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Introduction

This paper is part of a general comparative anatomical study involving two species of the genus, *Scrophularia*; namely, *S. marylandica* L. and *S. lanceolata* Pursh. These plants were once included in the same species and called *S. marylandica.* They are at present regarded as two distinct species and a comparison of their anatomy and development may help verify this separation. The present study is concerned chiefly with *S. lanceolata,* with only passing reference to *S. marylandica.*

Apparently the first adequate description of *S. lanceolata* was recorded by Bicknell (Bicknell 1896). He described the plant and gave it the appropriate species name of *leporella,* based upon the resemblance of the flower to a rabbit when viewed from the dorsal side. This name has been discarded, however, in favor of *lanceolata* (Pennell 1922), a name previously applied by Pursh (Pursh 1814), and which, according to Pennell, is the valid name. He reasons that the description given by Pursh was due to the accidental transfer of the flowering date "Aug. Sept." with a preceding description of *S. marylandica.*

Research of an anatomical nature has been done on this group by other workers and many of the findings of the present work correspond to their descriptions. Balicka-Iwanowska (Balicka-Iwanowska 1899) describes the mature megagametophyte of *S. vernalis* L. as large in the micropilar end and slender and elongated in the antipodal end. Schmid (Schmid 1906) found a similarly shaped megagametophyte in *S. nodosa* L. Schertz (Schertz 1919) worked out certain aspects of the reproductive organs of *S. marylandica.* Although the primary reason for an over-all study of these plants is taxonomic in nature, the present paper records morphological details not previously published.

Materials and Methods

Material for this study was collected outdoors under natural conditions during May and June, 1948. The point of collection was between the Chicago, Rock Island, and Pacific Railroad and U. S. Highway 218, approximately two miles south of Iowa City, Iowa. Material was fixed in both F. A. A. and Navashin's fluid. There was no significant difference in the efficacy of the two fluids. The procedure followed in this work was to collect all possible sizes of immature flowers ranging from one millimeter up to four millimeters in diameter. Flowers of nearly the same size were preserved in separate vials to facilitate sectioning in the same paraffin block. In this manner enough material could be collected in a few small vials to furnish enormous numbers of sections. When approximately four millimeters in diameter the flowers begin to open.

Material was dehydrated in butyl alcohol and embedded in paraffin. Flowers were embedded in groups of three to ten placed in the same plane and as close together as possible in order to obtain a maximum number of sections. Sectioning was done at ten and fifteen microns. Ten microns was found to be the best thickness for all stages except the mature or nearly mature megagametophyte.

Sections were stained in a modification of Fleming's triple stain and in safranin and fast green. The latter stain proved to be superior, especially for photographic purposes.

Observations and Discussion

The fruit of *S. lanceolata* is a septicidal two loculate capsule formed from two (rarely three) carpels. Numerous anatropus ovules are borne on two (rarely three) fleshy protruding axilliary placentas (Figure 1). Enough ovules are present so that a hundred seeds could develop in a single capsule but this rarely occurs due to the high degree of abortion, especially toward the distal end of the fruit. This contrasts with *S. marylandica* in which most of the ovules reach maturity and aborted ovules are seldom found. Many ovules of *S. lanceolata* may fail to mature, even when an excess of pollen is applied experimentally. The reason for the great number of abortions has not been determined by the writer.

Megaspore Development — The ovules first appear as small evaginations on the surface of the placentas and when still very small the megaspore mother cell can be seen differentiating immediately below the epidermis. At maturity the megaspore mother cell averages 20 microns in length and 10 microns in diameter. It appears elliptical (Figure 2) but may elongate concurrently with the first division (Figure 5). The megaspore mother cell with its surrounding megasporangium may extend more than half its entire length beyond the integument. This has been observed previously in other members of the *Scrophulariaceae*, (Schmid 1906), (Schertz 1919).

At this time the single massive integument begins to develop rapidly and by the time the linear tetrad has formed it is enclosed by the integument (Figure 8). Schertz stated that in *S. marylandica* the integument has fully surrounded the megaspore mother cell even as early as the time of reduction division.

The formation of the megaspores of *S. lanceolata* follows the typical pattern. The megaspore mother cell divides transversely (Figure 5) forming two daughter cells which in turn divide transversely (Figure 7) to produce four megaspores. Figure seven shows simultaneous division of the two daughter cells resulting from the division of the megaspore mother cell. Sections with three megaspores present, however, (Figure 6) prove that division does not always occur simultaneously.

Two-celled archesporia were occasionally found (Figure 3). Schmid (Schmid 1906) also observed them in *S. nodosa* L. He stated that only one of these cells undergoes division to form the megaspores, the other disintegrates. He also found two-celled archesporia in other members of the *Scrophulariaceae*. These included *Lathraea squamaria* L., *Pedicularis foliosa* L., and *Melampyrum silvaticum L.* Two-celled archesporia have been reported by another worker (Schnarf 1931). He stated that in rare instances there may be more than two megaspore mother cells in the archesporium.

