somewhat plicate, stylar primordia. They may be united pairwise at the base or slightly higher (fig. 34). In early stages the placentae show a low median furrow (fig. 35). Later they grow forward towards the centre and fuse. In late stages there are no hairs on the stylodia and the stamens.

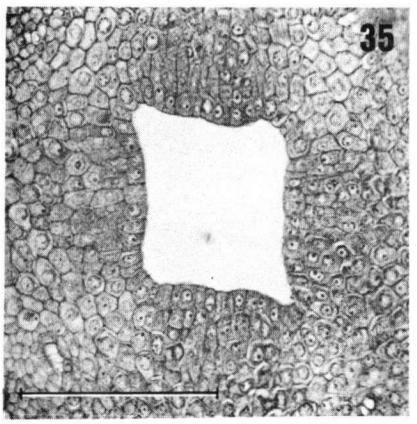


Fig. 35. *Thottea dinghoui*. — Cross section through the upper part of a young inferior ovary. Bar = 100 µm.

Thottea tricornis

We only had very limited material, comprising rather old flower buds. Two roughly triangular whorls of stamens surround the young gynoecium (fig. 36a). The stamens of the inner whorl alternate more or less with those of the outer whorl. However, the stamens are opposite in three radii which presumably pass through the corners between the perianth parts (arrows in fig. 36a). A dozen stylar primordia can be distinguished on the rim of a quadrangular crateriform gynoecial tube, the sides of the crater slightly protruding. On longisection, the flower bud shows the very narrow channel connecting the funnel-shaped stylar part and the dilated ovary (figs. 36c, d).

DISCUSSION

Androecium

The androecium in *Thottea* is obviously variable, both in number and position of the stamens, but is more or less constant for each species. The corners between the tepals may be occupied by one (*T. tomentosa, T. dinghoui*) or two (*T. tricornis*) stamens in line, or by one (*T. siliquosa*) or two (*T. spec.*) sterile organs in line. It is difficult to decide whether the sterile organs are homologous with stamens or petals or both. When comparing the corner primordia in *Thottea* with those in *Asarum cau-*

