V. *On the Mode of Development of the Pollinium in* Asclepias Cornuti, *Decaisne.*

By THOMAS H. CORRY, *M.A., F.L.S., M.R.I.A., Shuttleworth and Foundation Scholar, Gonville and Caius College, and Assistant Curator of the University Herbarium, Cambridge.*

(Plate XVI.)

Read December 21st, 1882.

So far as I have been able to ascertain, no observer has fully investigated, in an adequate manner, the whole mode of formation of the pollen-mass, or *pollinium*, in this genus and in the natural order to which it belongs.

Hofmeister* and Schacht† alone have thrown some light upon its history in the early stages, with, however, somewhat contradictory results, while Schleiden's‡ account of it is incorrect in several respects and very fragmentary. Francis Bauer, Ehrenberg §, Robert Brown ||, Adolphe Brongniart¶, and the younger Reichenbach**, have all recorded details more or less exact concerning its structure, but principally in some of the later stages, when the flower is becoming rapidly mature.

In the very young anther, which has the form of a very slightly flattened spatula with a strongly convex dorsal surface, I was able to trace in transverse section that a single cell of the hypodermal row lying laterally but towards the internal side of each lobe of the anther, and containing granular protoplasm and a prominent nucleus, had undergone longitudinal division parallel to the long axis of the anther. This hypodermal cell in which division occurs constitutes the *archesporium* of Goebel††. The archesporium so divided consists, therefore, of an inner and an outer segment. The inner segment in each lobe is in reality the *primary mother cell of the pollen* (Pl. XVI. figs. 1 & 2, *p m c*). Each of the primary mother cells, as seen in transverse section, will be found, when viewed longitudinally, to correspond to a single longitudinal row of somewhat cubical cells, rather higher, however, than they are broad or long. Since only a single row of primary mother cells is formed in each lobe, the anther is bilocular from the beginning, and never at any period quadrilocular. The outer or more superficial segment of the primitive archesporial cell then becomes successively divided longitudinally in a tangential plane, in such a manner that in transverse section three layers of cells are now apparent. In these latter, radial, horizontal, and further tangential

* "Zur Entwickelungsgeschichte der *Zostera*," Bot. Zeit, 1852, No. 7. pp. 121–131, plate iii.

† Das Mikroskop, 2. Aufl. p. 166 *et seq.*

‡ Grundzüge der wissenschaftlichen Botanik, Leipsic, 1850.

§ Linnæa, iv. p. 94; also Trans. Roy. Acad. of Sciences, Berlin, Nov. 1831.

|| Linn. Trans. vol. xvi. p. 717 *et seq*, 1833.

¶ Ann. des Sci. Nat. Ser. i. vol. xxiv. pp. 263–279, pls. 13–14 B.

** De Pollinis Orchidearum Genesi ac Structura: Leipsic, 1852.

†† "Beiträge zur vergleichenden Entwickelungsgeschichte der Sporangien," Bot. Zeit. 1881.

divisions successively occur. The cell which constitutes the innermost of these three layers forms by radial division a peculiar epithelium of rectangular cells, investing on the inside the primary mother cell: this is the *tapetum* (Pl. XVI. figs. 2, 3, & 4, *tap*). The cells of the tapetum *proper* are reinforced by a corresponding layer on the external side of the anther-lobe, formed by means of a series of internal segments, cut off vertically from the cells of the parenchymatous ground tissue in that region (Pl. XVI. figs. 3–9, *tap**). In this manner a limiting membrane is formed, which entirely surrounds and invests on all sides the primary mother cell of the pollen.

The tapetal cells *proper* are thus derived from a portion of the primitive archesporium, while those cells by which the layer is completed towards the outer side of the anther, and which appear in transverse section to be longer and more oblong than the real tapetal cells, are not so derived. Each cell of the limiting membrane contains a prominent nucleus surrounded by granular protoplasm.

