Floral organogenesis in *Antirrhinum majus* (Scrophulariaceae)

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Abstract. The various appendages (sepals, petals, stamens and carpels) in the flower of *Antirrhinum* are initiated in a centripetal sequence. The five sepal primordia are initiated in a rapid succession as discrete units. The calyx tube is formed due to the fusion of marginal meristems of adjacent sepal primordia. The corolla tube is also initiated by the fusion of marginal meristems at the back of stamen primordia. In the later stage of development, it extends in length by zonal growth. Of the five stamen primordia formed, the posterior one develops into a staminode. The septum, which bears placentae, grows from the summit of the floral apex as in typical axile placentation.

Keywords. *Antirrhinum majus*; floral organogenesis; axile placentation.

1. Introduction

Scrophulariaceae has received considerable attention from earlier morphologists who studied the floral anatomy and embryology in the family (see Davis 1966; Puri and Saxena 1972). Hartl (1956) made a detailed investigation of the morphology of the gynoecium and Leinfellner (1951) discussed the placentation in some Scrophulariaceae. Investigations on floral development are, however, completely lacking except for brief observations on the development of gynoecium by Hartl (1956) and some brief remarks on *Antirrhinum* by Esau (1977). In this paper a 3-dimensional account of the floral organogenesis in *Antirrhinum majus* based on the fine dissection technique is presented.

2. Materials and methods

Inflorescences of *Antirrhinum majus* L. of various stages of development were collected from the Botanical Garden, Meerut College, Meerut, in January and February 1975. They were fixed in formalin-acetic acid-alcohol and later preserved in 70% ethyl alcohol. Whole inflorescences were stained in 1% solution of acid fuchsin in ethyl alcohol for 48 hr and then differentiated in 70% to 95% ethyl alcohol. They were dissected and photographed completely immersed in 100% ethyl alcohol following the technique outlined by Sattler (1968).
3. Observations

3.1. Organography

An assortment of coloured flowers of *Antirrhinum majus* are borne in elongated terminal spikes. They are bracteate, bracteolate, bisexual, zygomorphic, pentamerous and hypogynous. The calyx is deeply five-lobed. The corolla is gibbous to saccate and bilabiate; the upper lip is erect and two-lobed and the lower lip is spreading and three-lobed. The lobes are imbricate. The stamens are four, didynamous and epipetalous; the fifth posterior stamen is represented by a filamentous staminode. The anthers are dithecous and introrse and dehisce longitudinally. The gynoecium is bicarpellary and syncarpous with a superior, bilocular ovary showing axile placentation. The numerous ovules are borne on enlarged placentae. The style is terminal with a bilobed stigma. A nectariferous disc surrounds the base of the ovary.

3.2. Organogenesis

The dome-shaped floral apex, formed in the axil of a bract, gives rise to five sepal primordia in a quick succession (figure 1). From their inception the sepal primordia are dorsiventral structures with broad bases. They grow faster than the other floral appendages. The bases of the sepal primordia extend and fuse to form a short calyx tube (figures 2 and 3).

Following the inception of the sepal primordia, the floral apex becomes nearly flat. Then it assumes a pentagonal shape as a result of inception of five petal primordia inner to and alternate with the sepal primordia (figure 2). The petal primordia are also dorsiventral but they have narrow bases in comparison to the sepal primordia. The growth of the petal primordia is slow to begin with and they are soon overtoped by the stamen primordia (figures 4–7). However after the formation of the gynoecial primordia the growth of the petal primordia is accelerated and they soon over-arch the growing stamens and the gynoecium (figures 8–10).

The petal primordia are very shortly followed by the four stamen primordia. The antero-lateral pair of stamens arises slightly ahead of the postero-lateral pair. A fifth stamen primordium is formed in the posterior position later (figure 4) but its growth is soon arrested and it develops into a filamentous staminode (figure 12). Unlike the sepal and petal primordia, the stamen primordia show a somewhat radial symmetry following their inception. Each of the four stamen primordia later becomes differentiated into a basal and a distal portion. The former develops into a filament and the latter into a two-celled anther (figure 12).

Shortly after the initiation of stamen primordia, there is an extension and fusion of the bases of the individual petal primordia at the back of the stamen primordia (figures 4 and 5). This results in the initiation of the corolla tube which develops further by the zonal growth of the common bases of petal and stamen primordia (figures 6–9). This also carries the stamen primordia above, such that in a mature flower the stamens are inserted at the mouth of the corolla tube. The free lobes of corolla also continue to grow and assume an imbricate aestivation (figure 10).
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Figures 1-8. (x 100). All figures in top view. 1. Floral apex after sepal inception. 2. Floral apex at the time of initiation of petal primordia (C). 3. Floral apex at a later stage of sepal development. 4. Floral apex at the time of inception of staminodial primordia (S). The inception of gynoecial ring can also be seen. The sepal primordia were removed. 5-8. Floral buds showing successive stages of petal (C), stamen (A) and gynoecial (G) development. Sepal primordia were removed.
Figures 9-12. (x 100). 9. Top view of floral bud at a later stage of gynoecium development. 10. Side view of floral bud showing aestivation of corolla lobes (C). 11. Gynoecium of a floral bud in side view. 12. A floral bud in top view showing a later stage of staminode (S), stamen (A) and gynoecium development. (A—stamen primordium; C—petal primordium; F—floral apex; K—sepal primordium; G—gynoecial primordium; S—staminodial primordium).
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The gynoecium arises as a pentagonal rim which surrounds the floral apex (figure 4). The five corners of this rim alternating with the stamen primordia are more developed toward outside and extend between the stamen primordia. The anterior and posterior parts of this rim grow rapidly to form two gynoecial primordia (figures 5 and 6). The basal region grows upward by zonal growth to form the ovary which narrows down into the style (figures 11 and 12). The two gynoecial primordia give rise to a bilobed stigma. The floral apex grows up in continuation with the lateral ovary walls. Thus the ovary is divided into two chambers with a solid upgrowth. This solid upgrowth (septum) extends on both sides to form the two placentae. Numerous ovules are initiated on each placenta in a basipetal succession. The ovary wall in the basal region outgrows into a nectariferous disc.

4. Discussion

The short calyx tube in Antirrhinum is initiated as a result of extension of the bases of separate sepal primordia, or in other words it is the fusion of the marginal meristems of the adjacent sepal primordia. Thus this corresponds to post-genital fusion (cf. Cusick 1966; Sattler 1977). The corolla tube is also initiated by marginal meristem fusion of adjacent individual petal primordia at the back of the stamen primordia. Subsequently, the corolla tube grows upward by zonal growth. A somewhat similar mode of corolla tube origin has been described for Pharbitis nil by Nishino (1976).

Although five stamen primordia are formed in Antirrhinum, the growth of the posterior stamen primordium is arrested and it develops into a staminode whereas the remaining four primordia form fertile stamens. The staminode also receives a single trace like other stamens (Varghese 1971a). Thus Antirrhinum represents an intermediate condition between typical five and four staminate forms occurring in the family.

In taxonomic literature the placentation in Scrophulariaceae has been described as axile on topographical considerations (e.g., Lawrence 1951; Hutchinson 1959). However, on the basis of anatomical criteria, Varghese (1971a, b) when discussing the placentation in Scrophulariaceae concluded that whereas in some taxa the placentation is truly axile, in others it is anatomically parietal. In Antirrhinum the septum (which bears placentae) grows from the summit of the floral apex (floor of the gynoecium) and not from the lateral walls of the carpel primordia. Hence the placentae are axial structures as should have been in typical axile placentation (cf. Hartl 1956).

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