NOTES ON THE DEVELOPMENT OF THE OVULE, EMBRYO SAC AND EMBRYO OF *HYDNORA AFRICANA*, THUNB.

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(With thirteen Text-figures.)

Introductory.

The genus *Hydnora* is confined to South Africa, Bourbon and Madagascar, and comprises several species, out of which three only occur in South Africa. They are all parasites, and the species which forms the subject of these notes, viz. *Hydnora Africana*, uses mainly the common milkbush of the karoo, *Euphorbia mauritanica, L.*, as its host, and is of fairly common occurrence in South Africa (3). The flowers appear as buds on the underground stem, but soon come above the surface of the ground, and open when mature by means of three longitudinal slits.

The material for this investigation was collected in the neighbourhood of Worcester, Cape Province, mostly by Prof. Saxton in December, 1912, and in part by Mr. Izak Meiring in May, 1912, and fixed in chromacetic acid with or without osmic acid. A short series of sections was prepared by Prof. Saxton, but pressure of other work prevented him from completing the series, and in November, 1919, he handed over the whole material to me. The fixed material consisted mainly of small pieces of the extensive placentas cut out from a series of about a dozen plants ranging from the youngest to the oldest that could be found.

Investigation.

The placentas are extensive and much branched, and bear radially enormous numbers of orthotropous ovules. The sections were cut, in the main, transverse to the longitudinal axis of the placentas, thus giving longitudinal sections of the ovules in great numbers. A very young ovule before the differentiation of the integument is shown in Fig. 1. Very soon a massive integument makes its appearance, at the top of which the cells divide by periclinal walls giving rise to four layers of cells, while it is only two cells thick on the sides. The very young ovules are nearly spherical but elongate afterwards. No definite archesporial cell or cells are clearly

EXPLANATION OF FIGURES.

All sections were cut with a Cambridge rocking microtome, the thickness varying from 4–7 μ. The figures were drawn with the help of a Leitz microscope and a Zeiss camera lucida. The sections were cut transverse to the placenta, giving longitudinal sections of the ovules.

In all figures: I. Integument; M.M.C. Megaspore mother-cell; N. Nucellus; E.S. Embryo sac; E.C. Egg cell; S.N. Synergid nuclei; P. Polar nuclei; P.T. Pollen tube. M. Male nuclei; A. Antipodal nuclei; E. Embryo; S. Suspensor; P.T.N. Pollen tube nucleus.

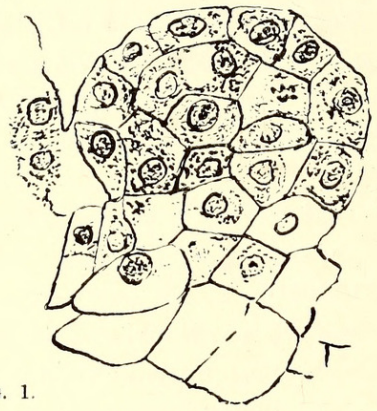


Fig. 1.

Fig. 6.

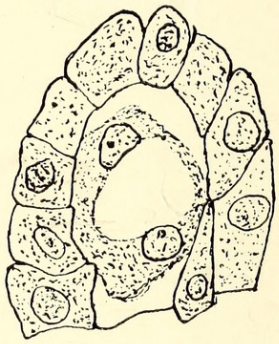


Fig. 4.