The primary mother cell of the pollen is, when viewed in transverse section, at first somewhat hexagonal in shape, single, and of relatively large size; for while the outer segment of the archesporial cell has continued to undergo division, no further division has taken place in the inner segment, which possesses very granular protoplasmic contents and a distinct nucleus (Pl. XVI. fig. 6, *m c*). Very soon, however, it may be found exhibiting two nuclei produced by the division of the single one; and this nuclear division is speedily followed by a division of the protoplasm into two portions, and formation of a longitudinal septum in a direction somewhat oblique to the surface of the anther. Each of these two cells now begins distinctly to elongate in a direction perpendicular to the surface of the anther; and by virtue of this elongation they become very sharply differentiated from the surrounding tissue. As the loculus expands by growth of its walls, this elongation becomes more and more pronounced. Immediately after this change has become fairly well marked, each of the two cells becomes divided by longitudinal division parallel to its longer axis; and this is followed by a transverse, *i. e.* horizontal division, also parallel to its longer axis, and therefore at right angles to the last. The cells, in consequence of this, take the form of short prisms, whose direction is inclined obliquely downwards from the surface (Pl. XVI. fig. 7). Of these prisms four appear in transverse section; and the free faces of the two lateral ones are somewhat rounded, so that the whole mass has now a slightly elliptic form. Further division of each of these prisms is then continued in both the longitudinal and horizontal planes parallel to the longer axis of the cell; the result of which is that the loculus of the anther now contains a large group of cells, comparatively narrow in proportion to their length, which appear in any transverse section as a single row, consisting of from eight to twelve or more cells. Seen in this view they are of extreme length, being six to ten times longer than they are broad, of large size, and rhomboidal or prismatic form, while they pursue a slightly oblique direction. Each possesses very granular protoplasmic contents, containing a large circular nucleus with a nucleolus, a large vacuole at each end, and a thin cellulose cell-wall. Their vertical or longitudinal walls form a common partition between these cells, on the one hand, and the cells of the tapetal limiting membrane, which closely surrounds them, on the other. Some of them may, at a slightly

later period, be found exhibiting two nuclei in close proximity to each other. In longitudinal sections they may be seen to lie in numerous obliquely directed rows, arranged one above the other.

But all the narrow prismatic cells contained in a loculus remain parallel and closely appressed together, in close and intimate connexion one with another, so that they cannot be separated one from the other without injury and rupture; in the relative thickness of their walls, moreover, they present no difference which would enable one to assert with any degree of certainty, when this stage has been reached, that any special aggregation of cells was the direct derivative of one of the segments of the primitive mother cell. The coherent tissue completely filling the cavity of the loculus, and bounded by the tapetal membrane, has throughout thoroughly the appearance of a cell-mass all of whose cells have been repeatedly bisected in succession by a series of divisions in two planes only.

At this stage of their development they correspond exactly to the contents of a single loculus in the young anther of *Zostera*, a genus of Monocotyledons whose mode of pollen-formation has been studied in a most masterly manner by Hofmeister *. Indeed the earlier stages of *Asclepias* and those of the last-named genus exhibit an extremely close correspondence with one another, the only marked difference between the two cases being that in *Zostera* the anther is quadrilocular. My observations up to this point accord at first with the single recorded observation of Schacht, rather than with those of Hofmeister, though they commence at a much earlier stage than was noticed by either of these writers. Hofmeister regards the pollen as derived, not from a *single* primitive mother cell, as seen in transverse section, but from a *group* of primitive mother cells. Being unable to trace his "group" of cells back any further, he regards Schacht's statement and figure † that in *Asclepias* only a *single* primary mother cell is formed in each anther-lobe as erroneous. The ultimate conclusion reached, if his observations on this point be accepted, is, of course, a multicellular archesporium; while my own results distinctly prove that it is unicellular, and that Schacht's statement really represents the true condition of the case. Apart from this, however, I have been able completely to confirm Hofmeister's researches, in so far as they relate to the pollen-development of *Asclepias* up to the stage at which the most obvious resemblance to that of *Zostera* is exhibited.

The cell-walls of the primary mother cell and its derivatives by division are thin, and always remain so, never being visibly thickened at any subsequent period. In this feature they resemble, so far as is known, only *Zostera* and its near ally *Naias* ‡, while they differ in it from the rest of Angiosperms generally.

At this point, however, the close analogy to, and correspondence with, the type of pollen-formation in *Zostera* ends. In the latter the granular protoplasmic contents

* *Loc. cit.* pp. 125–128, plate iii. figs. 4–15 *b*; also Neue Beiträge, ii. pp. 643–645; also Johannes Grönland, "Beiträge zur Kenntniss der *Zostera marina*," Bot. Zeit. 1851, pp. 185–192, and plate iv.

† Das Microskop, pl. iii. fig. 8; English edition, 1853, p. 105, fig. 21 *a*.

