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The Development of Flowers Within the Ovary of *Raphanus sativus* L.

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Introduction

In the greenhouses at the State University of Iowa, Radish plants (*Raphanus satisvus L.*) cultivated for other purposes were discovered to have some abnormal fruits with flowers developing inside in the place of ovules. These abnormal ovaries had normal ovules except for one, near the base, which was replaced by a flower or inflorescence with a perianth and several stamens in various stages of development (Figure 1).

Though a complete search of the literature has not been made, the older treatises on teratology contain no references to abnormalities of this type. Related floral anomalies have been reported in the Cruciferae more frequently than in other families. In his compendium of teratological facts, Masters (1869) cites a few instances of the formation of adventitious flowers and fruits within the ovary. In *Brassica kaber* (DC) Wheeler, "in the dilated upper portion of the ovary two flower-buds were found projecting from a raised central line, corresponding, as it would seem, to the midrib and not the margins of the carpel." These flower buds were not described further. Similar cases have apparently been reported for *Nasturtium amphibium* R.Br., *Brassica rapa* L. and *Passiflora quadrangularis* L. though Masters cites no references to these reports. In *Cheiranthus cheiri* L. a miniature adventitious silique within the normal one was illustrated by Masters (Page 182, Figure 94). This abortive ovary was produced on the placenta along the row of ovules. One interesting comparable instance is Masters' observation of the formation of stamens within the cavity of the ovary in flowers of the Myrtaceous *Baeckea diosmaefoli* Rudge. On cutting the ovary across numerous perfectly formed stamens with anther and distinct filament were found projecting inward from the walls of the ovary instead of the axial Placenta. No ovules were found on the placenta of abnormal ovaries. Worsdell (1916), though treating other teratological phenomena exhaustively, added no cases of adventitious flowers or floral parts in the ovary that Masters had not previously reported. Kausik (1938) described two abnormal flowers of *Allamanda grandiflora* Lam., in which the ovary was replaced by an elongated axis (gynophore) bearing, distally, a pair of leaf-like carpels. These develop into an open ovary bearing ovules on their adaxial surfaces some of which had the initial stages of an embryo

sac before observations were discontinued. The problem of self-incompatability in Cruciferae (Bateman 1955) and in radish (Sampson 1957) has recently been investigated intensively. There was no mention of the type of abnormality described herein. It seems evident that the abnormalities of ovary development reported thus far in the Cruciferea and other families do not include the replacement of ovules by flowers or inflorescences.

Observations

In attempts to obtain inbred lines of radish to be used in experimental studies of growth, plants grown from seed of the commercial variety Crimson Giant were self-pollinated by hand. Seed obtained by selfing were planted in May, 1956. Germination was good but the plants suffered in the extreme heat in the greenhouse during the summer. Surviving plants initiated flowers during the summer but normal fruits did not form until early autumn 1956. Many of these fruits had ovules and matured seeds. In many fruits 25 to 100 percent of the seeds germinated prior to drying. Among the siliques formed in the late autumn of 1956 were several with an abnormal flower-like structure in the position of one of the basal ovules. From casual observation while harvesting seeds these anomalous structures were mistaken for germinated seeds. Upon closer examination they were seen to have a curved pedicel arising from the placenta with numerous irregularly arranged stamens and a tubular, irregularly pleated, perianth-like covering (Figure 1). In each of the many fruits examined, the internal flowers seemed to arise from the basal portion of the placenta in the distended part of the ovary in place of one of the ovules. This was later confirmed through the study of serial sections. Across the fruit on the placental tissue opposite were several normally developing ovules which matured into seeds. Among the seeds used to start a new generation of radish were some harvested from the abnormal fruits. The radish plants upon which abnormal fruits were first found have been producing flowers continuously since August, 1956. When anomalous flowers in the siliques were first discovered almost all fruits exhibited the phenomenon. As recently as April 22, 1957, fruits collected from the original plants contained anomalous flowers. The frequency of their occurrence was still approximately 50 percent of the fruits collected. These plants are now almost 12 months old and still flowering. Inflorescences are several feet long on the surviving plants.

Many abnormal fruits in different stages of development were collected and dissected under a stereoscopic microscope. The flower-like structures inside were observed to have a tublar perianth and a central axis. The axis branched quite irregularly. Some of these branches had floral primordia at their apices from which two whorls

