TRANSACTIONS.

I.—Sphærostoma ovale (Conostoma ovale et intermedium, Williamson), a Lower Carboniferous Ovule from Pettycur, Fifeshire, Scotland.

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[Plates I. and II.]

CONTENTS.

I. INTRODUCTION.

The Palæozoic ovule, to which the generic name "Sphærostoma" is now given, was originally described by WILLIAMSON* in 1877 under the names *Conostoma ovale* and *Conostoma intermedium*. He referred sections of different individuals to different species owing to the imperfect condition of the material then available, but expressed the view that *Conostoma intermedium* "may possibly be a state of *Conostoma ovale*." The new material has rendered this interpretation a certainty. With respect to the reference of this ovule to the genus *Conostoma*, WILLIAMSON again expresses some hesitation, merely stating that "it appears to be of the same generic type." The genus *Conostoma* was established for an Upper Carboniferous ovule which WILLIAMSON designated *Conostoma oblongum*. This species, together with a new one, *Conostoma anglo-germanicum*, have recently been fully described,† and they show a greater

* WILLIAMSON, Eighth Memoir, *Phil. Trans.*, 1877, pp. 244 and 245.

† OLIVER and SALISBURY, "On the Structure and Affinities of the Palæozoic Seeds of the Conostoma Group," *Annals of Botany*, vol. xxv. No. xcvii., Jan. 11.

divergence from the type under consideration than was formerly suspected—in fact, as the authors of the above treatise suggest, the resemblances of *Sphærostoma* with *Lagenostoma* are greater than with *Conostoma*.* Hence one has been obliged to found a new form-genus for the geologically older type, and the term *Sphærostoma* was chosen because of the rounded form of the free part of the nucellus within which lies the pollen chamber. Before proceeding to describe the ovule, I wish to express my indebtedness to Professor I. Bayley Balfour, who presented me with the large block of Burntisland rock from which all but two of the slides used in the present paper have been obtained.

One of these is a slide most generously put at my disposal by Dr D. H. Scott, F.R.S. In the course of the paper it will be shown how much is derived from this slide which, as a section of a Pettycur petrifaction, cannot, I think, be surpassed for beauty of workmanship and interest of content. I take this opportunity of expressing my gratitude to Dr Scott for this loan. The other slide is a fine radial section of the ovule, cut by Dr Gordon, a photograph of which Dr Gordon has been kind enough to send me (*vide* Pl. II. fig. 8).

Sphærostoma ovale has so far only been recorded from Pettycur deposits of the Calciferous Sandstone series of Scotland. In these it occurs at rare intervals, but generally, when found, is fairly abundant. About fifty have been sectioned from the above-mentioned block, but owing to the impossibility of orienting such small objects, a large proportion are cut obliquely. They are always closely associated with the vegetative organs of *Heterangium Grievii*, and hence the ovule has long been suspected of being the megasporangial apparatus of this most fern-like of all would-be Pteridosperms.

Deferring the evidence which I consider places this surmise upon a surer basis, it will be best to describe the ovule in detail.

II. General Features of the Organisation of the Ovule.

(Text-figs. 1 and 2.)

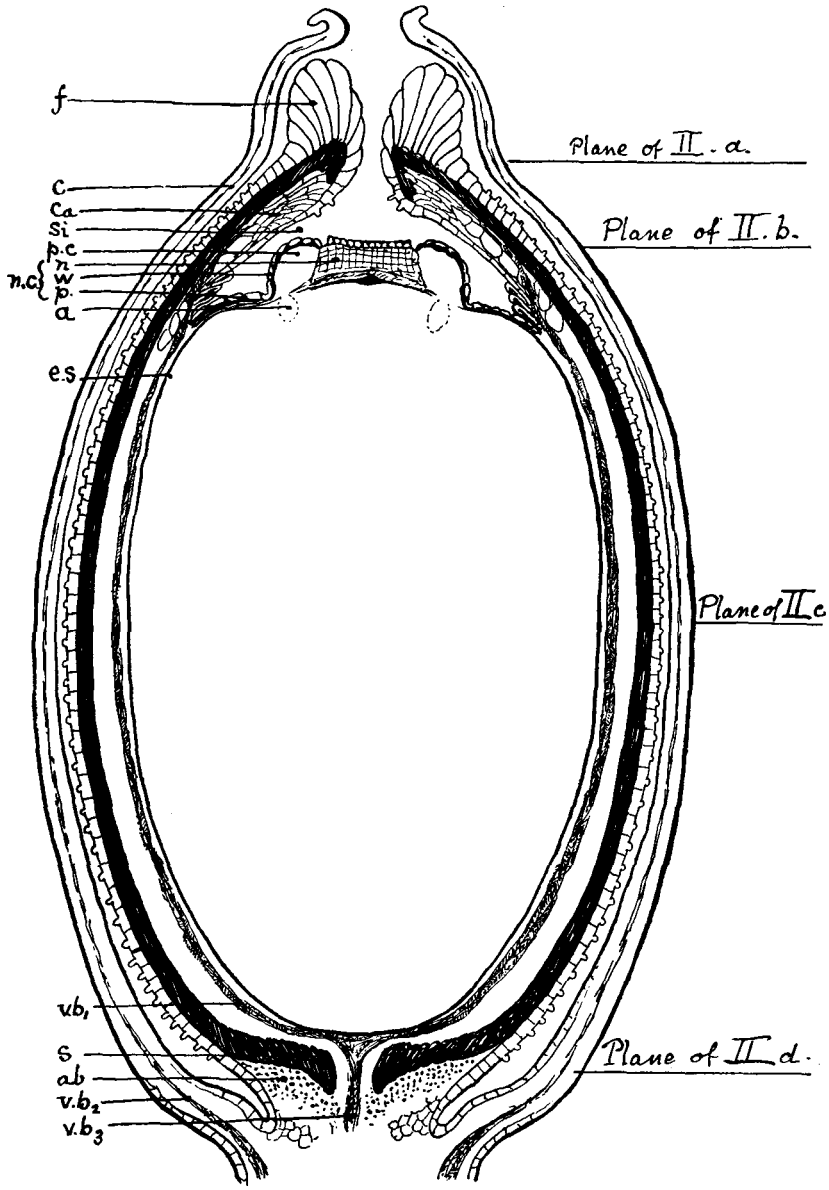
In its complete state the ovule consists of two parts—a central body representing the nucellus and inner integument, and an enveloping cupule or outer integument.

For convenience, the inner part will often be referred to as the ovule, for it is most common to find it bereft of its cupule. A reference to text-fig. 1, which represents a restoration of a median longitudinal section of both parts, will readily show their relationship to one another, especially if this restoration be compared with that in text-fig. 2, *c*.

