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FLORAL ORGANOGENESIS IN SOME BIGNONIACEAE[1]

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ABSTRACT

This paper reports on the floral organogenesis in three species of Bignoniaceae, *Jacaranda cuspidifolia, Millingtonia hortensis* and *Tecoma stans*. The sequence of inception of the floral appendages is acropetal except for overlapping in the formation of petal and stamen primordia in *Tecoma stans*. The five sepal primordia arise as discrete units but they soon unite to form a short calyx tube by ontogenetic fusion of their bases. The petal primordia are also initiated as discrete units adaxial to and alternate with the sepal primordia. Two processes are involved in the formation of corolla tube, zonal growth and the extension of margins of the petal primordia. The four stamen primordia follow quickly the petal primordia. A fifth stamen primordium appears slightly later in the adaxial position and it develops into staminode. At a time when the stamen primordia are as high as the petal primordia, two crescent shaped gynoecial primordia arise in antero-posterior plane. The residual floral apex grows parallel to the gynoecial primordia in the form of a septum, that extends on either side towards the ovary wall to form two massive placentae. The ovules are borne on these placentae which are extension of the septum and not on the gynoecial primordia. The early development of the flower suggests that the disc in Bignoniaceae is carpellary in nature as it arises from the basal region of the ovary wall as an outgrowth.

INTRODUCTION

The ontogenetic studies have proved very useful in the better understanding of the morphology of flowers. In view of the importance attached to the sympetalous condition in the construction of phylogenetic systems and the sporadic attention by investigators on developmental studies of this group a detailed study on the floral development in Bignoniaceae has been undertaken. This paper reports on the organogenesis of flowers in three taxa of the Bignoniaceae.

MATERIALS AND METHODS

Inflorescences of *Jacaranda cuspidifolia* Mart., *Millingtonia hortensis* L. and *Tecoma stans* (L.) H. B. & K. in various stages of development were collected from the plants growing in Meerut. They were immediately fixed in formalin-acetic acid-alcohol (F A. A.) and preserved in 70% ethanol. To obtain pictures of three dimensional developmental stages, entire young inflorescences were stained in 0.5-1% solution of acid fuchsin in 95% ethanol. They were differentiated in 70% to 95% ethanol and then dissected and photographed completely immersed in 100% ethanol, with the help of a Zeiss stereoscopic binocular with an incident light condenser. A high contrast copying film was used in conjunction with a green filter to obtain good contrast. The prints were made on hard paper (Sattler, 1968).

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OBSERVATIONS

Organography: The flowers are borne in three-flowered axillary lateral cymes which form axillary or terminal panicles. They are bracteate, bracteolate, hermaphrodite, zygomorphic and hypogynous. The bracts and bracteoles are small and narrow. The calyx is cupular-campanulate, truncate or shortly 5-dentate with narrow, lanceolate, equal (*Millingtonia hortensis*) or somewhat unequal (*Jacaranda cuspidifolia*, *Tecoma stans*) segments. The corolla is also tubular-campanulate or funnelform with a moderately long and narrow basal tube. The limbs are sub-bilabiate; in *Jacaranda cuspidifolia* and *Millingtonia hortensis* the upper lip is notched and the lower lip is rather large and three-lobed; in *Tecoma stans* the limbs, however, have five undulate, oblong or obtuse and somewhat subequal imbricate lobes. The androecium consists of four fertile stamens and a posterior staminode inserted on the corolla tube. The stamens are didynamous with dithecous and introrse anthers having divaricate cells. In *Millingtonia hortensis* the two anther lobes are unequal. The staminode is a dorsiventrally flattened structure varying in height and it may be awl-shaped (*Millingtonia hortensis*), spathulate (*Tecoma stans*) or club-shaped and villous (*Jacaranda cuspidifolia*). Frequently it is surmounted by an abortive anther in *Jacaranda cuspidifolia*. The gynoecium is bicarpellary and syncarpous with a superior bilocular ovary having numerous anatropous ovules on each placenta. The style is simple and filiform and the stigma is bilamellate. The base of the ovary is surrounded by a conspicuous annular or cupular nectariferous disc.

