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Organogenesis of Flower in *Nicotiana rustica* L. (Solanaceae)

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The inception of the floral appendages in *Nicotiana rustica* L. is centripetal. The five sepals arise in succession in clockwise or counter clockwise sequence as separated primordia. The calyx tube is initiated by the extension and fusion of the bases of the sepal primordia. The five petal primordia arise simultaneously also as discrete units. The corolla tube is initiated by the fusion of the bases of fully meristematic primordia on the base of the back of stamen primordia. Further upgrowth of the corolla tube takes place by zonal growth. The gynoecium arises as a rim which grows upward to form the ovary and the style. Two septa are initiated from the inner region of the ovary and they fuse post-genitally in the centre of the ovary. The floral apex also grows upward and fuses with these septa and thus a common septum is produced which enlarges to form two massive placentae. Hence, developmentally the placentation is intermediate between a typical axile and parietal condition.

Key Words: *Nicotiana rustica*, **Floral organogenesis, corolla tube, Zonal growth**

Introduction

The development of flowers in a few members of the Solanaceae has received attention of earlier workers. Floral development of *Solanum tuberosum* has been reported by Young (1923) and that of *S. lycopersicon* by Cooper (1927), Warner (1933) and Efeikin (1958). Sattler (1973) made a detailed study of the organogenesis of flower in *Solanum dulcamara* and more recently in another paper (Sattler 1977) he has discussed the inception of corolla tube in the same taxon. Satina and Blakeslee (1943) reported on periclinal chimeras in *Datura* in relation to carpel development. Shah and Patel (1970) described the ontogeny and development of the floral and vegetative buds in brinjal (*Solanum melongena*) and chilli (*Capsicum annuum*). Waterkeyn et al. (1965) and Diomaiuto-Bonnand (1966) have described the transition from vegetative to reproductive

phase and the ontogeny of inflorescence respectively in *Nicotiana*. In the present investigation a three-dimensional study of the floral organogenesis in *Nicotiana rustica* has been undertaken.

Materials and Methods

Inflorescences of *Nicotiana rustica* L. were collected from a local field. To obtain various developmental stages, they were collected at short intervals during February and March 1976. They were immediately fixed in formalin-acetic acid-alcohol and later preserved in 70% ethyl alcohol. Whole inflorescences were stained in 1% solution of acid fuchsin in 95% alcohol, differentiated in 70% to 95% alcohol, dissected and photographed completely immersed in 100% alcohol (Sattler 1968).

