POLLINATION MECHANISM IN *PASSIFLORA FOETIDA* LINN.

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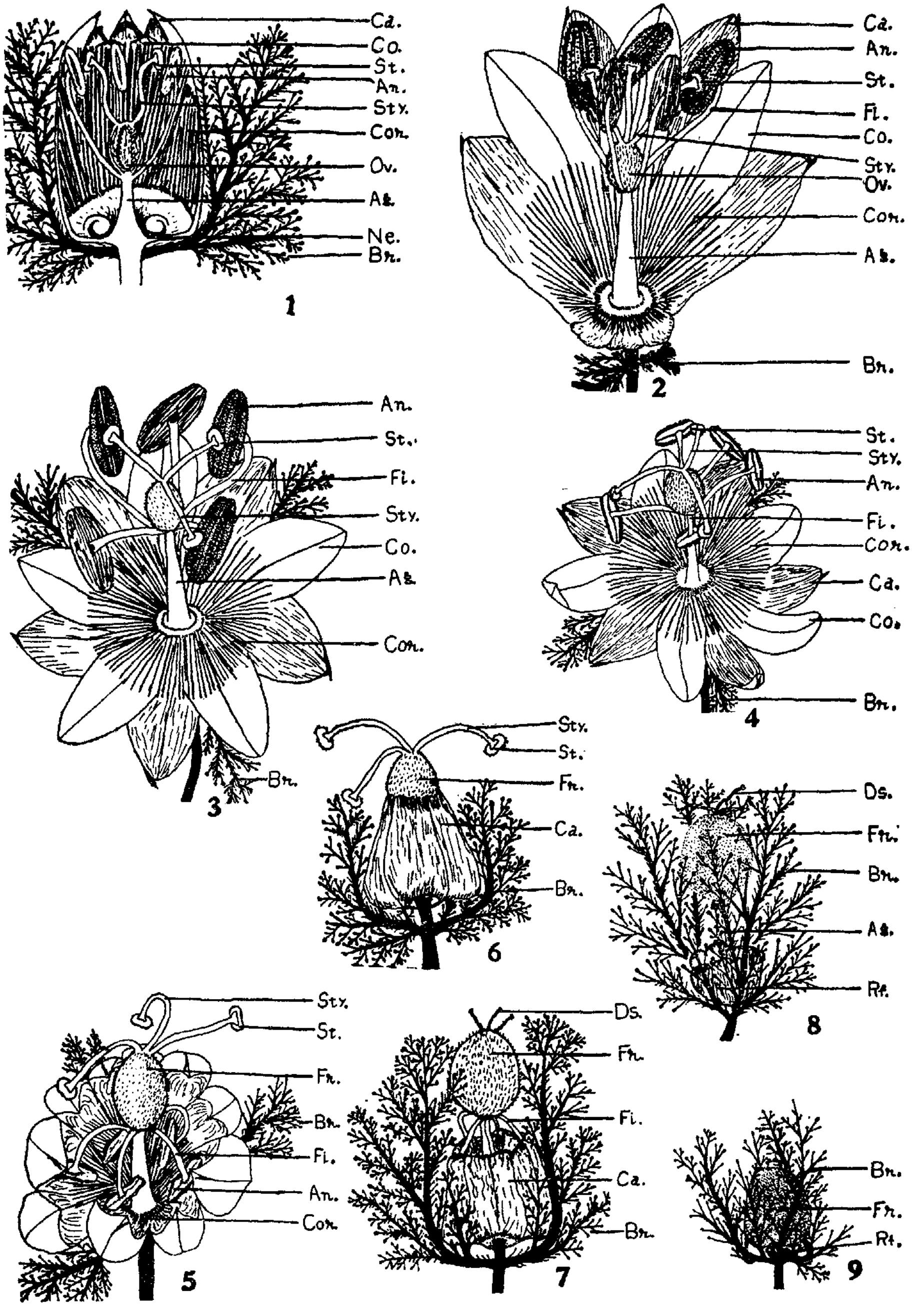
A detailed account of the various types of pollination mechanism has been given by Kerner (1891) in his monumental work entitled 'Natural History of Plants'. Information concerning the mode of pollination in members of the Passifloraceae is also available from the work of Knuth (1908). The information presented by these authors does not, however, appear to be quite precise in every case. In the course of an embryological study of some members of the Passifloraceae I was able to observe certain interesting details concerning the pollination mechanism of *Passiflora foetida* grown in the Central College Botanical Gardens.