Organogenesis: The bracts arise in opposite decussate pairs on the high dome-shaped inflorescence apex as broad dorsiventral organs. They sharply curve over the inflorescence apex as they grow. Shortly after the inception of the bract primordium, an apex of the lateral branch of the inflorescence is initiated in its axil (Figs. 1,20). This apex after producing two bract primordia of second order gets transformed into a floral apex. A floral apex is also initiated in the axil of each bract primordium. Thus, the lateral branch of the inflorescence has three flowers. In *Tecoma stans*, the apices formed in the axils of bracts, however, do not develop and hence the axillary inflorescence in this taxon has a single flower. The central flower of an axillary inflorescence is first to initiate followed by the two lateral flowers which in turn are formed almost simultaneously.

A young floral apex is a low dome-shaped structure before sepal initiation. The five sepal primordia are initiated on the flanks of the floral apex in a very rapid sequence (Figs. 2,11,21). In *Jacaranda cuspidifolia*, the primordium of the posterior sepal is larger since its inception (Fig. 2). Shortly after the initiation of sepal primordia a short calyx tube is formed as a result of interprimordial growth between the adjacent sepal primordia (Figs. 2,12).

After the formation of the sepal primordi the floral apex becomes nearly flat and assumes a pentagonal shape. The five petal primordia are initiated almost simultaneously adaxial to and alternate with the sepal primordia on the five corners of the rim (Figs. 3,12,13).

The four stamen primordia follow quickly the petal primordia but in *Tecoma stans* they arise with the petal primordia or even immediately before the petal primordia (Fig. 22). They appear approximately at the same time or they have a very rapid sequential inception (Figs. 3,14,22,23). A fifth stamen primordium appears slightly later in the adaxial position. The growth of this primordium is arrested at an early stage of development and it forms a staminode (Figs. 8,15,27, 29). However, in some floral buds of *Jacaranda cuspidifolia* it also develops abortive anthers. In some floral buds of *Tecoma stans* the fifth stamen primordium is completely absent even in its rudimentary form (Fig. 26). Each stamen primordium differentiates into a basal and a distal portion in later stage of development. The former gives rise to a short filament and the latter a dithecous introrse anther (Figs. 8,15,18,19,27). In *Millingtonia hortensis*, one of the two anther lobes of a stamen grows faster and as a result of this the two anther lobes become unequal in size (Fig. 19).

Soon after the formation of stamen primordia, growth between the petal primordia interconnects them in the form of a ridge which encircles the androecium (Figs. 14,24). This is the beginning of the corolla tube formation and the tube grows further as a result of zonal growth in the bases of petal and stamen primordia. The five corolla lobes are very conspicuous up to later developmental stages (Figs. 4,25), but they are not so prominent in the mature flowers of *Tecoma stans* where the corolla is funnelform. The free lobes assume imbricate aestivation (Fig. 4).

At a time when the stamen primordia are as high as the petal primordia, the gynoecium is initiated as an almost pentagonal rim which completely surrounds the central floral apex (Fig. 14). During the upgrowth of the gynoecial ring, the adaxial portions grow more and consequently the rim becomes two lobed (Fig. 6,15,24, 25). During further development the lobes form the stigma whereas the cylindrical portion below the free lobes forms the ovary which narrows into the style (Figs. 7-10,17,18,26-29).

As the lower cylindrical portion of the ovary grows, there is an outgrowth of the floral apex in continuity of the ovary wall. As a result of this a ridge is formed parallel to the long axis of the carpels which forms the septum. Thus, the ovary becomes sub-divided in two locules by one solid upgrowth (Fig. 16). This septum extends on either side towards the ovary wall to form two massive placentae each of which bears numerous ovule primordia in rapid basipetal succession. Each ovule becomes unitegmic and anatropous.

After the formation of the ovules, a nectariferous disc is initiated from the basal portion of the ovary wall (Fig. 10). It becomes 5-lobed and the lobes alternate with the stamens.

In *Jacaranda cuspidifolia*, an occasional increase has been observed in the number of the stamen and carpel primordia. One such bud showed as many as eight stamen and three carpel primordia (Fig. 5).

DISCUSSION

The primordia of the floral appendages in all the three taxa are initiated in acropetal (centripetal) sequence. However, there is an overlapping in the formation of petal and stamen primordia in *Tecoma stans*, a condition which has also been reported in *Pyrostegia venusta* (Jain and Singh, in press).