Observations

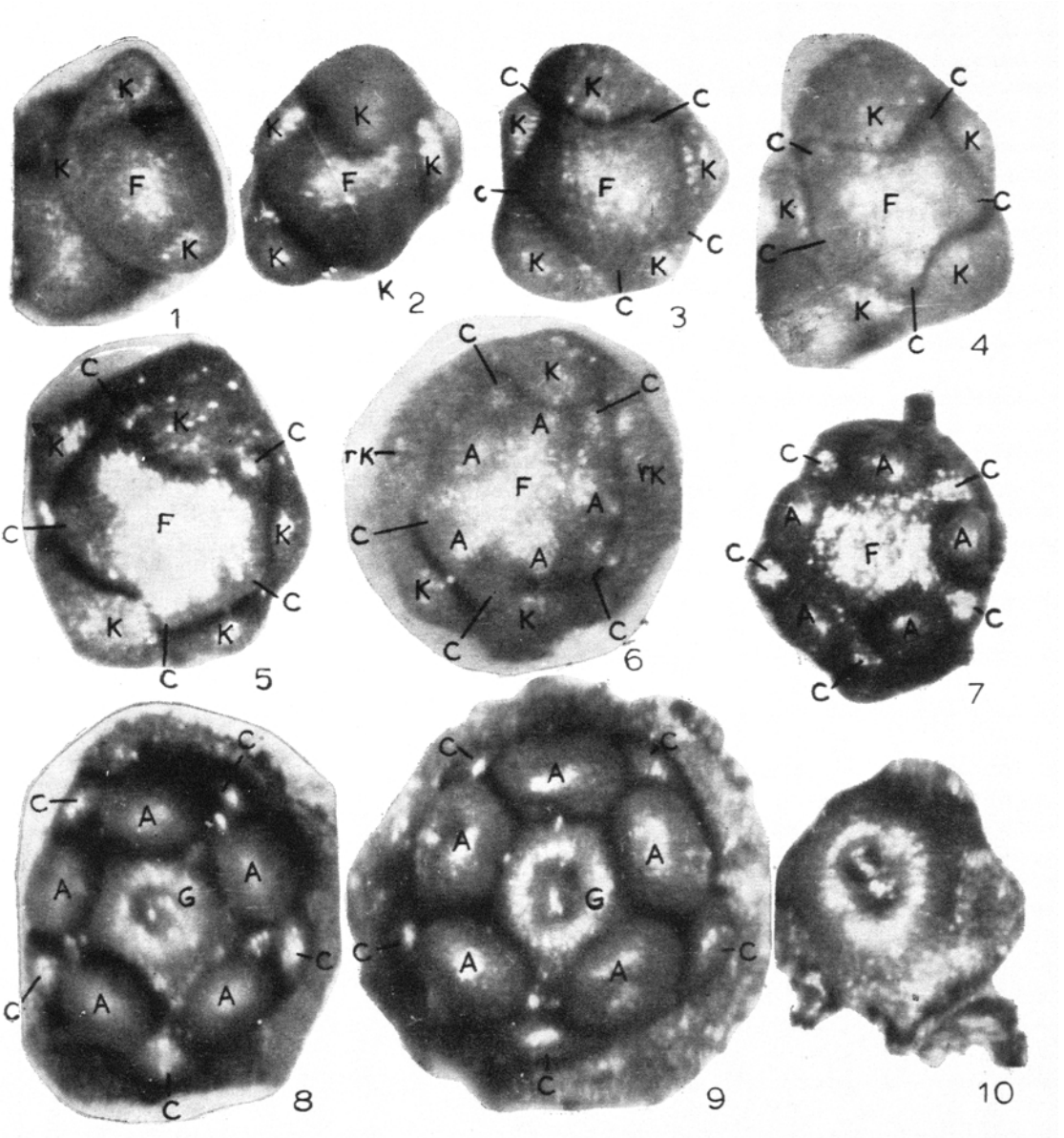
Organography

The greenish yellow flowers of *Nicotiana rustica* are borne in terminal racemes. They are ebracteate, bisexual, actinomorphic, pentamerous and hypogynous. The calyx is 5-lobed and persistent. The corolla is gamopetalous with a short tube and 5-lobed limb which is plicate in bud. The androecium consists of five nearly equal stamens which are attached to the throat of corolla tube alternating with its lobes. The filaments are short; the oblong anthers are narrowed upward and connivent in a cone and dehisce longitudinally. The gynoecium is bicarpellary and syncarpous with a superior, bilocular ovary bearing numerous ovules on two intruding placentae. The placentation is described as axile. The style is short columnar and the stigma is bilobed. A hypogynous nectariferous disc is present at the base of the ovary.