The solitary hermaphrodite flower has three highly dissected bracteoles at the base. The five calyx lobes enclose five white membranous petals. In the centre of the flower is an androgynophore around the base of which is a shallow cup with nectar bounded by one to many rows of filiform white or slightly violet coloured segments forming the corona. The androgynophore bears at its top the tricarpellary ovary with its three styles and stigmas. The stigmatic surface has a number of multicellular papillate outgrowths. At the base of the ovary five stamens emerge from the androgynophore. The anthers are oblong and introrse. The filament is stiff and flat and to this is attached the anther by a hinge-like arrangement. The filament shows two pegs which act as a pivot so as to allow the anther to rotate slightly with a jerky movement in any direction on the filament.

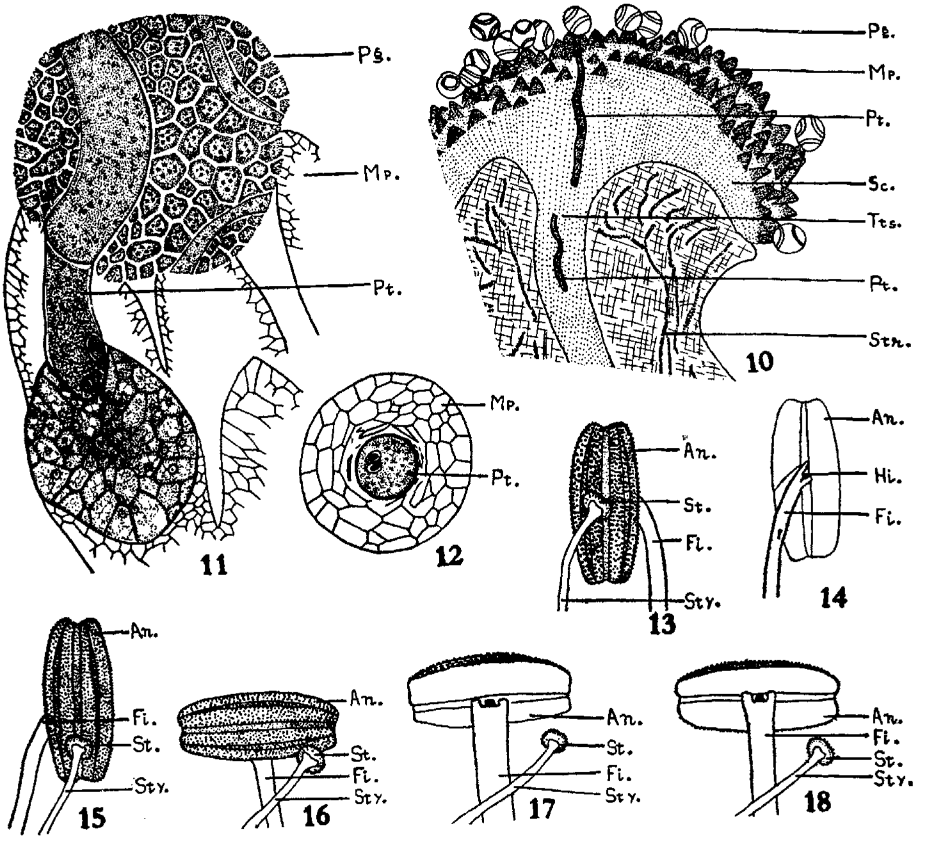
OBSERVATIONS

Figure 1 shows the arrangement of the floral parts as seen in a median longitudinal section of the flower bud prior to anthesis. The anthers are in close contact with the stigmatic lobes and the other floral members are erect in position (Fig. 1). The bracteoles are highly dissected, the branches forming ramifications and terminating in glands which secrete a highly sticky substance in later stages. Anthesis takes place during nights and lasts from a few minutes to a few hours. The first indication of anthesis is the horizontal spreading of the bracteoles and the subsequent opening of the calyx and corolla (Figs. 2–4). By about this time the anthers dehisce and their dehisced faces are pressed against the stigmatic lobes by a downward movement of the latter (Figs. 2–4). At first the anther lobes are in a line with the filament (Figs. 2 and 13). One of the stigmatic lobes comes in contact with the dehisced surface of the anther at its middle (Figs. 2, 3 and 13). Subsequently, the stigmatic lobe becomes closely pressed against the dehisced surface of the anther and a kind of mechanical tension is brought about by mutual pressure. The stigmatic lobe is now brushed against the pollen carrying surface of the anther, but finally slips out due to the slow jerking movement of the latter (Figs. 15–17). As a result, the tension originally created between the anther and the stigma is released and the anther begins to tilt suddenly on the filament (Figs. 15–18). Thus the dehisced surface of the anther now becomes directed downwards (Figs. 4, 5, 17 and 18).



