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THE EMBRYOLOGY OF VALLISNERIA SPIRALIS.*

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The material for this study was gathered in Sandusky Bay in July and August, 1902. It was killed in chrome-acetic acid, preserved in 70 per cent. alcohol, imbedded in paraffin, cut on a Minot rotary microtome, and stained in anilin safranin and gentian violet, and also in Heidenhain's iron-alum-haematoxylin. For the development of the embryo-sac the former was the best, and the latter for the staminate flowers. For the embryo, either stain gave satisfactory results.

The sections were cut 8-12 microns thick, the staminate flowers transversely and the carpels longitudinally. The older ovules were removed from the ovulary and imbedded separately. This was necessary on account of the mucilaginous material which was contained in the carpels.

The work was carried on at Ohio State University under the direction of Prof. J. H. Schaffner to whom I am greatly indebted for assistance and suggestions.

The carpellate flowers are borne on a long scape with a tubular, one-flowered spathe. The perianth has a linear tube adnate to the one-celled ovulary. There are three small petals, and three stigmas which are short and broad. The ovules are numerous and orthotropous, borne one the ovulary wall. The staminate flowers are numerous, nearly sessile, on a conic receptacle, enclosed in a spathe which is borne on a short scape. The perianth is three-parted, the petals being very small. The androecium (Fig. 9) is a two-parted structure which may be regarded as two stamens united at the base, or a single stamen, as described by Engler and Prantl. If the former view be held, the anthers

* Contributions from the Botanical Laboratory of Ohio State University. XIII.

must be regarded as being bilocular. The related plants, of the Alismaceae and Naiadaceae, as well as the Vallisneriaceae, are described by Britton and Brown as having two celled anthers.

Fig. 9 shows the microsporocytes in the pollen sacs. Before the pollen is shed the grains are three-celled, having a large tube nucleus and two smaller male cells (Fig. 10).

The young ovule has two integuments; the inner one is barely beginning to appear when the archesporial cell is organized (Fig. 1) The archesporial cell is hypodermal in origin. From this a tapetal cell is cut off and this divides into two (Figs. 2 and 3). The megasporocyte enlarges and four megaspores are finally produced by two transverse divisions, although in some cases some of the walls may be oblique (Figs. 4 and 5). The functional megaspore, which is the lowest, divides into two cells, forming the two-celled embryo-sac in the usual way (Fig. 6); one cell passes to the upper and the other to the lower end of the sac and by successive divisions the typical eight-celled embryo-sac is formed (Fig. 7). The polar nuclei are rather large and they conjugate in about the middle of the sac. A large number of these conjugations was observed, but there was no trace of a triple conjugation of polar nuclei and a male cell. The synergidae lie side by side, extending across the upper end of the sac, and beneath them is the oosphere. The antipodals have the same relative position in the lower end that the egg-apparatus has in the upper end.

At the first division of the definitive nucleus two cells are formed with a transverse wall across the sac between them. The upper one of these by further division forms a small amount of endosperm tissue. The lower one develops into a large vesicular cell with a large nucleus (Fig. 8). This same structure with the partition wall was found by Schaffner in *Sagittaria*, by Cook in *Castalia* and *Nymphaea*, and by Murbeck in *Ruppia*. It has also been found in other groups. Contrary to the case in *Sagittaria*, no direct division of this nucleus was observed. At this stage the antipodals are in a pocket at the base of the sac, where they persist for a long time.

The first division of the oospore is transverse. The lower cell elongates and divides transversely also, forming the first three cells of the proembryo (Fig. 11). The upper one of these does not divide but forms a very large suspensor cell as is usual in the Helobiae. The next division is in the middle cell and is also transverse. There is now a tier of four cells. The lowest one of the tier divides longitudinally (Fig. 12), and following this division there is a transverse division in the cell next to the large suspensor cell followed by another longitudinal division in the lowest tier and one in the tier above (Fig. 13). At this stage the pro-embryo is composed of nine cells arranged in five

tiers. Following this, the four basal cells (*c*) divide by transverse walls, thus forming an octant; the next tier (*b*) divides by longitudinal walls, forming a quadrant; the next tier (*d*) divides into two cells by a longitudinal wall, while at the same time there is a transverse division in the tier (*e*) below the suspensor cell. These divisions, therefore, give rise to a seventeen-celled embryo (Fig. 14.)

The eight cells from the basal tier give rise to the single terminal cotyledon; the lateral plumule develops in the next tier while the radicle is developed from tiers, *d*, *e*, *f*, etc. (Fig. 16). Following this seventeen-celled stage the number of transverse divisions is continued in the cell below the large suspensor until there are about nine or ten original tiers, the embryo being organized from the six or seven terminal ones, and the rest serving as suspensor cells. The dermatogen begins to be cut off in the cells of the incipient cotyledon and continues to develop toward the root-tip (Fig. 15). The original tiers of cells begin to divide by transverse and longitudinal walls and this also appears first in the cotyledon. The development of the embryo follows quite closely that of *Sagittaria*. It remains orthotropous and when nearly mature shows the usual four regions, cotyledon, plumule, radicle and root-cap (Fig. 17.)

SUMMARY.

1. The archesporial cell is single and hypodermal in origin.
2. From the archesporial cell, a tapetal cell is cut off, which divides into two.
3. The megasporocyte produces four megaspores; sometimes the dividing walls are oblique.
4. The pollen grain has three cells before the pollen is shed.
5. The embryo-sac is normal in development.
6. There is a large definitive nucleus, by the first division of which a lower vesicular nucleus is formed, cut off by a transverse wall from the upper nucleus which forms a small amount of endosperm tissue.
7. The embryo develops as in *Sagittaria*, with terminal cotyledon and lateral plumule, but remains orthotropous.

