PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Miadesmia membranacea, Bertrand; a New Palaeozoic Lycopod with a Seed-Like Structure

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Phil. Trans. R. Soc. Lond. B 1908 **199**, 409-425
doi: 10.1098/rstb.1908.0010

X. Miadesmia membranacea, *Bertrand; a New Palæozoic Lycopod with a Seed-like Structure.*

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Communicated by D. H. Scott, *F.R.S.*

(Received April 26,—Read June 13, 1907.)

[Plates 33–37.]

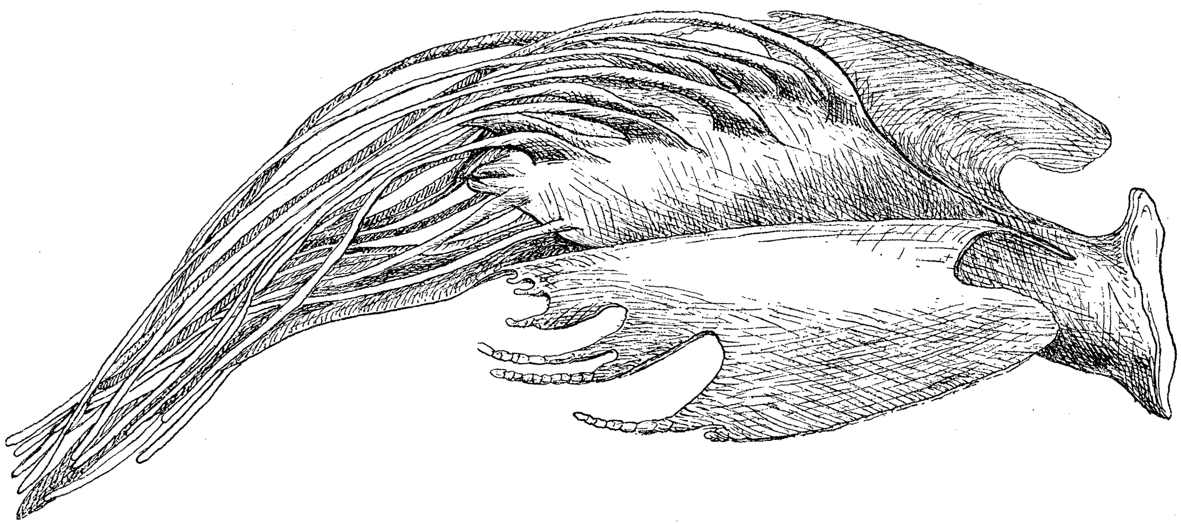
Professor Bertrand's account of this interesting little Lycopod ("Sur une nouvelle Centradesmide," Assoc. Franç. pour l'Avancement des Sciences, 1894), is based on English material. He found fragments of leaves and twigs, associated with those of *Lepidodendron Harcourtii*, in preparations from the nodules of the Gannister beds at Hough Hill, sent him by Mr. Lomax. In describing these for the first time, he gave them the name of *Miadesmia membranacea*. The leaves bear a large ligule of a definite form and characteristic structure and insertion. They are provided also with a thin margin. This feature is noted by Professor Bertrand as exceedingly useful in the diagnosis of Miadesmia. The sporophylls have only recently been obtained, and it is with these the present paper is chiefly concerned. The megasporophylls were first recognised by Dr. Scott in a series* of sections passing tangentially through a single large Lepidocarpon megasporophyll. These new structures proved to be exceptionally interesting, on account of their advanced seed-like character. Not only are the sporangia equipped with an integument and physiological stigma, but the single megaspore is retained in the sporange and resembles the embryo-sac of a Phanerogam in a very marked degree. I simultaneously received from Mr. Lomax a number of excellent preparations, and it is due to him to record that he recognised the seed-like nature of the new bodies. An investigation of older preparations in the R.H.C. Collection revealed several microsporophylls and foliage leaves of Miadesmia.

Professor Weiss, moreover, has kindly lent from the Manchester Collection several slides which are rich in Miadesmia. Dr. Scott has contributed not only a large number of invaluable preparations, but has helped most fundamentally in all the more difficult problems connected with the work. To Dr. Scott, then, I offer my best thanks, and also to Professors Oliver and Weiss.

The number of megasporophylls under investigation now amounts to over sixty, and in one case a young cone appears in longitudinal section (fig. 28, Plate 36).

* This series (*cc* 7*a*–*k*, O.) was prepared by Mr. Lomax, and sent to Professor Oliver, who handed them over to Dr. Scott, and later, with Professor Oliver's sanction, they were given to me.

The microsporophylls, which bear a similar ligule, are found associated with the megasporophylls and vegetative organs.



Further facts have been obtained relating to the foliage leaves which are present in great quantities in many of the slides. Sometimes they occur in their natural position on the axis, and these twigs occur in longitudinal and transverse section.

No roots nor organs of attachment have been identified.

An investigation of a series of sections from the same block as Professor BERTRAND's in the Williamson Collection at the British Museum (380 *a–h*), and of the various new sections already referred to, shows the general organisation of Miadesmia to be as follows.

The plant was exceedingly minute, its stem slender and without any trace of skeletal or secondary tissue. It is the first herbaceous Palæozoic Lycopod known structurally. The megasporophylls show a more advanced type of seed habit than has hitherto been met with in Cryptogams. The megasporange gives rise to but one thin-walled spore, which in development and structure resembles an embryo-sac, and germinates *in situ*. An integument, or velum, surrounds the sporange, leaving but a small distal orifice as micropyle (figs. 37 and 38). This is surrounded by numerous long processes of the integument, which formed a collecting and incubating apparatus for the microspores. There is no trace of an envelope about the microsporange. The carpellary leaf was shed at maturity, and resembles a winged seed (see accompanying text-figure).

The foliage leaves, which were only about a third the size of the seed, are delicate acuminate structures, very thin, and without stomates. Some show multiseriate hairs springing from the adaxial surface of the leaf base.

I will now proceed to describe the different organs in detail, dealing with them under the following heads:—

I.—The Foliage Leaf.
II.—The Stem.
III.—Megasporophylls and ♀ Cone.
IV.—Microsporophylls.
V.—Comparative Review.

I.—The Foliage Leaf.

Professor Bertrand says:—"The frond was thick in its inferior part where the bundle and ligular groove occur. There is a well developed ligule. It is a little tongue about 0·3 mm. long, 0·1 mm. wide at the base, 0·07 mm. in the middle, 0·04 mm. at the summit, attached to the posterior part of the ligular chamber. It consists of a layer of epidermal cells with thin walls surrounding a mass of tubular cells in regular tiers and without lacunæ."

Almost the whole of the ligule is inserted in a pit, which it fits as a cork does the neck of a bottle. This is shown in figs. 1, 4 (Plate 33) and fig. 33 (Plate 37). This pit is formed by a groove in the leaf base which is bridged over by tissue uniting the lateral margins of the groove where the leaf base abuts on the lamina. The extreme apex of the ligule can be seen projecting from the pit, but still resting on the uncovered part of the groove (fig. 32). Exceptionally it can be seen that the tissue above the ligular groove bears multiseriate hairs (fig. 31). The plane in which the leaf in this section is cut is obvious by reference to fig. 30. It is obliquely tangential through the base of the ligule. The tissue with its processes is an interesting homologue of the velum with its processes, which we shall find in the megasporophyll, and is a further confirmation of the view that the leaves and megasporophylls belong to the same plant.

The lamina is but a few cells in thickness, and is bordered like the leaf base with a thin membrane but one cell thick (fig. 33). The form and structure of the ligule is very characteristic of Miadesmia, and so is the thin border. But still more characteristic are the moniliform, uniseriate hairs which everywhere accompany the leaves. Bertrand's statement, "les cellules marginales n'étaient pas prolongées en poils," is due to his interpretation of them as vertical sections of the thin lamina. But though in some cases the lamina has disintegrated, giving rise to long rows of cells, these can, by their compressed and non-tapering form, be easily distinguished from the true hairs. The same difference would obtain in the case of sections of leaves which, moreover, would necessarily show their lamellar nature in the relatively thick sections which we have to employ. The cells are small and spherical, with an occasional elliptical one suggesting approaching division. Many of these hairs are composed of as many as seventy cells, and may be 4 mm. in length. The walls of their cells must have been cuticularised, judging from their excellent preservation. In its living state the border of the lamina must have been fringed with these hairs, which are indicated in several of the figures (figs. 1 and 5). In the latter figure we see two attached to a single cell, but as a rule they became detached before fossilisation. They occur also on the megasporophylls, where, however, they do not seem to reach so great a development, doubtless in correlation with the increased importance of the multiseriate hairs on these organs.

Disregarding the hairs, the leaves are found to reach a length and breadth of between 1 and 2 mm. The leaf base is about 0·3 mm. in depth. The mode of insertion of the leaf is shown in figs. 1 and 30. Not only the lamina but the multiseriate hair-like processes on the adaxial surface and the uniseriate peripheral processes were normally held at an acute angle with the axis, and thus the whole shoot with its imbricating leaves must have been an admirable apparatus for holding water by surface tension. Stomates appear to be wholly absent. No evidence of heterophylly among the foliage leaves, such as Professor BERTRAND suggests, has been forthcoming from the new slides.* Figs. 1 and 30 seem to support the view that Miadesmia was homophyllous. Detached leaves of different dimensions occur, but it is probable in these cases that we are dealing with leaves from axes of different orders or in different stages of development.

II.—THE STEMS.

A large number of twigs have been investigated, among the best being those in slides 51, 880, 881, 1125–1139, S.†

R. 416, M.
380 *b–c*, W.
87, H.

Both longitudinal and transverse sections have been figured (*e.g.*, figs. 1, 6, 13, and 30). We see from a comparison of these figures that while the internodes are short in some, there is a considerable interval between the nodes in others, *e.g.*, compare figs. 1 and 14.

The transverse sections also confirm this observation, as some show two or three leaves in attachment (fig. 10) and others only one (fig. 11).

The leaves seem to have been spirally inserted, but the number of orthostiches is difficult to determine. With BERTRAND we have a few cases which suggest a tetrastichous phyllotaxy (fig. 30 and possibly figs. 1 and 6); but that this was a constant arrangement seems improbable from a consideration of the majority of the specimens, and if we take into account the irregular form of the xylem, which is rarely, if ever, tetrarch. The xylem is that of a simple protostele, and is built up entirely of scalariform tracheides with peripheral protoxylem of spirally thickened tracheides.

* *Loc. cit.*: "Les frondes postérieures—un peu plus grandes."

† *Vide* foot-note to Description of the Figures.

The protoxylem groups vary in number, and may be three or four (slide 1131, S.), five (slides 1127, 1129, 1135, S.), or six (slides 880 and 1130, S.). These protoxylem groups are more conspicuous in some steles than in others. They project considerably in the sections 1129 and 1135, S. (fig. 6).

The new slides show no case of a bipolar xylem plate such as BERTRAND describes. The scalariform tracheides are hexagonal in section. The bars are rather remote, and there are very conspicuous Williamson striations connecting them (fig. 12).

Phloem seems to have surrounded the xylem, and is fairly preserved in sections 1135 and 1126, S. (fig. 13).

The stele bifurcates at intervals and the two branches travel together in the parent stem before the stem bifurcates. Thus there are several examples like that figured from slide 1126, S. (fig. 13). In one case one stele is larger than the other, which corroborates Professor BERTRAND'S statement that the branches of the dichotomy were unequal.

The cortex is two-fold in character. The outer cortex consists of about three layers of large cells about three times as great in their vertical dimension as in their radial or tangential. They offer a sharp contrast to the small-celled peripheral layer upon which they abut (fig. 14).

The inner cortex is lacunar, and trabeculæ of swollen cells pass radially from the central stele to the outer cortex (figs. 6 and 14). In one specimen the cells of the inner cortex are large and regular.

It is conceivable that the trabeculæ originated from such cells in the course of development. Such a stage makes the suggestion probable that the trabeculæ, as in Selaginella, represent an endodermis, although, as BERTRAND remarks, no characteristic endodermal thickening can be detected.