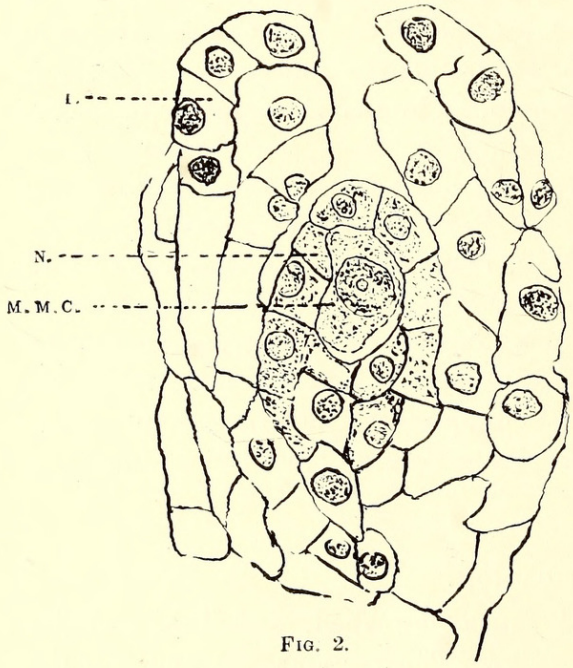


Fig. 2.

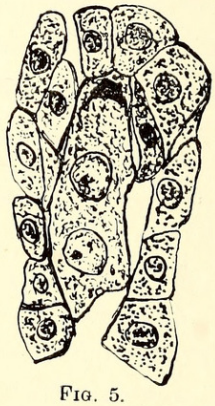


Fig. 5.

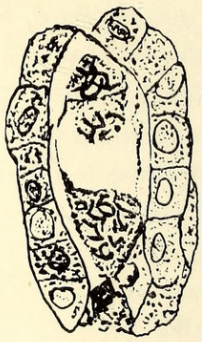


Fig. 7

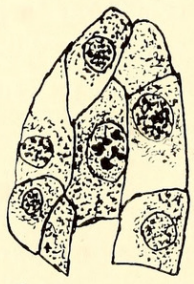


Fig. 3

Figs. 1–7.—1. Young ovule about the archesporial stage. × 196. 2. Young ovule showing M.M.C. which directly functions as the embryo sac. × 196. 3. Embryo sac nucleus dividing. × 196. 4. Equatorial arrangement of the chromosomes at the heterotypic division. × 196. 5. The embryo sac with two nuclei, with the curious thickening above. × 196. 6. Embryo sac showing two nuclei with the vacuole. × 196. 7. Division of two nuclei into four. × 196.

recognisable, but a hypodermal cell larger than the rest becomes at once the megaspore mother-cell (Fig. 2). At this stage a curious thickening is seen at the top of the megaspore mother-cell and persists till a later stage.

The megaspore mother-cell functions as an embryo sac directly, without first dividing into four megaspores. The nucleus divides into two by the heterotypic division (Figs. 3 and 4). The sporophyte number of chromosomes is believed to be twenty-four,* and in the reduction division twelve were counted. Vacuoles appear in the embryo sac after the first division and the two nuclei arrange themselves at the poles (Fig. 6). The stages showing the homotypic division of the two nuclei into four were also seen (Fig. 7). Fig. 8 shows the embryo sac with an egg cell nucleus, two synergids, two fusing polars, three antipodals and a pollen tube, with the pollen tube nucleus and two curved male nuclei. Stages were seen in the progress of the polar nuclei towards the centre of the sac, and they fuse before fertilisation (Fig. 8). The antipodals may also disintegrate and disappear before fertilisation. Cases believed to show actual fertilisation were observed, but they have not been figured as the evidence was inconclusive.

The embryo divides into two cells by a transverse wall and transverse divisions continue till a very long chain of cells is formed. As many as fifteen cells were counted in a chain in one proembryo. Then longitudinal divisions occur in about the fifth, sixth, seventh, eighth and ninth cells from the distal end and these cells alone give rise to the embryo proper. The longitudinal divisions begin even before the divisions in the distal part of the filament are complete. The cells of the suspensor slowly shrink and at least the proximal cells disappear gradually, while the distal cells persist in the most mature embryo observed. Fig. 12 shows two longitudinal rows of four and three cells each and Fig. 13 shows two longitudinal rows of five cells each.

Discussion.

The massive integument seems to be an unusual feature in this species, as generally two integuments prevail among Archychlamydeae, except in some species of Ranunculus and Leguminosae (4).