There has been a great deal of controversy with regard to the mode of development of floral tubes in angiosperms. The existing literature has been briefly reviewed by Singh and Jain (1979). In the taxa investigated for the present study, it has been observed that after the formation of the petal and stamen primordia, growth takes place in a ring zone below them. Later, there is a lateral union of the petal primordia by marginal growth. Thus, two processes are involved in the formation of corolla tube, zonal growth and the extension of margins of the petal primordia. The short calyx tube is resulted by interprimordial growth between the sepal primordia.

In later stages of development the stamen primordium is differentiated into a basal and a distal portion. The former gives rise to a short filament and the latter a dithecous introrse anther. The anther lobes grow at the same rate in *Jacaranda cuspidifolia* and *Tecoma stans* but in *Millingtonia hortensis* one of the anther lobes grows faster and as a result of this the two anther lobes in a mature stamen are of unequal size.

The form, position and structure of nectaries in angiosperms are very variable and from the morphological point of view they are usually distinguished into two types: (1) localized areas where nectar is secreted, and (ii) organs transformed from their original form and function (*see* Puri and Agarwal, 1976). The cupular or cushion-shaped nectariferous disc which surrounds the base of the ovary in all the three taxa investigated falis under the second category. Such nectaries have also been observed in several other families of Bicarpellatae e. g. Oleaceae, Boraginaceae, Apocynaceae, Convolvulaceae, Acanthaceae, etc., where they are vascular in some and nonvascular in others (*see* Puri and Agarwal, 1976). The disc in Bignoniaceae is richly vascularized and receives its vascular supply from many sources (Rao, 1954; Jain, 1977) and hence it has been variously interpreted. In mature flowers the base of the ovary appears to be quite distinct from the disc, and Rao (1954) considered it a strong argument against its carpellary nature. However, early developmental stages of the flowers are conclusive which shows that the disc is formed as a result of the outgrowth of the basal region of the ovary wall. This clearly suggests its carpellary nature. Fahn (1953) who examined the nectaries in some 52 families of angiosperms also classified the nectaries of Bignoniaceae as discoid (ovarial) type.

After producing two carpel primordia the floral apex grows up dividing the ovarian cavity into two locules. The ovules are borne on placentae which are extensions of this septum and not on the carpel primordia.

