

On the Embryogeny of *Angiopteris evecta*, Hoffm.

BY

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With Plate XV.
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NOTWITHSTANDING the attention which has for many years been bestowed upon the Filicineae and their allies, the embryogeny of no member of the eusporangiate Ferns is as yet known; a circumstance, the cause of which is to be attributed to the difficulty of obtaining the plants in a condition suitable for investigation.

When in Ceylon last year, I took the opportunity of securing as much material as possible of prothallia of *Angiopteris*, with the view of studying the development of the sporophyte, and although my results are incomplete on some points, it has been possible to make out clearly the more important features presented by the embryo of this plant.

The prothallium is remarkably deep green in colour and somewhat orbicular in shape. It is not unlike the thallus of *Anthoceros*, with which my specimens were often associated; it commonly however reaches a large size, occasionally attaining to as much as three quarters of an inch in diameter. The

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development of the prothallium has been followed by Jonkman¹ from the germinating spore, and he observed the formation of the sexual organs. The *antheridia* occur on the upper and lower surfaces of the oophyte, though they are more freely distributed on the lower side. They arise from single superficial cells. Each of these divides into an inner and an outer cell. The former by repeated division gives rise to the mother-cells of the antherozoids, whilst the latter or outer cell divides in planes at right angles to the free surface, thus forming the cover-cells, by whose separation the antherozoids are eventually liberated from the antheridium. The *archegonia* are confined exclusively to the lower surface of the prothallium, and arise from the 'cushion' region, which is exceptionally large in this plant. A superficial cell divides periclinally into an outer cell from which the neck of the archegonium originates, and an inner cell from which the neck-canal and ventral-canal cells are successively cut off, leaving the oosphere at the base. The neck-canal-cell grows between the cells of the short neck forcing them apart. It ultimately divides into two transversely, and the resulting cells are often separated by a true wall, as was observed by Jonkman, and by Campbell² also in the case of *Osmunda* as an occasional occurrence. It is by no means invariable in *Angiopteris*, and in Fig. 2 there is shown a case in which the cell-wall, though it had begun to be formed, was not completed, and was drawn away with the shrinking of the protoplasm, from the lining walls of the neck-canal. The ventral-canal-cell, which is very large in this fern, is converted like the two neck-canal-cells, into mucilage, which on the addition of water, bursts open the archegonium. In a few cases I observed an apparent deviation from the course just described, inasmuch as the inner of the two cells resulting from the first division of the archegonial primordium seemed to have divided again, before forming the axile row of cells;

¹ Jonkman, De Geslachtsgeneratie d. Marattiaceën.

² Campbell, On the Prothallium and Embryo of *Osmunda claytoniana* and *Osmunda cinnamomea*, Ann. Eot. VI, p. 67.

the lowest of the three first cells would thus be the equivalent of the basal cell of Janczewski. My material was however unfortunately not sufficient in quantity to enable this question to be conclusively settled.

I had not the opportunity of observing the process of fertilisation, and unfortunately none of my material showed the earliest divisions of the oospore, though in preparations of the youngest embryos, their succession could be determined without much difficulty. The basal wall is formed as in *Isoëtes* and *Equisetum*, at right angles to the long axis of the archegonium, that is, in the plane of the prothallium. The next wall in order of succession I believe to be the median one; it is at right angles to the basal wall, and parallel to the axis of growth of the prothallium. This wall can easily be distinguished, even in advanced embryos, as a well-defined vertical line. The transversal wall is much more indefinite, and soon becomes quite unrecognisable as the embryo grows in size. New cell-walls succeed each other very rapidly, and without much regularity (cf. Figs. 3 and 4 which represent almost identical stages), and they are far less easily followed than in the common types of leptosporangiate ferns. I was unable to determine the presence of segment-walls in most preparations of young embryos, though they are indicated in some cases. No doubt this comparative irregularity is to be connected with the absence of well-marked apical cells from the members into which the young embryo becomes differentiated. These members originate from the octants in a way recalling strongly the typical fern-embryo, as will be at once seen from what follows.