Without the cupule the ovule is 3·5 mm. in length and about 2·2 mm. at its widest part. At first sight its most striking feature is the series of crests forming the so-called "frill" around the micropyle (text-fig. 1, *f*.).

* Oliver and Salisbury, *loc. cit.*, p. 38.

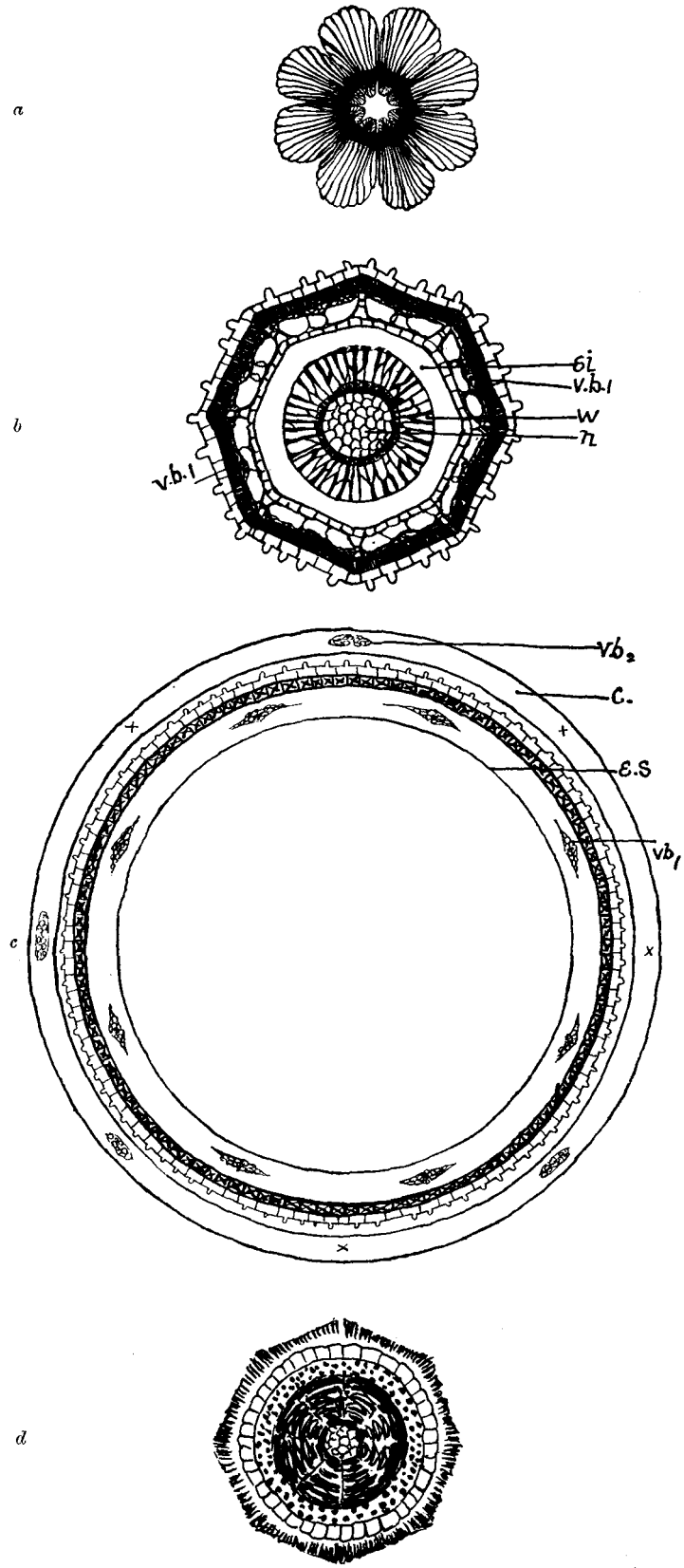
Within the sinus (*si.*), surrounded by the free part of the inner integument or "canopy" (*ca.*), may be seen the nucellar cap (*n.c.*) or free part of the nucellus. This



TEXT-FIG. 1.—Diagrammatic drawing of a median longitudinal section of *Sphærostoma ovale*, still surrounded by the cupule. The description is given in the text.

a. = archegonium.
ab. = abscission layer.
c. = cupule.
ca. = canopy.
e.s. = embryo sac.
f. = frill.
n. = central column surrounded by the pollen chamber.
n.c. = nucellar cap.
p. = plinth.
p.c. = pollen chamber.
s. = sclerotic hypoderm.
si. = sinus.
$v.b._1$ = a vascular strand of the cupule.
$v.b._2$ = a vascular strand of the inner integument.
$v.b._3$ = central supply strand to the ovule.
w. = wall of the pollen chamber.

consists of the plinth (*p.*) which is relatively flat, and the central nearly hemispherical dome or "lagenostome" which rises abruptly from the centre of the plinth.



TEXT-FIG. 2, *a*, *b*, *c*, *d*.—Diagrammatic representations of sections across the ovule in the planes indicated in text-fig. 1.

a, shows the eight crests outside, and the eight within, the micropyle. The cupule is omitted.

b, shows the extreme apex of the nucellus (column = *n*, and roof = *w*, of the pollen chamber) standing in the centre of the sinus, *si.*, surrounded by the canopy or free part of the inner integument. Traces of the vascular bundles of the inner integument can be detected as at $v.b._1$. The outer epidermis of the integument is excretory at this level. The section is octagonal in form. The cupule is omitted.

c, shows the widest part of the ovule still surrounded by the cupule, *c*. The vascular bundles of both integuments are inserted as far as they have been observed, $v.b._1$ and $v.b._2$. The epidermis of the inner integument is still secretory at this level, and the whole section is exactly circular, *e.s.* = embryo sac.

d, shows a cross-section of the pedicel of the ovule with the single supply bundle in the centre. Around the bundle is the base of the sclerotic sheath. Intervening between this and the epidermis is the layer regarded as the abscission layer. This abuts on the epidermis, which is no longer secretory in this plane. The section is represented as including the outline of a transverse section of the base of the ovule to show that the transverse section of the ovule is again octagonal at its base. This drawing is made partly from a section through a fallen ovule, and therefore the cupule is omitted (*cf.* Pl. II. fig. 11).

The "lagenostome" is differentiated in a manner which has so far been undescribed for any ovule. We find, it is true, a central column of nucellar tissue (*n.*), surrounded by a lysigenic annular cavity—the pollen chamber—as in *Lagenostoma* and several other genera of Palæozoic ovules, but *Sphærostoma* differs in the definite manner in which the roof of the pollen chamber closes the aperture made at dehiscence. As far as we know, the aperture was only adventitiously blocked, or the closure was due to growth phenomena in other seeds, but in *Sphærostoma* the pollen chamber is always found tightly closed by means of what appears to be an elastically acting mechanism.