There is absolutely no special skeletal tissue, and it is therefore obvious why such a structure became crushed when subjected to pressure previous to petrifaction. In the fairly numerous sections investigated there seems no other explanation needed of the non-circular form of the section. Professor BERTRAND, however, refers to the stem as dorsiventral in form.

It may be useful to state that the above description of the vegetative organs differs from Professor BERTRAND'S only in the following particulars. It has been found :—

(1) That the stele has an oligarch xylem which varies from a tri- to a hex- arch form, and that it has not been observed on any occasion to be diarch.

(2) That there are an abundance of hairs which are distinct from (not mere sections of) the thin lamina.

(3) That the new slides yield no evidence in support of the view that the stem was bifacial nor that the leaves varied in size in the different orthostiches, nor that they were regularly tetrastichous.

III.—The Megasporophylls and ♀ Cone.

The mature megasporophyll was a relatively bulky structure, extended at right angles with the plane of insertion. The lamina was bordered by a membrane only one cell thick. It was by means of this border to the lamina that Dr. Scott first identified the megasporophylls as belonging to Bertrand's new genus (figs. 17 and 25 should be compared with fig. 33). Further evidence has since accrued. The resemblance in the character and insertion of the ligules of the structure under discussion and of the foliage leaf of Miadesmia (figs. 4 and 19); the resemblance between the former in its young condition and the foliage leaf (figs. 1 and 35); the existence upon the tissue covering the ligule in the foliage leaf of multiseriate hairs very similar to those on the velum of the new organ (fig. 31) combine to render us fairly confident in referring these seed-like organs to Miadesmia. Lastly, we may compare the structure of the axis of the cone with the vegetative axis. Fig. 28 represents a megasporangial cone cut tangentially. If we compare this with fig. 14, we see the same differentiation of cortex into an inner and outer layer, the outer being continuous and built up of large cells, and the inner showing trabeculæ of swollen cells. The megasporophylls resemble those of figs. 29 and 35 and are evidently immature, but otherwise identical with the bodies now attributed to Miadesmia.

In the mature megasporophyll the vascular bundle which enters in the centre of the concave area of insertion traverses the leaf base and then, sinking abruptly at the base of the sporange, travels up the midrib of the lamina. At the base of the ligule it is supplemented by a sheath of tracheides.

The sporange, attached by its cylindrical pedicel to the leaf base, lies slightly inclined to the plane of the lamina, which extends to a considerable length beyond it.

The wall of the sporange is several layers of cells in thickness, but the outermost layer loses its palisade-like character as it matures. Within the wall, and generally very closely abutting on it, may be seen the thin coat of the single megaspore or embryo-sac (figs. 8 and 18–21).

In an immature sporophyll, such as that shown in fig. 29, the inner layers of the sporange wall are not yet fully absorbed, while in many the spore seems to have absorbed even the upper part of the wall (fig. 8). In the specimen shown in fig. 21 the sporangial wall and megaspore wall are indistinguishable; thus the Miadesmia fructification may have resembled a true seed in the nucellus, almost disappearing at maturity.

A noticeable feature in the sporangia of figs. 20 and 21 is their prolongation into a beak-like process (accidentally reversed in the former). The form is probably due to a special development of the germinating spore. In the beaked megaspore figured by Renault, in his 'Flore d'Autun,' Plate 34, fig. 11, the lumen is continued into the beak, and such megaspores occasionally occur in the nodules of the Gannister beds. These, however, were probably tetrahedral in form, while there is no sign whatever of a tetrahedral form in the megaspore of Miadesmia. One of the many remarkable features of the megasporophyll is that the sporange is roofed over by a velum in which the aperture is distal. It arises at the proximal end of the leaf base and roofs over the deep groove in which the ligule and sporange lie (figs. 37 and 38).

In fig. 23 the velum is on a level with the border of the lamina, and there is a well-marked keel on the abaxial surface. As the sporange gradually rises, the velum which surmounts it becomes more and more raised above the level of the lamina, as is shown in figs. 23–27. These should be compared with the radial section in fig. 18.

As the velum rises, its sides, which are continuous with the lamina, become steeper until, at the plane represented by fig. 27, they are vertical to it.

The sections so far available do not give completely satisfactory evidence as to the form of the micropyle. There are six approximately radial sections, two of which pass exactly through the micropyle (figs. 20 and 21), but there is no horizontal section passing exactly through the micropyle. The section which is nearest to this plane is shown in fig. 9. The radial sections indicate that below the apex of the sporange tissue rises from the lamina following the wall of the sporange to the micropyle and there engages with the margin of the upper part of the velum (fig. 20).

The horizontal section, which, however, passes slightly above the micropyle, indicates that the upper part of the velum narrows rapidly towards the apex of the sporange (fig. 9). The deduction, from which we can hardly escape, is that the micropyle was a circular orifice. The sporophyll shown in almost radial section in fig. 29 passing through both sporange and ligule longitudinally indicates further that the micropyle must have been small, as this section escapes it altogether.

The velum is smooth on the surface abutting on the sporange, but on the distal half of its outer surface bears long processes, which are generally so constructed that their whole length lies parallel with the lamina. There is one exception to this, showing the processes held at right angles with the surface. They form very striking objects, both in radial and tangential sections, and are obviously homologous with those of the foliage leaf, where, however, they do not seem to be constantly present.

The part of the velum below the apex of the sporange bears numerous processes like those above and beside the sporange (figs. 18 and 19). The micropyle is thus surrounded by these hairs, which doubtless subserved the function of a feathery stigma in an anemophilous flower. They must also have done duty for a pollen chamber, to which water was brought by capillary attraction.

If the micropyle, as above suggested, were a circular pore, it offers a great contrast to that of Lepidocarpon, in which, as Dr. Scott has shown, it is a long, slit-like aperture.

There is considerable probability that the megasporophylls were shed when mature. There are exceedingly few cases in which the foliage leaves or twigs occur together with the mature megasporophylls, whereas they are abundant with young sporophylls (slides 380*a*–*h*, W.; 1118, S.; and *cc* 7*a*–*k*, O). Moreover, such an immature sporophyll as that in fig. 35 shows part of the cortex torn away from the stem and still adherent to the leaf, which is never the case with a mature organ.

The structure of the megasporophyll will be made clearer by an examination of the various figures. The sections from which these are taken occur in various planes. A series of tangential sections is shown in figs. 22–27.

The longitudinal sections may be vertical or horizontal or oblique. If vertical, they may pass to the right or left of the median plane of the leaf, and if horizontal above or below the median plane. The sporophylls also vary in their stage of development.

The figures of radial sections are as follows:—

Median (figs. 18 and 19).

Obliquely radial, but exactly through the micropyle (figs. 20 and 21).

The figures showing horizontal sections are as follows:—

Above the median plane (fig. 9).

In the plane of the lamina and therefore oblique to the sporange (fig. 17).

The latter figure represents one of the two sections available in this plane. It shows the form of the wide border, and enables one to realise how similar the whole structure must have been to a winged seed. Whether there were any biological significance in this is not easy to estimate, but the view receives support from the fact that special appendages occur, as Mrs. SCOTT points out,* in the megaspores of *Lepidostrobus foliaceus.*

These admirable photographs, taken together with those of the tangential sections already referred to, enable one to obtain a clear conception of the form and structure of these mature sporophylls. The insertion of the sporange and ligule, the form and scope of the velum, the course of the vascular bundle, the embryo-sac with its beak and contents, all are revealed to us with a perfection that will surprise anyone who recalls that we are dealing with a plant that is only known to us from the Palæozoic rocks.

The Immature Megasporophyll.

Several specimens of the young sporophyll occur, which are shown in figs. 35, 28, 29. Fig. 35 is a camera drawing of one only a millimetre in length, and thus scarcely a quarter the size of the mature sporophyll. The section reveals the course of the vascular bundle and the insertion of the sporange and ligule. The peripheral part of the velum has, unfortunately, been injured, and the contents of the sporange have entirely perished. The wall at this stage is limited by a palisade layer. On the adaxial surface of the trace near the base of the leaf can be seen a layer of meristem which by division evidently gives rise to the tissue which causes a deflection of the sporophyll as it develops. The difference in the positions of the young and

* 'New Phytologist,' 1906.

of the mature megasporophylls, which is made clear by contrasting figs. 18–21 with figs. 35, 28, and 29, cannot but be regarded as of great biological significance. If we consider that the foliage leaf and, as we shall see later, the microsporophyll, retain a position more or less parallel with the axis, we realise that as the seed leaf developed it must have bent back through 90° to lie in a plane nearly at right angles to the plane of insertion. This deflection causes the vascular bundle to take the zig-zag course shown in radial sections. The biological import would be the need for increasing the receptive area for microspores.

One of these radial sections of a young megasporophyll before deflection has occurred (fig. 29) shows an interesting stage in the development of the megaspore. It is circular in section and solitary, and surrounded by uniform parenchyma which it is gradually absorbing. This condition is much more suggestive of the early stages in the development of an embryo-sac of a Phanerogam than those of any recent Cryptogam.

Another radial section of a very young sporophyll (which, however, from its external configuration we can hardly distinguish from a microsporophyll) (fig. 36) shows the tissue contained in the sporange with extraordinary perfection. The upper part is occupied with radially arranged series of cells like those in the apical part of the nucellus in many Phanerogamic seeds. There is an indication of a single cell being already marked out as the young megaspore. That we should be able to make out details such as these is but another instance of the excellent preservation of even delicate tissues in the calcite nodules, and may be compared with the discovery of germinating spores in a Fern sporange by Dr. Scott.

Another point of interest in these sections of the young sporophyll is the evidence they afford that, as in Recent Ligulatæ, the ligule reaches its full size very early in the development of the leaf.

Gametophyte.

A considerable number of the sections show the cavity of the megaspore to be filled with large celled tissue which is evidently prothallial. One of these is shown in fig. 8. The apex of the prothallus appears to have emerged. The emerging part has some resemblance to the neck of a large archegonium, but the appearance is probably quite fallacious.

IV.—The Microsporophylls.

Microsporophylls occur in the same blocks, and many even in the same sections, as foliage leaves and megasporophylls of Miadesmia. Some of these show ripe spores, and therefore are mature, as, for instance, the specimen shown in fig. 34. Here will be seen also the typical ligule of Miadesmia with a tapering apex (*cf.* the ligules of figs. 4, 19, 29, and 34). The sporange wall is formed of a palisade layer. There is no great development of the tracheal sheath, and the tissues as a whole are not well differentiated. The size of the microsporophyll is intermediate between that of the foliage leaf and that of the megasporophyll, and there is similar lacunar tissue on the abaxial part of their bases. There was a relatively large sporange with a short cylindrical pedicel which closed in the ligular groove. The whole leaf appears to have retained the bent form characteristic of the young megasporophyll and of the foliage leaf. Thus while the mature megasporange was held horizontal the microsporange was held erect. The microspores are tetrahedral in form and $0{\cdot}03 \times 0{\cdot}025$ mm. in size.

In a paper "On the Cone of *Bothrodendron mundum*," read by D. M. S. WATSON, B.Sc., at the Leicester Meeting of the British Association this summer, he points out the similarity between the microsporophylls of *Bothrodendron mundum* and Miadesmia. He has also kindly furnished me with full details of his newly identified microsporophylls, which enable me to make the following comparison. Both structures show the same general form, but if we deal with mature specimens containing spores we find the difference in dimensions as follows: the microsporophyll of Miadesmia, measured from apex of sporange to under surface of sporophyll, is only about 1·35 mm., while that of Bothrodendron is 2 mm. The inside height of the sporange in Miadesmia is about 0·75 mm., while that of Bothrodendron is 1·2 mm. Moreover, the tissues of the latter are much more compact and better differentiated than those of Miadesmia. Radial sections also offer no difficulty, as the ligules are distinct in form, those of Bothrodendron being rounded at the apex, and those of Miadesmia tapering. It is, however, confusing in many cases, as we may be dealing with immature forms of Bothrodendron in transverse section. Moreover, the two species seem to have been common together, and are associated in the same slide as, for example, in Dr. SCOTT'S slides 2277 and 2243, in which undoubted microsporophylls of Bothrodendron are found alongside of sections of megasporophylls of Miadesmia. In the case of the microsporophyll shown in fig. 34 we have not only satisfactory internal evidence that it is Miadesmia, but we find it and several others, like that of fig. 15, associated on the same slide with stem, foliage leaves, and megasporophyll of Miadesmia.