‡ W. Hofmeister, Neue Beiträge zur Kenntniss der Embryobildung der Phanerogamen, part ii. Monokotyledonen, pp. 642, 643, plate i. figs. 1–12, 1859.

of each of these long, narrow, prismatic cells becomes surrounded by an exceedingly thin and delicate but readily observable cellulose membrane, and forms an elongated club-shaped or fusiform pollen-grain, exhibiting therefore perhaps the most primitive type of pollen-formation known in the Phanerogams. In *Asclepias*, on the contrary, further division of each of the prismatic cells takes place, resulting ultimately in the formation of the special mother cells of the pollen in the following manner:—

Succeeding the division of the nucleus of each of the prismatic cells into two parts (which feature, it has been already mentioned, was observable in some of the cells), the protoplasmic contents now divide vertically into two at right angles to the long axis of the cell, and therefore in the direction of the breadth of the anther, and at right angles to all the previous planes of division; simultaneously the formation of a cell-wall takes place in the plane of division, *i. e.* parallel to the short sides of the prism. By means of this septum the prismatic cell becomes divided into two smaller segments of oblong form and equal size *. The conspicuous nucleus of each of these oblong cells then becomes further subdivided by vertical division at right angles to the length of the cell. This division is followed by division of the protoplasm and formation of a cellulose septum running in the same plane.

The walls formed by the two last series of divisions are, of course, only visible in transverse sections. In the upper narrower part of the anther-lobe, the number of longitudinal divisions which the primary mother cell undergoes is very small; and in consequence of this, fewer long narrow prismatic cells are visible in a transverse section through this part. Further, in this portion, sometimes only one of the two oblong cells formed by vertical division of the narrow prism divides again vertically; so that in transverse section three cells only are apparent in an oblique row, viz. one larger and two slightly smaller. The cells formed by these successive vertical divisions of the narrow prisms, each with a conspicuous nucleus, are at first cubical; and in longitudinal section they are seen to be disposed in numerous more or less horizontal rows one above another. Soon, however, they become spherical in form (Pl. XVI. fig. 8), owing to the rounding-off of their walls on all sides, though they still remain firmly adherent together, and at the points where they touch adjoining cells there still exists only a common partition-wall. They are the *special mother cells of the pollen* (*s m c*, fig. 8). At this period the mass of granular protoplasm contained in each of them cannot be discovered to have any special cellulose coat or wall deposited on it, but is surrounded only by the wall of the special mother cell.

Thus none of the cell-walls so far produced in the whole course of the development of the pollen undergo absorption, as is commonly the case, and as Reichenbach has shown to take place in the waxy pollinia of the Orchids (where the mother cells are broken down, and form a viscid pulp in which the tetrads lie), but persist †—the cells which

* The effect of all these divisions in the primary mother cells is merely to increase the number of mother cells from which the special mother cells are subsequently to be derived.

† Schleiden (*loc. cit.*) states that the walls of the primary mother cells *are* absorbed in *Asclepias*, and that at a very early period. Such, however, is not the case. In *Naias*, according to Hofmeister, they are resolved together with those of the special mother cells.

they bound, though now become rounded, adhering, as has just been mentioned, closely to one another. Their contents also never become, now or subsequently, set free, except on the rupture and bursting of the pollinium. By the unequal extension of the whole loculus the special mother cells contained in it now become polyhedral (Pl. XVI. fig. 9). They are formed by division of the single primitive mother cell in three planes, at right angles to each other; but the succession of the divisions is quite unique, and is not that usually characteristic of Dicotyledons.

That vertical wall of each of the limiting tapetal cells which is adjacent to the special mother cells now undergoes, at least in part, conversion into cutin, and in so doing increases considerably in volume; the chemical change is likewise accompanied by a change in colour from colourless to pale yellow. This change is followed successively by a like conversion of all the walls surrounding the special mother cells, which assume the same tint. On treating these walls with concentrated sulphuric acid a pale ruby-red colour is produced in all alike.

In this manner the pollinium is produced; and it can at this period be extracted from the anther-loculus in the form of a single, definite, compact, solid, coherent mass, of considerable size, with a deep golden-yellow colour and a waxy look externally. Its surface, which is perfectly smooth, and not in the least viscid, as it is stated to be by Thomé, presents the appearance of being divided in a reticulate manner into areolæ or hexagonal meshes, the apparent bulging of each areola being caused by the shape of the underlying cell filled with protoplasm (Pl. XVI. fig. 10).

Each pollinium contains all the adherent or firmly united special mother cells produced in one anther-loculus or pollen-sac. In transverse section it exhibits a cellular appearance and structure, consisting of three series or rows of cells * parallel to its sides, the middle series being more or less interrupted. These cells are enclosed by thick pale yellow-coloured semitransparent cell-walls, the cell-walls of those belonging to the two outer rows being continuous at certain points with, and surrounded by, a deep-golden-yellow, pellucid, cuticularized membrane, which has a resistant horny texture, cuts with great ease, and is derived from the change of those portions of the surfaces of the tapetal cell-membranes immediately adjacent to the special mother-cells. This membrane, forming an unbroken sheet, encloses and envelops completely every part of the entire, compact, solid, concrete mass of coherent special mother cells filling the anther-loculi, thus forming a general coat of considerable thickness. Brongniart (*loc. cit.* p. 267) and Schleiden ('Principles of Scientific Botany,' ed. 3, 1849, p. 356) both believed that this yellow investing membrane, which I have shown to be formed from the tapetum, was itself really of a cellular nature, *i. e.* composed of cells; for the former observer tells us that the areolate appearance is due "not to the underlying cellular mass, but to the cells themselves which constitute the membrane, and which are disposed after the fashion of epidermal cells;" while the latter regards it as formed "of the outermost layer of the special mother cells in which no pollen-grains are developed."