Beneath the lagenostome and plinth lies the large embryo sac (*e.s.*) encased in a framework of eight vascular bundles (text-figs. 1 and 2, *c* (*vide b*, 1)). These spring at the base from a single delicate strand which passes up the pedicel. In this particular *Sphærostoma* differs from the ovules included in Messrs Oliver and Salisbury's groups Conostomeæ and Physostomeæ, as they are supplied by a ring of bundles.

Accompanying the vascular bundles are large, thin-walled cells, which probably formed an aqueous storage tissue. They are, however, rarely preserved in the fossil except in the canopy. The wall of the ovule is strengthened by a layer of hypodermal fibres which ceases at the base and is here supplemented by deeper-lying fibres closely investing the single vascular strand of the pedicel, thus making the sheath complete when the ovule falls (Pl. II. fig. 8).

Below the sheath in the pedicel may be seen (text-figs. 1 (*ab.*) and 2, *d*) a region where rupture normally took place, suggesting that the cupule was left on the plant when the ovule was shed.

Two series of four transverse sections through single ovules enable one to state definitely that the ovule is exactly circular in section in its median region, but at the extreme base and in the region of the canopy the transverse section gradually assumes an increasingly octagonal form (*cf.* text-fig. 2, *c*, with text-fig. 2, *a*, *b*, and *d*; *vide* also Pl. II. figs. 10 and 11).

The outermost part of the micropyle is formed by eight lobes of the canopy, which bear each a large crest or lobe of the frill on the outside and a smaller one within. Text-fig. 2, *a*, is a restoration of a transverse section through this region. It is based on a section in slide 253, which is figured in part on Pl. I. (*vide* fig. 3). The individual epidermal cells constituting the crest enlarge and become hexagonal in section distally. They may be regarded as representing a special development of the epidermal cells which are characteristically developed in all the Lagenostomales, constituting the structure called the "blow-off" by Professor Oliver.

Sphærostoma is most often found without the cupule, hence this organ is only represented in one of the transverse sections in text-fig. 2 (*vide* 2, *c*).

III. Details of Structure.

1. *The Outer Integument or Cupule.*

The cupule is probably a youth organ which did not accompany the ovule when it separated from the parent plant. In some sections it is represented by fragments, but seems to owe this preservation to the fact that parts had adhered to the slimy surface of the inner integument. The tissue is far more uniform than that of the inner integument, and the vascular bundles more rounded in transverse section.

The preservation does not admit of a decision as to the relative position of the phloëm and xylem in each strand, nor have I been able to ascertain the number of the latter, but the distribution of those which can be made out is such as to suggest there are eight, which is also the number of the strands in the inner integument (text-fig. 2, *c*, *v.b.*).

It is possible that, at the apex, the cupule was lobed like that of *Lagenostoma Lomaxii*,* but most of the transverse sections passing through it show it as a continuous sheath (Pl. I. fig. 5).

In the specimen shown in fig. 2 of the same plate, there are at the base of the cupule a few longitudinally disposed fibres of cylindrical form, which are similar in character and position to those in the neighbouring petioles of *Heterangium Grievii*. With the exception of these and the tracheides of the vascular strands, the only tissue elements preserved in the cupule are parenchymatous.

2. *The Inner Integument.*

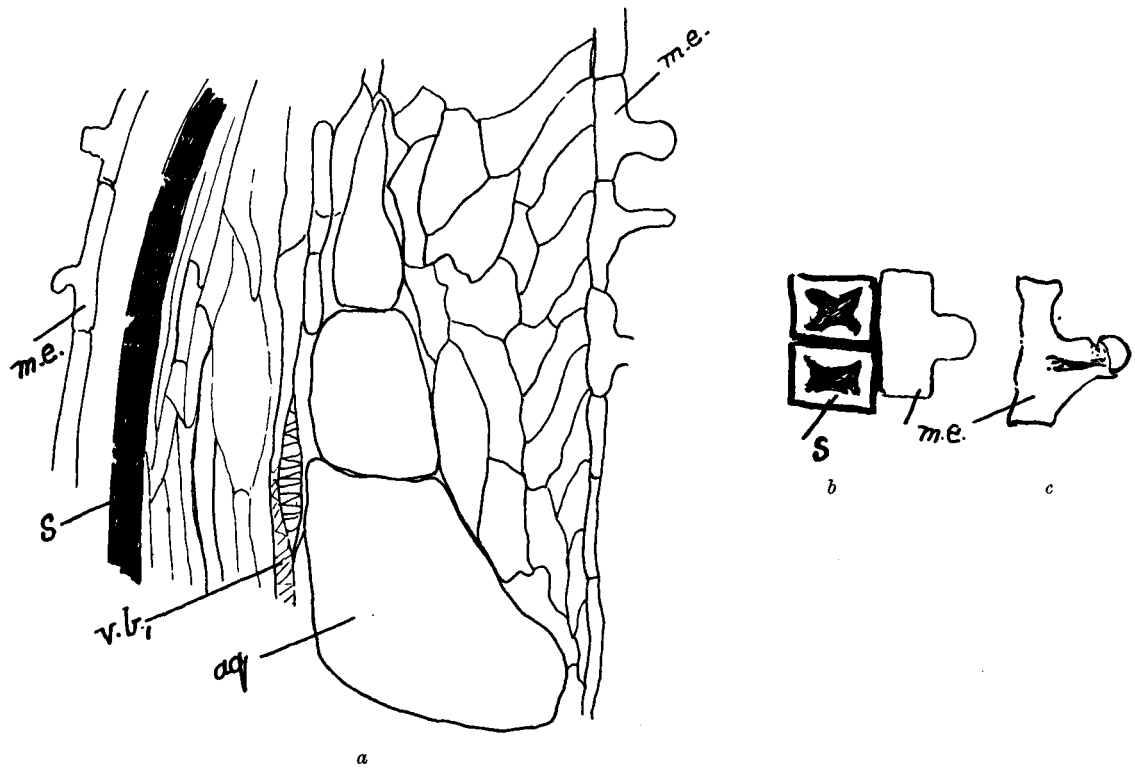
The inner integument is only free from the nucellus in the upper part, where it corresponds in many respects with the so-called canopy of *Lagenostoma*. In the basal three-fourths of the ovule there is no distinct layer of demarcation between the nucellus and the peripheral vascular part commonly regarded as the part of the integument adherent to the nucellus. The whole of the ovule, irrespective of the cupule, is surrounded by a remarkably well-differentiated epidermis, which eventually becomes secretory for the most part. On the exposed surface of the inner integument, from the pedicel up to the margin of the micropyle, the epidermal cells are longitudinally disposed, brick-shaped bodies. Each cell bears peripherally a small papilla, which later increases in size and eventually ruptures near the apex—a hemispherical cap being pushed aside by the emerging mucilage as in *Lagenostoma Lomaxii*† (text-fig. 3, *a*, *b*, and *c*).