FIGS. 1–9. Fig. 1. L.S. young flower bud just before anthesis showing the arrangement of flower parts. Fig. 2. L.S. view of a flower just after anthesis with dehisced surfaces of anthers in contact with the stigmatic lobes. A few calyx and corolla lobes removed. Fig. 3. Still later stage after anthesis showing the horizontal spreading of bracteoles, calyx, corolla and corona; and bending of the styles over their respective anther lobes. Fig. 4. Pollinated flower showing the incurving of the margins of sepals and petals. Fig. 5. A view of the flower with inrolling petals and sepals gradually enveloping downwardly

bent stamens. Fig. 6. Side view of flower with erect bracteoles and the margins of petals and sepals lying at the base of the ovary also enveloping the stamens completely. Fig. 7. Flower showing downward shrinking of sepals with the enclosed petals, corona and stamens. Fig. 8. Fruit with fading styles and drying floral parts at the base of the androgynophore. Fig. 9. Same at later stage showing the fruit enveloped by the sticky bracteoles. (*Ag*, androgynophore; *An*, anther; *Br*, bracteoles; *Ca*, calyx; *Co*, corolla; *Cor*, corona; *Ds*, fading style; *Fi*, filament; *Fr*, fruit; *Ne*, nectary; *Ov*, ovary; *Rf*, remnants of floral parts; *St*, stigma; *Sty*, style.) All figures diagrammatic.



FIGS. 10–18. Fig. 10. Longitudinal free-hand section of the stigmatic lobe showing multi-cellular outgrowths bearing pollen grains; note the penetration of pollen tube through the outgrowth and into the transmitting tissue, ×50. Fig. 11. A portion of the stigmatic crest showing the germination of a pollen grain and the entry of the pollen tube in the multi-cellular outgrowth, ×485. Fig. 12. T.S. of the multi-cellular outgrowth and the pollen tube, ×485. Fig. 13. Stigma in contact with the dehisced surface of the anther. Fig. 14. Back-view of the same showing the hinge attachment. Figs. 15–18. Stages showing the movement of anther with respect to the stigmatic lobe. (*An*, anther; *Fi*, filament; *Hi*, hinge; *Mp*, multi-cellular papillate outgrowth; *Pg*, pollen grain; *Pt*, pollen tube; *Sc*, stigmatic crest; *St*, stigma; *Str*, stylar tracheids; *Sty*, style; *Tts*, transmitting tissue.) (Figs. 13–18. All diagrammatic.)

The movement of the anther takes place in both the vertical and horizontal planes (Figs. 13 and 15–18). In the final stage when the dehisced surface becomes downwardly directed, the anther comes to lie at right angles to its filament (Figs. 17 and 18). The movement itself seems to be due largely to the peculiar hinge-like mechanism which aids in drawing down the anther and also in helping it to become laterally tilted (Figs. 14, 17 and 18). The anthers of a flower which are not in contact with any of the stigmatic surfaces also perform these movements. The dehisced anthers may also touch the stigmatic lobes and deposit their pollen subsequently.

Early in the day, after pollination is over and as the temperature begins to rise, the bracteoles, sepals and petals gradually move towards the centre of the flower (Figs. 4 and 5). Concurrently, the stamens also begin to droop down (Figs. 5 and 7). The inrolling sepals, petals and coronary filaments thus begin to enclose the stamens and touch the base of the developing fruit (Fig. 6). Later, the petals and sepals begin to dry up and move towards the base of the androgynophore (Fig. 7). The developing fruit is now well protected against ants and other insects by the latticed bracteoles which secrete a sticky fluid. Frequently ants were found to be caught in the meshes of the bracteoles. At the base of the androgynophore, inside the bracteoles, the shrivelled sepals, petals and coronary filaments as well as the dried up anthers can be seen (Figs. 8 and 9). The bracteoles themselves dry up finally and wither away only when the fruits are fairly old.

The stigmatic lobe is slightly reniform in shape and possesses multi-cellular papillate outgrowths on its surface (Fig. 10). The pollen grains with their reticulate exine are easily caught by these outgrowths on account of their rubbing against their anther surfaces. Beneath the papillate outgrowths is the expanded stigmatic crest through which the pollen grains send their pollen tubes which grow ultimately through the transmitting tissue of the style and reach the ovary (Figs. 10–12).

Discussion and Conclusions

The above observations confirm those of Warnstorf, especially regarding the movement of the anthers and the styles (*see* Knuth, 1908). Warnstorf has pointed out that anthesis lasts for a whole day. From my observations, however, made on a large number of flowers, I find that anthesis occurs only for a brief time during the early hours of the morning when the atmosphere is relatively cool.