Among Archychlamydeae nearly all the species investigated have three or four megaspores (except in three genera of Piperaceae), and a row of four megaspores seems to be less common than a row of three (4). In this plant the megaspore mother-cell does not divide at all but directly functions as the embryo sac.

The curious thickening which is seen at the top of the megaspore mother-cell, and which persists till a later stage, was thought at first to be the remains of a parietal cell cut off from the archesporial cell, and a careful examina-

* Twenty-three were actually counted, but it is presumed that twenty-four were present.

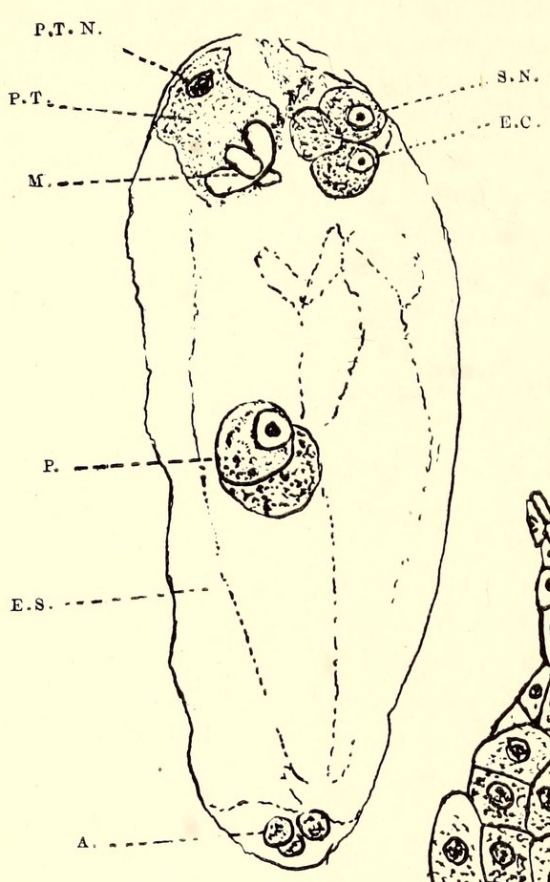


FIG. 8.

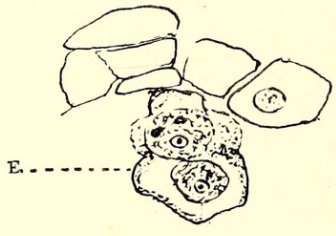
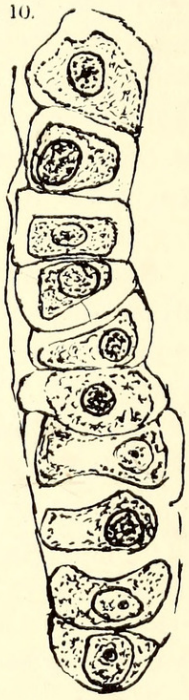


FIG. 9.

FIG. 10.



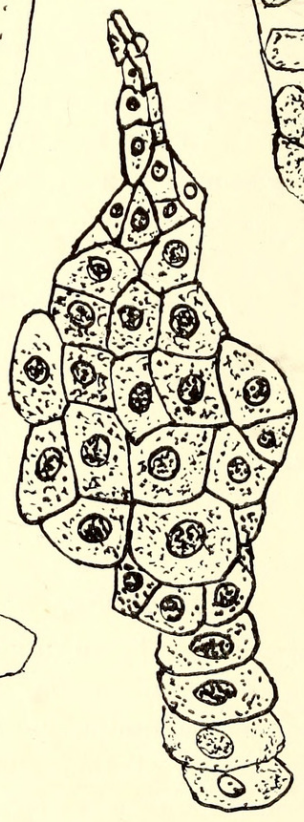


FIG. 13.

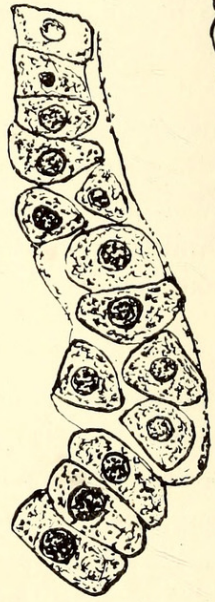


FIG. 11.

