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DOUGLAS HOUGHTON CAMPBELL

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THE DEVELOPMENT OF THE OSTRICH FERN,

BY DOUGLAS HOUGHTON CAMPBELL, Ph.D.

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II. The Development of the Ostrich Fern, Onoclea struthiopteris.

By Douglas Houghton Campbell, Ph.D.

(Walker Prize Essay, 1886)

Among the most characteristic ferns of the northern United States are those belonging to the genus Onoclea, represented by three species, two of which, *O. sensibilis*, L., and *O. struthiopteris*, Hoffm., are found throughout the northeastern United States, the latter species, the subject of this memoir, being less generally distributed, though locally abundant. It also occurs throughout northern Europe and Asia.

The sporangia in this fern are borne in great numbers on the back of the fertile fronds, and as these remain standing through the winter after the sterile fronds have decayed, spores can be obtained at all seasons of the year. These retain their vitality for several months after being gathered, so that when the plants are common, abundance of material is constantly on hand. This fact, together with the ease with which the spores can be germinated, makes the plant a specially valuable one for study.

The observations here recorded were begun in the spring of 1882, and were continued, with more or less interruption, through the autumn of 1885. The points of most importance discussed are the following:

The presence of a third coat in the spore.

The marked dioecism displayed by the prothallia.

Formation and development of the apical cell of the prothallium.

Continuity of the protoplasm in the cells of the prothallium.

Development of the antheridium and antherozoids.

Absence of the ventral canal-cell in the archegonium.

Succession of the divisions of the embryo and the establishment of the apical cells of its different members.

Development of the different tissues of the embryo.

Development of the leaf from the apical cell, and the relation of the different tissues of the leaf to the segments of the apical cell.

Method of formation of the pinnae.

Development of the stem from the apical cell.

Development of the sporangium.

Section I. Prothallium.

The spores are of the so-called bilateral form, oval in shape and protected by a firm, dark brown outer coat, the exospore, which is provided with ridges or folds, usually arranged so as to enclose an irregularly polygonal area, other ridges running from the angles. The spore is slightly flattened on the side originally in contact with its fellow, in the mother-cell, and the exospore on this side is smooth. Besides the exospore there are two other coats: a middle one that does not appear to have been previously noted in ferns, and the endospore. The middle coat is not readily seen before germination, but that it is not unmodified cellulose is shown by the fact that the prolonged action of sulphuric acid and iodine does not color it blue. It is plainly seen in cases where the opaque exospore has become detached before germination, as it must be ruptured before the endospore can protrude. The exospore seems to be only slightly attached, readily separating on slight friction, and is often thrown off by the swelling of the spore on the absorption of water.

On examining dry spores after the removal of the exospore, they are found to be flattened on one side, but in a few minutes after being placed in water, by its absorption they become distended and all trace of flattening disappears, the spore then being almost perfectly oval in form (Pl. 4, fig. 1). They contain abundant chlorophyll which is sometimes nearly uniformly distributed throughout, but is commonly more abundant in the center. Besides the chlorophyll, the protoplasm contains other granules, not, however, of starch. Oil is often to be detected in drops of considerable size but is usually uniformly distributed. At the center of the spore, but usually nearly concealed by its dense contents, is a small, but sharply defined nucleus.

Under favorable circumstances, the spores begin to germinate in from three to five days. The early stages can best be observed by simply growing the spores in water, and keeping them in a warm place in a moderately strong light; but perfect prothallia cannot be thus obtained.