In no case do multiseriate hairs occur, and there is no velum. There is no evidence so far as to whether they occurred with the megasporophylls in ambisporangiate cones or otherwise.

V.—COMPARATIVE REVIEW.

The habit, anatomy, and ligule of Miadesmia show that it is undoubtedly a member of the *ligulate Lycopodineæ*, of which there have been hitherto only two other genera known with an integumented sporange, *i.e.*, Lepidocarpon among the Palæozoic plants and Isoëtes among the Recent.

These two types differ in common from Miadesmia, in having a radially elongated insertion of the sporange and in having both the micro- and the mega- sporangium integumented. The velum to the microsporangium of Lepidocarpon was, however, incomplete and possibly inconstant, and there are many species of Isoëtes with an incomplete velum and others, such as *Isoëtes Tasmanica*, with none at all. The velum of Lepidocarpon and that of Miadesmia agree in both enclosing the ligule. In Isoëtes the opening is proximal, in Lepidocarpon radially extended, in Miadesmia it is distal. In fact, the velum differs so much in these three cases that we are compelled to regard each as of independent origin. This rather surprising conclusion points to there having been a widespread tendency to vary towards seed formation in the Palæozoic era. Lepidocarpon and possibly Miadesmia date back to the Lower Carboniferous flora. So also does Mazocarpon, another Lycopodinean genus, which is shortly to be described, showing an incipient velum originating from the wall of the megasporange. Probably this will be shown to be connected with fertilisation rather than protection, and it is possible that it was primarily for the collection of microspores that the Miadesmia velum was evolved.

Among the Calamites the formation of an upgrowth of tissue in the form of radially placed lamellæ from the abaxial surface of the coherent whorl of bracts has been recorded by Renault.* Protection was thus afforded to the sporangia of the whorl below.

The Pteridosperms were, in the Lower Carboniferous Epoch, far advanced in the seed habit. The ovule showed not only a greater elaboration of mechanism but was shed independently of the sporophyll. Moreover, there seem to have been *two* envelopes to the nucellus or sporange, and it has been suggested† that the inner of these is of synangial origin and only the outer, if any, comparable with the velum of Miadesmia. The form among the Ferns which is most analogous to Miadesmia is the sporocarp of Azolla, but even here the envelope surrounds micro- and mega-sporangia equally. Miadesmia is unique among the Lycopodineæ, so far known, in retaining an absolutely cryptogamic type of microsporophyll, while it has advanced to a high degree of elaboration of the megasporophyll. An analogous case is found in the Pteridosperms and in all Phanerogams—the microsporophylls being relatively cryptogamic in character, but the seed leaves highly specialised.

If we then regard the velum as of little taxonomic value, there can be no doubt that the aggregate of characters corroborates BERTRAND'S view that Miadesmia is nearly allied to Selaginella. BERTRAND concludes his paper on Miadesmia with these words:—"La découverte de nouveaux matériaux plus complets permettront peut-être d'identifier complètement au genre Selaginella."

Although the discovery of new material has not led to this result, all will agree that Selaginella is the genus most nearly allied to Miadesmia among forms so far described. The stele bears a very fair resemblance to that of the erect stem of

* RENAULT, 'Flore Fossile,' p. 136, Plate LXII.

† BENSON, "*Telangium Scotti*," 'Annals of Botany,' vol. 18.

Selaginella selaginoides (L.). There are not often in the stele of Miadesmia so many tracheides as occur in the stele referred to, but we have a few cases in which they do not fall far short. The protoxylems are not quite so definite, nor the trabeculæ of Miadesmia quite so long, but on the whole the steles show a fair resemblance. The leaf-traces in both pass off at a very similar angle. The sporange also, in its insertion upon a cylindrical pedicel close to the ligule, is more like that of Selaginella than that of any other known genus except Bothrodendron. But we must remember that the thickened base of the leaf which intervenes between the sporange and the axis is an archaic character, which is not found in Recent Selaginellas. In this particular, Miadesmia recalls in a slight degree the radially elongated leaf bases of Lepidostrobus, and closely resembles Bothrodendron.

Moreover, in the great majority of the Selaginellas there is no approximation to the seed habit. In *Selaginella apus* and *Selaginella rupestris*, described by Miss LYON,* we have a slight advance in that direction as fertilisation takes place within the sporange, and germination occurs before the cone is disintegrated. But even in these suggestive cases there is no great structural adaptation as in Miadesmia.

In *Selaginella apus* a complete tetrad of megaspores developes in each sporange, and though in *S. rupestris* the tetrad is incomplete, each spore has a rigid multiple coat. The prothallus emerges from the respective spores, but not from the sporange. The sporophylls remain attached to the axis of the cone, and are not shed like seeds.

In Miadesmia, on the other hand, it has already been shown at length that but one megaspore arises in each megasporangium and its wall is a thin membrane. There is an integument with a well-developed receptive and incubating apparatus for the microspores. The megasporophyll falls at maturity like a winged seed.

Many of the Selaginellas diverge widely in anatomy from Miadesmia and the bulk of the species, forming a characteristic feature of the rain forests of the Tropics, are markedly dorsiventral in habit and heterophyllous. In comparison with these, the vegetative organs of Miadesmia appear relatively primitive, and it is not until we investigate the reproductive organs that we see how far the little Palæozoic plant has advanced. We have in it an illustration of two well recognised laws of advance—firstly, that variation need not necessarily affect all organs of an individual plant equally; and secondly, that the smaller members of a race may be from an evolution standard the most advanced.

HALLE's paper† on "Some Herbaceous Lycopodiaceæ of Palæozoic and Mesozoic Age" gives an interesting summary of what is known of Palæozoic Selaginellas. None of them, so far, are known structurally, but in the case of two of GOLDENBERG's

* LYON, 'Botanical Gazette,' 1901.

† HALLE, "Einige krautartige Lycopodiaceen Paläozoischen und Mesozoischen Alters," 'Arkiv für Botanik,' Stockholm, 1907.

species of Lycopodites, *i.e.*, *elongatus* and *primævus*, HALLE has found sufficient evidence of heterospory to lead him to transfer them to ZEILLER'S genus, Selaginellites. He points out that impressions of these plants show *Selaginellites elongatus*, like *S. Suissei*, ZEILLER, to have had more than one tetrad of megaspores per megasporangium, and *Selaginellites primævus* to have had but one tetrad. In the latter species there was an indication in the older shoots of a dorsiventral habit.

These results are interesting, as they show the great antiquity of the herbaceous ligulate Lycopod. Meanwhile, the new light cast on Bothrodendron by Mr. WATSON'S work, already referred to, shows us that a member of the Lepidodendreæ also produced a non-radially extended sporange like that of the Selaginelleæ.

As our knowledge thus increases of the ligulate Lycopodineæ, we find but little to elucidate the long-standing problem of the origin of the homosporous eligulate type—Lycopodium. If, however, as in the ligulate series, there existed in the Palæozoic era an ancestor with a radially extended leaf base, we should recognise a possible affinity between Lycopodium and Spencerites. In the latter genus, as was recently shown by Miss BERRIDGE* in her reconstruction of the sporophyll, the sporange is attached to a ventral hump on the sporophyll. This appears to be a non-vascular vestige of the ventral lobe, so characteristic of the sporophyll of the Sphenophyllales. If, then, as is readily conceivable, this hump flattened out in the course of evolution of the shorter leaf, we should get a type of sporophyll not far removed from that of Lycopodium.

We owe it to Dr. SCOTT that we have the interesting conception of the group, Sphenophyllales, as the point of convergence of the Lycopodineæ and Equisetinæ. Spencerites seems clearly derived from the Sphenophylls with which, perhaps, it should be associated systematically. Hence, in tracing a possible derivation of Lycopodium from such a form as Spencerites, we bring Lycopodium into closer touch with the Sphenophyllales.

In conclusion, we may enquire whether Miadesmia throws any light on the homology of the ligule. Possibly not, but it confirms us in the view that the ligule is a very ancient organ and not a mere colleter, as its early origin suggests to some. So far as we know, the presence of a ligule is co-extensive with heterospory in the Lycopodineæ, and this suggests that it may have had some significance in the early stages of this phenomenon. But none of the resources at our command have as yet given us a satisfactory interpretation of this curious organ.

* BERRIDGE, 'Annals of Botany,' vol. 19, 1905.

DESCRIPTION OF THE FIGURES.*

Plates 33–36 contain photomicrographs. Plate 37 contains camera drawings. Approximate linear magnifications are given. The small letters attached to the pointers are used as follows:—

b = border of lamina.
c = cortex.
e = embryo sac.
h = uniseriate hair.
l = ligule.
la = lamina.
m = micropyle.
m. h. = multiseriate hair.
p = prothallus.
s = sporange wall.
sp = microspores.
t = trabeculæ.
v = velum.
v. b. = vascular bundle.
w = Williamson striations.

PLATE 33 (figs. 1–9).

FIG. 1.—Longitudinal section of twig, with several leaves cut radially. (× about 40.)
380 *b*, W. Dulesgate.

FIG. 2.—Tangential section in plane of ligule of two leaves, apparently attached to an axis. (× 55.) 880, S. Hough Hill.

FIG. 3.—Ditto of one leaf in plane of lamina. (× about 100.)
380 *c*, W. Dulesgate.

FIG. 4.—Good radial section of the ligule of a foliage leaf, showing the tapering apex. (× about 125.) 1133, S. Hough Hill.

FIG. 5.—Ditto, showing the course of the vascular bundle of leaf. Outside are various detached uniseriate hairs. (× about 100.)
R, 221, M. Hough Hill.

FIG. 6.—Transverse section of twig, showing insertion of three leaves. The oligarch protostele can be seen. Outside this are the trabeculæ of the inner cortex. This is bounded by the large-celled outer cortex, which in turn is surrounded by a peripheral layer of small cells. Two uniseriate hairs are shown, which possibly formed part of a fourth leaf. (× about 80.)
1135, S. Hough Hill.

* The letter added to the number of a slide indicates its owner—S = Dr. SCOTT, O = Professor OLIVER, M = Manchester University, W = the Williamson Collection in the British Museum, H = the Royal Holloway College.

FIG. 7.—Transverse section of twig, showing one or more leaves in continuity. The lacunar cortex is destroyed, but the xylem of the stele is fairly preserved and appears to be hexarch. (×about 50.) 880, S. Hough Hill.

FIG. 8.—An obliquely tangential section of a megasporophyll, showing the embryo-sac, with contained tissue, which is evidently prothallial. (×35.) 82, H. Cloughfoot, Dulesgate.

FIG. 9.—A horizontal section of a megasporophyll above the plane of the lamina and above the micropyle. It shows well the pointed apex of the sporange and velum. (×about 64.) *cc* 7 *f*, O. Dulesgate.

PLATE 34 (figs. 10–17).

FIG. 10.—A transverse section of a twig, showing the insertion of several leaves. Its compressed form may be due to imperfect preservation. (×about 55.) 1137, S. Hough Hill.

FIG. 11.—A transverse section through an internode. Only the xylem and peripheral layer of small cells preserved. (×45.) 51, S. Hough Hill ?

FIG. 12.—A longitudinal section of xylem, showing the character of the scalariform tracheides. The Williamson striations are clearly shown. The elongated elements at the side of the xylem are probably phloëm. (× about 270.) 1125, S. Hough Hill.

FIG. 13.—A transverse section through a bifurcating stem. It is circular and shows one leaf in continuity. The phloëm is shown in fair preservation in the stele near the leaf. (×about 40.) 1126, S. Hough Hill.

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FIG. 15.—A tangential section through a microsporophyll in the plane of the insertion of the ligule. (×about 35.) 84, H. Dulesgate.

FIG. 16.—A tangential section through a megasporophyll at the plane through the apex of the ligule. The velum, sporange, and thin border can be seen. (×about 35.) 2237, S. Cloughfoot, Dulesgate.

FIG. 17.—A nearly horizontal section of a megasporophyll in the plane of the lamina for the proximal half. The distal part of the lamina beyond the apex of the sporange is not present. (×32.) 82, H. Cloughfoot, Dulesgate.