Near the micropyle the epidermal cells change their character. Outside, they form the structure to which I have referred as the "frill." It is seen in Pl. I. fig. 1. There are several sections which demonstrate that the "frill" is not continuous. In

* Oliver and Scott, "On the Structure of the Palæozoic seed *Lagenostoma Lomaxii*," *Trans. Roy. Soc.* (*Lond.*), 1904 (p. 217).

† Oliver and Scott, *loc. cit.*, pl. x. fig. 28 B.

the tangential section shown in fig. 4 we see two lobes which in the specimen can be shown to be distinct. In an obliquely transverse section of the micropyle (fig. 3), which passes through the "frill" on one side, the lobe cut through is seen to be distinct from its neighbours, and its outline corresponds at its base with one of the small crests within the micropyle. Thus it can be stated that the micropyle at its extreme apex was surrounded by eight lobes of the canopy, each crowned by an outer



TEXT-FIG. 3, *a*.—A radial section of that part of the inner integument which lies immediately above the plane of text-fig. 2, *b*, as plotted on text-fig. 1.

aq. = ? aqueous tissue of the canopy ; *s*. = sclerotic sheath ; $v.b._1$ = the extreme apex of one of the eight vascular bundles that pass up the inner integument.

b and *c*.—Figures to show transverse sections of young and old epidermal secretory cells, *m.c.*

b = a young intact cell with papilla. Also two hypodermal fibres from the sclerotic sheath, *s*.

c = an epidermal secretory cell showing liberation of hemispherical cap.

and an inner epidermal crest, of which the outer was the larger. Lower down the micropyle, the epidermis contracts into a uniform layer over the eight sides of the octagonal sinus. Just as the sinus widens out below the micropyle, the epidermis again becomes papillate and secretory. The papillæ are numerous and basiscopic. Below the surface formed by the secretory tissue lies a mass of parenchyma, behind which terminates the tracheal system (text-fig. 3, *a*, $v.b._1$).

The epidermis on a level with the pollen chamber again becomes smooth and apparently non-secretory. Below its surface we find the large rounded cells accompanying the vascular bundles throughout their entire length (text-fig. 3, *aq*.). They

are fairly frequently preserved in the canopy, but are rarely seen in the periphery of the embryo sac (slide 292, 1).

The eight regions respectively supplied by the eight vascular bundles correspond with those of the crests. Lower down on the same radii on which the vascular bundles lie, but at the very base of the sinus, between the canopy and the plinth, the epidermis shows some curious tongue-shaped cells which have pitted thick walls and generally dark brown contents (Pl. I. figs. 1 and 6, *h.*). They differ in form and appearance from the papillate mucilage cells, which are thin-walled and of a pale yellow colour.

The eight vascular strands approximate closely to these cells, often obviously bending towards them and then retreating again above. There are probably eight groups rather than a continuous ring of these cells, since occasionally the radial plane of section does not pass through any. Such sections escape also the bundles.

The form of these cells and their close approximation to the vascular strands suggest an excretory function, but their different mode of preservation suggests that the excretum was non-mucilaginous and hence possibly merely water.

Let us turn now to the hypodermal structure of the exposed surface of the inner integument. One sees in a well-preserved specimen a uniform single layer of fibres approximately square in transverse section (text-fig. 3, *b*) and several times longer than broad.

The layer appears to be less regular in some ovules—some growth in length and displacement probably taking place among the fibres.

This sheath forms the only special mechanical tissue the ovule possesses, and must have given toughness to the coat although it was unable to afford it any great degree of rigidity. In several cases the ovule has been indented, or even folded like a collapsed bladder, before fossilisation. The sheath is not continued beneath the epidermis of the pedicel, but is completed by deeper-lying sclerotic cells forming a transverse plate, which is only perforated to allow of the entry of the single vascular strand into the ovule (text-fig. 1, *s.*). This plate forms the base of the great majority of the ovules examined (Pl. II. figs. 8 and 11).

3. *The Abscission Layer.*

Immediately outside the sheath, as it leaves the epidermis, the tissue in the pedicel shows signs of breaking down. Remains of this layer have been demonstrated in a transverse section of an ovule which had probably been naturally severed from the parent plant (Pl. II. fig. 11, *ab.*). The tissue is seen also in the radial section of the ovule in slide 387 (Pl. II. fig. 9, *ab.*) which shows the layer of separation still *in situ.* In this case the degeneration of the tissue has not yet encroached on the epidermis, which is still regular and continuous.

If this be the true interpretation of this region, it indicates that the ovule normally fell out of the cupule, leaving that upon the parent plant. Thus it would seem probable that such of the ovules in Dr SCOTT'S slide 387 as are still surrounded by a cupule had

not become at any rate normally detached. I will refer to the significance of this deduction later when discussing the grounds of reference of this ovule to *Heterangium Grievii* (*cf.* p. 12).

4. *Vascular Supply of the Ovule.*

It has already been demonstrated by an earlier reference to figs. 9 and 11 that a single delicate strand of tracheides enters the pedicel. This gives rise to eight strands which terminate behind the parenchyma abutting on the papillate epidermis near the micropyle (text-figs. 1, 2, and 3, *a*, $v.b._2$ and $v.b._3$). The constituent tracheides have their thickening disposed in a manner approximately spiral, and are of small dimensions. In several cases the strand of xylem is obviously mesarch.

At the extreme base of the embryo sac the tracheides lie almost contiguous to one another, forming a sheath of which the constituent elements gradually diverge into the eight strands. Very frequently one or two or even three of these strands may be duplicated, *i.e.* respectively represented by two smaller, more or less laterally connected strands. In such cases we may meet with from nine to eleven bundles, but the position and size of the branching strands indicate their relationship to one another.

5. *The Nucellus and Embryo Sac.*

The nucellus exhibits features of great interest. The lower part is entirely occupied by the embryo sac, which never shows much contained tissue. In all the material investigated the embryo sac had already expanded until it almost abuts on the vascular strands, only a few layers of much flattened cells intervening (text-figs. 1 and 2, *c*, and Pl. I. figs. 1, 5, and 6 (*e.s.*)).

In the upper part the nucellus is represented by the plinth (text-fig. 1, *p.*, and Pl. I. and II., figs. 1, 7, and 8), and by the dome-like lagenostome already referred to as consisting of a central column, surrounded by the annular pollen chamber. The plinth and dome are covered with a well-characterised but apparently non-secretory epidermis.