The first sign of germination, in cases where the exospore has been thrown off, is a splitting of the second, or middle coat, for nearly the whole length of the spore, and through the fissure thus formed the endospore protrudes (Pl. 4, figs. 2, 3). Usually one end of the spore at this time is more transparent than the rest, being wholly, or in part, destitute of chlorophyll. This transparent end becomes shut off from the body of the spore by a septum nearly at right-angles to the longer axis of the spore, and becomes the first root-hair (Pl. 4, figs. 2–4, 6). This elongates rapidly, attaining in the course of two or three days four or five times the length of the original spore. The body of the spore has also elongated by this time to more than twice its original size, and becomes further divided by a septum nearly parallel to the first. The terminal cell continues to increase in length, and new septa parallel to the first are formed thus causing the prothallium to assume the filamentous or protonemal stage (Pl. 4, figs. 4, 6). By the end of the first week many of the prothallia show divisions at right angles to those first formed, this sometimes occurring in the second or third cell, but not usually until a row of three or four cells has been formed. About the same time a second root-hair is formed from the basal cell. A small papilla is formed on one side which is cut off from the cell by a septum, and rapidly elongating assumes the form of the first (Pl. 4, fig. 5 r'). Like this it contains little or no chlorophyll. As growth progresses the chlorophyll granules, which had at first been crowded together, become more separate and very distinct. The protoplasmic layer in which the chlorophyll granules are embedded lines the walls of the cells, the center of the cell being occupied by a large sap-cavity. The nucleus, which is sharply defined, and usually contains an evident nucleolus, is round in outline, and lies close to the wall of the cell. In the root-hairs the protoplasm, near the growing end, is finely granular, and a few larger granules are scattered through the peripheral protoplasm. In the young hairs, some of these are faintly colored with chlorophyll but this seems to be finally lost.

If the protoplasm of the cells of the prothallium is contracted, *e. g.*, by a solution of sodium chloride, and then stained, the continuity of the protoplasm can be easily demonstrated. Delicate threads of protoplasm can then be detected connecting the protoplasmic masses of adjacent cells, apparently passing through small openings in the wall.

By the end of the second week the flattened form of the older prothallia begins to be marked, on account of the division of the cells in two planes, and about a week later the larger ones show the beginning of the sinus in the front margin, causing it finally to assume the heart-shape usually met with in the larger prothallia of ferns. This form is usually quite pronounced by the end of the first month (Pl. 4, fig. 13). It is brought about in the following way: after a row of several cells has been formed, the terminal cell becomes divided by a wall nearly at right angles to the earlier ones. In the cells thus formed, transverse walls are formed which, however, generally diverge somewhat from an exact right angle with the median wall, being turned slightly forward, thus forming two cells that are nearly triangular in shape. One of these becomes the apical cell of the prothallium, the other behaving like the ordinary cells. The apical cell becomes next divided by a wall parallel to one of its lateral walls, and next by a similar one parallel to the other side. This process is repeated, resulting in two series of segments lying alternately right and left, thus rapidly increasing the breadth of the apex of the prothallium (Pl. 4, figs. 7–11). Occasionally, two segments appear to be cut off from the side in succession, but this is probably exceptional. The first division in each segment is transverse, and divides it into an inner and an outer cell. The succeeding divisions do not always follow the same order, but usually the next wall divides the outer cell into two equal parts, and is perpendicular to the first one. Following this, the inner cell is divided into two by a transverse wall. Beyond this point there is great irregularity. However, the longitudinal growth of the segment exceeds the lateral growth, so that the end of the segment is pushed out beyond the apical cell. This combined with the rapid division of the marginal cells of the segment results in the formation of a deep sinus or cleft, in the front of the prothallium, in the bottom of which lies the apical cell. Where this growth is excessive, the two lobes of the prothallium sometimes overlap. Sooner or later the apical cell ceases to form lateral segments, and becomes divided by a transverse wall into an inner and an outer cell, in the same way that the segments were first divided (Pl. 4, fig. 12). The outer cell divides into two equal cells by a wall at right angles to the first, and the apical cell thus becomes obliterated, acting from this time on like the other cells. In cases where the prothallium is branched, as frequently occurs in the male prothallia, a new apical cell, dividing in the same way as the original one, may be formed at the end of a branch. One case was observed where the prothallium was divided into two branches, each having a perfect apical cell, the whole looking very much as if these two cells had originated from a bipartition of the original apical cell.

Soon after the obliteration of the apical cell, or sometimes before, the cells in its vicinity, which hitherto have divided in two planes only, now divide also by walls parallel to the surface of the prothallium, thus giving rise to a mass of cells occupying the bottom of the cleft in its front. In cases where the prothallium continues to grow for a long time and this process begins early, a thickened mid-rib is formed, running for nearly its whole length.