PLATE 35 (figs. 18–21).

FIG. 18.—An excellent radial section of a mature megasporophyll, showing the lamina beyond the apex of the sporange, the course of the vascular bundle, and the ligule. The apex of the sporange is seen to be considerably above the level of the lamina, and the velum is shown below the apex as well as above it. (×38.) 2240, S. Cloughfoot, Dulesgate.

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FIG. 21.—An approximately radial section through a mature megasporophyll passing exactly through the micropyle into which the beak of the sporange extends. The embryo sac seems to have destroyed the upper part of the wall of the sporange, and to have contained prothallial tissue. Two short marginal uniseriate hairs are seen on the lamina. (×38.) *cc* 7 *h*, O. Dulesgate.

PLATE 36 (figs. 22–29).

FIGS. 22–27.—A series of tangential sections of the megasporophyll from the base upwards.

FIG. 22.—A tangential section through the base of the megasporophyll. The narrow border has perished. (×about 80.) 2241, S. Cloughfoot, Dulesgate.

FIG. 23.—Ditto through ligule and base of sporange. The walls of the ligular groove are shown, and also the velum, but the thin border to the lamina has perished. (×about 40.) 2242, S. Cloughfoot, Dulesgate.

FIG. 24.—Ditto through ligule and sporange. The keel is prominent in this plane. The thin border to the lamina has perished. (×about 40.) *cc* 7 *d*, O. Dulesgate.

FIG. 25.—Ditto of one side of the free lamina in a section approximately in the plane of fig. 16, Plate 2. (×40.) *cc* 7 *k*, O. Dulesgate.

FIG. 26.—Ditto still more distal, showing the velum now giving off processes. This section is oblique, as otherwise the ligule would not be seen in the same plane as the processes. (×about 40.) 91, H. Dulesgate.

FIG. 27.—The last of the series. The velum is breaking up over the apex of sporange into processes. The more proximately inserted processes, as seen in section, form a halo-like circle. The free part of the lamina is now at a much lower level relatively to the sporange and is of considerable width. (×about 40.) *cc* 7 *c*, O. Dulesgate.

FIG. 28.—A tangential section of part of a young cone with four megasporophylls in continuity. It should be compared with the vegetative shoot in fig. 1. The stem in the upper part shows the trabeculæ of the inner cortex and can be compared with those of fig. 14. (×18.) 88, H. Cloughfoot, Dulesgate.

FIG. 29.—An obliquely radial section of part of a young megasporophyll, showing the bent form and ligule, velum and sporange. The young spore is circular in section, and no trace of sister cells is to be seen. (×about 55.) 81, H. Cloughfoot, Dulesgate.

PLATE 37 (figs. 30–38).

FIG. 30.—A longitudinal section of a twig, showing the insertion of four leaves. (×about 80.) 87, H. Dulesgate.

FIG. 31.—An obliquely transverse section of a leaf, showing multiseriate hairs on the tissue covering the ligule. This section also shows the thin border to the lamina. (×120.) 87, H. Dulesgate.

FIG. 32.—A transverse section of a leaf, showing the exposed apex of the ligule. (×about 90.) 84, H. Dulesgate.

FIG. 33.—Ditto, more proximal, showing the tissue covering the ligule and the border of the lamina. (×about 90.) R, 194, M.

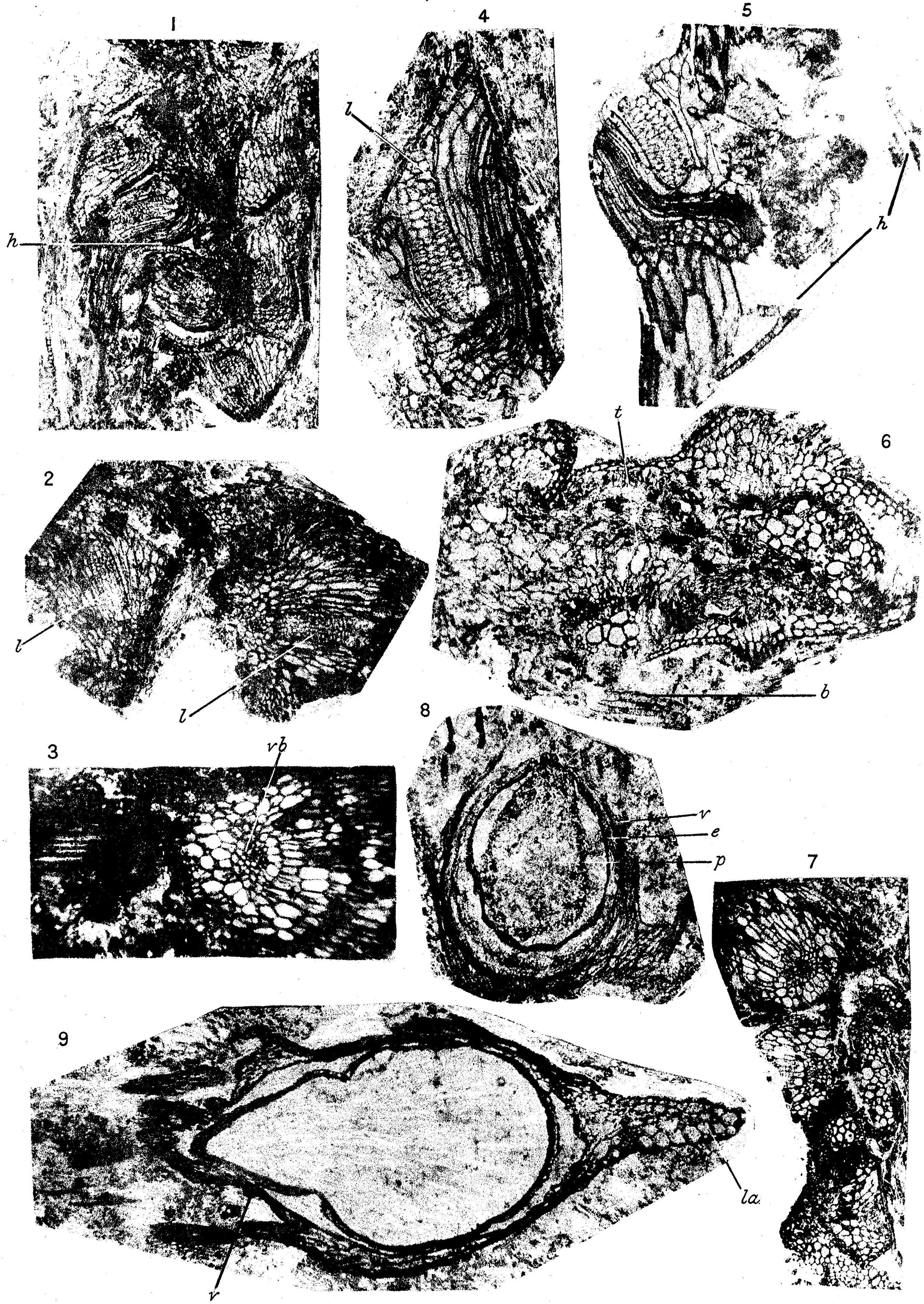
FIG. 34.—A longitudinal section of a microsporophyll escaping the attachment of the sporange, but showing the form of the ligule. Microspores are seen in sporange. (×about 80.) 84, H. Dulesgate.

FIG. 35.—A radial section of a young megasporophyll, showing mode of attachment to cone axis. This should be compared with fig. 28. The distal part of the velum was injured before petrifaction. The leaf is 1 mm. in length. (×about 90.) 94, H. Dulesgate.

FIG. 36.—A longitudinal section of a very young sporange, showing regular arrangement of cells. The ligule at this stage is two-thirds the size of the sporange. (×about 250.) 95 *b*, H. Dulesgate.

FIG. 37.—Diagram of a seed-leaf in radial plane. It shows sporange with embryo-sac, ligule, velum with its appendages, micropyle, and course of vascular bundle.

FIG. 38.—Diagram of a section through plane *ab* of above diagram. It shows the sporange and ligule roofed over by the velum.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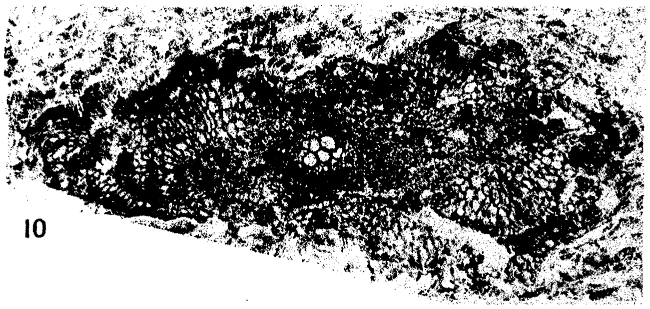

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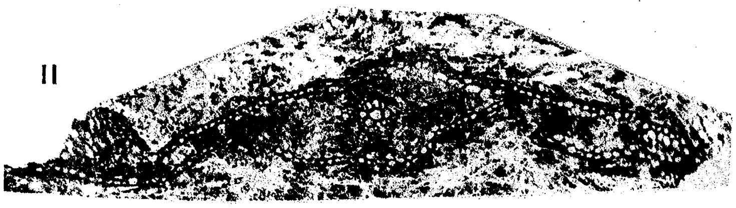

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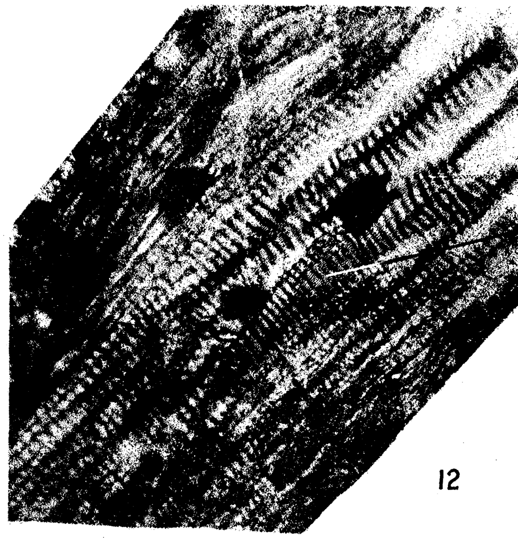

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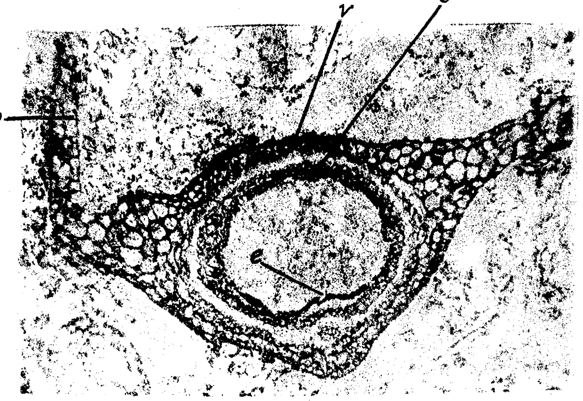

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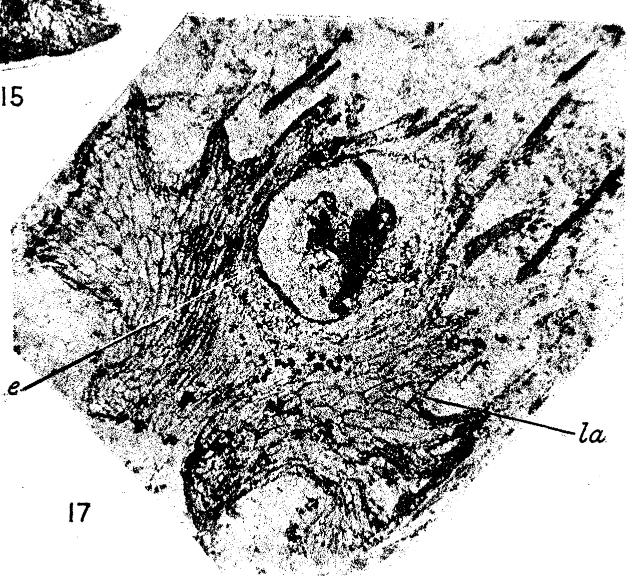