The large size of the flower, the occurrence of the complicated brightly coloured coronary filaments, the hidden nectary and the elevated position of the essential organs all suggest that cross-pollination occurs and that it is aided by some special insect visitors. Knuth (1908) says: 'In the first stage of anthesis a large insect (such as a humble-bee) when sucking nectar, receives pollen on its back from the downwardly dehiscing anthers. In the second stage the styles have curved downwards to such an extent that the now receptive stigmas are lower than the empty anthers. It follows that the older flowers are fertilized by pollen from younger ones.' According to my observations, however, the second stage described by Knuth occurs only subsequent to pollination, when the styles move up and the stamens move down so that once again a contact may be established between dehisced surfaces of anthers and the stigmatic crests. Warnstorf explains the upward deflection of purple-flecked styles from the anthers as suggesting that autogamy would be excluded under such circumstances, but that the stigmas and anthers may be brought into contact when the flower closes at the end of single day's anthesis (*see* Knuth, 1908). The above observations of Warnstorf make one feel doubtful about the statement that 'the older flowers are fertilized by pollen of younger ones'.

In *Passiflora foetida* the flower undoubtedly closes gradually after pollination. This makes the dehisced anthers which have moved down after pollination to become enclosed by the corona, corolla and the calyx and no contact can, therefore, be brought about between the stigma and such anthers at this stage. Thus Warnstorf's suggestion probably owes itself to his having found the styles spread out and the anthers with their dehisced surfaces directed downwards. The mechanism involved in the downward and later upward movement of the styles or the movement of the anthers themselves on their filaments with reference to the apposed stigmatic surfaces seem to have been overlooked by him. Basing his observations on plants grown in a green house, his interpretation of the chasmogamic flower being adapted to authogamy appears to be exaggerated. Perhaps, some of the post-pollination features like the downward movement of the styles and stamens and displacement of anthers were presumed by Warnstorf to be stages preceding actual pollination.

Delpino's (*see* Knuth, 1908) suggestions of humming birds as pollinating agents and a subsequent corroboration of the same by Müller in some of the Brazilian Passifloras probably deserve further study and confirmation. In *Passiflora foetida*, occasionally, insects were found to be moving about on the floral parts during post-pollination stages. The insects were very small, however, and it is improbable that they can be considered as pollinating agents. Very rarely, especially in the mornings when there is bright sunshine, a small honey bee would seem to alight on the corona in a flower completely spread out. By this time, however, pollination is completed and pollen tubes were actually observed to have reached the transmitting tissue. Doubtless, the honey bee collects some pollen grains on its back and legs, but this takes place only subsequent to pollination. The suggestion made by earlier workers that the honey bee alone brought about cross-pollination, is therefore erroneous.

'It is true that cross-pollination appears to be the primary object aimed at, but it is not true that autogamy is avoided. If cross-pollination takes place there is naturally no necessity for subsequent autogamy, but if cross-pollination fails autogamy assumes an importance of its own, and the contrivances which have been observed to bring about autogamy are no less numerous than those which favour cross-pollination. That flowers should be adapted at different times to two such diverse purposes as cross- and self-pollination is one of marvels of floral construction' (Kerner, 1891). One of these marvels of floral construction adapted to autogamy is seen in *Passiflora foetida.* The structure and behaviour of different entities and their unified action have made autogamy a successful mode of pollination in this plant. A good example of an intermediate case between cleistogamy and chasmogamy seems to be demonstrated in *Passiflora foetida.*

The pollen grains have such characteristic thickenings that they are easily caught by the stigmatic crest. The pollen tubes emerging out from the furrows of the pollen grains penetrate directly into the multicellular outgrowths and not in between them. The highly dissected bracteoles form a lattice work enveloping and protecting the fruits in later stages. The glandular tips of their ramifications secrete a juicy fluid which, probably, attracts the neighbouring ants or small insects. The remnants of those ants are later seen on the bracteoles.

Summary

Pollination mechanism in the flowers of *Passiflora foetida* grown in Central College Botanical Gardens has been studied. Anthesis of flowers occurs during nights and lasts for a brief time. The unified action of the different entities of the flower helps in self-pollination. The stigmatic crests with their multicellular papillate outgrowths easily catch the pollen grains which have reticulate exine thickenings. The pollen tube emerging out from one of the furrows of the pollen grain penetrates directly into the multicellular outgrowth. During post-pollination stages the latticed bracteoles protect the developing fruits. Autogamy is successfully ensured in the flowers of *Passiflora foetida* and it can be taken as a good example of an intermediate case between cleistogamy and chasmogamy.

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