The foregoing account applies only to the larger prothallia, which are, for the most part, female. Many exceptions occur in the male prothallia, and the younger prothallia that are exposed to unfavorable conditions. If the spores are germinated in water, the cells become much longer and more slender, sometimes attaining four or five times the normal length without dividing. On the other hand, prothallia grown under normal conditions are to be met with in which no protonema is formed, but the second cell of the prothallium dividing by a longitudinal wall, the flattened form is assumed almost from the beginning. Where the spores are sown thickly, the male prothallia sometimes do not pass beyond the protonemal stage, the row of cells being terminated by an antheridium, and these simple prothallia are sometimes destitute of any root-hair (Pl. 4, fig. 15). While many of the male have much the form of the female, differing simply in their smaller size, they are more commonly of very irregular shapes, especially if they have attained some size, often being much branched and lobed, reminding one strongly of those of certain species of Equisetum. In some irregular forms, either no definite apical cell is formed, or else it is early lost.

Under favorable circumstances the first antheridia are mature in from five to six weeks from the time the spores are sown, and the first archegonia about three weeks later. With care they can be kept alive for a comparatively long time. A quantity of prothallia raised from spores sown Aug. 31, 1884, were kept through the winter, growing but little for about two months, from the last of November. They were removed to a warm room in January and given abundant light and moisture. Growth was resumed and an abundance of antheridia and archegonia were produced. The greater part of the female prothallia produced young plants, but a few that were not fertilized were alive a full year from the time that the spores were sown. Most of the male prothallia had died a month or two previously. As the growth of the prothallium continues, new root-hairs are formed from the cells near its base; these arise sometimes from the margin, but more commonly from the lower surface of the cells; in exceptional cases from the upper surface.

Section II. The Sexual Organs.

The antheridia originate in the same way as the root-hairs. In the young prothallia they arise from the marginal cells; in the older ones, from the upper and lower surfaces as well. They begin as small prominences, usually close to the wall separating two adjacent cells. The protoplasm in the papilla is dense, especially in the middle, and contains small chlorophyll granules. A septum is then formed, by which the papilla, now the mother-cell of the antheridium, is shut off. This may be followed by a second wall parallel to the first so as to form a pedicel, but this is unusual (Pl. 4, fig. 29, P). Ordinarily, the first wall to be formed in the mother-cell is funnel-shaped, the base of the funnel being upward and the smaller end of the funnel in contact with the wall by which the mother-cell was first cut off (Pl. 4, fig. 16). Sometimes this wall is almost flat, or it may be convex downward but not reaching to the base of the antheridium. The second wall (Pl. 4, fig. 17) is nearly constant in form, dome-shaped or hemispherical and follows pretty closely the outline of the antheridium which has by this time grown rapidly and become nearly globular in shape. Finally, a third wall is formed in much the same way as the first, and like it subject to considerable variation (Pl. 4, fig. 18). The cell thus formed is the cap-cell and has its inner surface in contact with the upper part of the second wall. The antheridium now consists of four cells: an inner cell containing dense, finely granular protoplasm, but no chlorophyll; and three others which surround this, in which there is less protoplasm, but some small chlorophyll granules. Of the three outer cells the two lower are thus annular in form, except in cases where the first wall formed is not sufficiently convex to touch the basal wall of the antheridium, in which case the lower cell is discoid. About the time the cap-cell is formed, or sometimes before, the central cell begins to divide. The first wall (Pl. 4, fig. 20) is vertical, dividing the cell into nearly equal parts. This is followed by a second vertical wall (Pl. 4, fig. 23) at right angles to the first, so that when the antheridium is seen from above, the cells are arranged like quadrants of a circle. These undergo further divisions (Pl. 4, fig. 22) until there are about twenty cells. Their form is polyhedral, but the outer walls are rounded so that those on the outside of the mass appear almost globular. The protoplasm is highly refractive and finely granular and each cell is provided with a small but evident nucleus.