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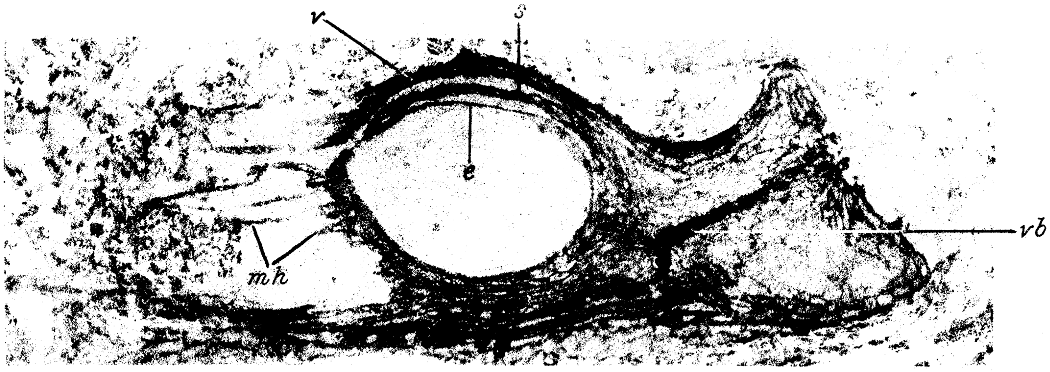

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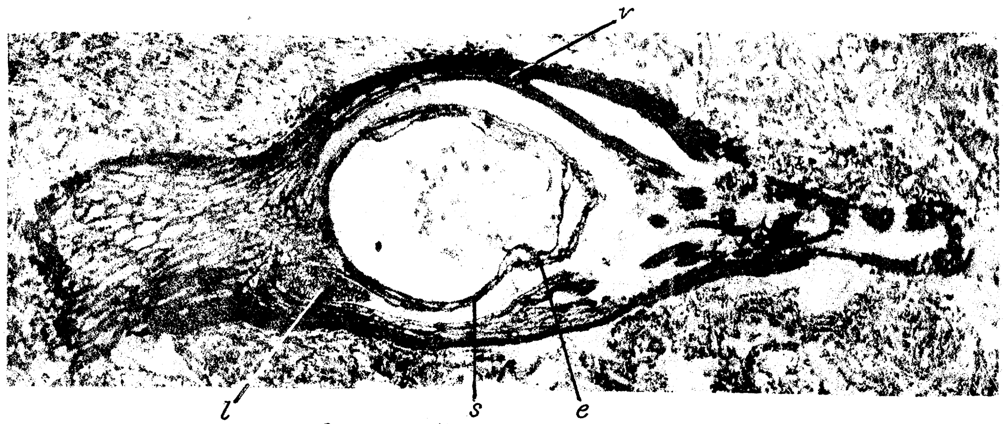

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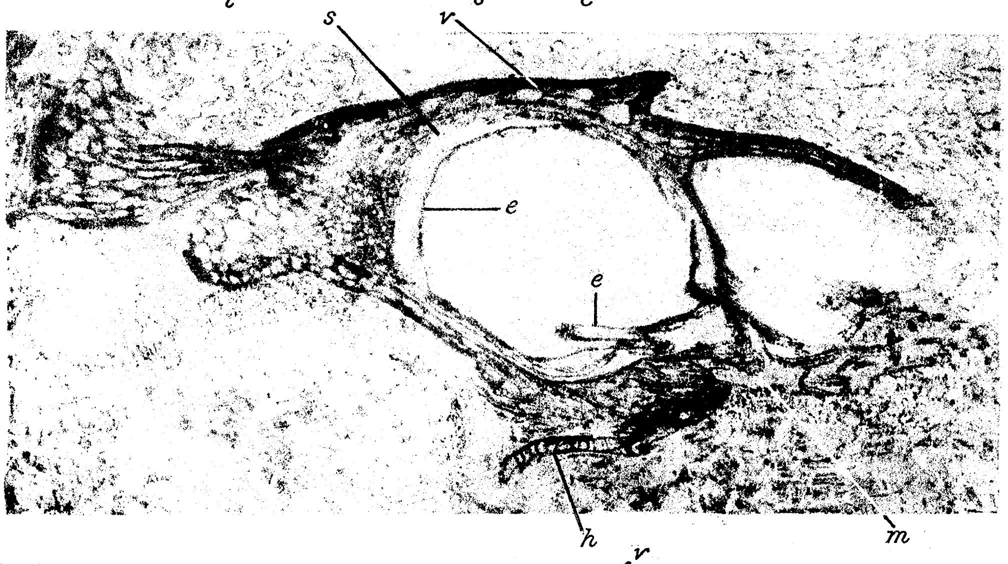

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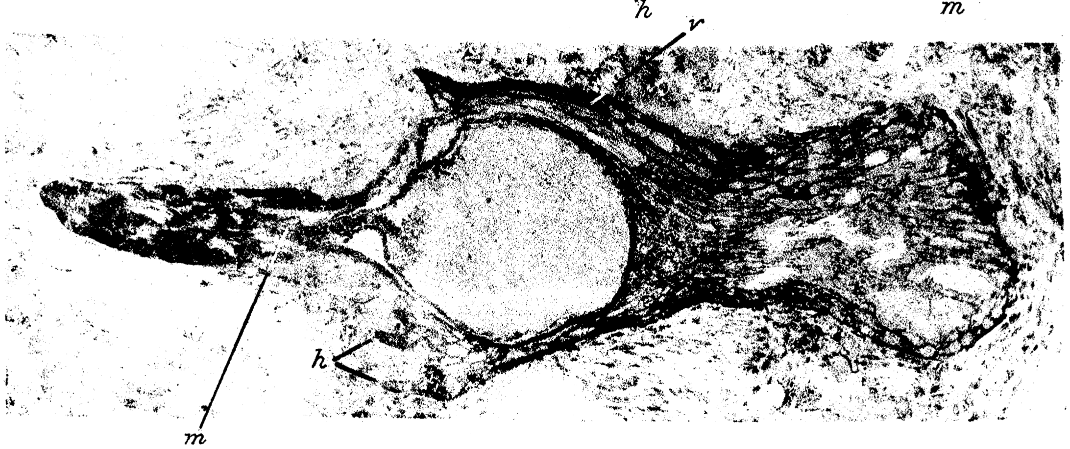

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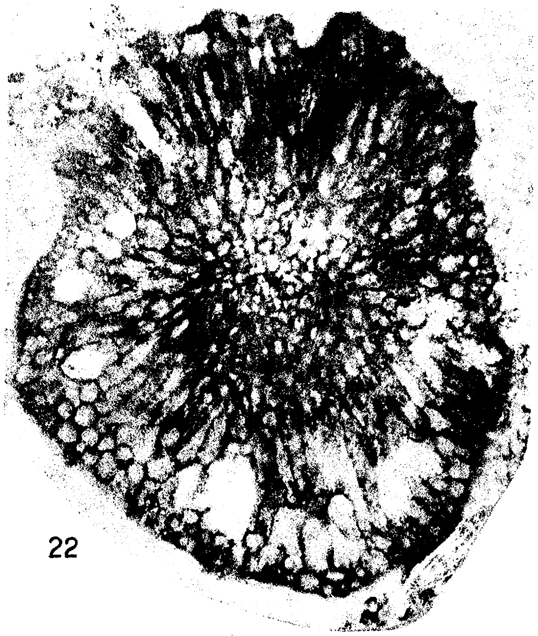

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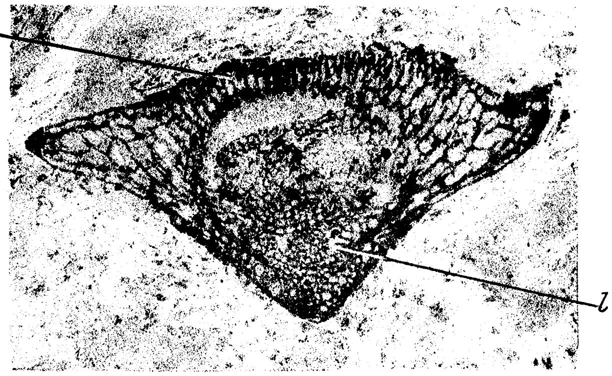

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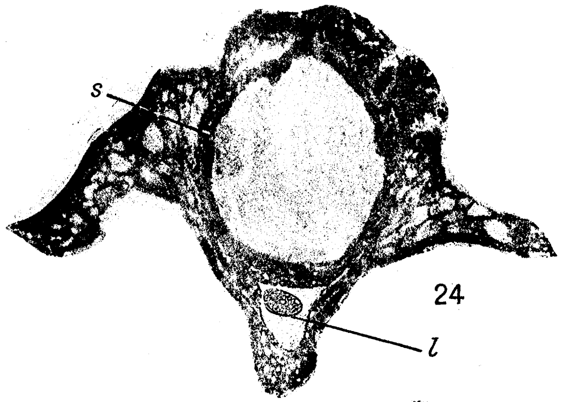

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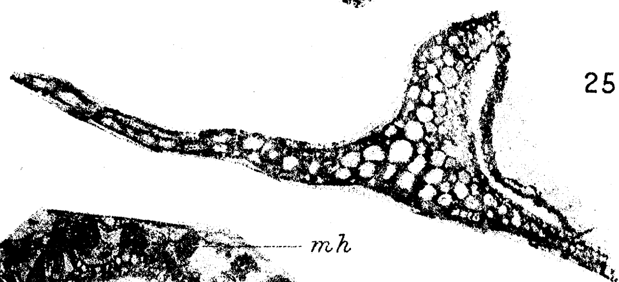

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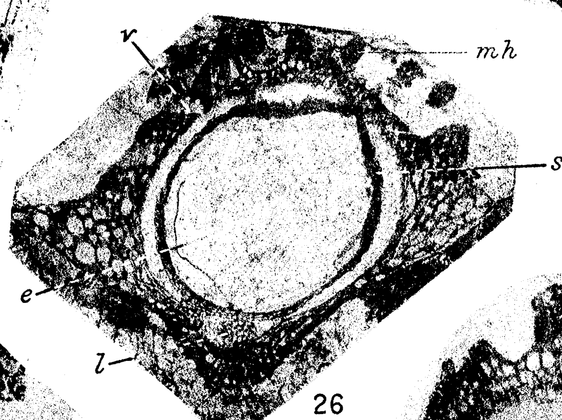

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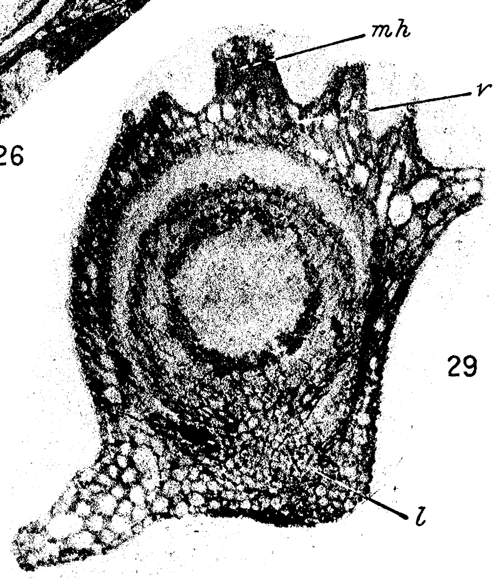

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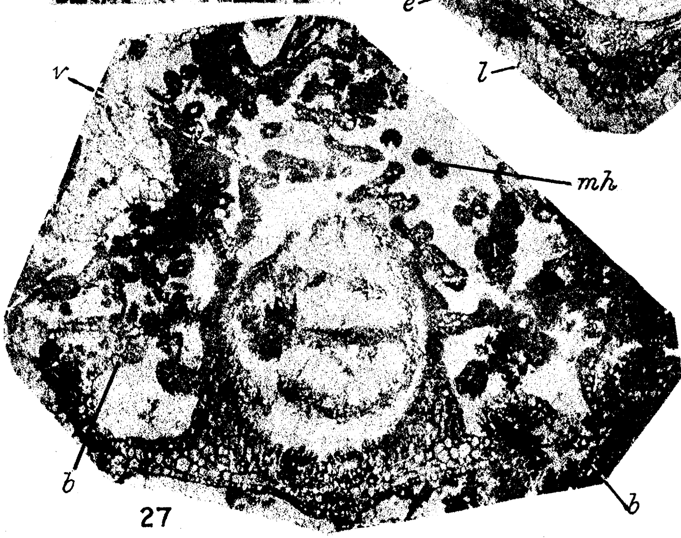