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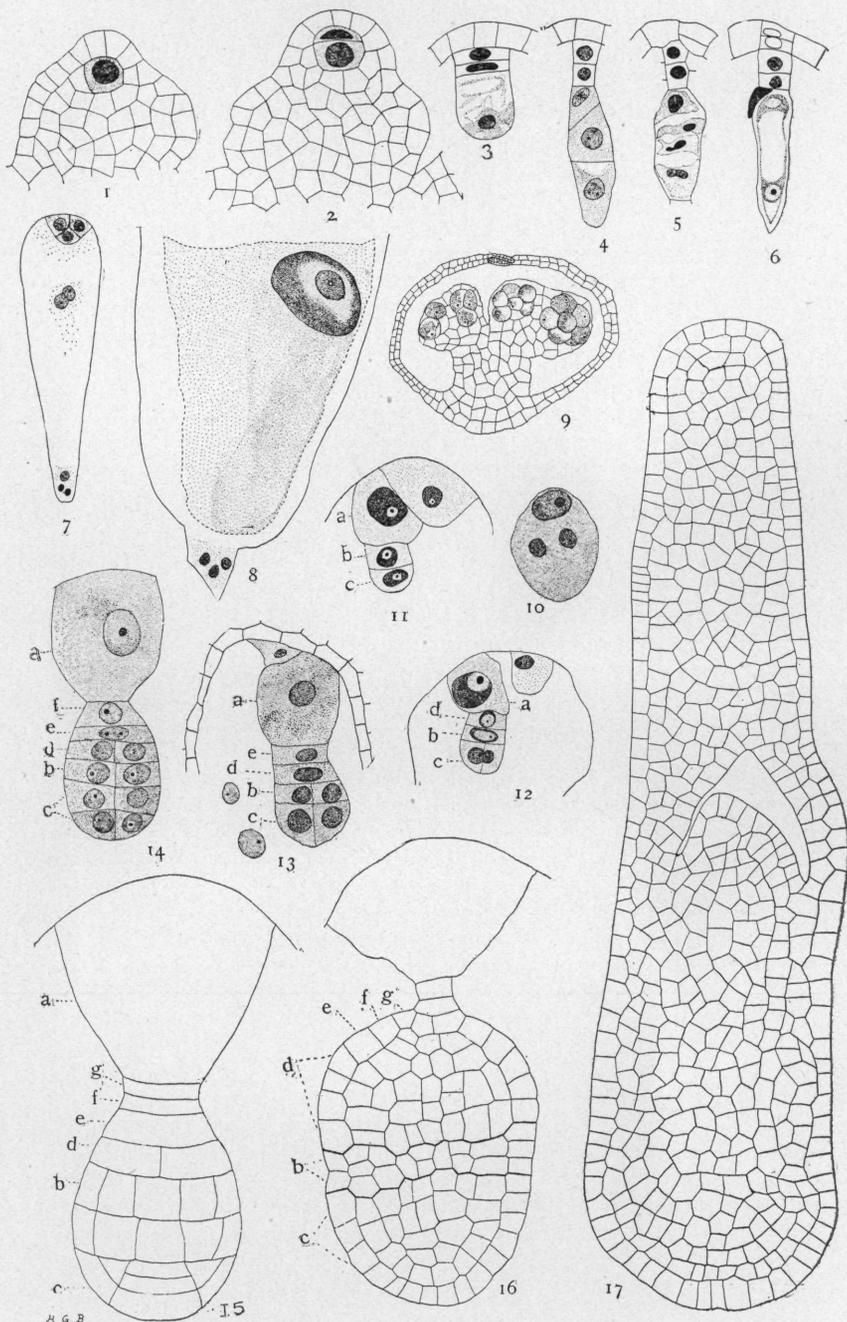
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EXPLANATION OF FIGURES.

For the drawings, a Leitz stand and a Bausch and Lomb camera lucida were used. For Figs. 7 and 16, a No. 2 Leitz ocular and No. 7 Leitz objective were used; for Fig. 9, a No. 8 Leitz ocular and No. 3 Leitz objective; for Fig. 17, a No. 2 Leitz ocular and $\frac{1}{6}$ Bauch and Lomb objective; for the others a No. 6 Zeiss ocular and a No. 7 Leitz objective were used. The magnifications given are those of the original drawings, which in the plate are reduced to $\frac{3}{8}$ of their diameters.

- Fig. 1. Archesporial cell. x 950.
- Fig. 2. Sporocyte and tapetal cell. x 950.
- Fig. 3. Megasporeocyte and two tapetal cells. x 950.
- Fig. 4. Three megasporas and two tapetal cells. x 950.
- Fig. 5. Four megasporas and two tapetal cells. x 950.
- Fig. 6. Two-celled embryo-sac with remains of megasporas. x 950.
- Fig. 7. Eight-celled embryo-sac showing the egg apparatus, conjugation of polar nuclei, and antepodals. x 630.
- Fig. 8. Large lower endosperm nucleus and antipodals. x 950.
- Fig. 9. Staminate flowers showing pollen-sacs and microsporocytes. x 230.
- Fig. 10. Pollen grains. x 950.
- Fig. 11. Three-celled embryo and persistent synergid. x 950.
- Fig. 12. Five-celled embryo. x 950.
- Fig. 13. Nine-celled embryo. x 950.
- Fig. 14. Seventeen-celled embryo. x 950.
- Fig. 15. Older embryo showing dermatogen. x 950.
- Fig. 16. Embryo showing origin of cotyledon (*c*), plumule (*v*), radicle (*d, e, f*). x 630.
- Fig. 17. Nearly mature embryo showing growing point, cotyledon and radicle. x 450.



BURR on "The Embryology of Vallisneria spiralis."