* In the oblique planes of the original prismatic mother cells, each row consists of four cells, not three. The relation of the descriptions framed from the two points of view, viz. perpendicular and oblique, is easily seen, however, on reference to the figures.

A very slight examination will easily afford convincing proof that both of these views are at variance with the facts.

No other observer, with the exception of Payer, has attempted to fathom the mode of origin of this membrane; and this observer held that the viscid gum forming the "appendages" or "processes" of the stigmatic corpusculum—which he believed was a liquid secreted by a gland (the corpusculum)—flowing in lateral channels or grooves, when it arrived at the anther-lobes on which the lateral grooves abut, penetrated into the interior of these lobes, and agglomerated the grains of pollen, uniting them afterwards through their whole extent (*vide* 'Traité d'Organogénie comparée de la Fleur,' vol. i. page 569). This same investigator did not examine the method of development of the pollinium by means of sections; or it would have been clearly evident to him that the investing membrane is formed and completed at a period long prior to the dehiscence of the walls of anther-loculi and consequent exposure of the pollinium, also that the only function performed by the corpuscular appendages, when the anther-loculi have opened by dehiscence, is that of firmly attaching the pollinia to their free ends, the substance of the two bodies, though externally united, being never confounded, but always remaining completely distinct, and moreover giving different reactions with micro-chemical reagents. Schacht believed (on what evidence he does not state) that the investing membrane was "of the nature of a secretion; and such is the view held by Prof. Oliver" *. But such is certainly not the case; and Dr. Maxwell T. Masters, in his article "Asclepiadeæ" †, hazards the statement that it is derived "from the separable inner lining of the anther-cell," probably referring to Brongniart's view above cited.

It is at once obvious that the pollen-grains subsequently formed in the special mother cells so enclosed cannot be dispersed in the ordinary way; nor can the pollinia fall out of the open anthers spontaneously, but remain seated there undisturbed, so that pollination without foreign aid is impossible; and, moreover, the flower is so very peculiarly contrived and adapted for the visits of insects in search of honey, that the pollinia are by their agency extracted and removed *en masse* from their place of origin, and applied by the same medium to a distant part of another flower.

Each special mother cell contains within its cuticularized wall a mass of protoplasmic contents, which have assumed a frothy condition owing to the presence of a number of vacuoles or oil-drops.

In this protoplasm spherical granules are to be met with in considerable numbers, and a distinct nucleus may be detected.

Very soon, however, by the aid of reagents, especially the aniline colour methyline-blue ‡, a delicate thin transparent hyaline membrane or wall (in fig. 11) is found to clothe and to have been formed all over its surface by the protoplasm, which has in some cases,

* 'Lessons in Elementary Botany,' p. 216.

† Lindley and Moore's 'Treasury of Botany.'

‡ I owe the suggestion that I should make use of this staining reagent to my friend Mr. W. Gardiner, who has employed it largely in his researches on "the Continuity of the Protoplasm in the Motile Organs of Leaves," Proceed. Camb. Phil. Soc. vol. iv. pt. v. pp. 266–271; also Quart. Journ. Mic. Sci. N. S. vol. xxii. no. lxxxviii. Oct. 1882, pp. 365, 366.

where the preparation has been treated with alcohol, slightly contracted away from this wall. The membrane, however, is exceedingly difficult to detect at this stage. This change takes place simultaneously in all the special mother cells. The newly formed cell, consisting of a very thin and delicate cellulose wall, closely applied to the internal side of the pale-yellow cuticularized wall of the special mother cell by which it is surrounded, but from which it may be made to contract away by means of alcohol, enclosing protoplasm loaded with vacuoles and rendered dark with minute granules and a nucleus, is the equivalent of the pollen-grain of other plants, and, to indicate this feature, is here designated by the same title.

