Spermatogenesis in *Asterella hemisphaerica*, Beauv.

BY

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With Plate XX.

THE material for this paper was collected several years ago, about five miles south-east of Bloomington, Indiana ; and it was killed in chromic-osmic-acetic acid. Upon working up the material the writer found that certain stages were not abundant, especially the last divisions of the spermatogenous tissue and the early stages in the development of the androcyte, or the protoplast which functions as a sperm. However, since so many definite stages in spermatogenesis and many cytological phenomena are clearly demonstrated, it was thought best briefly to summarize the data at present available.

Within recent years, investigators of the Hepaticae (especially in spermatogenesis) have reported cytological phenomena so varied that further information seems desirable. In an article by the writer on *Mnium*, in 1915, certain of these reports prior to that date were very briefly summarized². Other papers by various investigators have appeared since. Without repeating here in detail, we may say that the evidence indicates considerable variation, throughout the group consisting of the Hepaticae and the Musci, in two rather important respects: first, as to the origin, nature, and general prevalence of a centrosome-like structure, which is apparently the primordium of the blepharoplast ; second, as to the presence and nature of certain accessory bodies found in the cytoplasm of spermatogenous cells.

The student of botany to-day dare not draw dogmatic conclusions from isolated results of investigation. We are too well aware of the fact that extreme variability and plasticity constitute most prominent characteristics of the plant cell. Yet it seems reasonable to expect that we may find underlying this variability the expression of certain laws which are constant

¹ Owing to the death of the author this paper has been arranged for publication by Professor Atwell, of Northwestern University, and Professor Mottier, of Indiana University.

² Ann. Bot., xxv. 299-313, 1911 ; *ibid.*, xxvii. 93-100, 1913 ; *ibid.*, xxix. 441-56, 1915.

in operation, and the regular appearance of fundamentally significant structures which indicate natural relationships. The visible architecture of the cell is constantly changing. A nuclear or cytoplasmic structure of a certain pattern may be organized, pass through a series of changes, and then apparently be resolved again into less highly differentiated protoplasm. While throughout the majority of the plant groups we recognize the constant separation of the protoplast into nucleus and cytoplasm, the majority of certain forms (for example, the Schizophyta) fail to exhibit this differentiation. There is also a time in the life-history of a Bryophyte when an intimate union, if not an intermingling, of nucleus and cytoplasm seems to exist. The protoplast which forms the male gamete exhibits at early stages the usual sharp division into nucleus and cytoplasm. As the sperm reaches maturity, this sharp distinction between nucleus and cytoplasm becomes less defined. Perhaps in no other case is the morphological unity of the protoplast as a whole more clearly demonstrated. Within this unit there is a distinct organization of the elements, which are constantly mobile, and which become grouped according to definite laws, with the consequent appearance of visible protoplasmic structures. The individual protoplast as a unit of organization is clearly apparent. The writer does not wish to minimize the value of minute structural details, but merely to emphasize at the same time the power of the protoplast to develop along definite morphological and physiological lines with considerable plasticity of structure. The following data from *Asterella* confirm largely the writer's previous conclusions in regard to other Bryophytes.

THE PROPHASE IN ANTHERIDIAL TISSUE.

The fixed and stained cytoplasm of an antheridial cell in a resting condition contains very finely divided granules (Pl. XX, Figs. 1 and 2). These granules are not evenly distributed, but are aggregated irregularly into flocculent masses. These masses are of varying density and structure. One may find more or less uniform gradation from open, granular cytoplasm, through areas of more closely grouped granules, to larger, deeply-stained lumps. That these larger granules appear in any definite number or pattern, the writer finds no evidence.

The nucleus contains an irregular network of relatively large granules with one larger, centrally-placed, spherical body which resembles a nucleolus (Figs. 1 and 2). A faintly-stained or quite clear region may completely surround this central body. In or around this body, or nucleolus, the chromatin gradually collects during the prophase of division (Figs. 1, 2, and 3). As a result, this central mass gradually loses its regularly spherical form and becomes a larger group of irregular chromatin lumps, which presents somewhat the appearance of synapsis in spore-mother-cells (Fig. 4). Occasionally (Fig. 4) one lump stains like a nucleolus as compared with the

larger masses of chromatin. In most cases, however, the original nucleolus seems to enlarge through a concentration of the chromatin. As the nucleolus continues to enlarge and becomes more loosely arranged (Figs. 4 to 7), the chromosomes assume definite form. The number of chromosomes seems to be not less than eight. A continuous and distinct spireme was not observed.

THE FORMATION OF THE SPINDLE.

The first indication of the development of the spindle which was observed was the formation of cap-like areas of cytoplasm at opposite sides of the nucleus (Figs. 8 and 9). These caps may be closely applied to the nuclear membrane (Fig. 8), or only slightly removed from it (Fig. 9). These caps may remain for some time slightly beyond the extremities of the poles of the spindle. Soon after their appearance the nucleus becomes drawn out along the axis in which these cytoplasmic caps lie (Fig. 5). From this material, very delicate intranuclear spindle fibres soon become organized (Figs. 5, 10, and 11). As the spindle reaches maturity, remnants of the polar cap may occasionally be seen (Fig. 10). Occasionally a small granule may occupy the sharp-pointed pole of the spindle (Fig. 10). However, the poles may be sharp-pointed without the presence of either polar caps or granules (Fig. 11). Or, again, the poles may be broad and truncated (Fig. 12). Sometimes the spindle may be multipolar (Figs. 12 and 13) with more or less conspicuous granules occurring where the fibres converge. A careful study of Figs. 8, 9, 11, 12, and 13 would lead to the conclusion that, while polar granules occur with irregularity, no bodies are evident which partake clearly of the nature of centrosomes. Similar granules may occur with irregularity in number and position throughout other portions of the cytoplasm.

