MORPHOLOGICAL AND CYTOLOGICAL STUDIES IN THE SCROPHULARIACEÆ

Part IV. The Development of the Embryo-sac and Endosperm in *Scoparia dulcis* Linn.

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I. Introduction

Scoparia dulcis is a tropical American plant now run wild and very common in India on waste lands and fallow fields. It is a glabrous undershrub about three feet in height. The flowers arise usually in twos from the axils of leaves. There are four fertile stamens.

II. Material and Methods

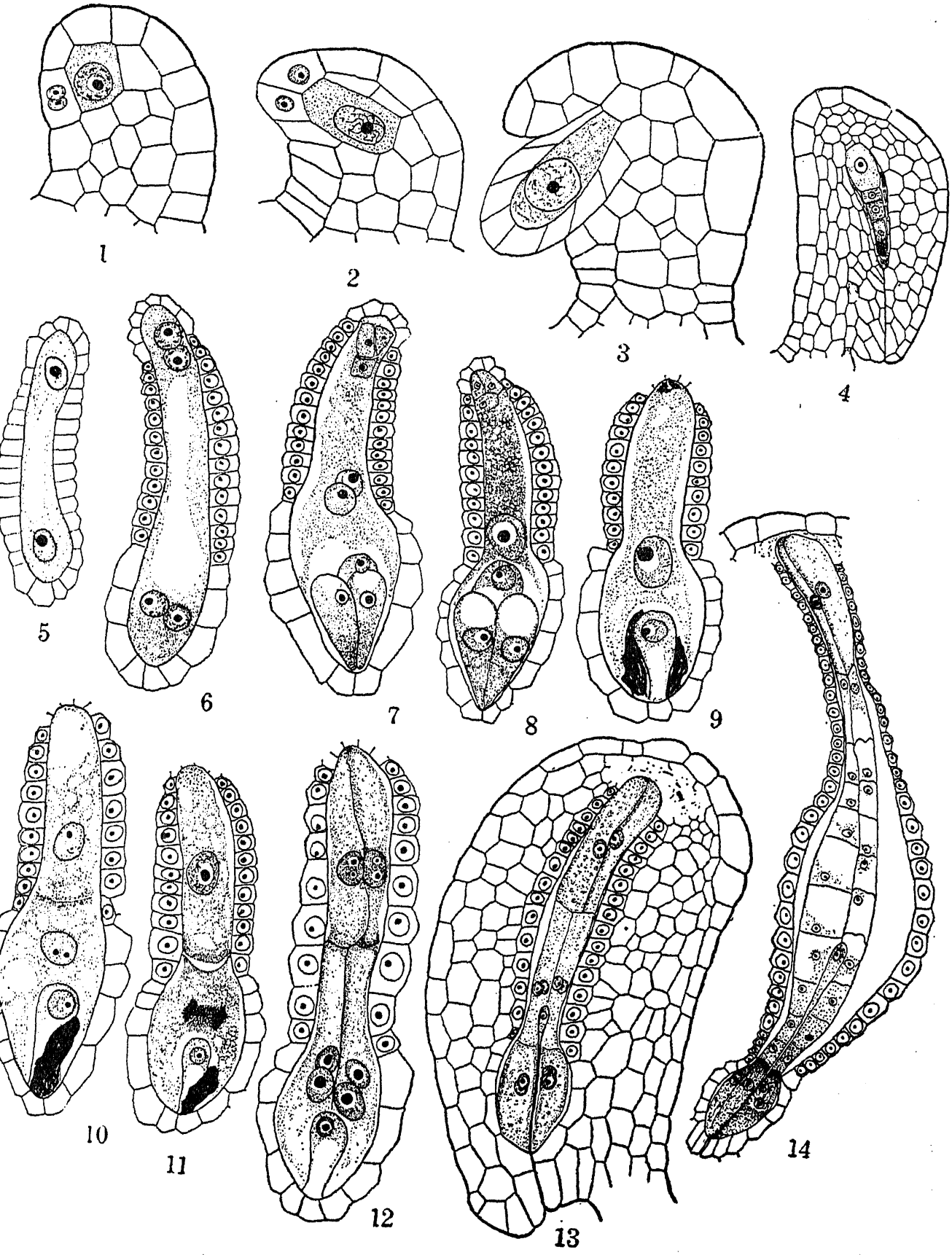
Material for the present work was obtained from plants grown in the University Botanical Gardens, Annamalainagar. Ovaries of various stages of development were fixed either in formalin acetic alcohol or in hot corrosive sublimate formalin acetic alcohol fixative. Sections were cut at thicknesses varying from 6 to 14 microns. All the preparations were stained in Haidenhain's iron-alum hæmatoxilin.