The mode of formation of the pollen, then, in *Asclepias* is very different from that which is the characteristic and prevalent type in the majority of Dicotyledons or Monocotyledons, and, so far as our present knowledge extends, exhibits in its *entire* details a perfectly unique, isolated, and peculiar case of development. The earlier stages are only to be found paralleled in the single instance of *Zostera*, which affords either the most primitive or most aberrant type of pollen-formation known. The later stages find no precise parallel in the entire range of the vegetable kingdom. This is the more remarkable, since another member of the Asclepiadeæ, viz. *Periploca græca*, exhibits, according to Reichenbach, a type of pollen-formation exactly comparable to that of the Orchid genera *Neottia* and *Epipactis* *.

Observations on the mode of development of the pollen in *Asclepias* are fraught with extreme difficulty; and its history can only be revealed by careful study of extremely thin transverse and longitudinal sections.

In many of the pollen-grains, especially when the flower was fully mature, I was able, by careful observation, and by having recourse to osmic acid of one per cent. strength, and to staining reagents—such, *e. g.*, as hæmatoxylon, Grenicher's carmine, and some of the aniline colours, viz. gentian-violet, saffranin, and methyl-green, to the latter of which a few drops of solution of acetic acid, one per cent. strength, had been previously added —to detect not a single nucleus only, but two nuclei, one of which was invariably larger than the other.

The smaller nucleus was often found lying close to the cell-wall; and in these cases I believe that, surrounded by a small quantity of protoplasm, it is cut off from the rest of the grain by a cellulose wall, although I was not always able to show this satisfactorily. This discovery is especially of interest in connexion with the recent researches of Elfving † and Strasburger ‡, since further confirmation of their observations has thereby been obtained in the pollen-grains of plants which they did not investigate, and in

* Dr. S. H. Vines suggests that probably in *Asclepias* and likewise in *Zostera* the phase of the special mother cells, as it occurs in other plants, is omitted, and hence we get the departure from the normal types. On this view, what I have termed the special mother cells are really the last series of the mother cells produced by repeated division of the single primary one.

† Jenaische Zeitschrift für Naturwissenschaft, 1879, part i., and Quarterly Journal of Microscopical Science, N. S. vol. xx. 1880, pp. 19–35.

‡ "Ueber Befruchtung und Zelltheilung," Jenaische Zeitschrift für Naturwissenschaft, Bd. xi.; (neue Folge, Bd. iv.) 1877, Heft iv. page 450.

which the very presence of nuclei of any kind whatever had not been previously detected.

I consider the smaller nucleus of the Asclepiad pollen-grain to be the representative of what Elfving terms the "vegetative nucleus," and others have designated as the "passive nucleus," which nucleus is genetically the last remnant of the male prothallium of a vascular Cryptogam type, such as *Equisetum*, while the larger nucleus, equivalent to the "active nucleus," is genetically the last remnant of the antheridium of such a type.

In shape the pollen-grains are always nearly spherical, though usually slightly angular, so as to be really irregularly polyhedral (Pl. XVI. fig. 11); their membrane is, as previously stated, single, very thin at first, ultimately becoming thicker, smooth, hyaline, and transparent, and formed of unchanged cellulose. There is at this stage no appearance whatever of the tubes which are afterwards produced.

Strasburger, in his most recently published work *, mentions the fact that he has observed the presence of only a single coat in the pollen-grains of the following plants —*Gaura biennis*, L., *Clarkia elegans*, Dougl., *Senecio vulgaris*, L., *Cobæa scandens*, Cav., *Allium*, L., *Naias major*? †, and Orchids; and the same phenomenon was first described by Fritszche ‡, and has long been known to occur in *Zostera*, L., while *Asclepias Cornuti*, Decaisne, must now be added to this interesting list of exceptions to what is otherwise the universal rule among phanerogamous plants.

The ultimate changes and fate which the tapetal membrane undergoes appear to be as follows:—The cells composing it which lie on the outer side of the anther divide each by means of a vertical tangential wall, parallel to the original tangential walls of the cell, so that the membrane becomes two cells broad on this side. Those tangential walls which are furthest from the pollinium in that row of limiting cells which is next the cavity of the loculus, together with the adjacent portions of the radial walls of these cells, become broken down and disintegrated. The tangential walls, on the other hand, which are nearest the pollinium, together with the internal portions of the said radial walls, persist for some time, forming a continuous membrane, surrounded by a layer of small cells. These latter, on the outer side of the anther, are segments from those cells which completed the tapetum *proper* on this aspect, and were themselves derived from the parenchyma, while on the inner side of the anther they constitute simply that row of cells which were formed immediately external to the tapetum *proper*, at the same time that it was differentiated, and which have persisted. Such is the condition immediately prior to the opening of the two anther-loculi to expose the pollinia. The mode in which the dehiscence of the anther takes place will be fully described in a subsequent paper, the result being that the whole of the

* Ueber den Bau und das Wachsthum der Zellhäute: Jena, 1882.

