CERTAIN SALIENT FEATURES IN THE FLORAL ANATOMY OF *BURMANNIA*, *GYMNOSIPHON* AND *THISMIA*

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Introduction

Earlier work on the floral anatomy of Burmanniaceae is very limited. Pfeiffer (1914) dealt with some features of the anatomy of vegetative organs and the external morphology of the flower of *Thismia americana*. Saunders (1939) gave a short general account of the anatomy of the flower in this family. Pai (1966 *a*) described the floral anatomy of *Burmannia pusilla* but made a number of wrong observations in important structures (Rao, 1967, 1968). Moreover, he dismissed Saunders' account saying that it was mainly in connection with her theory of carpel polymorphism, ignoring completely her account of the vascular supply to floral parts other than the gynoecium.

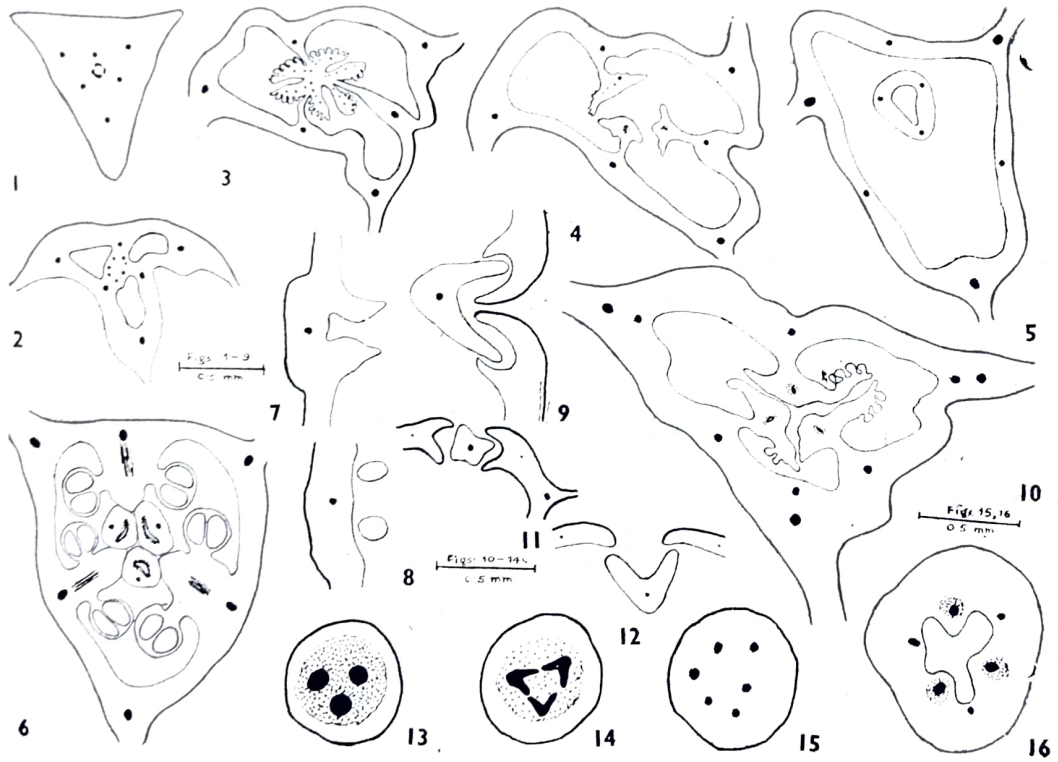
The present paper deals with the floral anatomy of *Burmannia disticha* L., *B. nepalensis* (Miers.) Hook. f., *Gymnosiphon cymosus* (Benth.) Benth. *et* Hook., *G. aphyllus* Bl., and *Thismia aseroe* Becc. Of these, *Thismia* is extremely rare and even taxonomic accounts are based on single collections (Jonker, 1939). The customary methods of observing serial microtome sections and cleared entire flowers were followed for *Burmannia* and *Gymnosiphon*. On account of the very limited amount of dried material of *Thismia* made available to the present author, only serial microtome sections were studied for the species of this genus.

