Polyembryony in Erythronium americanum.

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With Plate XIX.

DURING the Spring of 1894 I collected a large amount of material of the ovules and seeds of *Erythronium americanum* in various stages of development with the intention of studying the process of fertilization and development of the embryo. When some of the seeds, which had reached their full size, but had not yet become filled with the characteristic horny endosperm of the Liliaceae, were cut into series by means of the turpentine-paraffine method, they were seen to present the phenomenon of polyembryony. A detailed examination of serial sections of the embryos in all stages of development resulted in the conclusion that the polyembryony here differed from any which has yet been described. Publication has been delayed till this year in the hope of adding other examples of polyembryony in native Canadian Liliaceae, a hope which has not however been realized.

It is hardly necessary to refer to the well-known work

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of Strasburger on polyembryony in *Funkia*, *Nothoscordon*, *Euonymus*, *Citrus*, &c.[1]

In these forms the multiplicity of embryos was shown to be due to the adventitious buds derived from the nucellus growing into the cavity of the embryo-sac after fertilization. Later Guignard has described in *Mimosa Denhartii* a polyembryony arising from the fertilization of one or both of the synergids in addition to that of the normal egg-cell [2].

He has not explained however how the *two* generative nuclei of the pollen-tube are able to fertilize the nuclei of the *three* cells which give rise to the embryos. He also observed polyembryony in *Schrankia uncinata*, but from lack of material was unable to discover its mode of origin.

More recently Dodel and Overton have described polyembryony in *Iris sibirica*, which they refer to synergidal fertilization[3].

In February of this year (1895) Tretjakow published an account of polyembryony in *Allium odorum*, originating from the formation of embryos from the antipodals [4].

It will be seen from the above that the place of origin of the supernumerary embryos being considered, there are two kinds of polyembryony which may be conveniently termed *extrasaccal* (*Funkia*, *Nothoscordon*, &c.), and *intrasaccal* (*Mimosa*, *Iris*, and *Allium odorum*). The embryos of *Erythronium* are intrasaccal, but differ from the others described in *all* taking their origin from the fertilized egg-cell.

The youngest ovules of *Erythronium americanum* procurable in the early spring show the embryo-sac in the binucleate state. The two nuclei divide in the usual way, giving rise to four and then to eight nuclei. The nuclei of the micropylar and antipodal ends of the embryo-sac are generally markedly different in size, but sometimes the micropylar and

[1] Ueber Befruchtung und Zelltheilung, Jen. Ztsch. Bd. XI. Ueber Polyembryony, Jen. Ztsch. Bd. XII.

[2] Annales des Sci. Nat., Sér. 6, tome XII.

[3] Dodel, Beitr. z. Erkenntn. der Befruchtungsersch. bei *Iris sibirica*. Zürich, 1891.

[4] Ber. d. Deutsch. Bot. Gesells., Feb. 1895.

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sometimes the antipodal ones are the larger. The differences are specially noticeable in the quadrinucleate condition of the embryo-sac. The number of chromosomes could not be made out, as the nuclei were not seen in the process of division. The final condition of the embryo-sac is similar to that which has been shown to obtain generally. The embryo-sac, at the time of fertilization, is imbedded in a richly protoplasmic nucellus. There is a considerable amount of tissue in the chalazal region of the nucellus, but at the apex there is only a single layer of cells over the embryo-sac. The cells of the nucellus are strikingly marked off from those of the integument by their richness in protoplasm and by their avidity for stains.

The pollen-tube penetrates the ovule in the usual manner and the egg becomes fertilized, the stages in the union of the male and female nuclei being made out with special facility on account of the large size of the elements. No attempt was made to demonstrate the existence of centrosomes and astrospheres[1].

Fig. 1 shows the essential parts of a just fertilized ovule. Two nuclei are seen in process of fusion in the egg. The synergids have disappeared entirely, as is usually the case in *Erythronium*. The egg-cell subsequently divides into two generally, but not invariably, by a division at right angles to the axis of the embryo-sac. The first division is followed by others which have no fixed order or plane.