III. Observations

(*a*) *Megasporogenesis.*—The ovary is typically bicarpellary with indefinite number of ovules. The ovules are anatropous and are arranged on an axile placenta. The ovules arise as epidermal protrusions from the placenta. A hypodermal archesporium appears very early in the development of the ovule (Fig. 1). This hypodermal archesporial cell without cutting off any wall cell, increases in size and becomes the megaspore-mother cell. As the archesporial cell increases in size and elongates, the epidermal cells just above it undergo repeated anticlinal divisions to form a nucellar cap (Figs. 2 and 3). The single massive integument grows rapidly and at the same time, the ovule curves to assume the anatropous configuration. The megaspore-mother cell is surrounded by a single layer of nucellar cells (Fig. 3). The megaspore-mother cell enlarges considerably before its nucleus undergoes the heterotypic division to produce a dyad. The two cells by a second division form a linear tetrad of megaspores (Fig. 4). During the formation of the tetrad, the nucellar layer is pressed against the integument and it begins to degenerate. Its place is taken up by the innermost layer of cells of the integument, which becomes the tapetal tissue and appears as a row or band of cells on either side of the embryo-sac (Fig. 6). The chalazal megaspore of the linear tetrad is the functional one, while the three micropylar ones degenerate.

The nucleus of the functional megaspore divides into two to form a bi-nucleate embryo-sac (Fig. 5). Further divisions of these two nuclei result in the formation of the four and eight-nucleate embryo-sacs (Figs. 6 and 7). The mature embryo-sac is somewhat dilated towards the micropylar portion. The integumentary tapetum surrounds only the non-dilated chalazal portion of the embryo-sac (Fig. 8). The cells of the tapetum are of the usual shape and are uni-nucleate. Their function is to absorb nutrition from the cells of the massive integument and pass it on to the endosperm during the period of its formation and later to the developing embryo. The mature embryo-sac consists of two rather prominent synergids, an egg-cell, three antipodals and the two large polar nuclei (Fig. 7). Both the synergids and the antipodals are ephemeral and degenerate soon after fertilization.

(*b*) *Endosperm haustoria.*—In the post-fertilization embryo-sac the triple fusion nucleus is the most prominent and is situated near the oospore (Fig. 9). It undergoes a period of rest, after which it divides. This first division is transverse to the long axis of the embryo-sac. This transverse division is followed by a cross-wall, which separates the embryo-sac into



FIGS. 1–14

Fig. 1. Hypodermal archesporium. × 1500. Fig. 2. Same at a later stage. Note the ticlinal division of the epidermal cell. × 1500. Fig. 3. Megaspore-mother cell surrounded a single layer of nucellar cells. × 1500. Fig. 4. Ovule showing the linear tetrad of megaores and the degenerating nucellus. × 700. Figs. 5, 6, 7 and 8. Two-nucleate, four-nucleate,

eight-nucleate and seven-nucleate embryo-sacs. Note the tepetal layer. × 1200. Fig. 9. Pos fertilization embryo-sac. × 1200. Fig. 10. Transverse wall separating a micropylar and chalazal chamber. × 1200. Fig. 11. Shows the longitudinal division of the nucleus of t micropylar chamber. × 1200. Fig. 12. The two uni-nucleate chalazal haustoria and t micropylar chamber consisting of two tiers each of two cells. × 1200. Fig. 13. Ovule sho ing the differentiation of the four uni-nucleate micropylar haustoria. × 355. Fig. 14. No the endosperm tissue, the elongated embryo, the tapetal layer and the chalazal and the micropyl haustoria. × 355.