The two anterior epibasal octants (i.e. the two anterior upper ones) give rise to the cotyledon. Of the two posterior epibasal octants one probably contributes the larger share in the formation of the stem, but, during the earlier stages at any rate, *both* are devoted to this purpose (Fig. 5*b*). There is no single apical cell, and on each side of the median wall cells are seen clearly marked out by their contents and large nuclei, as merismatic cells. The foot originates from the

posterior pair of hypobasal octants, beneath the stem; its cells which border upon the prothallium afford a good example of digesting and absorbing cells; their contents and general appearance contrasting strongly with those of the surrounding prothallial cells.

The root is formed from one of the octants beneath the cotyledon, that is from an anterior hypobasal one. The sister octant merely undergoes a few irregular divisions and rounds off the embryo on that side. The root is first indicated by a triangular apical cell, and is best seen in sections cut at right angles to the basal and median walls. It offers considerable difficulty in tracing out the course of its further development, as the apical cell which is at no time very clear, is subsequently replaced in *most cases* by a group of initials (see Fig. 8), as I convinced myself by an examination of a number of sections specially cut obliquely, in order to determine this point. In some instances however I was unable to satisfy myself that a cell-group was formed at the young root-apex, and there seems no doubt that some variability exists in respect of the structure of the latter. This is well shown in the Figs. 13-17, which were drawn from transverse sections of the roots of young plantlets in which not more than two leaves had been found. It may easily be seen that not only does the number of apical cells vary, but also the direction of the early division-walls is very inconstant, even giving rise in one case (Fig. 15) to an appearance almost suggesting the presence of an apical cell. It is obvious however that this construction would break down if the attempt were made to derive the daughter-cells from such a supposed cell, even in the section figured, which was one most favourable to such a hypothesis. Possibly a connection may exist between the relative robustness of the root and the structure of its apex, and this may perhaps account for the discrepancies existing in the statements given by different authors. I regret that my own material was not sufficient to determine this point conclusively in the case of the young embryos, but we know that some latitude of variation exists in certain ferns, e.g.

Osmunda as described by Bower¹; however this may be, it is a fact of some importance that in a number of cases at any rate, the root-apex in the embryo contains a group of meristematic cells, instead of the single apical cell so characteristic of the leptosporangiate ferns.

The vascular bundle of the embryo is formed at an early age, and is first differentiated in the cotyledon; it joins directly on to the bundle of the root, the first tracheids appearing at the point where the leaf-trace curves into the stem, and from thence fresh ones are differentiated in an upward and downward direction. The vascular bundle is accompanied in the cortex surrounding it, by rows of cells containing tannin (Figs. 11, 12). These are differentiated in the embryo at a very early age, long before it issues from the prothallium. Their development is best observed in the cotyledon, where they are seen to arise as cells, which elongate with the growth of the leaf, and finally coalesce by the disappearance of their transverse septa much as do the cells composing the laticiferous tissue of *Chelidonium*. I saw no instance of any lateral extension of these tannin-cells, though sometimes short blind protuberances are pushed between other cells of the cortex.

When the embryo has reached a certain size, it bursts the prothallium, the root boring through the lower surface, whilst the cotyledon and stem break through the cells of the upper surface. This manner of issuing from the oophyte serves at once to distinguish *Angiopteris* from those other ferns whose embryogeny is known; for it will be remembered that in them the cotyledon and stem appear through the archegonial region on the *lower* surface, and, so to speak, grow up round the edge of their prothallium. The peculiarity of *Angiopteris* in this respect may be connected with two facts in its earlier history; namely, first, with the occurrence of the archegonia at some distance behind the apex of the somewhat large oophyte, and secondly with the position of the basal wall which separates the shoot and root portions of the embryo, it

¹ Bower. Comparative examination of the meristems of Ferns: Ann. Bot. III, p. 310.

being formed in this plant in a plane parallel to, instead of at right angles to, that of the prothallium, as in most ferns.

Fresh leaves and roots speedily arise on the young plantlet, the second leaf appears nearly opposite to the first one, and immediately above the first root. Its own root emerges just beneath the cotyledon. The third leaf arises (continuing the spiral) close to the side of the cotyledon and its proper root also emerges on the opposite side of the stem. The first two leaves are destitute of stipules, but these structures appear at once on the third leaf, where they are relatively large, and quite functional. The leaf-stalks, especially in the stipular region are covered with hairs containing a large quantity of tannin.

EXPLANATION OF FIGURES IN PLATE XV.