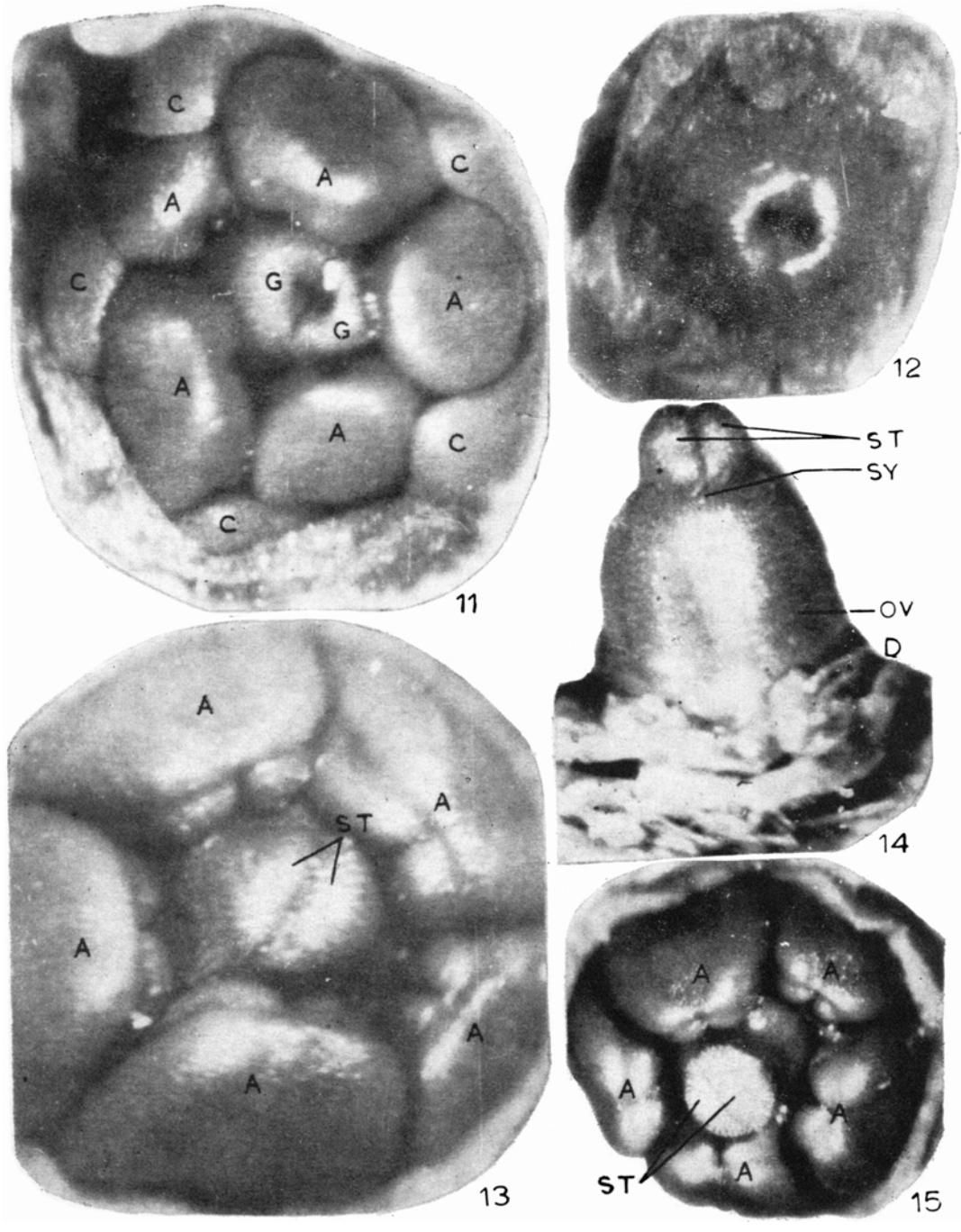
Organogenesis

The five sepal primordia are formed on the flanks of the dome-shaped floral apex in a spiral sequence (figures 1–3). The sequence of inception may be clockwise or counter clockwise. The posterior sepal primordium is always first to initiate and it is followed by one of the antero-lateral sepal primordia. If the sequence of inception is clockwise the antero-lateral primordium on the right side of the bud is the first to initiate (figure 1) but when the sequence is counter clockwise the antero-lateral primordium on the left side is formed first (figures 2, 3). Next, the two postero-lateral sepal primordia are formed in a rapid succession. Finally the second antero-lateral sepal primordium is initiated (figure 3). The plastochron between the inception of first and fifth sepal primordium is fairly long as is evident from the difference in their size. This difference in size of the sepal primordia is maintained in early stages of the sepal development (figures 4,5). The sepal primordia grow fast and cover the floral apex by the time the stamen primordia are initiated. After the inception of the fifth sepal primordium, a calyx tube is initiated by the extension and fusion of the bases of the distinct sepal primordia (figures 3–6).

Following the inception of the last sepal primordium, five petal primordia are initiated almost simultaneously alternating with the sepal primordia (figures 4,5). As a result of petal inception, the floral apex becomes pentagonal and each of the five angles of the apex (petal primordia) project between the two sepal primordia. As compared to sepal primordia, the petal primordia have very narrow bases but they too have a dorsiventral symmetry since their inception. The growth of the petal primordia is very slow in early stage of development and the stamen primordia outgrow them. Although the petal primordia emerge as discrete units on the floral apex, shortly after the gynoecial incep-



Figures 1–10 *Nicotiana rustica* (× 97). *1–3*, Floral buds in top view showing successive stages of sepal inception (**K**). Figure 1 shows a clock-wise sequence of sepal initiation, whereas figures 2 and 3 show a counter clock-wise sequence; *4 & 5*, Floral buds in top view showing inception of the petals (**C**); *6*, A floral bud in top view at the time of inception of stamen primordia (**A**). Two sepal primordia were removed (**rK**) to exhibit inner floral appendages; *7*, A floral bud in top view where sepal primordia were removed to exhibit a later stage of petal (**C**) and stamen (**A**) development; *8*, A floral bud in top view (sepals removed) at the time of inception of gynoecial rim; *9*, Top view of a floral bud where sepal primordia were removed to show the gynoecial ring at a later stage of development; *10*, Gynoecium of a floral bud in top view



Figures 11–15 *Nicotiana rustica* (11–13 × 100; 14 × 62; 15 × 40). *11*, A floral bud in top view (sepals removed) showing formation of corolla tube and a stage of stamen and gynoecium development; *12 & 14*, Gynoecia of floral buds in topandlateral views respectively at two stages of development; *13 & 15*, Androecia and gynoecia of flower buds at late stages of development

A, stamen primordium; **C**, petal primordium; **D**, disc; **F**, floral apex; **G**, gynoecial rim/gynoecial primordium; **K**, sepal primordium; **OV**, ovary; **rK**, sepal primordium removed; **ST**, stigma; **SY**, style

tion, a corolla tube is formed by the fusion of the marginal meristems of the adjacent petal primordia on the base of the back of the stamen primordia (figures 9,11). The corolla tube thus initiated grows upward by zonal or intercalary growth.