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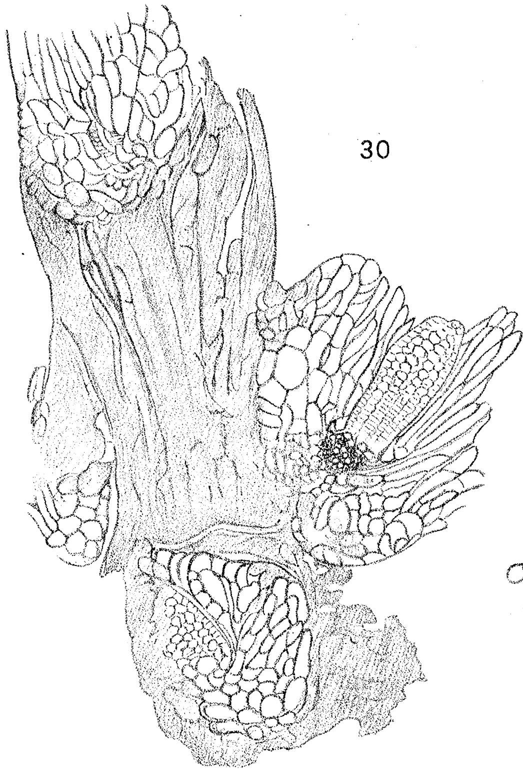

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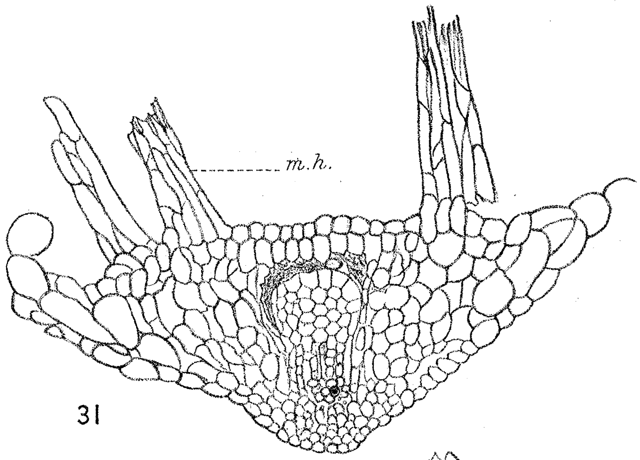

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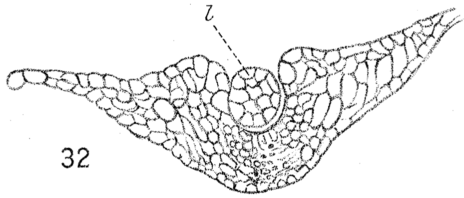

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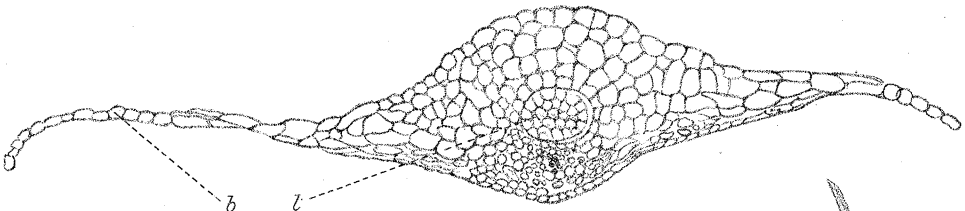

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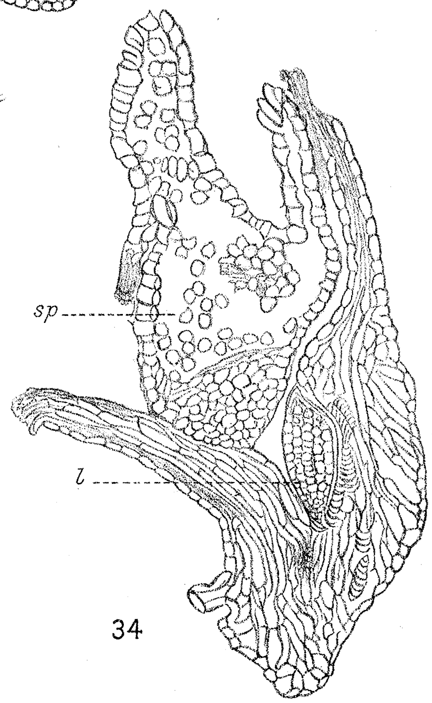

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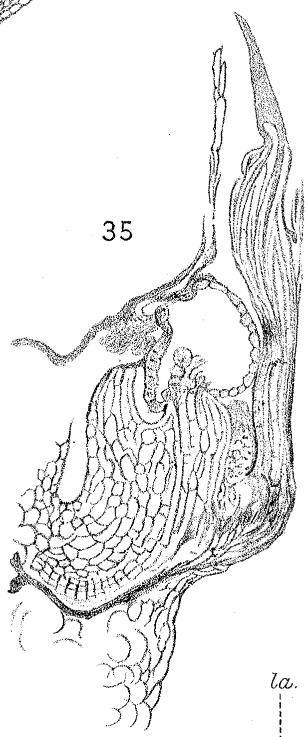

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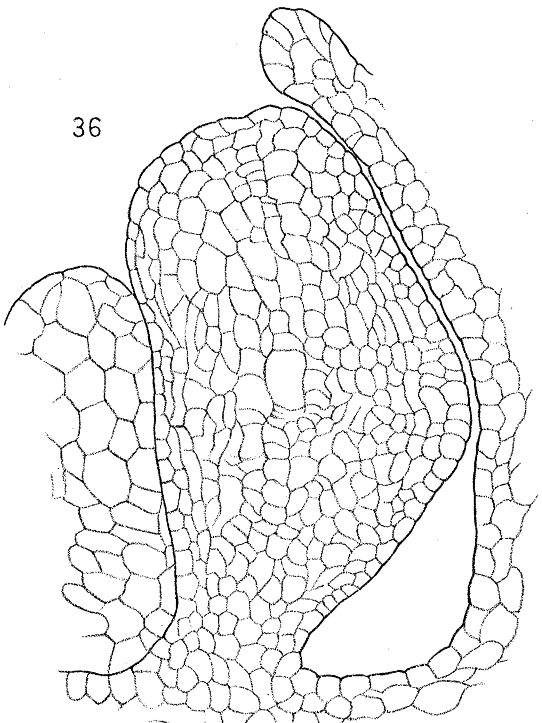

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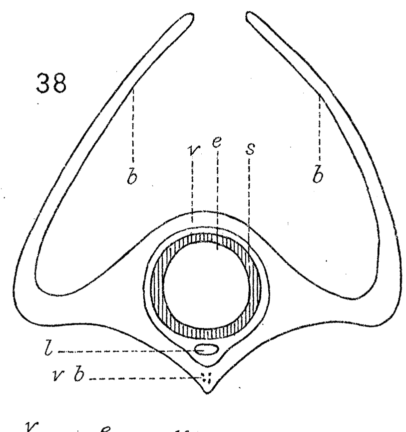

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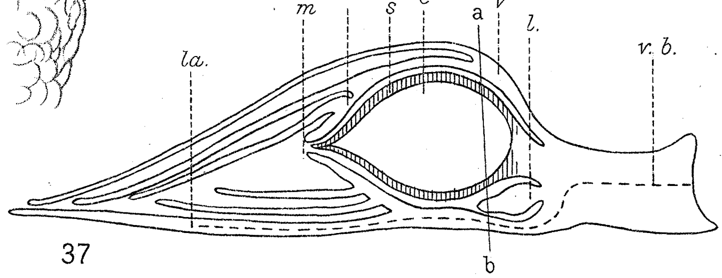

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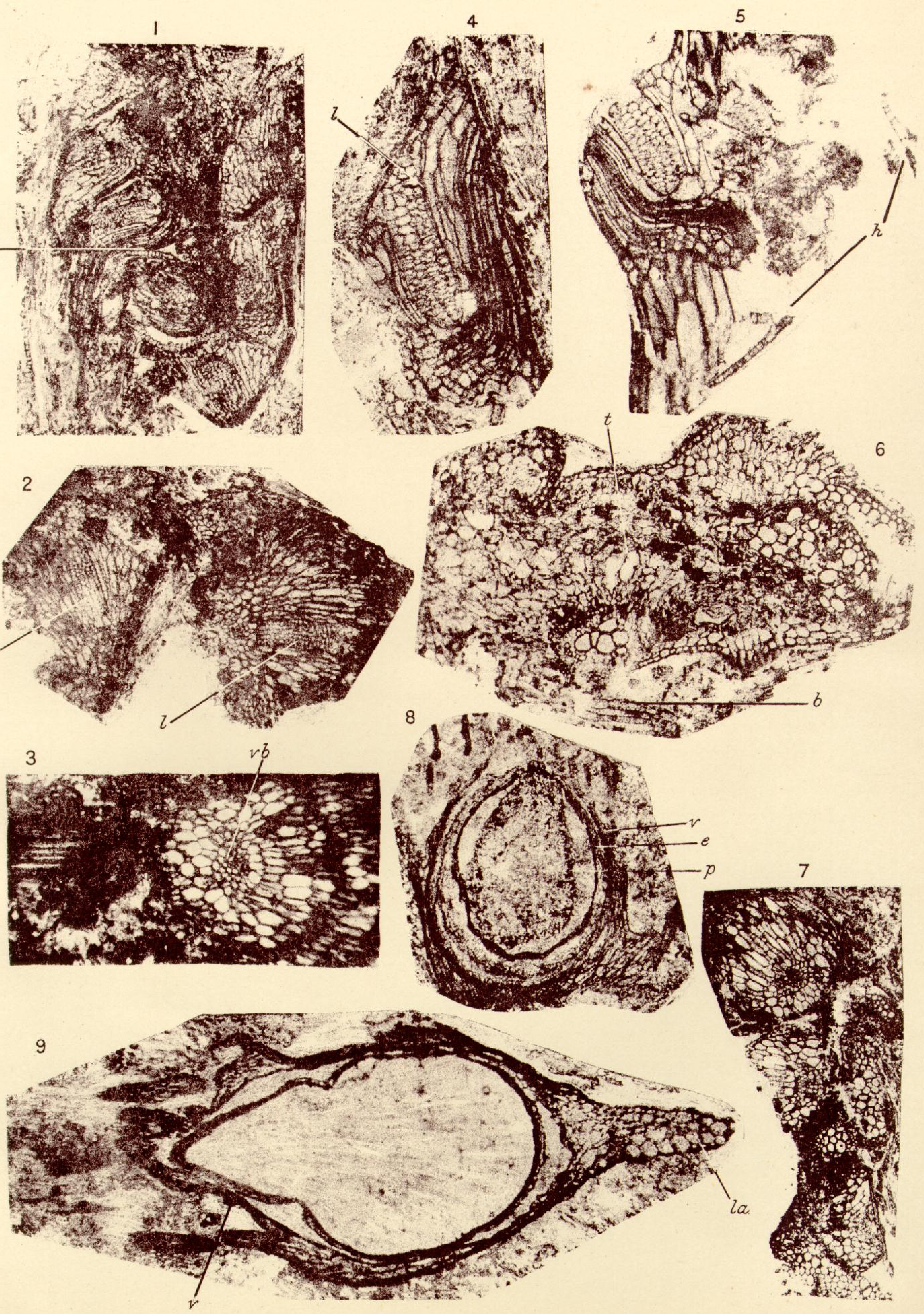