In *Burmannia* the epigynous flower has a perianth tube which divides into 3 sepals and 3 petals. There are 3 subsessile anthers inserted on the perianth tube below the petals. The connective in most species has 2 apical crests and a basal short truncate spur. The ovary has 3 prominent wings which are continued upwards on to the sepals also. There are numerous ovules on axile placentae, which project into the 3 loculi of the ovary. *Gymnosiphon* has parietal placentation and each placenta bears at both sides of its top a large globose gland. The anthers are 3, sessile and inserted below the petals. The perianth limb is deciduous below the insertion of the stamens. *Thismia* has 6 anthers which hang downwards from a prominent annulus at the mouth of the perianth tube. They are laterally coherent, forming a tube which

surrounds the style. The ovary has 3 parietal placentae bearing many ovules.

OBSERVATIONS

Burmannia disticha.—The axial vascular cylinder sends outwards 6 strands in alternating sets of 3 each for the ovary wall. The bundles of the first set run in positions of the carpellary dorsals and those of the second set are opposite the septa. The emergence of these 6 strands leaves 3 bundles in the centre which divide into a number of strands for the placentae (Figs. 1, 2). These increase in number higher up. In the ovuliferous zone the placentae have a prominent tangential row of vascular bundles (Fig. 3). The ovary is trilocular in the basal part and unilocular above with inwardly projecting placentiferous septa. In the terminal part of the ovary the placental bundles disappear and just above their ending, a small septal gland lined by deep staining epithelial tissue is formed for a short distance (Fig. 4) towards the inner end of each septum. The glands end in solid tissue and do not open to the exterior.



FIGS. 1–16. Figs. 1–10. *Burmannia disticha*. Fig. 1. T.s. through top of pedicel. Figs. 2, 3. T.s. ovary showing increase in placental bundles. Fig. 4. T.s. upper region of ovary showing septal glands in two of the septa. Fig. 5. T.s. through perianth tube and style. Fig. 6. T.s. at anther level. Fig. 7. Shows the two crests of a connective attached to the perianth tube. Fig. 8. T.s. at higher evel showing the crests free. Fig. 9. Shows the petal margins enclosed by the double margins of a sepal. Fig. 10. T.s. anther ovary of *B. disticha* showing early separation of carpellary dorsal bundles from the sepal traces within the ovary walll Fig. 11. A petal and adjacent sepal margins of *B. nepalensis*. Fig. 12. A peta. and adjacent sepal margins of *B. pusilla*. Figs. 13–16. *Gymnosiphon cymosus*. Figs. 13–15. T.s. pedicel of *Gymnosiphon cymosus* at successively higher levels. Fig. 16. T.s. near base of ovary.

The ovary wall has 3 prominent wings opposite the loculi and they are continued on the perianth tube and the sepals as well. At the top of the ovary the 3 bundles opposite the loculi divide into an inner carpellary dorsal bundle which travels into the style and an outer sepal median trace (Fig. 5). The perianth tube receives the 3 sepal traces and the alternating 3 bundles of the ovary wall which are on the septal radii. These latter function as the petal-stamen cords. High up on the perianth tube are inserted the 3 subsessile anthers. The petal-stamen cords divide into an outer petal trace and an inner stamen trace which moves into the connective in a radially inward direction (Fig. 6). The inner margins of the connectives are wedged in the grooves that separate the three stigmatic branches. The upper margin of the connective bears 2 acute crests. These are attached in their basal regions to the perianth member on their back for a short distance (Figs. 7, 8). In the basal part the sepal margins are double and forcipate, with the petal margins more or less enclosed by the double margin (Fig. 9). Higher up the margin of the sepals becomes single by a gradual reduction of the inner lobe. The style has a hollow canal. In its upper region, 3 strands of transmitting tissue are formed a little inside of the dorsal bundles. They increase in size and become arc-shaped, with the concavity outwards. At the level where the style divides into its 3 branches, the transmitting tissue strands give place to 3 crescentic hollow canals which widen very greatly to open to the outside in the funnel-shaped stigmas.