† Hofmeister (Neue Beiträge, 1859, part ii.) describes the existence of "a very thin but distinct extine" in the pollen-grains of this species; but in his figure (pl. i. fig. 11) he represents this extine as extending with the intine along the pollen-tube produced from the grain! It is therefore highly probable that Strasburger's observation is more accurate.

‡ "Ueber den Pollen," Mémoire présenté à l'Académie Impériale de St. Pétersbourg, iii. 1837.

tapetal membrane, together with a large portion of the substance of the anther, is broken down and disintegrated. The comparatively late period to which the tapetal membrane persists in *Asclepias* is a noteworthy point; in other Dicotyledons it usually breaks down, in consequence of the growth of the pollen-grains, *immediately after* the absorption of the walls of their special mother cells, while in the group of Monocotyledons it becomes either diffluent or absorbed at an early period, and the mother cells themselves in consequence float freely about in the loculus quite separate from one another.

Asclepias therefore appears to present at first sight a closer analogy in the period of resolution of its tapetum to the Monocotyledons than to the group of which it is a member, since the pollinium, which consists, among other parts, of the persistent though altered walls of the mother cells, comes ultimately to lie in the cavity formed by its resolution. Inasmuch, however, as the period of its resolution is coincident with that of the dehiscence of the anther-loculus, I believe that it more closely approaches the type of the group to which it really belongs than that of the Monocotyledons, though it differs from both, so far as we know of them at present.

DESCRIPTION OF THE PLATE.

PLATE XVI.

Development of the Pollinium.

Fig. 1. Very early stage of one half of an anther, seen in transverse section, showing division of the single archesporial cell into inner and outer segments, the former, which alone is shaded, constituting the primary mother cell of the pollen, *p m c*; *z*, the outer segment; *epi*, the epidermis covering the anther; *par*, ground-tissue of the anther. The fibro-vascular bundle of the connective is not yet visible.

2. A slightly later stage, also seen in transverse section. The primary mother cell, *p m c* (alone shaded), has now longitudinally divided into two mother cells. The outer segment, *z*, of the previous stage, has divided tangentially into three rows of cells, and these, again, vertically. The innermost row of these adjacent to the primary mother cell is the tapetum *proper*, *tap*.

3. A later stage. The two mother cells of the previous stage have now divided each in a longitudinal plane, so that four mother cells, *m c*, are seen; *tap*, tapetum *proper*; *tap**, segments cut off from the surrounding parenchyma, by which the tapetum is completed on the external side. The hypodermal layer of the previous stage, formed from *z*, has now become divided into two by longitudinal division.

4. Later still. The mother cells, *m c*, have become more numerous by longitudinal division of each of the four seen in the previous stage into two; and they have at the same time become longer. At this stage the contents of the loculus very closely resemble those of *Zostera* immediately before the formation of the pollen-grains. The other parts as before. The fibro-vascular bundle of the connective, *v*, has become visible a little before this stage.

5. Longitudinal section of an anther-lobe when the stage represented in the last figure (fig. 4) has been reached. The parts are lettered as in the previous figures.

Fig. 6. A stage still later. The mother cells, *m c*, of the last stage have each divided longitudinally into two in a plane at right angles to their length, so that they now form two rows; the other parts are lettered as before; *con*, the connective tissue.

7. Still more advanced. Each mother cell has again divided longitudinally into two in a plane at right angles to its length, so that from each mother cell a row of four cubical cells has been derived; these are the special mother cells of the pollen, *s m c*. The other parts are denoted by the same lettering as in the previous figures.

8. Portion of an anther seen in transverse section at a later period, the parts named as in the last figure. The special mother cells have now become rounded, but are still connected with one another. Considerable changes have taken place in the cells immediately external to those, *tap*, *tap**, which form together the limiting tapetal membrane; the walls of the former are much compressed, and the cell-cavity in some cases is almost obliterated.

9. The same at a more advanced stage still. The tapetal cells, *tap**, have become divided to form two layers; the wall of each of the tapetal cells, *tap*, *tap**, which is adjacent to the special mother cells has become in part cuticularized; and this transformed portion forms a continuous sheet of a pale yellow colour, *p w*, enclosing the whole of the special mother cells, *s m c*, the cell-walls of which are still unchanged. This sheet forms the external coat of the pollinium; *l*, compressed remnants of the rows of cells external to the tapetal membrane in earlier stages; *q*, the row of cells originally internal to the single row of tapetal cells proper which has persisted.