In surface view the epidermis of the plinth is seen to consist of isodiametric hexagonal cells (fig. 7), and thus offers a sharp contrast to that forming the pollen chamber wall (fig. 10). The embryo sac has in all cases flattened or absorbed all the cells beneath the epidermis of the plinth. It also abuts on the base of the dome, but no trace of a membrane has been found beneath the excavated pollen chamber—a fact which probably indicates that the archegonia were formed on that part of the prothallus which forms the floor of the annular pollen chamber. In this position traces of them are occasionally found. Under the central column only a thin pellicle can be demonstrated, and that only occasionally. In the exact centre a thickened mass is sometimes seen, but it is possibly due to the destruction of the overlying cells and not to any special formation on the apex of the spore, as is rather suggested by its appearance.

Directing our attention to the dome, we are very fortunately able to trace to some extent the development of the pollen chamber.

6. *The Structure of the Pollen Chamber.*

In the older ovules there is a clear broad space seen in radial section on either side of the central column and roofed over by a single layer of epidermal cells. In longitudinal sections it will be observed that the column consists of regularly arranged tiers of cells. In this latter feature *Sphærostoma* resembles *Lagenostoma*.

In transverse section the form of dome and column is found to be circular.

In the nearly radial section of a young ovule, shown in Pl. I. figs. 1 and 2, the tissue in the annular region, to be later replaced by the pollen chamber, is seen to be undergoing lysigenic degeneration. A difference between the younger and older domes is seen also in the character of their epidermis. In the younger, the epidermis is composed of thin-walled cells with flat peripheral walls. In the older, the epidermis over the pollen chamber has entirely changed its character, while that over the column has remained unchanged. Each cell over the pollen chamber has its walls sharply differentiated, *i.e.* the outer and basal walls remain thin, and all the four walls vertical to the surface are thickened in such a way that they appear of an opaque dark brown colour, while the outer and basal walls are quite transparent. Thus the whole roof or wall of the pollen chamber has much the appearance of a multiseriate annulus of such a sporange as that of *Senftenbergia*. The resemblance is heightened by the obliquity of the end walls of the cells (Pl. II. figs. 7 and 10).

The circumscissile dehiscene, by means of which presumably the pollen grains entered the chamber, is effected in a very definite manner. The central column becomes severed entirely from the roof of the pollen chamber along a line just within the margin of the epidermis of the column.

Thus marginal epidermal cells of the column remain attached to the roof-cells (*vide* Pl. I. fig. 6). There is no loss of surface cells, the dehiscence is schizogenic, and in some respects the whole apparatus is curiously reminiscent of the peristome in the sporogonium of *Polytrichum*, which opens around a persistent, circular diaphragm. The mechanism, however, of the closure in the two cases must have been very different, and the resemblance between them merely adventitious.

There are tetrahedral spores found in the pollen chambers of seeds in slides 217, 241, 270·1, and 304·4. Occasionally they occur still arranged as tetrads. These spores, which are presumably the pollen grains, are from 27–29μ in their widest dimension, and thus much smaller than those * attributed to *Lyginodendron*, which are from 50–70μ in diameter.

Traces of a species of microsynangium do, however, occur with the *Sphærostoma*, and its spores resemble in size and form those in the pollen chamber. Description of

* Kidston, "On the Microsporangia of the Pteridospermeæ," *Trans. Roy. Soc.*, 1906, vol. cxcviii. p. 423.

this body must be deferred until another occasion. So also must the description of some curious bodies which often accompany the ungerminated grains in the pollen chamber.

No satisfactory specimen has yet come to hand in which the pollen chamber is open. One of Williamson's slides, preserved in his collection at the British Museum at South Kensington, and figured in his Eighth Memoir,* suggests this condition, but the appearance may be due to injury before fossilisation, as only one side is open.

7. *The Processes assumed to occur during the Opening and Closing of the Pollen Chamber.*

That the important function of securing and nursing the pollen was correlated with a series of progressive changes cannot be doubted. When the excavation of the pollen chamber was complete, the epidermis of the nucellar cap underwent circumscissile dehiscence along a line just within the periphery of the persistent column of tissue in the centre. The roof of the chamber was thus made to overlap the column when it returned, after dehiscence, to its original position (*cf.* figs. 1 = state before dehiscence and 6 = state after closure). In fact, the relation of the margin of the column to the roof of the pollen chamber resembles that of the rebate of a box to its lid. Hence the downward curvature of the roof is prevented from being so excessive as to obliterate the pollen chamber.

The growth in length of the roof-cells and the deposition of thickening on their vertical longitudinal walls would necessarily have set up a centrifugal strain tending to bring about the circumscissile dehiscence. This was further aided by the mucilaginous degeneration of the subjacent tissue.

After dehiscence the roof would straighten elastically and thus an annular stomium would be formed. Passage to the lower part of the sinus would be at least partially blocked because the liberated margin of the roof of the pollen chamber would nearly abut on the basiscopic papillæ around the upper part of the sinus. Pollen would thus be prevented from straying into the sinus.

The mucilage glands would meanwhile have come into play, thus completing the preparation for pollen. If grains were now to enter the micropyle they would be caught in the freshly exuded watery mucilage and be drawn with it into the pollen chamber. The entry must have been aided by the subsequent downward curvature of the roof of the chamber.

This return to the former position may have been due to an increase in their turgescence on the part of the roof-cells. This is suggested by the domed form of the peripheral cell-walls of the epidermis covering the older pollen chambers. These peripheral walls offer a marked contrast not only to the thick vertical cell-walls, but even in this respect to the basal walls, which, although thin and transparent, are flat.

* WILLIAMSON, *loc. cit.*, pl. xii. fig. 83.

The tongue-shaped cells already described, which otherwise seem so enigmatic, receive their interpretation if they were the source of the water required for the closure of the pollen chamber.

Summary of Stages.

1. Growth in length and special thickening of the roof-cells of the pollen chamber. Concomitant lysigenic degeneration of the subjacent tissue leading to the excavation of the pollen chamber.

2. Circumscissile dehiscence and consequent formation of a stomium by the upward movement of the free margin of the roof.

3. The retention of the pollen grains on the downward curvature of the roof, which thus returns again to its original position and closes the pollen chamber.

8. *Diagnosis of Sphærostoma, n.g.*

The ovule resembles those of the *Lagenostoma* series in its general organisation, *e.g.* the nucellus is surrounded by an inner integument of radial symmetry and apparently multiple origin, and also by an outer integument or cupule. The inner integument is only free around the pollen chamber, but the cupule is free from the base upwards. Both integuments have a multiple vascular supply—the strands of the inner integument taking their origin from the single central bundle of the pedicel. *Sphærostoma* is distinguished from the ovules of the *Lagenostoma* series by the following characters:—

1. The whorl of epidermal crests around the micropyle.

2. The nearly hemispherical form of the lagenostome which rises from a somewhat flat plinth.

3. A pollen chamber relatively wider than that of *Lagenostoma*.

4. The persistence of the epidermis over the central column of the lagenostome.

5. A skeletal structure of less robust charater, with an indication of aqueous tissue in the region of the canopy.

Dimensions.—The ovule is a little under 3·5 mm. in length without the cupule and 2·2 mm. at its widest part.