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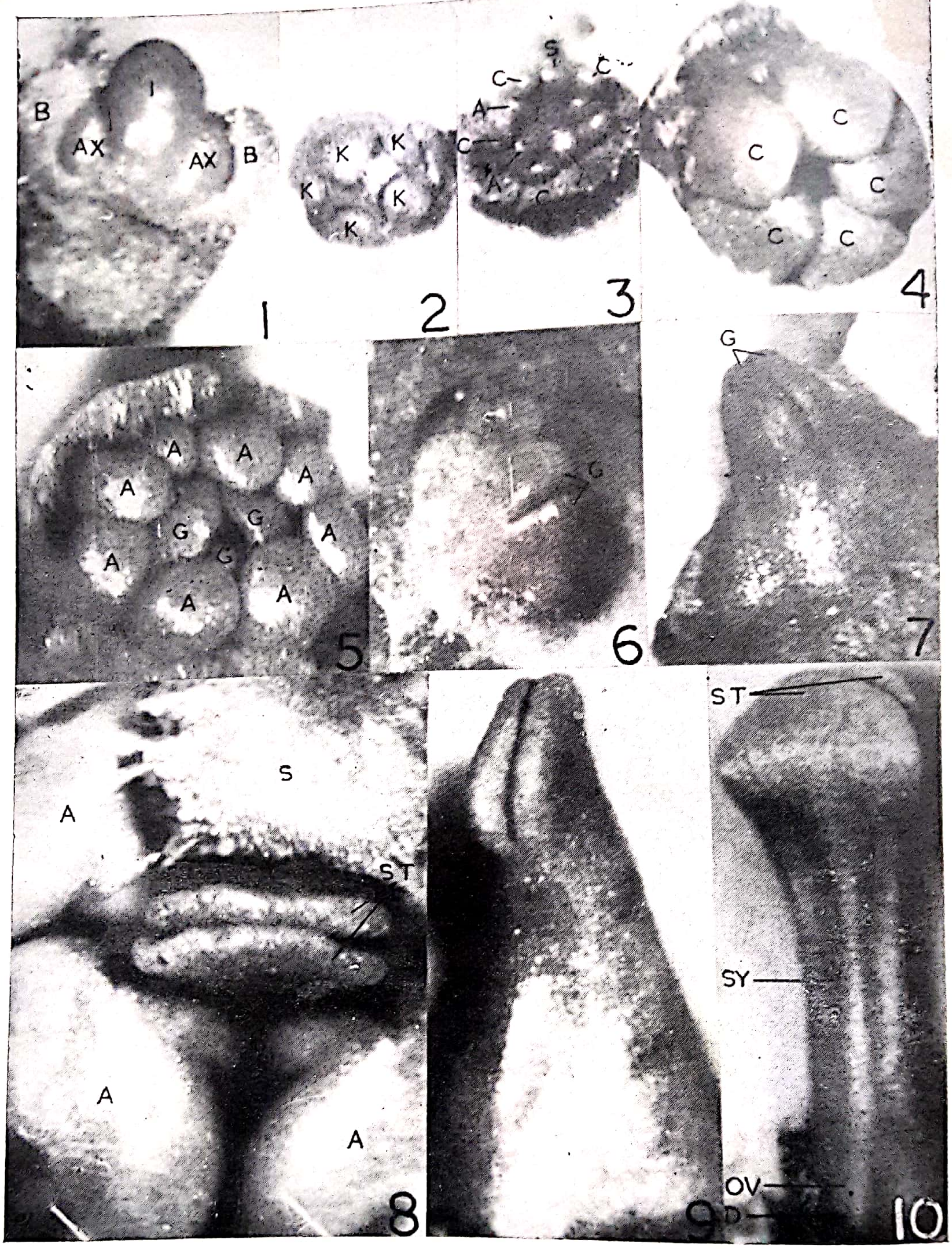
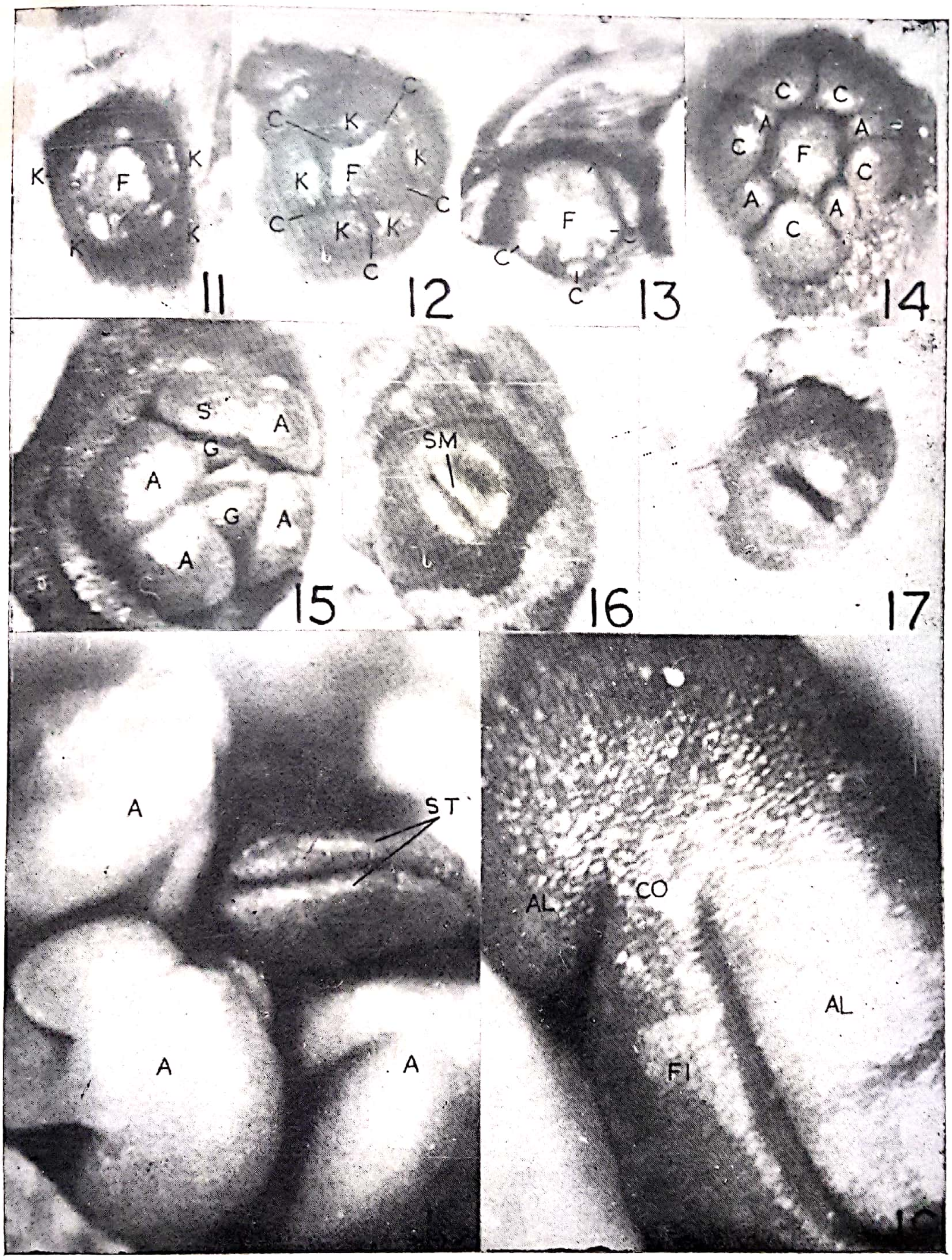