As soon as the sperm cells are fully grown the formation of the antherozoids begins. The protoplasm becomes somewhat more coarsely granular and the nucleus indistinct, though it does not actually disappear and can usually be demonstrated by staining. When it becomes more evident again, it is seen to have changed form and to have increased in size (Pl. 4, fig. 25). Instead of being globular, it is now crescent-shaped. It grows larger, becoming at the same time more curved (Pl. 4, fig. 26). This continues until it is soon evident that what was the nucleus of the cell is assuming the appearance of the complete antherozoid. Growth continues until the body of the antherozoid is in contact with the wall of the mother-cell, and lies coiled up within it, leaving, however, some remains of the protoplasm of the mother-cell lying between the coils. When the antherozoids are nearly mature, the walls of the sperm cells, which were hitherto in close connection, become partially absorbed leaving the separated sperm-cells free in the cavity of the antheridium. If an antheridium, in which the walls of the sperm-cells have undergone degradation, is placed in water, a very marked movement of the contents of the antheridium may sometimes be observed, due apparently to the absorption of water by the mucilaginous walls and their breaking down and dissolving through its action. Enough of the wall is left, however, to still enclose the antherozoid. By the time that they are ready to escape, the sperm-cells are so crowded as to press with sufficient force against the walls of the parietal cells to diminish their cavities very considerably (Pl. 4, fig. 24). These cells at the same time absorb much water, and if a ripe antheridium is placed in water, the tension resulting from the combined pressure of the cells within, and the turgidity of the parietal cells from the absorption of water, are sufficient to cause a rupture in the wall of the antheridium. This usually takes place between the two upper cells, the cap-cell being torn in the operation, but sometimes by a rent in the cap-cell only. As this occurs the lower parietal cells become much swollen and press inwards upon the mass of sperm-cells which are thus forced out through the opening. Their discharge is accompanied by a small amount of mucilaginous matter, evidently the remains of the disintegrated walls of the mother-cells. After lying quiescent for a few moments (Pl. 4, fig. 27) the vesicle in which the antherozoid is contained bursts and the antherozoid swims rapidly away with a twisting movement due to its spiral form. It consists of hyaline protoplasm, somewhat flattened and enlarged at the forward end, which sometimes shows two or three indistinct and close coils, the hinder part being composed of one or two open and complete turns of the spiral (Pl. 4, fig. 28). The cilia are numerous, being developed principally on the anterior coils but also extending back to the beginning of the larger ones. They are directed somewhat backward, as is plainly seen in treating the antherozoid with iodine, which causes it to become deeply stained and somewhat contracted and the cilia rigid and sharply defined. The end tapers to a point which sometimes is much prolonged. When the antherozoid has recently escaped, the movement of the cilia is so rapid as to render them almost invisible, but as it dies the movement becomes slower and is then seen to be undulatory, the movement seeming to begin at the point nearest the body and to proceed outward toward the tip of the cilium. This movement continues for some time after it ceases to be strong enough to propel the antherozoid.

It sometimes happens that the antherozoid does not become entirely free from the membrane of the cell in which it lies so that its movements are much hampered, the vibrations of the cilia being only sufficient to cause a rotation of the cell. It may subsequently free itself entirely or it may never escape completely. As the antherozoid swims away, there is seen attached to it a delicate vesicle which absorbs water and becomes much distended. Contained in this are several fine granules, the whole being the remains of the mother-cell of the antherozoid. This vesicle is sometimes attached to the pointed end of the antherozoid, sometimes it adheres for a considerable part of its length.

It occasionally happens that the antherozoids are imperfect in form, the hyaline protoplasm that constitutes the body not being sharply differentiated from the granular protoplasm of the central parts of the mother-cell. In such cases the antherozoid is club-shaped with the cilia at the pointed end, and the movement is less decidedly rotary.

The archegonia, like the antheridia and root-hairs, arise from the superficial cells of the prothallium and are, therefore, morphologically trichomes. Unlike the antheridia they are confined to a special part of the prothallium, being formed only on the lower surface of the cushion of tissue which lies at the bottom of the cleft in the front of the prothallium. If the earlier archegonia are not fertilized, new ones continue to form as long as the prothallium grows, the latter in such cases reaching a considerable size and bearing, sometimes, a hundred or more archegonia. In such cases, the cushion of tissue,