Horizon and Locality.—*Sphærostoma ovale* has so far only been recorded from the Calciferous Sandstone Series of the Lower Carboniferous rocks of Pettycur, Fifeshire, Scotland.

IV. The Grounds for the Provisional Reference of the Ovule Sphærostoma ovale to Heterangium Grievii.

As already mentioned, this ovule has long been surmised to be the megasporangial apparatus of *Heterangium Grievii*. The association between the two is of a very constant and striking nature. For example, there are some score of plants

of *Heterangium Grievii* in the same block with the ovules here described. Many of the plants are exceptionally well developed, and three are giving off adventitious roots. In the course of three years, during which time I have had hundreds of slides from this block under observation, I have not been able to detect a trace of any other plant the nature of whose sporangia is not known, except two undescribed stems apparently belonging to immature plants or other species of *Heterangium.*

Hence the fact that numerous ovules lie among the petioles and rooted stems of *Heterangium Grievii* is undoubtedly suggestive of actual reference.

The argument from association is supplemented by internal evidence. The ovule shows an unmistakable resemblance to *Lagenostoma*, which is acknowledged to be the type of ovule borne by *Lyginodendron.*

But *Lyginodendron*, both in the external morphology of its vegetative organs and in their anatomy has long been regarded as showing close affinity with *Heterangium.* The resemblance between their megasporangial members would be similarly great if *Sphærostoma ovale* belonged to *Heterangium.* Such differences as do obtain between the two ovules are such as would be expected between an older and a later type. In *Sphærostoma* the canopy shows less complete integration (*i.e.* the crests are free) and the mechanical tissue is less developed than in *Lagenostoma.* The method of dehiscence of the nucellus is more fern-like and the pollen grains are smaller. These differences are all consistent with the view that we are dealing with a more primitive ovule in *Sphærostoma* than in *Lagenostoma*, but with one in which *the ground-plan of the Lyginodendron ovule had been laid down.*

This evidence from comparative considerations receives important corroboration from certain features of Dr SCOTT's slide, C.N., 387, already referred to.

Many of the ovules are still surrounded with an intact cupule and hence, if the interpretation of the tissue in the pedicel as an abscission layer be correct, must have been still attached to the frond, or part of the plant on which they grew.

To investigate this matter the three longitudinal sections which were nearest the median plane were examined, with the following results :—

a was found to be exactly radial at its base;

b was radial at the micropyle but slightly tangential at the base;

c was in the plane which passed through the plinth but just escaped the pollen chamber. At the base it also just escapes the pedicel of the ovule.

Sections *a*, *b*, and *c* were found in each case to be accompanied by a petiole in the expected position and cut in a plane exactly corresponding to that of the ovule. Thus *a* shows a radially cut petiole, *b* shows one in which the vascular bundle is just touched upon, and *c* shows one with only the cortex occurring. For the case referred to as *a*, reference should be made to Pl. II. fig. 9.

As already pointed out in an earlier part of the paper, most of the ovules show no cupule. Such ovules in no single case, although they are far more frequently met with, show similarly disposed petioles of *Heterangium.*

To conclude, the evidence in support of the reference of *Sphærostoma ovale* to *Heterangium Grievii* may be summed up as follows:—

1. Association.
2. Comparative morphology, *i.e.* resemblance to *Lagenostoma*.
3. Strong suggestions of continuity in the only three cases in which sections have been obtained in a suitable plane, of ovules judged by independent evidence to have been still attached to the parent plant.

In conclusion, I wish to bear testimony to the steady and able help I have had from my laboratory attendant, C. H. WELLS, who has made all but two of the preparations used in this paper.

V. EXPLANATION OF PLATES.

S. = Scott Collection.
R.H.C. = Royal Holloway College Collection.

Lettering of Figures.

a. = archegonium.
ab. = abscission layer.
c. = cupule.
ca. = canopy.
e.s. = embryo sac.
f. = frill.
h. = tongue-shaped cells at the base of sinus.
m. = micropyle.
m.e. = mucilage epidermis (Prof. OLIVER'S "blow-off").
n. = persistent column of nucellar tissue.
p. = plinth.
p.c. = pollen chamber.
pet. = petiole.
s. = sclerotic hypodermal sheath.
si. = sinus.
$v.b._1$ = vascular bundle of inner integument.
$v.b._2$ = vascular bundle of cupule.
$v.b._3$ = vascular bundle of the pedicel of the ovule.
w. = wall of the pollen chamber.

PLATE I. FIGS. 1–6.

FIG. 1. Radial section of the upper part of a young specimen of *Sphærostoma ovale* enclosed in a cupule (*c.*). The lagenostome shows an early phase in the development of the pollen chamber (*i.e.* excavation incomplete). The tongue-like cells (*h.*) are formed, but the mucilage papillæ are not yet developed on the inner surface of the canopy. Those on the outer surface are not yet dehisced (*m.e.*). The embryo sac (*e.s.*) shows traces of an archegonium (*a.*). Supporting the crests are seen horn-like prolongations of the sclerotic sheath (*s.*).

S., C.N., 387 × 70 × $\frac{3}{4}$.

FIG. 2. Drawing from a photograph of the whole section of a young ovule, part of which is represented in fig. 1.

S., C.N., 387 × about 30 × $\frac{3}{4}$.

FIG. 3. Part of an obliquely transverse section through the micropyle in the plane plotted on fig. 1. It shows the corresponding crests on the inner and outer surfaces. At this level the sclerotic sheath is interrupted between the pairs of crests.

R.H.C., C.N., 253 × about 70 × $\frac{3}{4}$.

FIG. 4. A tangential section through the upper part of a similar ovule, showing two crests of the "frill."

S., C.N., 387 × about 80 × ¾.

FIG. 5. Drawing from a photograph of part of a transverse section of an ovule still enclosed in the cupule. The vascular bundles of cupule and inner integument can be seen, also the embryo sac and mucilage epidermis (*m.e.*).

S., C.N., 387 × about 60 × ¾.

FIG. 6. A slightly tangential section of the upper part of an ovule, showing a pollen chamber after dehiscence. The column (*n.*) is well preserved, and shows the ledge referred to in the text as a "rebate."

R.H.C., C.N., 241 × 70 × ¾.

PLATE II. FIGS. 7–11.

FIG. 7. Drawing from a photograph of an oblique section through an ovule to show the distribution of the eight vascular bundles of the inner integument. This section also exhibits the surface cells of the plinth and column, and the contrast they afford to those of the pollen chamber wall (*w.*).

R.H.C., C.N., 287 × about 70 × ¾.