10. Transverse section of a nearly adult pollinium removed from the anther-loculus: *p w*, external cutin coat of the pollinium; *s m c*, special mother cells, now become polyhedral, whose walls, *s m w*, have likewise become cuticularized.

11. Fully adult pollinium, seen in transverse section. The contents of each of the special mother cells have contracted slightly from its cutin wall, and formed over the whole surface a thin, delicate, cellulose membrane, *in* ("intine"), thus becoming converted into a pollen-grain. The section has been treated with absolute alcohol, so that the contents have contracted away from the newly formed wall, *in*, which is then rendered evident by staining with methyline blue. Several of the pollen-grains are seen exhibiting two nuclei.

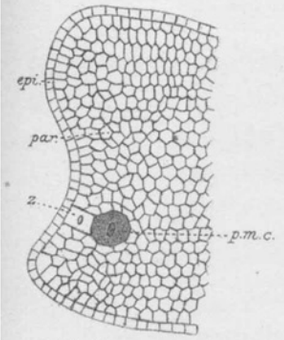

Fig. 1.

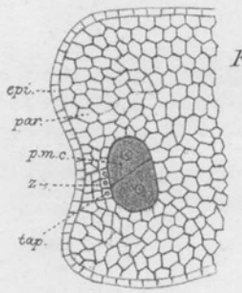

Fig. 2.

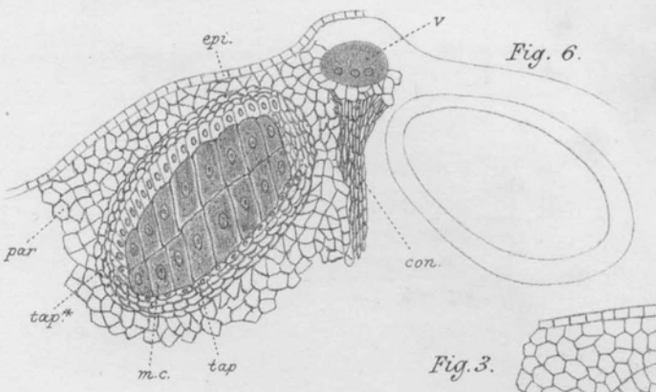

Fig. 6.

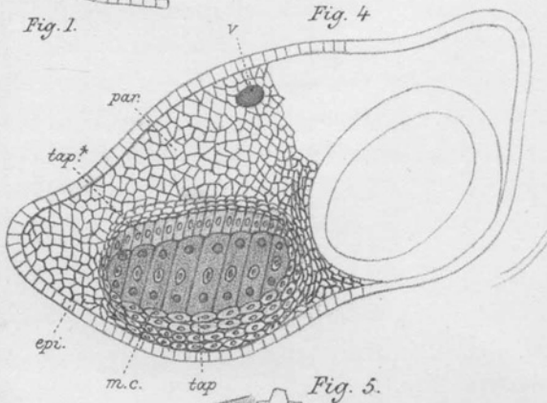

Fig. 4

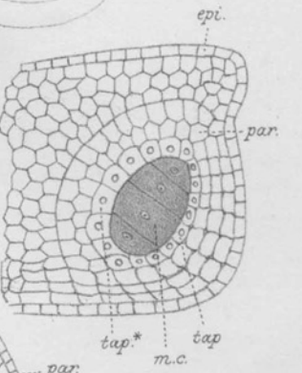

Fig. 3.

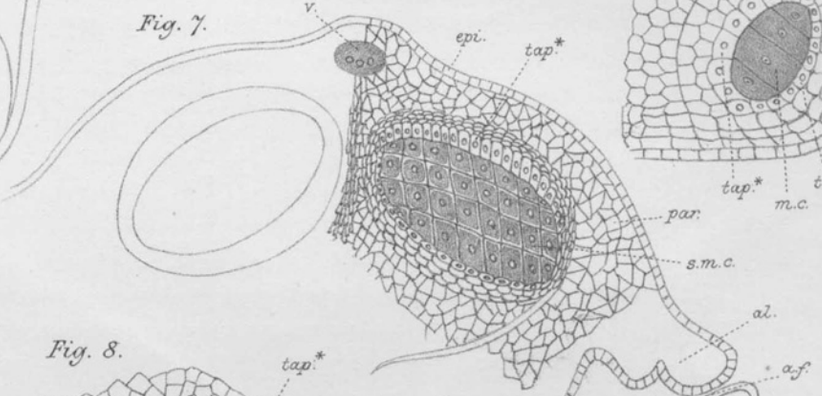

Fig. 7.