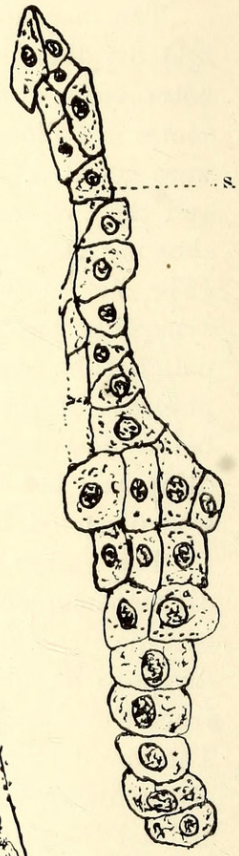


FIG. 12.

FIGS. 8–13. Embryo sac showing egg cell nucleus with two synergids, two fusing polars, three antipodals and the pollen tube with a pollen tube nucleus and two male nuclei. × 252. 9. Two-celled embryo. × 196. 10. Older embryo consisting of a chain of cells. × 196. 11 and 12. Beginning of the formation of a massive embryo. × 196. 13. The massive embryo. × 196.

tion of earlier stages was undertaken to test the point. So far as can be ascertained, however, it seems clear that no parietal cell is formed at all.

The long filament of cells produced by transverse divisions from the fertilised egg is unusual among Dicotyledons though paralleled in certain Leguminosae (2). Generally the formation of the embryo proper takes place in the distal cell of the proembryo amongst flowering plants, but in this plant it is approximately in the fifth, sixth, seventh, eighth and ninth cells from the distal cell that the formation of the embryo proceeds. So there are three regions in the proembryo: (1) the suspensor, (2) the embryo proper, and (3) the cells beyond the embryo. The most mature embryo observed (Fig. 13) is still undifferentiated, and the material available does not admit of the investigation of later stages, but field observations indicate that probably these would only be met with in germinating seeds. A small embryo in which neither radicle nor cotyledons are differentiated has been described for a number of parasitic and saprophytic Dicotyledons, but none of them shows an embryo of precisely the same type observed and figured for *Hydnora*. In Engler and Prantl's 'Pflanzenfamilien' (1) there is figured a mature embryo of *Prosopanche Burmeisteri*, De Bary (the only genus allied to *Hydnora*), but the latter does not appear to show the peculiar features described here for *Hydnora*, so far as such features are shown in Solms' figure cited.

In conclusion I have to thank Prof. Saxton for advice, suggestions and criticisms on various points in this investigation. Thanks are also due to Mr. Izak Meiring for his help in the collection of material.

Summary.

(1) The ovule of *Hydnora* is orthotropous with a single integument.

(2) The megaspore mother-cell is hypodermal and becomes the embryo sac.

(3) The proembryo consists of a row of about fifteen cells.

(4) The embryo is produced from the middle region of the proembryo, and no differentiation had taken place in the latest stages seen (probably from nearly ripe seeds).

Note.—This investigation was carried out in the Botanical Laboratory of the Madhavlal Ranchhodlal Science Institute, Ahmedabad.

Literature Cited.

(1) Solms, H. Graf zu.—"Rafflesiaceae" and "Hydnoraceae" in Engler and Prantl, 'Pflanzenfamilien,' III Teil. Ab. 1, 1889.

(2) Guignard, L.—"Recherches d'embryogénie végétale Comparée. I: Legumineuses," 1881. (In Coulter and Chamberlain's 'Morphology of Angiosperms.')

(3) Marloth, R.—"Notes on the Morphology and Biology of *Hydnora africana*," 'Trans. S. Afr. Philos. Soc.,' vol. xvi, Part v, 1907.

(4) Coulter and Chamberlain.—'Morphology of Angiosperms,' 1912.