FIG. 8. A radial section through the ovule, enlarged from a negative kindly lent for the purposes of this paper by Dr GORDON. The tissue (*c.*) outside the inner integument is probably cupular.

× about 27 × ¾.

FIG. 9. Drawing from a radial section of a somewhat crushed young ovule. At + the epidermis of the radially cut petiole of *Heterangium Grievii* is wrinkled and appears continuous with the tissue of the cupule, but the cell-walls are not well preserved. The cupule is obviously continuous with the ovule by its epidermal cells on the left of the section. The pedicel bundle can be traced down the centre and is seen to give rise to the inner integument bundles. The section suggests that the ovule grew terminally on the petiole.

S., C.N., 387 × 62.

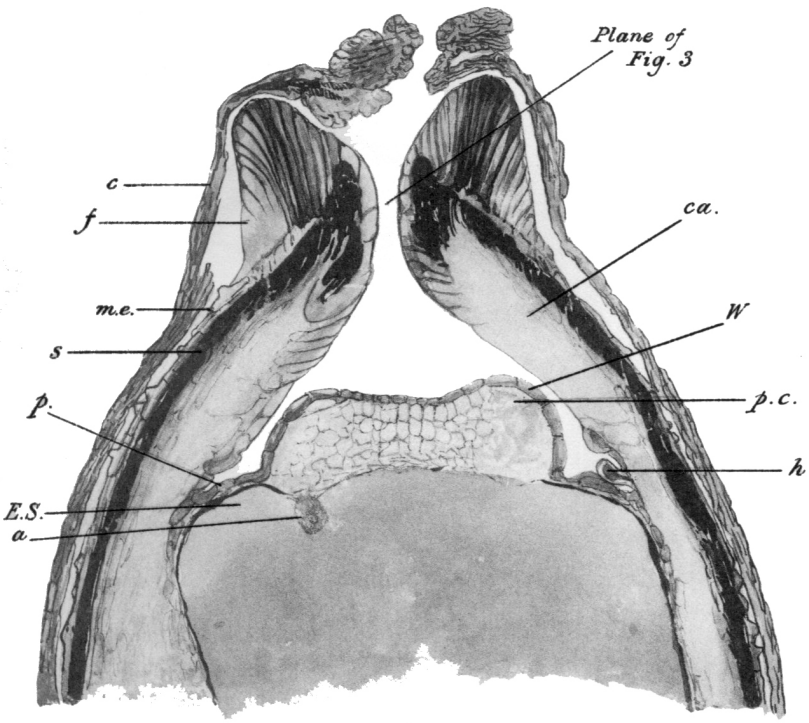
FIG. 10. Part of a transverse section at the level of the roof of the pollen chamber, showing it in surface view. The integument is octagonal, and the vascular bundles are well developed at this level.

R.H.C., C.N., 290·3 × about 70 × ¾.

FIG. 11. A transverse, slightly oblique section across the base of an ovule after it has fallen. In the centre can be seen the delicate strand of tracheides which perforate the basal sheath of sclerotic cells. The disorganised cells immediately outside this sheath to the left may possibly represent remains of the abscission layer shown in fig. 9 (from an ovule probably still attached to a petiole). On the right may be seen the sclerotic sheath cut tangentially and clearly indicating the octagonal form of the base of the ovule. The mucilage epidermis is shown in a condition very characteristic of the shed ovule. The cells have become so swollen that they are detached from the hypoderm and form a pale-yellow, halo-like area all round the section.

R.H.C., C.N., 246 × 87 × ¾.

BENSON: SPHÆROSTOMA OVALE.



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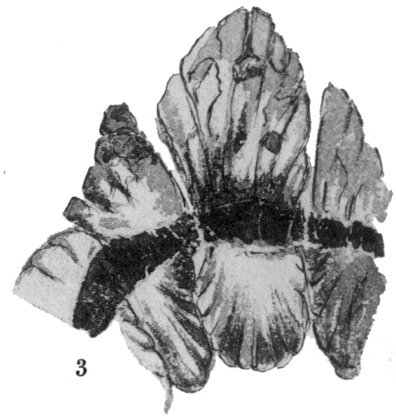

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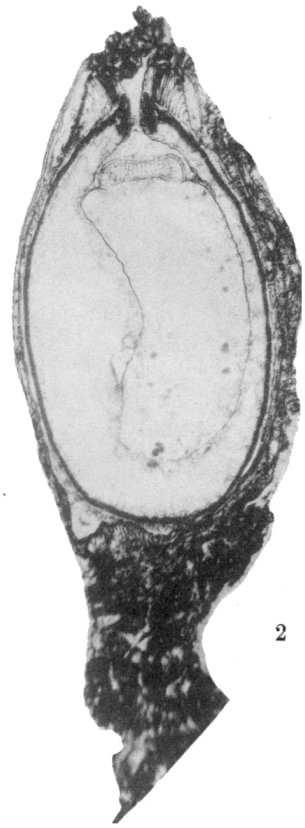

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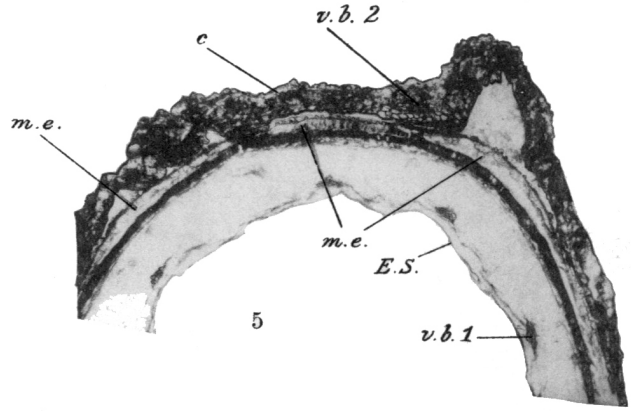

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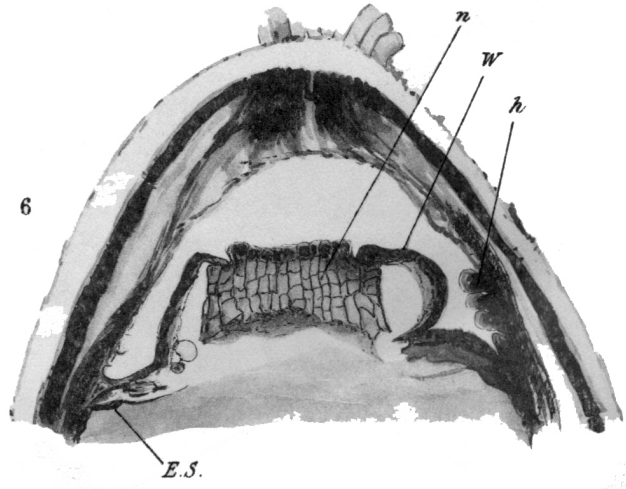