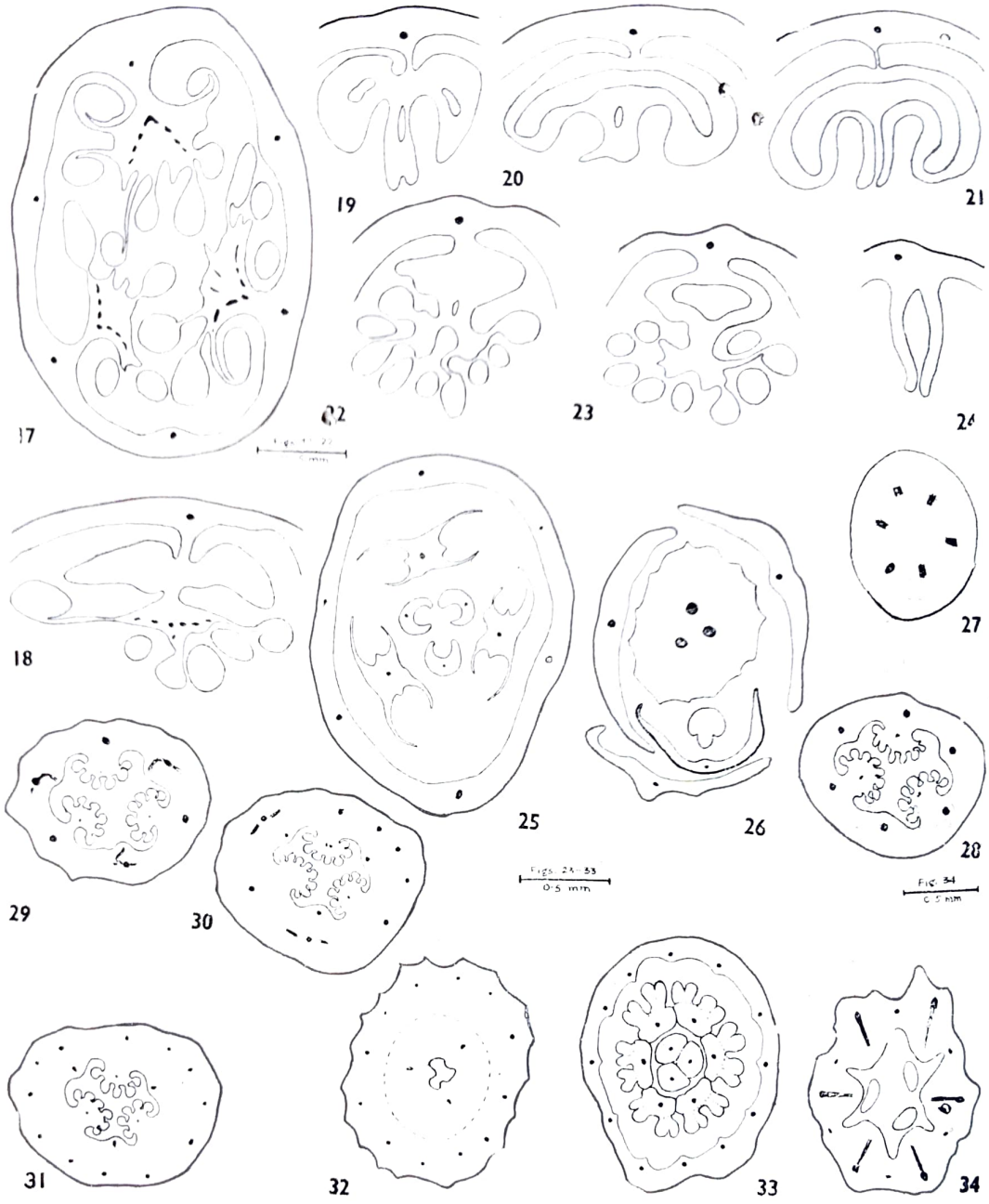
In one specimen of *B. disticha* the 3 cords opposite the loculi bore inwards the carpellary dorsal bundle in the upper half of the ovary and the separation of the perianth tube from the carpellary tissue occurred not at the top of the ovary but much beneath that level (Fig. 10).