After the four megaspores are formed (Figure 8) the three nearest the micropyle disintegrate (Figure 9). This disintegration begins with the third cell from the micropyle and proceeds toward it. The nuclei of the disintegrating cells stain heavily with safranin while the nucleus of the functional megaspore stains lightly. Several nucleoli commonly occur in the nucleus of the functional megaspore. The megagametophyte develops from this functional megaspore in typical angiosperm fashion (Schnarf 1936).

Megagametophyte Development — Shortly after the disintegration of three micropylar megaspores, the remaining functional one enlarges preparatory to division (Figure 10). As it elongates the nucleus divides to form a two nucleate stage (Figure 11). The two nuclei resulting from this division migrate, one to each end of the embryo-sac (Figure 12), and again divide to form a four nucleate stage (Figure 13). A third division follows, resulting in the eight nucleate stage commonly seen in the development of the megagametophyte (Figure 14). After this final division there is a reassortment of the nuclei and two, one from each end, migrate to the center of the embryo-sac where they fuse to become the primary endosperm nucleus. The nucleus from the antipodal end is smaller than the micropylar nucleus at first, but as it migrates toward the center of the embryo-sac it enlarges until it is the same size as the micropylar nucleus at the time of fusion. The three remaining antipodal nuclei form walls and remain near the antipodal end of the embryo-sac. They are seen with difficulty and soon disappear completely.

The three nuclei of the micropylar end differentiate, two forming the synergids and the remaining one the egg. The synergids are large and conspicuous, assuming the form of a curved cone. They lie one on each side of the egg with their pointed ends toward the micropyle (Figure 14). The egg stains with difficulty and at the best is inconspicuous, becoming progressively more so from this point. This same difficulty was encountered by Schmid (Schmid 1906) in his studies of *S. nodosa*. The egg is slightly oblong in shape and lies between the enlarged ends of the synergids (Figure 15), or just beyond their enlarged tips, toward the center of the embryo-sac. The megagametophyte at maturity averages 100 microns in length and 13 microns in diameter at the center. It is long and thin in the antipodal end and much enlarged at the micropylar end (Figure 14).

Summary

1. The megaspore mother cell of *S. lanceolata* extends beyond the main part of the ovule. It is at all times covered by the megasporangium.
2. Megaspore development follows the usual pattern. The megaspore mother cell divides transversely to form two daughter cells which in turn divide transversely, forming a linear tetrad.
3. Rarely a two-celled archesporium was seen.
4. Only one of the four megaspores are functional, the three micropylar ones disintegrate.
5. Megagametophyte development follows the typical angiosperm pattern.
6. At maturity the megagametophyte is long and slender at the antipodal end and much enlarged at the micropylar end.

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Explanation of Plate I

Photomicrographs showing megaspore development.
Figure 1, X440, all others X970.

Figure 1. Anatropous ovule forming, the protruding spore mother cell and the surrounding megasporangium are evident.

Figure 2. Mature spore mother cell with the megasporangium and the prominent nucleus showing. The integument may be seen to the right.

Figure 3. Two-celled archesporium. This phenomenon has been observed in other members of the *Scrophulariaceae*. See text.

Figure 4. Transverse section of the spore mother cell. Placental tissue may be seen to the left.

Figure 5. Spore mother cell in the process of division.

Figure 6. Three of the four megaspores showing.

Figure 7. Simultaneous division in the formation of the linear tetrad.

Figure 8. The four megaspores of the linear tetrad.

Figure 9. The remaining megaspore enlarging after the three micropylar ones have distintegrated.

Explanation of Plate II

Photomicrographs showing megagametophyte development.
Figures 10 through 14 X970. Figure 15 X1455.

Figure 10. Enlarging megaspore.

Figure 11. First nuclear division in the formation of the megagametophyte.

Figure 12. Two nucleate stage. The nuclei have migrated to the ends of the megagametophyte.

Figure 13. Four nucleate stage.

Figure 14. Mature megagametophyte, all cells and nuclei showing except the egg.

Figure 15. Micropylar end of mature megagametophyte with egg showing.