Illustrating Mr. Farmer's paper On the Embryogeny of *Angiopteris evecta*, Hoffm.

[B=Basal wall. M=Median wall. T=Transversal wall. x=Apical cell.]

Figs. 1, 2. Archegonia.

Fig. 3. Consecutive sections through a very young embryo.

Fig. 4. Median section through a similar embryo.

Fig. 5. Section of embryo cut parallel to transversal wall; (a) through the cotyledonary end, (b) through the stem-apex (shaded).

Fig. 6. Longitudinal section of older embryo with root-cell.

Fig. 7. Section, almost transverse, through embryo showing apical cells of the root.

Fig. 8. Embryo cut obliquely with apical cells of root.

Fig. 9. Median longitudinal section of embryo in the prothallium, with tannin-cells (shaded) in cotyledon.

Fig. 10. Section (not quite median) of embryo in the prothallium.

Figs. 11, 12. Longitudinal sections of part of the cotyledon showing tannin-cells (shaded).

Figs. 13-17. Transverse sections of root-apices of young plantlets.—The curved wall in Fig. 15 is unusual. The arrangement of the cell-walls in Fig. 17 is irregular.

Figs. 18-23. Young plantlets in various stages of development. In Fig. 21 two embryos are shown to have been formed on one prothallium.



Fig. 1.

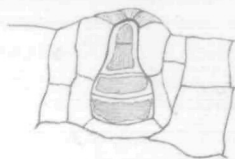


Fig. 2.

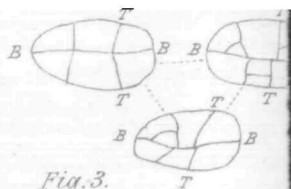


Fig. 3.

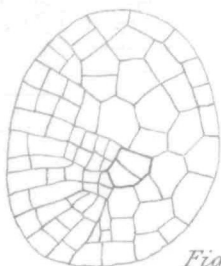


Fig. 7.

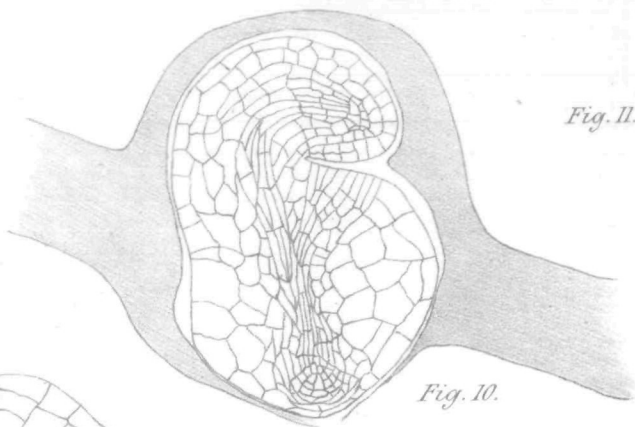


Fig. 10.

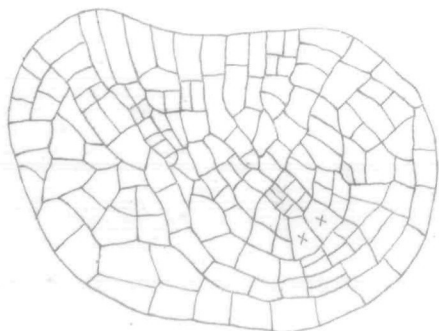


Fig. 8.