B. nepalensis.—Dr. F. P. Jonker identified some of my *Burmannia* material as *B. nepalensis.* It resembles *B. pusilla* in most characters, but the sepals have a double margin at the base, the inner lobes being involute (Fig. 11). *B. pusilla* does not have a double margin for the sepals (Fig. 12). Moreover, there is a clear difference in the appearance of the double margins of the sepals of *B. nepalensis* and *B. disticha.* Those of the latter appear claw-like (Fig. 9). An anatomical difference is that in the axile zone of the ovary of *B. nepalensis* there is a prominent cylindrical strand of thick-walled cells close to the periphery of which lie the ventral strands. In *B. pusilla* there is no such axile strand. The aestivation of the perianth members of *B. pusilla* differs from that of the other two species studied and a double margin is absent for the sepals (Fig. 12).

Gymnosiphon cymosus and *G. aphyllus.*—These two species agree very closely in their floral anatomy. As Jonker (1938) said, "the greatest difficulty in investigating the species of this genus is the fact that the perianth limb with the stamens and the stigmas is deciduous. The material becomes incomplete and then it is impossible to determine the specimens".

There are 3 closely placed vascular strands embedded in thick-walled tissue in the pedicel. These divide and form 6 bundles for the ovary wall (Figs. 13–15). Three of them run in positions of the dorsal bundles of the carpels and 3 are opposite the parietal placentae. The placentae are borne at the inner margins of inwardly projecting incomplete septa. The bundles of the ovary wall standing opposite the placenta send a large branch into the placenta. This placental bundle bears many branches which run into the ovules (Figs. 16, 17). In the upper part of the ovary each partial septum bears a prominent "gland" on either side. This gland is obviously formed through a lateral bulging of the partial septum on either side. It develops a hollow space which extends tangentially within the gland and also radially inwards for some length (Figs. 18–24). For some distance the septum bears the gland near its outer margin and the ovuliferous placentae which are often bifid at this level, at its inner margin. Above the ovuliferous zone this inner margin clearly shows a double nature for some distance, indicating that it is composed of the margins of two adjacent carpels (Figs. 21, 24). At the top of the ovary the 3 vascular strands opposite the loculi divide into an outer sepal trace and an inner dorsal bundle of a carpel. The latter enter the style while the perianth tube receives the sepal traces and the 3 bundles of the ovary wall on the septal radii. The latter are the petal-stamen cords which function as in *Burmannia*, dividing at the anther level into an outer petal trace and an inner trace which supplies the stamen (Fig. 25). The stamens are inserted much beneath the level of splitting of the perianth tube into its lobes. In the upper region of the style the carpels are loosely coherent by their margins.