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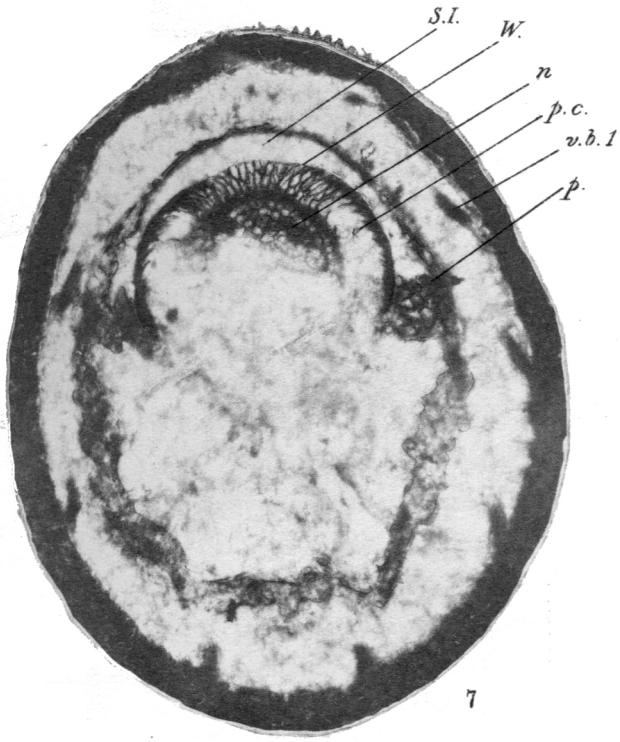
M'Farlane & Erskine, Lith., Edin.

BENSON: SPHÆROSTOMA OVALE.



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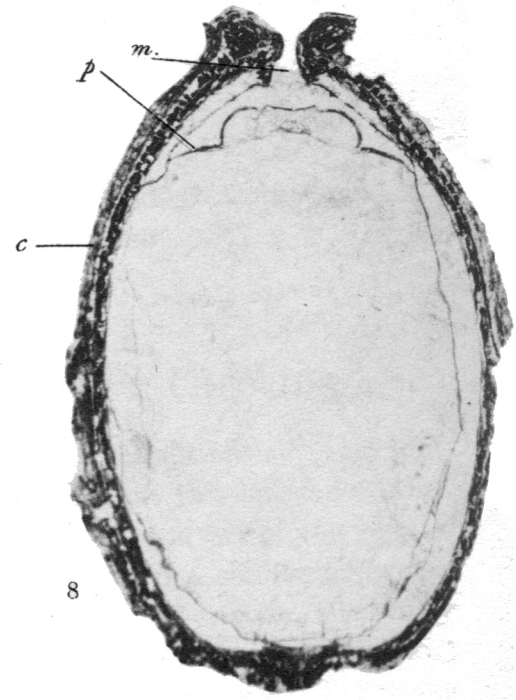

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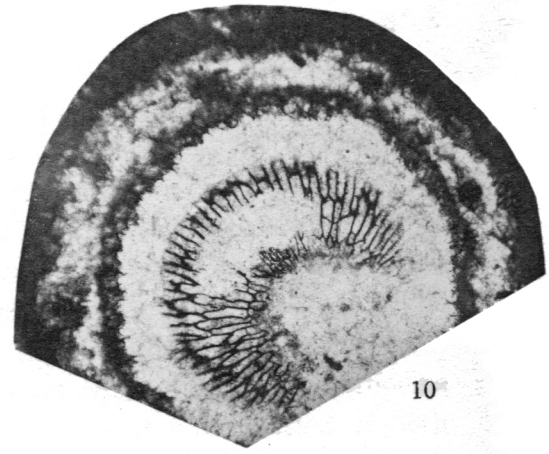

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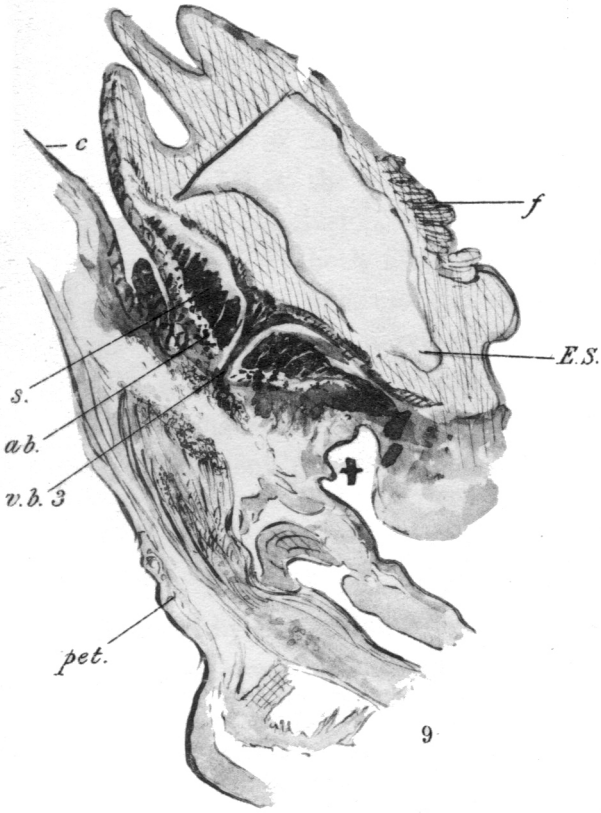

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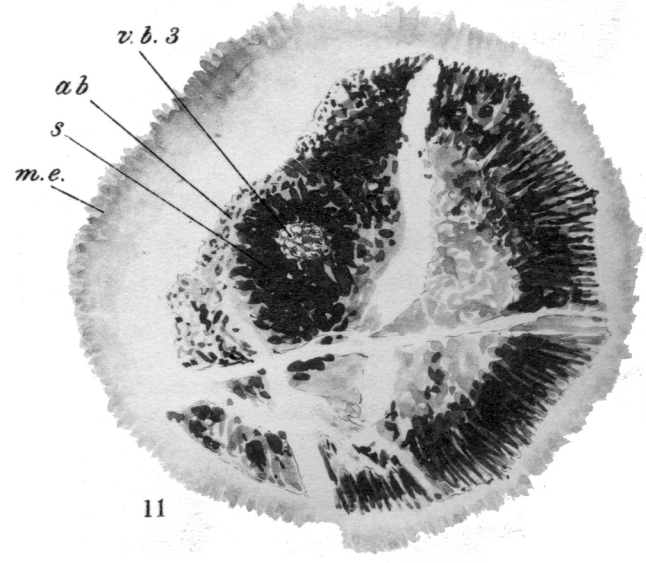

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M'Farlane & Erskine, Lith., Edin.