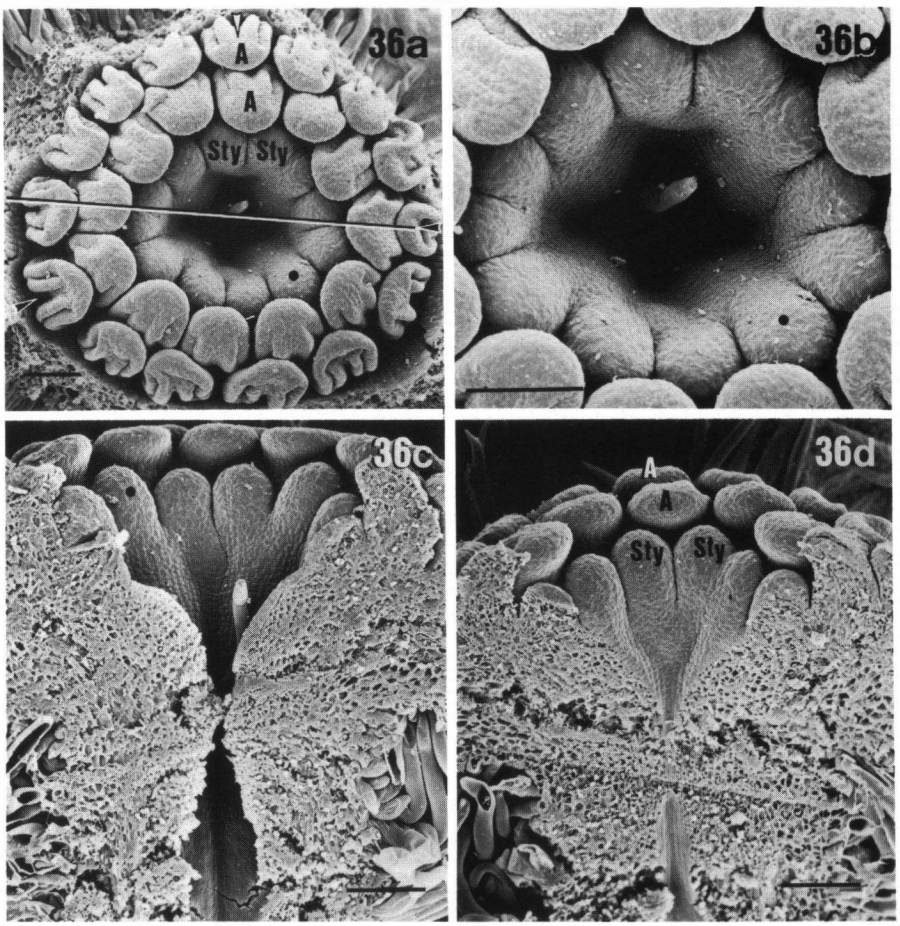


Fig. 36. *Thottea tricornis*. — One late flower bud from above (a, b) and in longitudinal section (c, d). Plane of section indicated in a. A = stamen, Sty = stylar organs, arrows indicate the presumed corner places between the removed perianth parts (see text), dots mark the same stylar organ. Bar = 100 µm.

datum or *A. europaeum* (cf. Leins & Erbar, 1985), we consider that in the latter they are rudimentary petals, whereas in the former they represent specialised organs bearing hooked hairs similar to those on the anthers (*T. siliquosa, T. spec.*) and stylar organs (*T. siliquosa*). Whereas in *T. tricornis* and *T. dinghoui* a second whorl of fertile stamens is formed, in *T. spec.* (cf. *Bragantia dalzellii*) this whorl consists of organs similar to those in the three corners.

Only *T. siliquosa* has an androecium pattern that resembles the one in *Asarum* (especially of *A. europaeum*) in very early stages (paired stamen primordia). However, in *Asarum* additional stamens originate later between or outwards from the six first stamen primordia (Leins & Erbar, 1985).

The relatively high plasticity of the androecium in *Thottea* is probably a derived character within the family. The number of organs (stamens and sterile appendages) presumably depends on the correlations between the size of the primordia and the size of the floral axis at the time of initiation. The first available space defines the number and position (frequently alternate) of the organs. Also when the number is high all stamens, also those in the corners, originate more or less simultaneously within one whorl. We consider the multiplication of stamens in one whorl as a sudden phylogenetic change.

Gynoecium

The gynoecial development differs considerably from the usual pattern. The stylar organs cannot be associated with the ovary so easily. The inferior ovary constantly has four placentae, but the stylar organs vary in number and position. In some *Thottea* species (Ding Hou, 1984) the number of stylar lobes is very high, for instance in *T. pentilobata* (up to 14), in others very low, for example in *T. paucifida* (only two or three). On comparison it may be found that generally the whorl of stylar primordia follows upon the whorl of stamens or sterile organs in the same way as the second whorl of stamens or sterile organs follows upon the first. Three of these are situated in the corners and the others alternate with the primordia of the preceding whorl, if the whole pattern is regular. Irregularities frequently occur, by increasing as well as decreasing in number (see figures of *T. siliquosa*).

After this preliminary investigation we nevertheless hazard to explain the gynoecial structure by offering a new hypothesis. According to our view the 'stylar organs' do not originally belong to the gynoecium. The superior part of the gynoecium seems to be fully reduced and to be substituted by new organs. The loss of the distal gynoecium part is shown by the fact that the inferior ovary tube is not covered by a roof as usual, but is open above. The distal protection is brought about by the very narrow upper part of the floral tube at the level of the perianth (figs. 11, 36c, d). The new organs possibly function only to capture pollen. We could not discover any undisputable stigmatic protuberances present on the 'stylar organs'. It is necessary to investigate the germination of the pollen in the flowers. Maybe pollen tubes grow downwards to the 'jelly-like substance' at the base of the stylar arms noted by Ding Hou (1981: 314, fig. 42).

REFERENCES

GERSTBERGER, P., & P. LEINS. 1978. Rasterelektronenmikroskopische Untersuchungen an Blütenknospen von Physalis philadelphica (Solanaceae). Anwendung einer neuen Präparationsmethode. Ber. Deutsch. Bot. Ges. 91: 381–387.

HOU, DING. 1981. Florae Malesianae Praecursores LXII. On the genus Thottea (Aristolochiaceae). Blumea 27: 301–332.

— 1984. Aristolochiaceae. Flora Malesiana ser. I, 10: 53–108.

LEINS, P., & C. ERBAR. 1985. Ein Beitrag zur Blütenentwicklung der Aristolochiaceen, einer Vermittlergruppe zu den Monokotylen. Bot. Jahrb. Syst. 107: 343–368.

RENUKA, C., & K. SWARUPANANDAN. 1986. Morphology of the flower in Thottea siliquosa and the existence of staminodes in Aristolochiaceae. Blumea 31: 313–318.