Thismia *aseroe*.—Above the level of the bracts, each of which receives a single trace, the pedicel has 3 vascular strands (Fig. 26) which bifurcate to form 6 bundles (Fig. 27). These diverge outwards to traverse the ovary wall. Three of these are opposite the parietal placentae while the other three alternate with them in positions of the carpellary dorsal bundles. The former send branches into the placentae (Fig. 28). Near about the middle of the length of the ovary the 3 cords alternating in position with the placentae bear lateral branches. One of these diverging suddenly turns inwards towards the inner surface of the ovary wall (Fig. 29) and constitutes the dorsal bundle of the carpel. Above this level the ovary wall shows 12 bundles in a ring, in addition to the 3 dorsal bundles of the carpels that form another inner ring (Figs. 30, 31). Of the 12 outer bundles three are the strands opposite the placentae while the remaining 9 are the strands opposite the carpellary dorsals and the two lateral branches of each of them. At the top of the ovary, the perianth tube with the 12 bundles mentioned above separates from the style which receives the 3 carpellary dorsal bundles (Fig. 32). The 6 stamens are pendulous from a collar-like inward projection of the perianth tube. The six main strands of the ovary wall (the other 6 are lateral branches of three of them) send inward staminal traces into the annulus (Fig. 34). These run downwards into the connectives of the anthers which are laterally connate, forming a sort of a cylinder round the stylar branches (Fig. 33).



FIGS. 17–34. Figs. 17–21. *Gymnosiphon cymosus* (*contd.*). Fig. 17. T.s. ovary showing placentation. Figs. 18–21. T.s. at successively higher levels through a "placental gland". Figs. 22, 23. T.s. through "placental gland" of *G. aphyllus* at successively higher levels. Fig. 24. T.s. just above placental gland of *G. aphyllus*. Fig. 25. T.s. through anther level of same species. Figs. 26–34. *Thismia aseroe*. Fig. 26. T.s. passing through pedicel and four bracts, one of which has a rudimentary axillary bud. Fig. 27. T.s. top of pedicel. Fig. 28. T.s. basal part of ovary. Fig. 29. T.s. ovary showing origin of the dorsal bundles of the carpels. Figs. 30, 31. Branching of three strands of the ovary wall. Fig. 32. T.s. at level of separation of style from perianth tube. Fig. 33. T.s. at anther level Fig. 34. T.s. at annulus level showing origin of the six staminal traces.

DISCUSSION

Burmannia disticha, *B. nepalensis*, and *B. pusilla* agree in general morphological features but show certain anatomical differences. In all these three species the inner margins of the connectives are wedged in longitudinal furrows of the upper part of the style or in the spaces that separate the 3 stigmatiferous branches of the style. It has been shown earlier (Rao, 1967) that Pai's statement (1966 *a*) that the stamens of *Burmannia pusilla* are connected with the style by broad bands of parenchymatous tissue is wrong. Hence his theorizing (Pai, 1966 *b*) about the relationships of the entire family of Burmanniaceae on the basis of wrong observations of one species of the genus *Burmannia* is meaningless. There is no actual fusion at all between the stamens and the style in any species of *Burmannia*. Even if there were a fusion (assuming it for the sake of an argument), it is a far cry between Burmanniaceae on the one hand and Orchidaceae on the other. In the former, the stamens are epipetalous high up on the perianth tube, the adhesion being between the perianth and the androecium. In Orchidaceae as well as in the Apostasiaceae the adhesion of the androecium is not at all with the perianth but with the gynoecium.

There are many placental bundles in *B. disticha* while in *B. pusilla* and *B. nepalensis* they are either 3 or 6, consistent with the number of composite or separate ventral bundles of the carpels. The orientation of the ventral bundles in *B. disticha* and *B. nepalensis* is not clear. Pai (1966 *a*) stated that in *B. pusilla* the ventral bundles have a normal orientation. This again is a wrong observation because in that species the orientation is unmistakably clear and the ventral bundles have a very definite inverse orientation (Rao, 1968). The ovary of *B. nepalensis* has a central strand of thick-walled cells at the periphery of which the ventral bundles are present. *B. disticha* and *B. pusilla* do not have such a strand. There are many monocotyledons in which the septal glands are reported to open freely to the outside, and Pai (1966 *a*) reported that such is the case in *B. pusilla*. In *B. disticha* they end in solid tissue. It is quite likely that they end freely to the outside in some species of this genus, and it is not of much significance. There might be variation in this character depending upon even the age of the flower-bud, the septal glands being closed at one stage and open at another. *B. disticha*, *B. nepalensis* and *B. pusilla* differ in the aestivation of the perianth members.