A careful examination of the stages represented in Figs. 1, 5, 8, and 13 has convinced the writer that, in *Asterella*, polar caps and granular bodies arise *de novo* as the nucleus enters upon division. There seems to be no basis for assigning to them morphological rank more than to the fibres of the spindle. They seem to be temporary structures of protoplasmic development, as are the spindle fibres. The caps no doubt actually become a part of the spindle. There is no evidence that the polar caps or granules (Figs. 5, 8, 9, and 10) are permanently organized structures. Their appearance and behaviour suggest rather a visible structure which is built up temporarily and which performs definite functions, and then is resolved into less differentiated cytoplasm. This conception, supported by cytological evidence, seems to the writer to throw some light on the questions suggested above.

The reaction of the delicate protoplasmic structures to killing fluids is also significant, as a comparison of different cells in different parts of the antheridium will show.

TELOPHASE.

Various stages of telophase were carefully examined, but no body was discovered which might with certainty be termed a centrosome or a blepharoplast (Figs. 14-17).

FORMATION OF THE BLEPHAROPLAST AND DEVELOPMENT OF THE SPERM.

The blepharoplast was first seen as a densely-staining body, somewhat elongated, lying close to the boundary of the protoplast which later functions as a sperm.

Two sperms are formed from one of the cubical cells (androcyte mother-cells) of the antheridium. The last spindle does not occur obliquely with the same regularity as in *Marchantia* or *Conocephalum*. All of the cytoplasm of the androcyte mother-cell is not used in the formation of the two sperms. Each of Figs. 19 to 21 shows one of the pair of sperms found in each of three mother-cells. A definite membrane develops some distance away from the nucleus, but does not enclose all of the peripheral cytoplasm. The blepharoplast first makes its appearance upon the inner surface of this membrane, as a deeply-staining lump or short band of cytoplasm (Figs. 19 and 20). The cytoplasm becomes more dense just within the enclosing membrane, leaving the space around the nucleus somewhat vacuolate. Very densely-staining material often collects on the inner surface of this membrane (Fig. 21). It is along this course that the blepharoplast develops. The material which produces the blepharoplasts collects in a rather lumpy granular band. The writer has earlier emphasized the possible close association or intermingling of nuclear and cytoplasmic material during the metamorphosis of the androcyte, and that in certain cases the nucleus and blepharoplast become quite indistinguishable. There is here additional evidence of the outward diffusion of material from the nucleus. In some cases it consists of finely divided or scarcely stained material; in others of larger lumps of coagulated substance. Careful observations were made to determine the effect of the killing fluid upon the structure of the protoplasm. At this stage, cells near the periphery of the antheridium, where the killing fluid had penetrated rapidly, appear as in Figs. 19 and 20; while those into which the fluid had filtered more slowly frequently showed the protoplasm much coagulated, as in Figs. 17 and 18.

Other writers have described the extrusion of material from the nucleus into the cytoplasm during this period.

[Figs. 22 to 27 indicate the remaining steps in the development of the sperm. Manuscript pertaining to this part of spermatogenesis was not found.]

SUMMARY.

The last division in the spermatogenous cells may be oblique, as in *Marchantia*, but it is not always so.

The number of chromosomes is eight.

Prior to the formation of the spindle, small, dense cytoplasmic caps appear on opposite sides of the nucleus near the positions which will be occupied by the poles of the future spindle. These caps arise *de novo*; they are neither permanent cell-structures nor are they centrosomes.

The blepharoplast arises near the plasma membrane as a newly-formed structure.

The most completely developed sperm shown consists of a curved, club-shaped part, the nucleus, tapering to a slender point which is continued by the thread-like blepharoplast bearing two cilia at its anterior end.

EXPLANATION OF PLATE XX.

Illustrating Professor W. L. Woodburn's paper on Spermatogenesis in
Asterella hemisphaerica, Beauv.

Figs. 1 to 17 pertain to the last nuclear and cell division in the spermatogenous cells (androcyte mother-cells) in the antheridium.

Fig. 1. Cell with nucleus in resting condition.

Fig. 2. The chromatin has become more coarsely granular. A large nucleolus lies in a colourless cavity.

Fig. 3. The chromatin shows a tendency to accumulate about the nucleolus.

Fig. 4. The entire nuclear content has contracted near the centre of the nucleus.

Fig. 5. The nucleus has become elongated.

Figs. 6 and 7. The formation of the chromosomes.

Figs. 8 to 13. The formation of the spindle. In Figs. 8 and 9 densely staining caps of cytoplasm appear on opposite sides of the nucleus. In Fig. 10 the caps have almost disappeared. Fig. 11 represents a pointed spindle, while in Figs. 12 and 13 the poles are broadly truncated.

Figs. 14 to 17. Telophases.

Figs. 18 to 27. Transformation of the sperm initial into the mature sperm.

Fig. 19. The plasmic contents have rounded up. A dense body, probably the primordium of the blepharoplast, is seen near the plasma membrane. Finely granular material is indicated between the cell-wall and the rounded protoplast.

Figs. 20 and 21. Later stages.

Figs. 22 and 23. The blepharoplast is now elongated and thread-like; the nucleus is oval or elliptical.

Figs. 24 and 25. Two young sperms of a single androcyte.

Figs. 26 and 27. The cilia are present.

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