After petal inception the floral apex becomes nearly flat and the five stamen primordia are initiated almost at the same time (figure 6). A stamen primordium has a nearly radial symmetry soon after its formation but shortly afterward, as a result of lateral growth, it becomes dorsiventral in symmetry (figures 7–9). During further growth each stamen primordium is differentiated into a basal and a distal portion. The former develops into a short filament by intercalary growth and the latter undergoes a specialized type of growth which eventually results in a dithecous introrse anther (figures 11, 13 & 15). There is a slight difference in the size of stamen primordia since their inception and the difference in size is reflected even in mature flower. The zonal growth carries up the stamen primordia so that in a mature flower the stamens are inserted on the throat of the corolla tube.

As compared to the other floral appendages, there is a longer plastochron between the stamen and gynoecium inception. The gynoecium arises as a rim on the remaining floral apex. This rim is circular in outline on the inner side and a pentagon on the outer side as it ingrows between the stamen primordia where more space is available (figure 8). This gynoecial rim grows upward to form the ovary wall and then narrows down to give rise to a short style and two stigma lobes (figures 9–14). The two stigma lobes fuse post-genitally to form a nearly discoid stigma (figures 13–15).

As the gynoecial rim grows upward, two septa are initiated from the inner region of the ovary wall (figure 9). They grow inward, meet in the centre of the ovary and fuse post-genitally. The floral apex also grows upward (in the plane of the septa) and fuse with these septa to form a common septum (figure 10). The latter enlarges toward the ovary wall to form two massive placentae. Numerous ovule primordia are initiated basipetally on each placenta. The ovules are unitegmic as they develop a single integument.

The basal region of the ovary wall grows outward to form a nectariferous disc (figure 14).

Discussion

The floral appendages in *Nicotiana* appear in a distinct centripetal order. The same sequence was observed in *Solanum dulcamara* by Sattler (1973) and *S. lycopersicon* by Cooper (1927). But Young (1923) reports simultaneous inception of the petals and stamens in *Solanum tuberosum*. Except for the sepals, the primordia of other whorls arise simultaneously or nearly simultaneously in *Nicotiana rustica*. The sepal primordia are initiated in a sequence as discrete units and the calyx tube is initiated at a later stage of development by extension and fusion of the marginal meristems. Sattler (1973) also observed in *Solanum dulcamara* that the five sepal primordia are initiated before the formation of the primordial calyx tube. Contrary to this, in *Solanum lycopersicon*, Warner (1933) reports a common girdling primordium of the calyx on which five sepal primordia are formed.

In *Nicotiana* the gynoecium arises as a circular rim. A similar mode of gynoecial inception has been observed by Young (1923) in *Solanum tuberosum*. Studying *Solanum dulcamara*, Sattler (1973), however, observed that two distinct, crescent-shaped gynoecial primordia arise simultaneously which give rise to a cylindrical portion at their bases as a result of growth occurring between these two primordia immediately after their inception.

Sattler (1977) has discussed at some length the origin of corolla tube in *Solanum dulcamara*. According to him the five petals emerge as discrete primordia on the periphery of the floral apex. In the beginning these primordia are fully meristematic. During their growth, gradually, marginal meristems are differentiated in them. The marginal meristems of the adjoining primordia extend in the basal region and fuse at the base of the back of the stamen primordia. In this manner the marginal meristems form a continuum adjacent to crown petal primordia. Thus the corolla tube (with the crown lobes) is the product of meristematic activity in this continuum. He did not comment on subsequent developmental stages.

Our observations on *Nicotiana* agree with those of Sattler (1977) as in this taxon also the corolla tube is initiated by the fusion of the bases of fully meristematic petal primordia on the base of the back of the stamen primordia. The corolla tube of *Nicotiana* is much longer in comparison to that of *Solanum dulcamara*. Hence further upgrowth of the corolla tube in *Nicotiana* takes place by zonal growth by a basal meristem.

Topographically the placentation in Solanaceae is axile and is described so in taxonomic literature (e. g. Lawrence 1951, Hutchinson 1969). Bhatt (1974) who made a detailed study of floral anatomy in the family, however, concluded that the placentation in most of the Solanaceae (including *Nicotiana*) is anatomically parietal. In typical axile placentation the placentae are continuation of what represents the summit of the floral apex, whereas in parietal placentation the placentae arise from the lateral walls of the carpel primordia. In *Nicotiana* two septa are initiated from the inner wall of the ovary. They fuse postgenitally among themselves and upward growing floral apex. The placentae arise on this common septum. Thus developmentally *Nicotiana* shows a condition which is intermediate between typical axile and parietal placentation.

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