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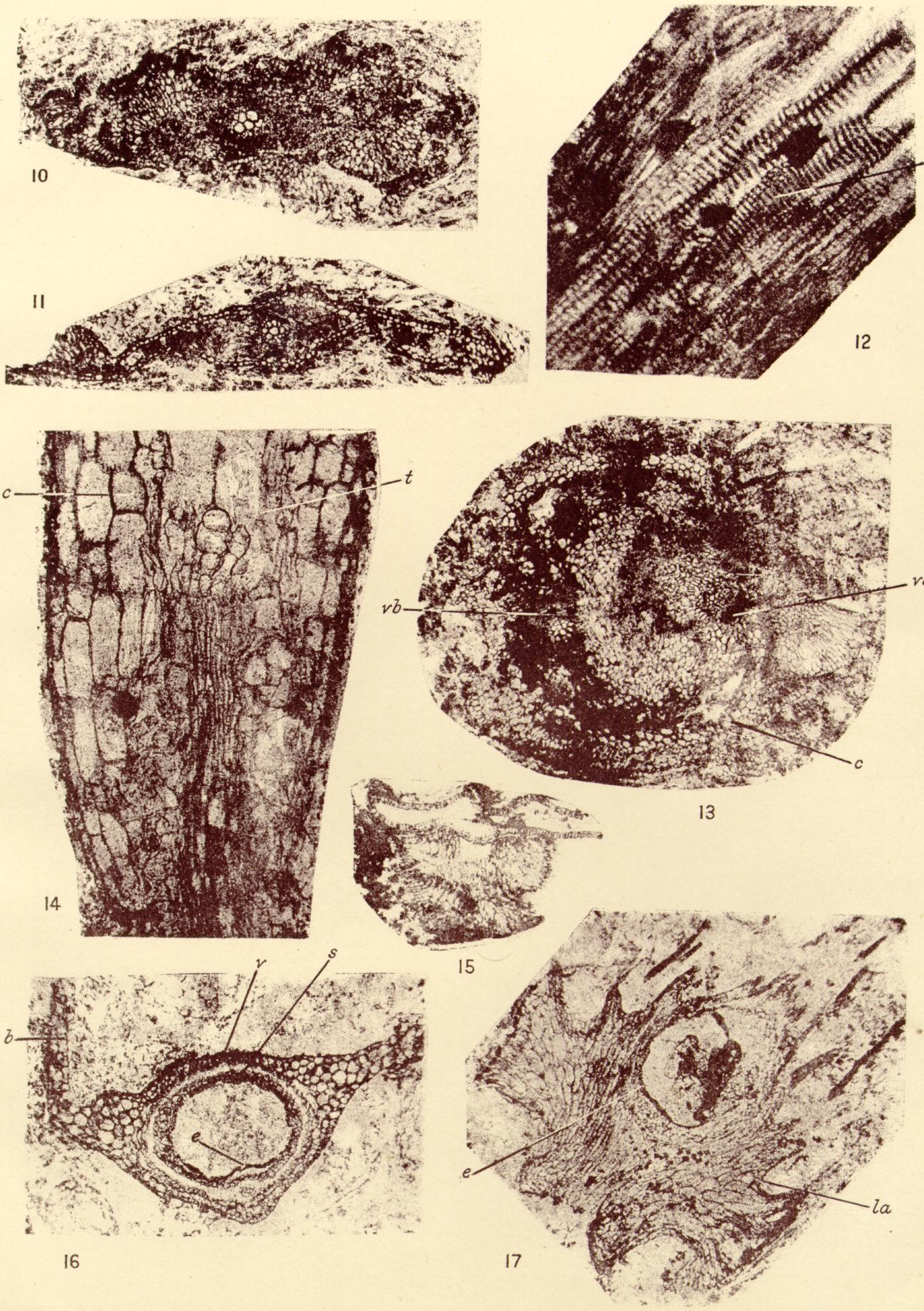

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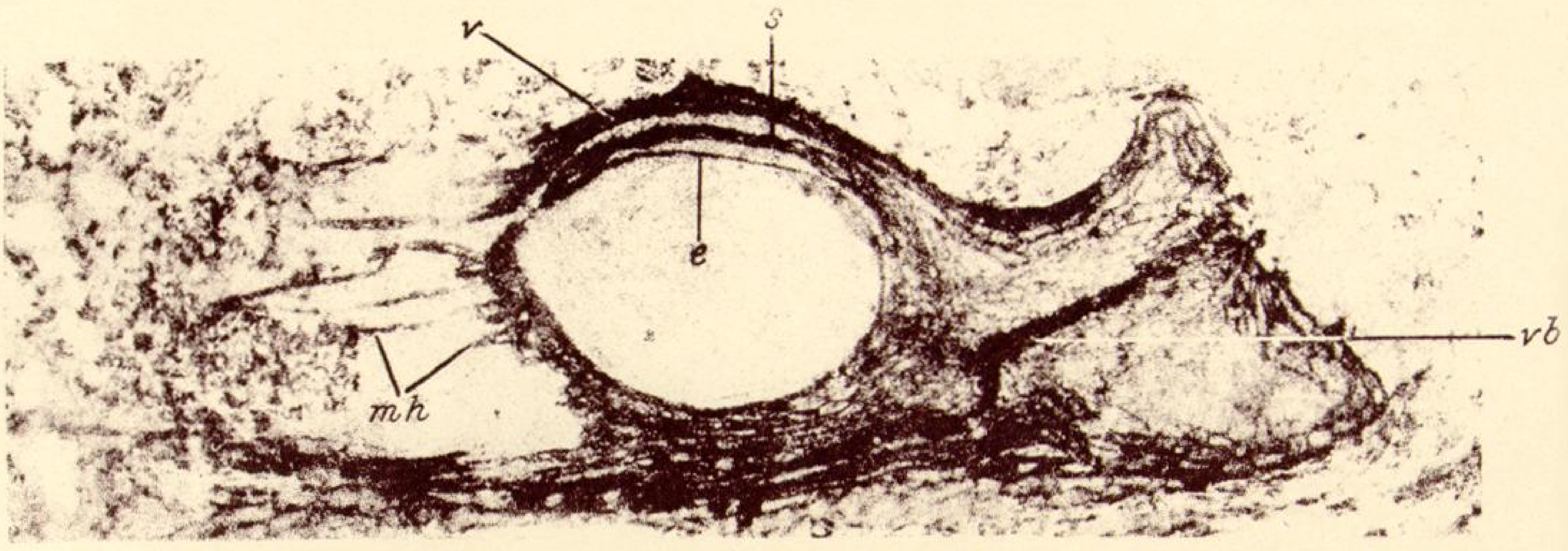

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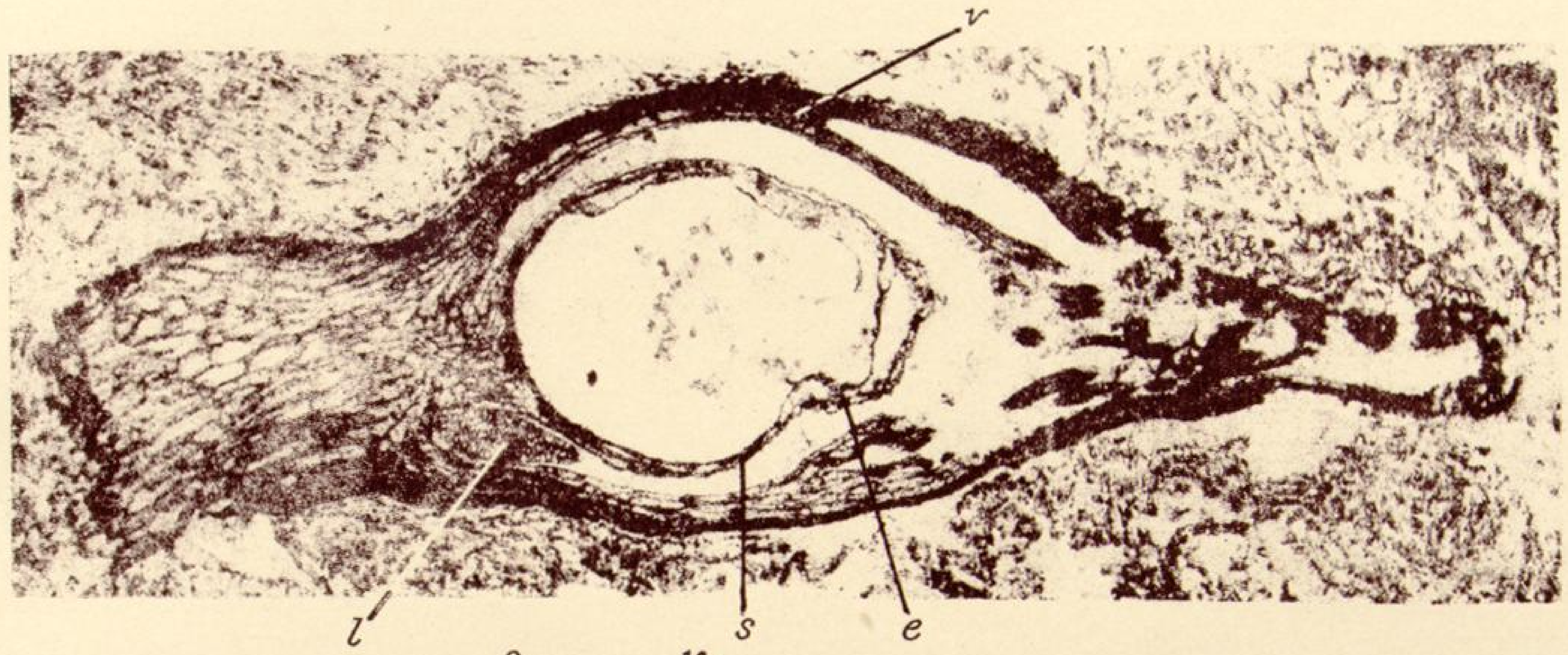

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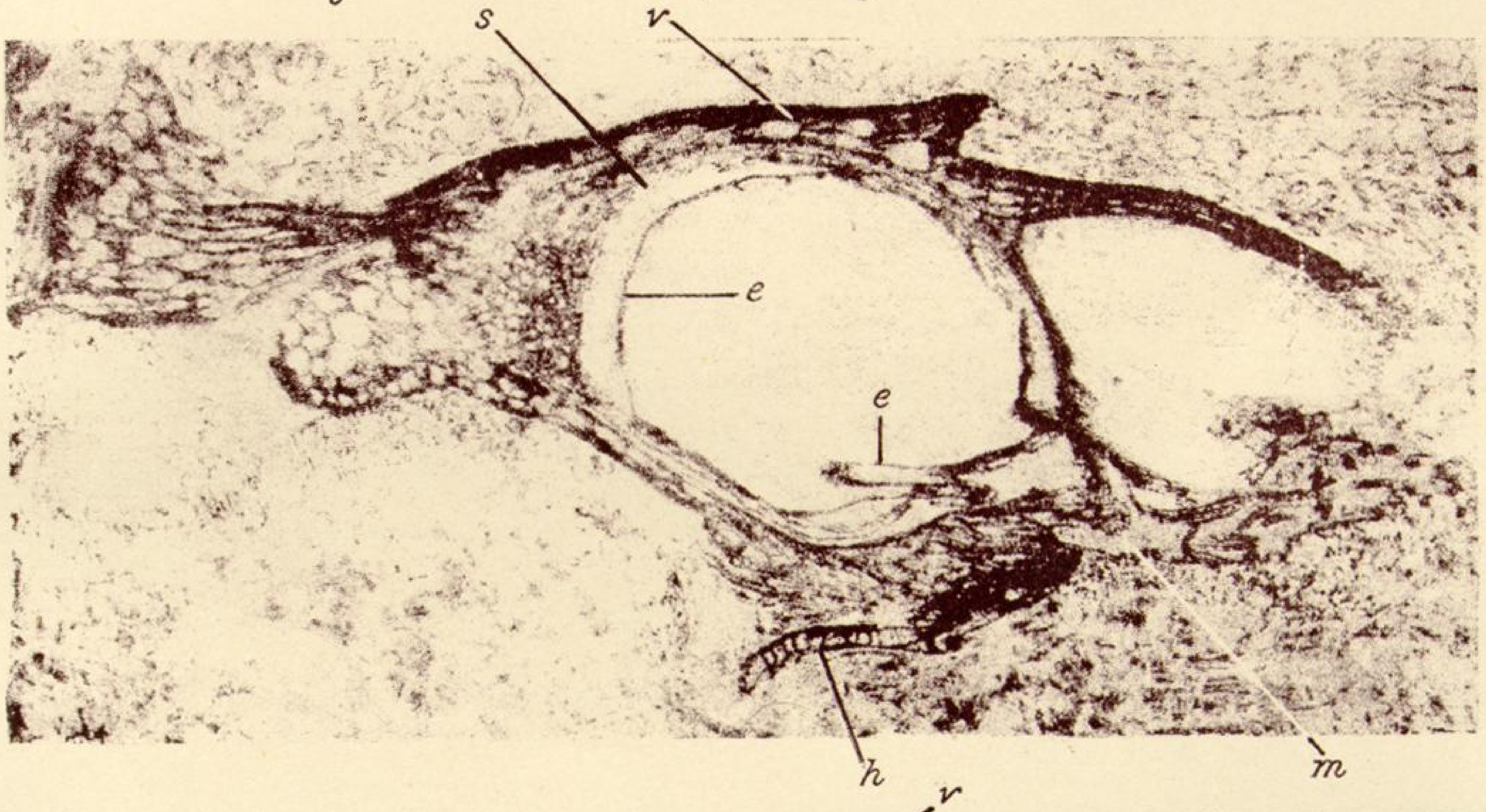