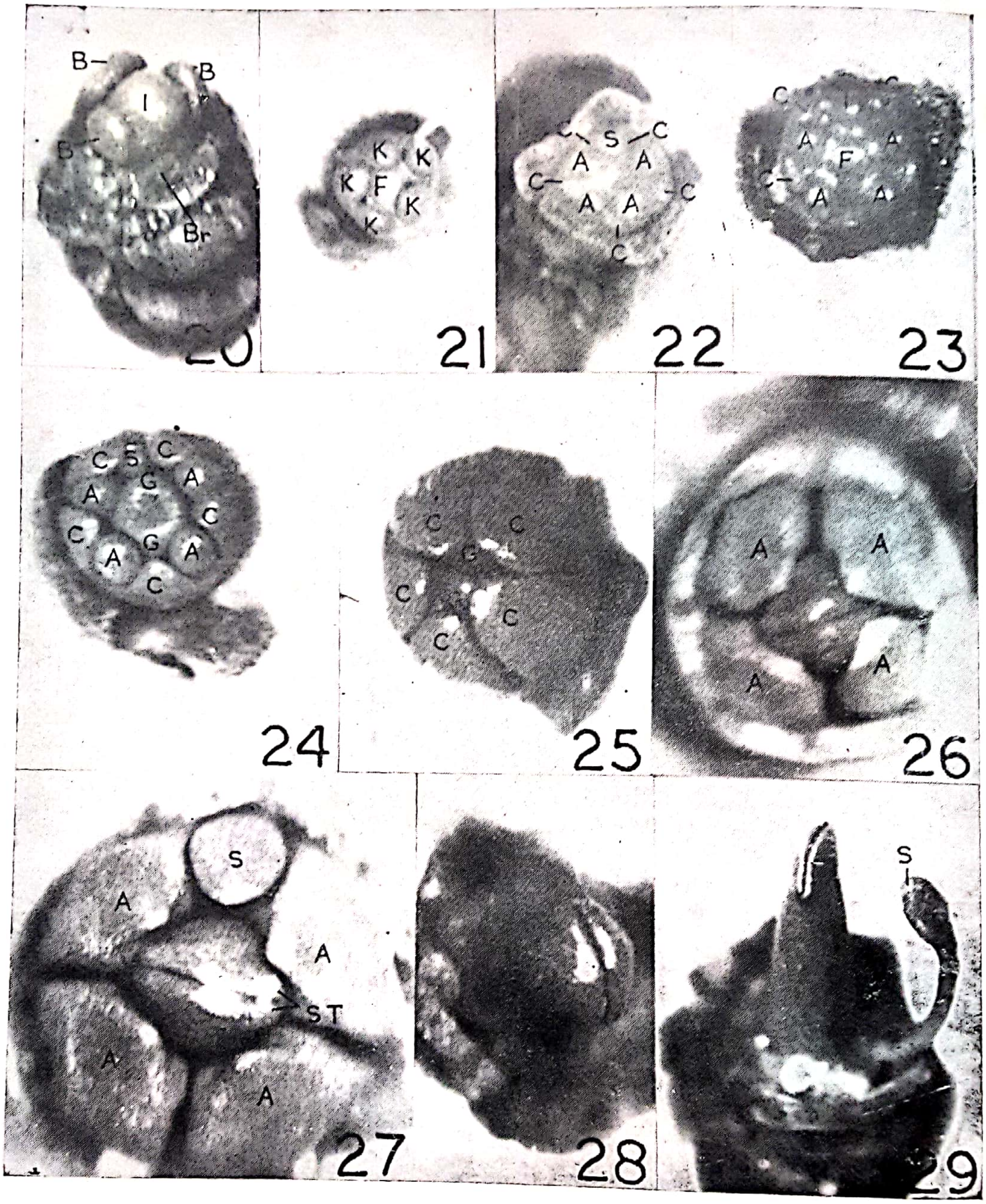
Figs. 1-10. Floral organogenesis in *Jacaranda cuspidifolia*. Fig. 1. An inflorescence apex (I) in side view showing bract primordia (B) and axillary branches (AX) of the inflorescence. Fig. 2. A floral bud in top view after the inception of sepal primordia (K). Fig. 3. A floral bud in top view where sepals were removed to exhibit petal (C), stamen (A) and staminodial (S) primordia. Fig. 4. A floral bud in top view showing the aestivation of the corolla lobes. Fig. 5. An abnormal floral bud in top view with eight stamens (A) and three gynoecial (G) primordia. Figs. 6-10. Gynoecia of floral buds showing stages of pistil development. Stamens (A) and staminode (S) at a later stage of developement can also be seen in figure 8.