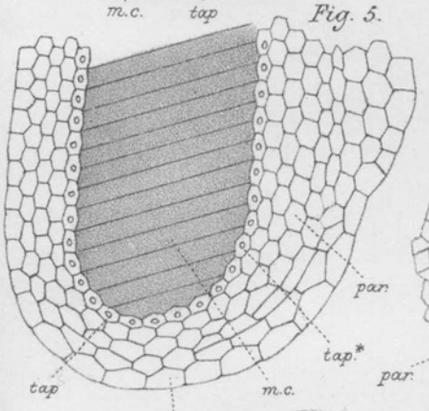

Fig. 5.

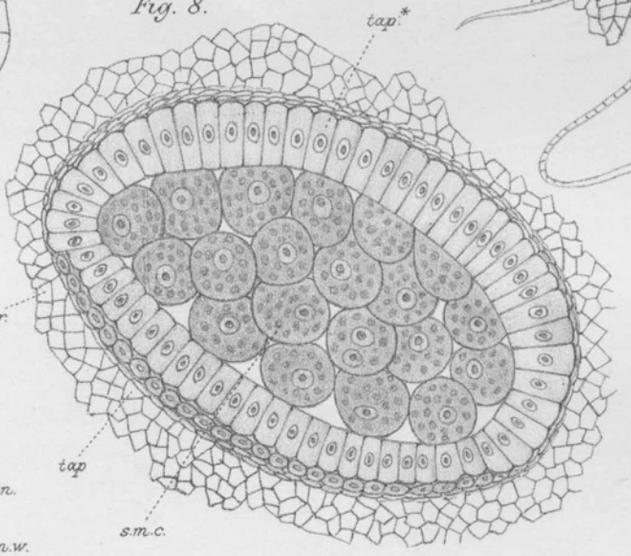

Fig. 8.

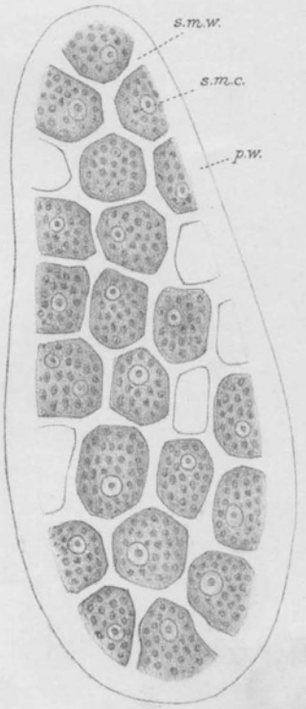

Fig. 10.

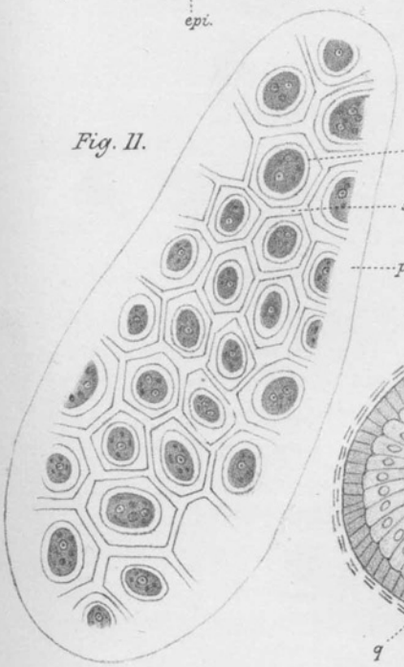

Fig. II.

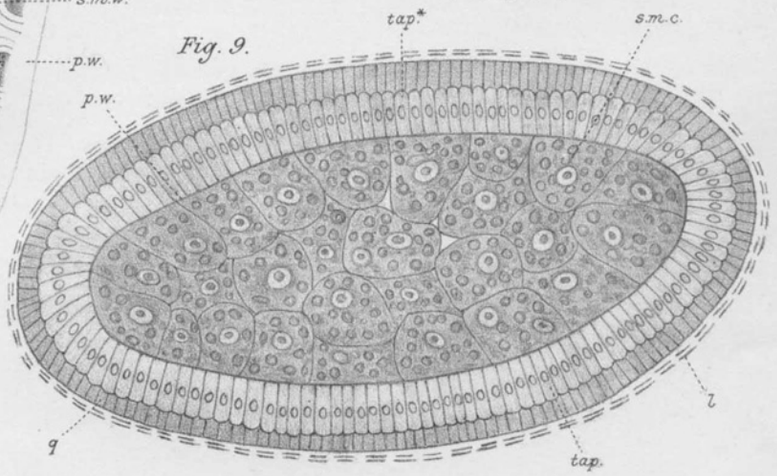

Fig. 9.