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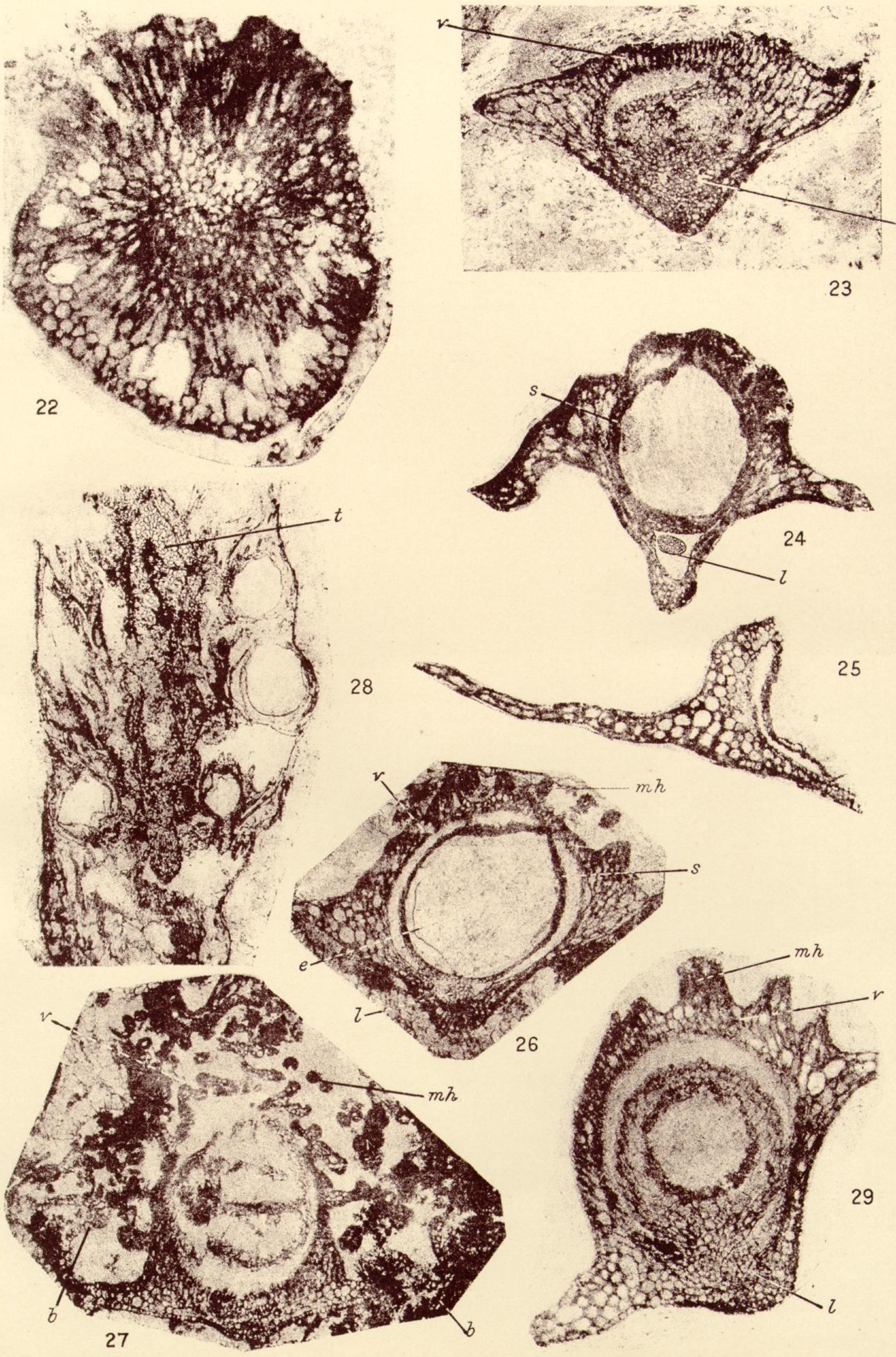

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FIGS. 22–27.—A series of tangential sections of the megasporophyll from the base upwards.

FIG. 22.—A tangential section through the base of the megasporophyll. The narrow border has perished. (×about 80.) 2241, S. Cloughfoot, Dulesgate.

FIG. 23.—Ditto through ligule and base of sporange. The walls of the ligular groove are shown, and also the velum, but the thin border to the lamina has perished. (×about 40.) 2242, S. Cloughfoot, Dulesgate.

FIG. 24.—Ditto through ligule and sporange. The keel is prominent in this plane. The thin border to the lamina has perished. (×about 40.) *cc* 7 *d*, O. Dulesgate.

FIG. 25.—Ditto of one side of the free lamina in a section approximately in the plane of fig. 16, Plate 2. (×40.) *cc* 7 *k*, O. Dulesgate.

FIG. 26.—Ditto still more distal, showing the velum now giving off processes. This section is oblique, as otherwise the ligule would not be seen in the same plane as the processes. (×about 40.) 91, H. Dulesgate.

FIG. 27.—The last of the series. The velum is breaking up over the apex of sporange into processes. The more proximately inserted processes, as seen in section, form a halo-like circle. The free part of the lamina is now at a much lower level relatively to the sporange and is of considerable width. (×about 40.) *cc* 7 *c*, O. Dulesgate.

FIG. 28.—A tangential section of part of a young cone with four megasporophylls in continuity. It should be compared with the vegetative shoot in fig. 1. The stem in the upper part shows the trabeculæ of the inner cortex and can be compared with those of fig. 14. (×18.) 88, H. Cloughfoot, Dulesgate.

FIG. 29.—An obliquely radial section of part of a young megasporophyll, showing the bent form and ligule, velum and sporange. The young spore is circular in section, and no trace of sister cells is to be seen. (×about 55.) 81, H. Cloughfoot, Dulesgate.

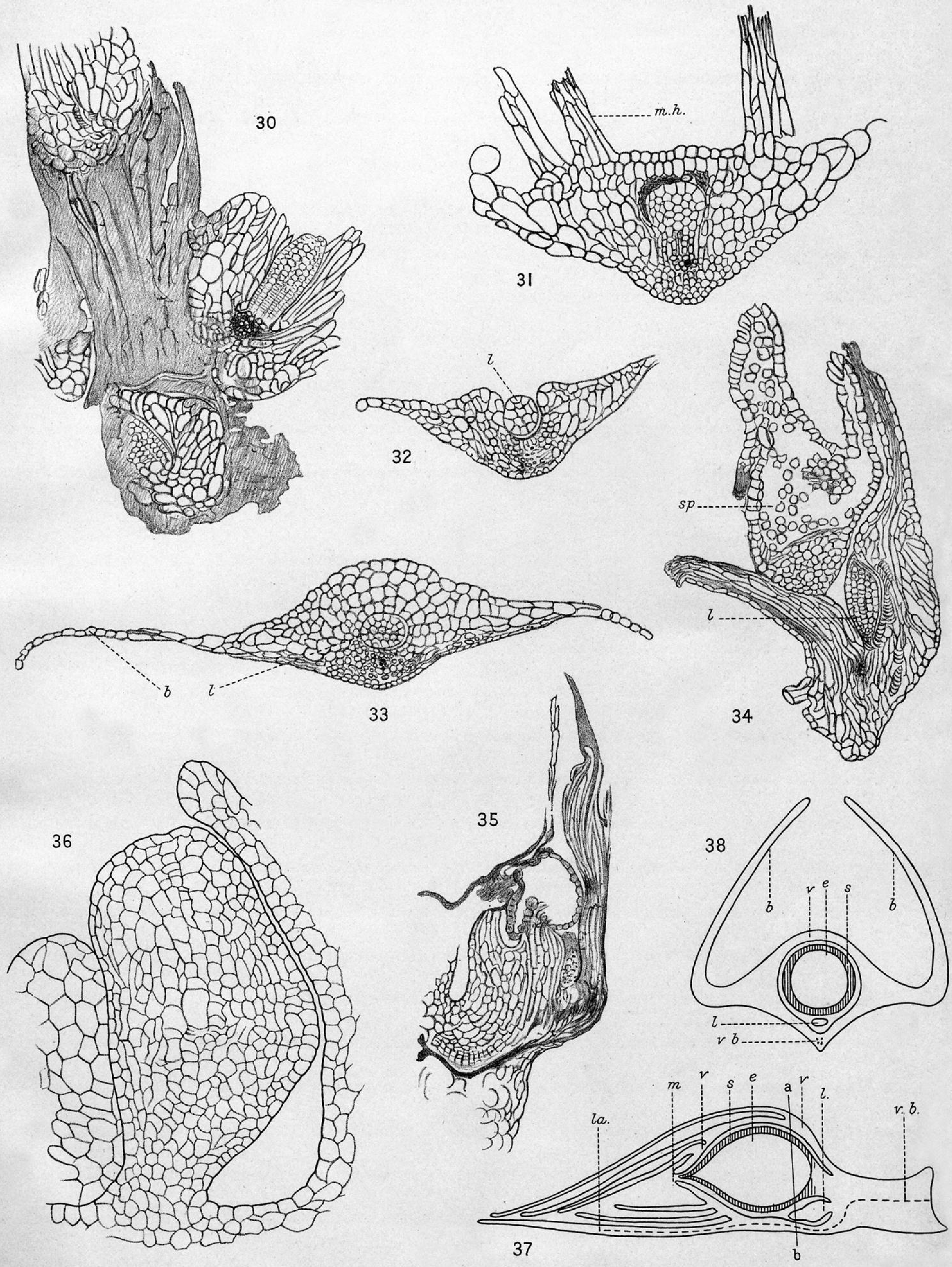

PLATE 37 (figs. 30–38).

FIG. 30.—A longitudinal section of a twig, showing the insertion of four leaves. (×about 80.) 87, H. Dulesgate.

FIG. 31.—An obliquely transverse section of a leaf, showing multiseriate hairs on the tissue covering the ligule. This section also shows the thin border to the lamina. (×120.) 87, H. Dulesgate.

FIG. 32.—A transverse section of a leaf, showing the exposed apex of the ligule. (×about 90.) 84, H. Dulesgate.

FIG. 33.—Ditto, more proximal, showing the tissue covering the ligule and the border of the lamina. (×about 90.) R, 194, M.

FIG. 34.—A longitudinal section of a microsporophyll escaping the attachment of the sporange, but showing the form of the ligule. Microspores are seen in sporange. (×about 80.) 84, H. Dulesgate.

FIG. 35.—A radial section of a young megasporophyll, showing mode of attachment to cone axis. This should be compared with fig. 28. The distal part of the velum was injured before petrifaction. The leaf is 1 mm. in length. (×about 90.) 94, H. Dulesgate.

FIG. 36.—A longitudinal section of a very young sporange, showing regular arrangement of cells. The ligule at this stage is two-thirds the size of the sporange. (×about 250.) 95 *b*, H. Dulesgate.

FIG. 37.—Diagram of a seed-leaf in radial plane. It shows sporange with embryo-sac, ligule, velum with its appendages, micropyle, and course of vascular bundle.

FIG. 38.—Diagram of a section through plane *ab* of above diagram. It shows the sporange and ligule roofed over by the velum.