Figures 1-9 ×100 ; Figure 10 ×63.

Abbreviations used : A—Stamen primordium ; AL—Anther lobe ; AX—Axillary branch of inflorescence ; B—Bract primordium ; Br—Bract primordium removed ; C—Petal primordium ; CO—Connective ; Dt Disc ; F—Floral apex ; FI—Filament ; G—Gynoecial primordium ; I—Inflorescence apex ; K—Sepal primordium ; OV—Ovary ; S—Staminodial primordium ; SM Septum ; ST—Stigma ; SY—Style.



Figs. 11-19. Floral organogenesis in *Millingtonia hortensis*. ×100. Fig. 11. Top view of a floral bud after the inception of sepal primordia (K). Figs. 12-13. Top views of floral buds at the time of inception of petals (C). The sepal primordia were removed in figure 13. Fig. 14. A floral bud in top view at the time of initiation of gynoecium which arises as a pentagonal rim surrounding the floral apex (F). Fig. 15. Top view of a floral bud where sepals and petals were removed to exhibit stamen (A), staminodial (S) and gynoecial (G) primordia. Figs. 16-17. Gynoecia of floral buds showing stages of pistil development. Figure 16 shows the formation of a septum (SM) which divides the ovary cavity in two locules. Fig. 18. A floral bud in top view showing later stage of development of stamen (A) and gynoecium. Fig. 19. A developing stamen showing two unequal anther lobes (AL).



Figs. 20-29. Floral organogenesis in *Tecoma stans*. Fig. 20. An inflorescence apex (I) in top view showing bract primordia (B). Fig. 21. Top view of a floral bud after the inception of sepal primordia (K). Fig. 22. Top view of a floral bud during inception of petal (C), stamen (A) and staminodial (S) primordia. The sepals were removed. Fig. 23. Top view of a floral bud (sepals removed) showing a later stage of development of petal (C), stamen (A) and staminodial (S) primordia. Figs. 24-25. Top views of floral buds (sepals removed) showing the stages of gynoecial (G) development. Early stages in the formation of the corolla tube can also be seen. Figs. 26-27. Top views of the floral buds (sepals and petals removed) to show stages of stamen (A), staminode (S) and gynoecial development. Note that staminodial primordium is not formed in figure 26. Figs. 28-29. Gynoecia of floral buds showing two successive stages of development. Staminode (S) at a late stage of development can also be seen in figure 29.

Figures 20-28 ×100 ; Figure 29 ×40.