Gymnosiphon cymosus and *G. aphyllus* resemble each other very closely in floral anatomy and in other morphological features like the placental glands. In both, it seems best to regard the small inwardly projecting placentiferous parts of the ovary wall as 'partial septa'. These bear the placentae at their inner margin. (The term partial is used in the sense that it does not extend up to the centre.) The placentation of course is parietal and the placentae are prominently vascularized. Although taxonomic literature refers to glands of the placentae, it is really not the placentae but the partial septa that bear

them between the placentiferous end and the ovary wall. For convenience in description, however, it is best to retain the term placental gland, realizing that it is the septum and not the actual placenta that bears it. The term 'gland' here should not be taken in a physiological sense. The very great similarity between these two species of *Gymnosiphon* proves that Jonker (1938) is correct in merging *Ptychomeria* with *Gymnosiphon*. *G. cymosus* was earlier kept in *Ptychomeria* as *P. cymosa* Benth.

Thismia aseroe has a separation of the dorsal bundles of the carpels from the cords alternating with the placentae, near about the middle of the length of the ovary. It is peculiar that these dorsal bundles do not travel directly inwards but start as lateral branches which then suddenly turn inwards to occupy the carpellary dorsal positions. The number of bundles that traverse the perianth tube is 12 as contrasted with the 6 in *Burmannia* and *Gymnosiphon*. The stamens are 6 in *Thismia* but only 3 in the other two genera studied. The 6 anthers are pendulous from an annular in-growth of the perianth tube. It is at the level of the annulus that the 6 main strands of the perianth tube bear the staminal traces which move inwards and downwards into the connectives. The anthers of *Thismia* are laterally coherent, forming a tube round the style.

It is difficult to make out from Saunders' (1939) account which species of Burmanniaceae formed the basis of her descriptions of floral anatomy. According to her, the vascular system below the flower generally consists of three cords. This is more correct of *Gymnosiphon* (including *Ptychomeria*) and *Thismia* than of *Burmannia*. Each of the three cords is said by her to trifurcate, the median branch running on a sepal radius, while the adjoining lateral branches of adjacent cords fuse to form a bundle on the petal radius. Thus on each of the perianth radii there is a vascular strand. Those on the sepal radii supply the sepals and the sterile carpel midribs, and if an antesepalous set of stamens is present, that also is supplied. Those on the petal radii supply the petals, the antepetalous stamens and the placental bundles of the fertile carpels. She has also mentioned the formation of septal glands above the upper ends of the placental bundles. What she called as the sterile carpels are the carpels in the classical interpretation. As described by her, in *Burmannia* (species not stated) the 6 strands of the ovary wall have anastomozing branches at the top of the ovary, and these form a complete girdle. This feature is not seen in any of the species of *Burmannia* studied by the present author.

Pai (1966 *a*) called the wings of the ovary of *Burmannia* as "median lateral extensions of the sepals". They are median outward, and not median lateral (compare the use of the term "median lateral" bundles of the ovary wall).

Summary

The floral anatomy of *Burmannia disticha*, *B. nepalensis*, *Gymnosiphon cymosus*, *G. aphyllus*, and *Thismia aseroe* is studied. In *Burmannia* the inner margins of the connectives are merely wedged in

furrows of the style and there is no fusion between the androecium and the gynoecium. The two species of *Gymnosiphon* have the same type of floral morphology. The partial septa bear glands on either side at the top. The placentae in these two species are richly vascularized. The vascular anatomy of the flower of *Thismia* differs from that of the other genera. The dorsal bundles of the carpels are organized near about the middle of the length of the ovary as laterally inward branches of three of the cords of the ovary wall. There are 6 pendulous anthers which are laterally coherent to form a tube round the style. The 6 main cords of the perianth tube bear the staminal traces at the level of the annulus of the perianth tube, and these descend downwards into the connectives of the anthers.

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