two chambers, the micropylar and the chalazal (Fig. 10). The nucleus of t micropylar chamber now divides, this division being longitudinal (Fig. 1 A longitudinal wall is formed and the micropylar chamber is divided in two, by the longitudinal wall. The nucleus of the chalazal chamber al divides longitudinally, followed by wall formation. The resulting two cel without any further division assume the rôle of the chalazal haustoria (Fig. 12 The nuclei of the two micropylar chambers now undergo a second long tudinal division, the plane of this division being at right angles to the fir longitudinal division. As a result, the micropylar chamber consists of tw layers of two cells each (Fig. 12). A transverse wall formed across the four cells results in the differentiation of a middle tier also consisting of tw layers of two cells each (Fig. 13). The four cells towards the micropyl end, become the four micropylar haustorial cells, while the four cells of t middle tier, by repeated divisions build up the endosperm tissue. The tw chalazal haustorial cells are long, narrow and tubular with their distal en rather enlarged (Fig. 14). They elongate and absorb food materials from t chalazal region of the ovule. The resultant breaking-up of the cells in tha region can be seen (Figs. 13 and 14). The four micropylar haustorial cel are comparatively less efficient as haustorial organs. The four haustori cells later become a single four-nucleate haustorium, by the disintegratio of the cross-walls (Fig. 14). In the present investigation, the method of de elopment of the endosperm haustoria is thus found to be similar to tha recorded previously in *Stemodia*, *Dopatrium* (Srinivasan, 1940) and *Ilysanth* (Raghavan and Srinivasan, 1941).

(*c*) *Embryo*.—Most of the stages in the development of the embryo hav been observed and they are quite normal and similar to the method c development described in *Ilysanthes parviflora* (Raghavan and Srinivasa 1941).

IV. Discussion

There are practically no genera known in the Scrophulariaceæ wher haustoria are not present. Schertz (1919) in his comprehensive study c *Scrophularia marylandica*, has mentioned that the genus *Scoparia* exhibite no endospermal haustoria. In an earlier paper of this series (Srinivasa

1940) it was found that of a number of genera investigated, the genus *Angelonia* which had not received any attention till then, was found to exhibit no haustorial structures. Curiously enough, there was in this genus a highly interesting phenomenon shown namely the persistence of the synergids till a late stage of embryo formation. This phenomenon was however not seen in any of the other genera that were investigated and since this was found only in a genus where the usual haustorial formation was conspicuous by its absence, it was suggested that a correlation might exist between the absence of haustoria and the persistence of synergids. Other genera investigated since then also failed to reveal any such absence of haustoria such as was encountered in the genus *Angelonia*. In the literature on the Scrophulariaceæ, so far as we are aware, only the genus *Scoparia* is mentioned as exhibiting no haustorial structures (Schertz, 1919). But in that Schertz (1919) has made no mention of the synergids, their persistence or otherwise. Perhaps they escaped his observations. We were therefore, curious to find out whether the hustoria were absent and if so whether this phenomenon was in any way correlated to any abnormal behaviour of the synergids. It was with this intention that this genus was investigated. The chromosome number of this species has already been recorded by us in a previous paper (Raghavan and Srinivasan, 1940). The embryo-sac development has revealed that the formation of the endosperm haustoria is just like that in other genera investigated. Therefore, there can be no question of the absence of haustoria in the genus. The synergids are quite normal upto fertilization and degenerate soon after fertilization. There is no persistence on their part. It would thus appear that this case also proves at least in a negative manner the validity of the tentative suggestion made previously, of the existence of a correlation between the absence of haustorium and the persistence of synergids. So far only the genus *Angelonia* has exhibited this absence and revealed the correlation mentioned above. The only other genus namely *Scoparia* which was supposed to have no haustoria, has in the present investigation, been shown to be quite normal in the matter of haustorium formation. It would be interesting if future investigation on other genera would reveal any genus exhibiting no haustoria. In those few that may show this, the synergid behaviour should be watched with care to see how far the suggestion made previously could be generalised.

V. Summary

A hypodermal archesporium directly functioning as the megaspore-mother cell produces a linear tetrad of megaspores, the chalazal one of which produces a normal 8-nucleate embryo-sac. The synergids are normal and degenerate soon after fertilization.

The tapetum surrounds only the non-dilated chalazal portion of the embryo-sac.

There are two uni-nucleate chalazal haustoria and the four uni-nucleate micropylar haustorial cells later fuse into a single 4-nucleate haustorium.

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