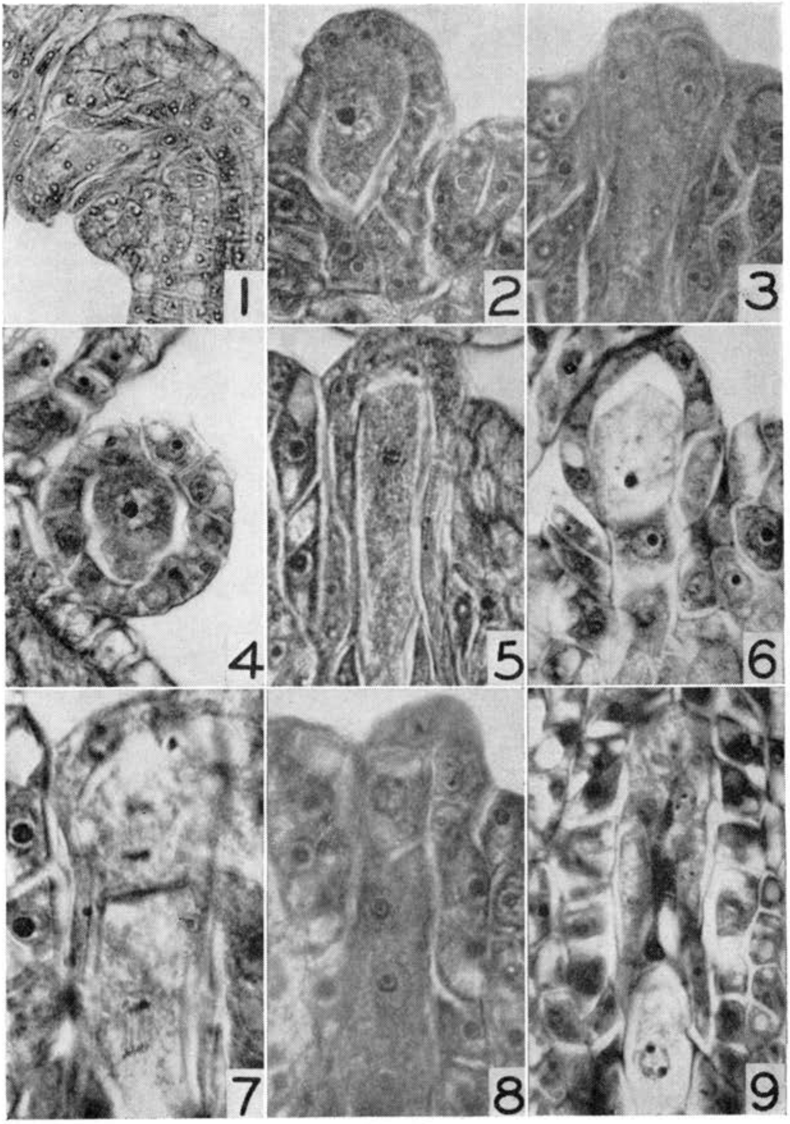

Plate I

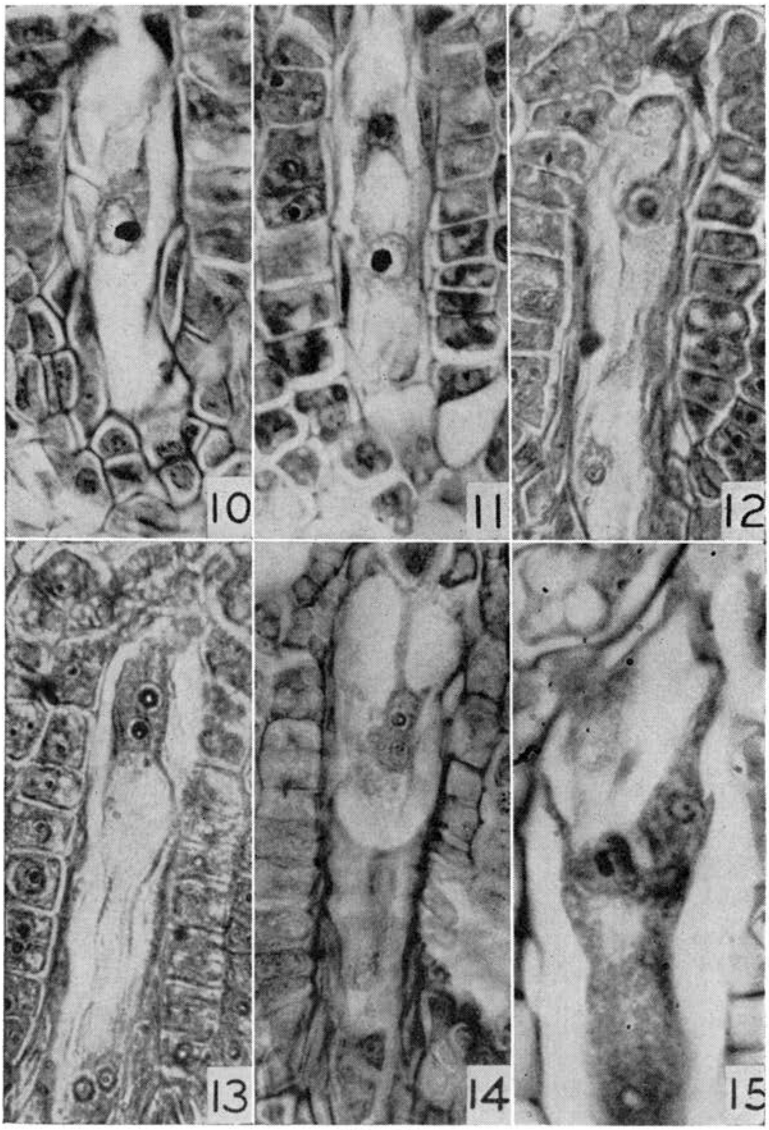

Plate II