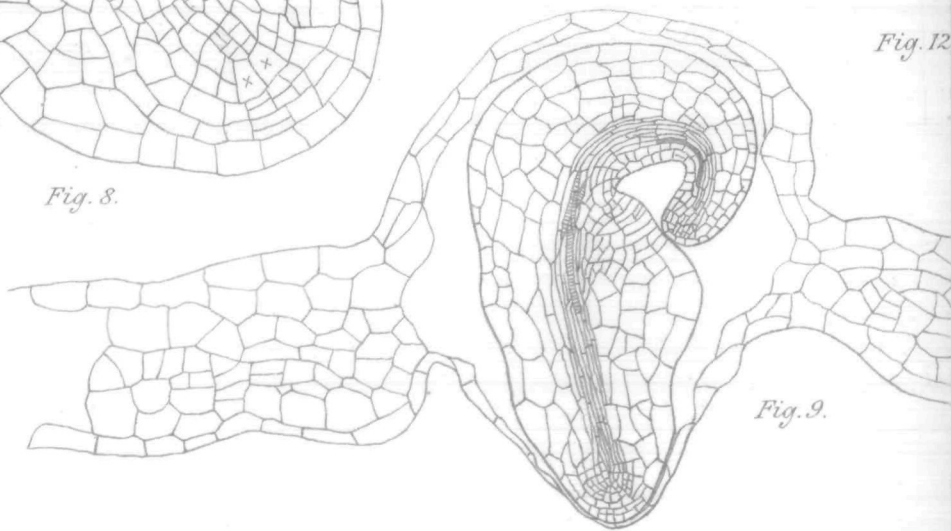


Fig. 9.



Fig. 18.



Fig. 19.



Fig. 20.



Fig. 21.

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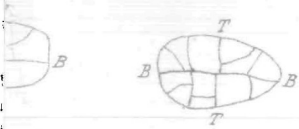


Fig. 4.

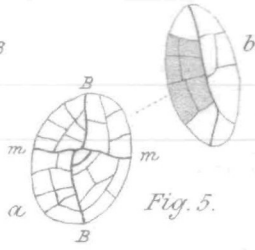


Fig. 5.

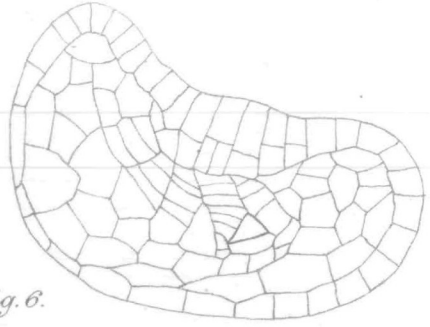


Fig. 6.

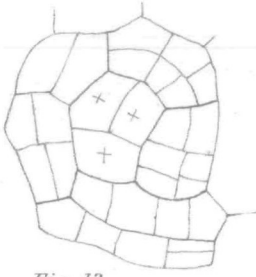


Fig. 13.

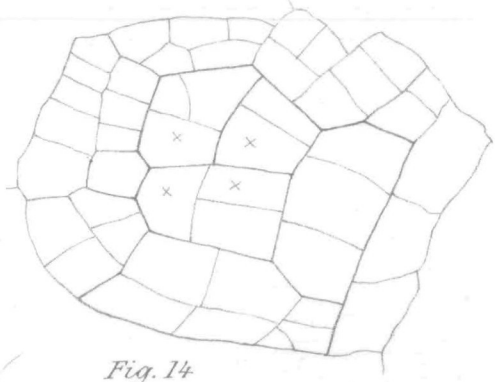


Fig. 14

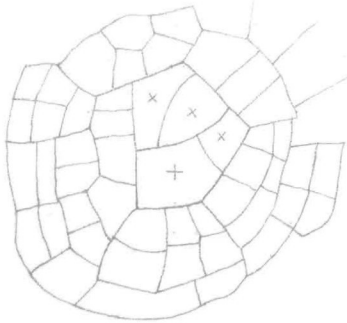


Fig. 15.

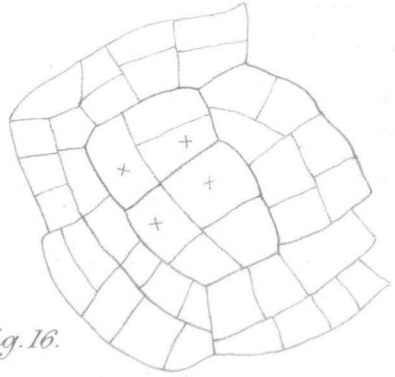


Fig. 16.



Fig. 22.



Fig. 23.

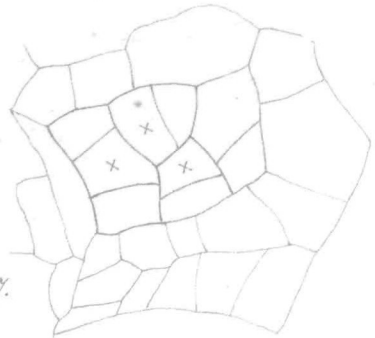


Fig. 17.