In Fig. 2 a division is represented taking place in the upper cell of the two-celled embryogenic mass. The single layer of nucellar tissue over the apex of the embryo-sac is seen to be densely filled with protoplasm. Strasburger found the same peculiarity in *Funkia*, in which plant it is these 'inhaltsreiche Zellen' which give rise to the multiple embryos. In *Erythronium*, however, as before stated, *all* the tissue of the nucellus is rich in protoplasm. The same is true of *Lilium canadense* and species of *Trillium*, so the phenomenon is probably of general occurrence.

[1] Strasburger, Hist. Beiträge, IV.

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Fig. 3 shows an embryogenic mass in a later stage of development. In Fig. 4 the embryogenic mass appears still further increased in size; whilst in Fig. 5 the mass is seen not only increased in size, but beginning to send forth outgrowths from the free end, the future embryos. The single layer of nucellar cells over the apex of the embryo-sac still persists, but their dense protoplasm is for the first time vacuolated. At no time do the cells of this layer show any signs of division. In Fig. 6 four embryos are seen at the free end of the embryogenic mass. The preparation here represented shows an unusually large number of embryos. Generally there are but two or three of them to be made out. The single investing layer of nucellar tissue has disappeared by absorption. As is the case in *Mimosa Denhartii*, only one embryo persists in the ripened seed[1]. This is buried in the endosperm resting on the broad base furnished by the persistent embryogenic mass, or, as it may be better termed at this stage, the suspensor. The large size of the latter in the case of *Erythronium* suggests the possibility that the equally enlarged suspensor of the Viceæ[2] may be a relic of polyembryony. No investigation, however, has been made as yet in this direction.

The fact that the single layer of densely protoplasmic nucellar tissue over the apex of the embryo-sac in *Erythronium* does not give rise to the multiple embryos, suggested a reinvestigation of *Funkia* in the expectation that the employment of the improved technique now in vogue might give similar results in that form. Detailed examination of *Funkia* showed, however, that Strasburger's description of the origin of the embryo was in all respects exact.

Guignard himself suggests the possibility of doubt as to the multiplicity of embryos in *Mimosa Denhartii* being due to the fertilization of the synergids, and offers the alternative that they may have come from the segmentation of the egg-cell. The latter supposition seems to gain force from the difficulty of conceiving that the *three* cells which give rise to

[1] Guignard, op. cit. [2] Vide Guignard, op. cit.

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embryos[1] should be fertilized by the *two* generative nuclei of the pollen-tube. The conditions in *Erythronium* also lend strength to this opinion. From lack of material I have not been able to reinvestigate the facts in *Mimosa*.

Iris versicolor was examined in the hope of finding polyembryony, but it was found to possess normal embryos. As *Iris sibirica* was not available, it was not possible to compare it with *Erythronium*.

The polyembryony of *Erythronium americanum* is also of interest, in that it is exactly homologous with the polyembryony which is so commonly found among the Gymnosperms. The resemblance extends even to the ultimate persistence of only one of the multiple embryos.

[1] Op. cit., Plate I, Fig. 31.

EXPLANATION OF FIGURES IN PLATE XIX.

Illustrating Mr. Jeffrey's paper on Polyembryony in *Erythronium*.

Fig. 1. Embryo-sac just after fertilization has taken place. In the oospore the male and female nuclei are seen in process of union. The synergids have disappeared. × 180.

Fig. 2. A later stage. The embryonic mass consists of two cells, in the upper of which a mitosis is just taking place. × 250.

Fig. 3. The embryogenic mass has increased in size. × 250.

Fig. 4. The embryogenic mass has grown still larger. × 250.

Fig. 5. The still more enlarged embryogenic mass is beginning to give rise to embryos. × 250.

Fig. 6. Four embryos are seen projecting from the embryogenic mass. × 180.

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