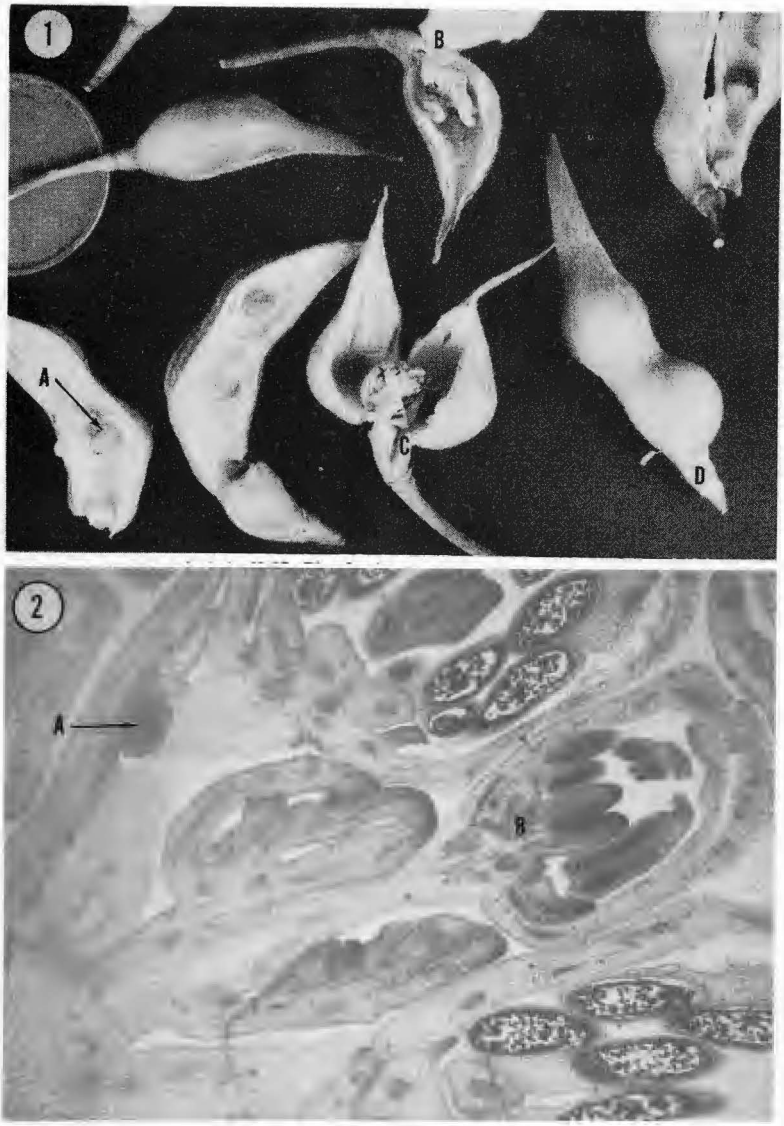

Figure 1. Fruits of radish. (A) A germinated seed in the freshly opened fruit. (B) and (C) Opened fruits with anomalous floral structures. (D) A normal unopened fruit.

Figure 2. Longitudinal section of a portion of the central axis (inflorescence) of an anomalous floral structure. (A) An ovule on a lateral enation. (B) A floral promordium with an incipient ovary, young stamens and perianth parts.

of perianth lobes, numerous stamens and incipient ovaries were initiated. Some of the enations along the axis bore single ovules in their axils. It might be concluded that the axis, arising at is does from the very base of the placental tissue of the parent ovary, retains this placental function during the development of the anomalous "flower." Observations from initial dissections indicated that, the internal floral structure was a crudely irregular, reduced inflorescence ensheathed by a tubular or flask-shaped bract.

After removing most of the ovary wall, fruits with anomalous floral structures were fixed and imbedded in paraffin. Transverse and longitudinal serial sections were cut and stained in order to study more intensively the organography of the abnormal material.

Serial sections confirm the observations made from dissected fruits. The numerous stamens had microsporangia in many different stages of development (Figure 2). Some were in the pollen-mother-cell stage, others had mature pollen. Typical binucleate tapetal cells were evident in several anthers. The sporogenous tissue was dividing synchronously in the normal process of meiosis. Pollen dyads and tetrads were also observed. The mature pollen grains were structurally similar to those produced in the stamens of normal radish flowers. In general, stamen development, except for the variety of filament lengths, appeared to be comparable with that in normal flowers.

From the study of sectioned material the previously stated interpretation of the central axis is further revealed. It seems to be an inflorescence axis bearing branches or enations some of which have floral primordia at their apices. At the apices of major branches, in addition to stamens, ovary initials were observed. Most of these were exceedingly immature, in the material studied thus far, but some contained the primordia of ovules in two regular rows. In a few young ovaries the primary archesporium and megaspore-mother-cell as well as the initials of the integuments were seen. Other ovules observed in the anomalous floral structures occurred singly in the axils of minor branches or small enations from the axis. A few of the more mature ovules were found attached to the inner epithelial tissue of the tubular "perianth" or bract near the base of the axis. Ovules in the latter position were developing normally with embryo sac, nucellus and integuments. Ovules in the axil of enations were intermediate in position between the ultimate apex of the axis and its base and were also intermediate in stage of development. In general the development of ovules was slower than stamens. Since fewer of them have been studied their complete development in the anomalous floral structures awaits the examination of more material.

Conclusions

Concerning the significance of teratological phenomena in plants there appear to be two extremes of viewpoint (Arber (1931). Some botanists hold that teratology contributes nothing to our understanding of phylogeny and classification. Others believe abnormalities of structure are atavistic and seek out anomalous organs studying their development as a primary means of explaining interrelationships. It seems unlikely that the modified radish ovaries described in this preliminary account have any value in suggesting phylogenetic relationship in the Cruciferae or in elucidating the affinities of the family.

The phenomenon studied is presently referred to as an anomalous floral structure because one cannot be certain of its morphology. It seems to be, more than anything else, a modified inflorescence with an irregular subtending bract. That proliferation of organs is compounded in the anomaly is strikingly clear, when one can observe developing ovules in recognizable ovaries, in recognizable flowers, on an inflorescence initiated from the placenta within an ovary of a normal flower.

To state that the casual mechanism of such an abnormality is as yet illusive, is indeed an understatement. The frequency of abnormal fruits on the generation of plants presently under investigation would seem to warrant study of later generations of this strain in the hope of finding some explanation.

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