
On the Structure and Affinities of Fossil Plants from the Palaeozoic Rocks. II. On Spencerites, a New Genus of Lycopodiaceous Cones from the Coal Measures, Founded on the *Lepidodendron Spenceri* of Williamson

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Phil. Trans. R. Soc. Lond. B 1897 **189**, 83-106
doi: 10.1098/rstb.1897.0011

References

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III. *On the Structure and Affinities of Fossil Plants from the Palæozoic Rocks.—II.*
On Spencerites, a new genus of Lycopodiaceous Cones from the Coal Measures,
founded on the Lepidodendron Spenceri of WILLIAMSON.

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Received November 2,—Read November 18, 1897.

[PLATES 12–15.]

INTRODUCTION.

THE fossils which form the subject of the present paper are Cryptogamic strobili showing evident Lycopodiaceous affinities, but differing in important points from other fructifications of that family, so that it appears necessary to establish a new genus for their reception. The specimens are derived from the Coal-measures of Lancashire and Yorkshire, and are calcified, the internal structure being thus preserved in considerable perfection.

As our present knowledge of the forms in question is entirely due to the researches of the late Professor W. C. WILLIAMSON, it will be necessary to give a short historical summary of the results which he attained, before going on to my own observations.

The first specimen described by WILLIAMSON* was a strobilus, of which he received sections from Mr. SPENCER and Mr. BINNS, of Halifax. From this material he gained a general idea of the structure of the axis, and showed that the sporangiophores are spirally arranged, and of peltate form, each bearing a single sporangium on its upper surface. He pointed out the peculiarities of the sporangial wall, in which this fossil differs from typical *Lepidostrobi*, and described in great detail the form and structure of the remarkable winged spores, as to the true nature of which he was in much doubt. It is unnecessary to follow his arguments in detail, but it may be mentioned that he had at that time already detected the minute spore-like bodies which sometimes occur inside the large spores, and that he interpreted the wings of the latter as consisting of their barren sister-cells, a view which no longer appears to be tenable.†

* "Organization of the Fossil Plants of the Coal Measures," Part IX., 'Phil. Trans.,' 1878. Read in 1877.

† *Loc. cit.* pp. 340–344, Plate 22, figs. 38–47 and 52–57.

At that time WILLIAMSON called the cone merely a *Lepidostrobus*, without giving it any specific name, though he quite recognised its peculiar characters.

In his next memoir,* the author described a second specimen of the strobilus, of which he had received two transverse sections, also from Mr. SPENCER. He was thus enabled to give a fuller account of the anatomy than before, and to show that it possessed a "generally Lycopodiaceous aspect." He points out, however, that we do not see in this cone "any traces of transverse sections of" the leaf-trace bundles "grouped around the vascular axis, such as constitute so striking a feature of true *Lepidostrobi*." He emphasizes the "very distinctive individuality" of the strobilus, and names it *Lepidostrobus insignis*. This name, therefore, has priority, as the first given to the species.†

Ten years later, in 1889, WILLIAMSON, in his 16th Memoir, described specimens from Mr. SPENCER, of a supposed vegetative stem, to which he gave the name of *Lepidodendron Spenceri*.‡ The anatomical features are described and figured, and attention is especially called to the occurrence of partially-developed tracheæ in the middle of the woody axis, thus proving its centripetal development. The author overlooked the remains of foliar organs, the bases of which are often visible in these specimens, and was under the mistaken impression that the outermost cortex had perished, which is certainly not the case. At that time he made no suggestion of any relation between *Lepidodendron Spenceri* and the strobilus previously described.§

In the last Memoir of the series, however,|| WILLIAMSON established the connection between the two. He says (p. 24): "Since the last of the above Memoirs (Part XVI.) was published, I have obtained specimens highly suggestive of the probability that the strobilus of Memoir IX., and the twigs named *L. Spenceri*, belonged to the same plant. This probability is now converted into a certainty by a specimen received from Mr. LOMAX, and now represented by fig. 41, Plate 7. It is an obliquely transverse section through a branch of *L. Spenceri* (C.N., 624E, $\times 10$), but at its upper extremity A, it bears a portion of the strobilus of Memoir IX." There is no doubt that the conclusion at which WILLIAMSON thus arrived is correct; as we shall see, the so-called vegetative specimens of *Lepidodendron Spenceri* are nothing but the peduncles of cones. Unfortunately, the true vegetative organs, to which the fructifications belonged, are still unknown or unidentified.

In this Memoir, the author maintained his former opinion that the annular wing surrounding each spore, consists of its three sterile sister-cells. A very important addition to our knowledge is the description in Memoir XIX., of a fine longitudinal section of a strobilus; from this, WILLIAMSON rightly (though with some reserve)

* "Organization," &c., Part X., 'Phil. Trans.,' 1880, p. 501. Read in 1879.

† *Loc. cit.* pp. 501-2, Plate 15, figs. 11 and 12.

‡ "Organization," &c., Part XVI., 'Phil. Trans.,' 1889.

§ *Loc. cit.*, p. 199, Plates 7 and 8, figs. 19-22.

|| "Organization," &c., Part XIX., read 1892, published 1893.

determined the mode of attachment of the sporangia to the sporophylls, a point which, as we shall see, is of the greatest importance in fixing the taxonomic position of the species.

In his 19th Memoir, WILLIAMSON points out that "the marked individuality of this rare type," "seems to justify its recognition as a distinct species." In his "General Index," however (Part II., p. 24, 1893), he goes further, and speaks of *Lepidodendron Spenceri*, as "a small and rare Lepidodendroid form, which presents so many peculiarities in its fructification, that it may possibly be necessary sometime, to make it the type of a new genus." In the "Index" the author gives an account of the variations met with in the structure of the central cylinder, and gives a fuller description of the cortex than before.

The only other account of the fossil known to me, is a short statement in Count SOLMS-LAUBACH'S 'Fossil Botany,' in which the structure of the spores is described, and the resemblance of the axis to that of *Lepidodendron Harcourtii* pointed out.*

The chief object of the present paper is to show, by means of a connected account of the whole structure, based on a comparative examination of the fairly numerous preparations now available, that WILLIAMSON'S suspicion of the generic distinctness of this fossil is fully justified, and that it thus represents a new type of Lycopodiaceous cone. A second species of the same genus will also be described.

A word as to nomenclature is necessary at the beginning, in order that the same name may be used throughout the paper.

As mentioned above, the specific name *Spenceri*, must be dropped, for that of *insignis* has the priority over it by ten years. As the fossil is a cone and not a vegetative stem, it would thus bear WILLIAMSON'S original name of *Lepidostrobus insignis*, were it not that its peculiarities, as will be shown below, demand generic separation. In order that the discoverer of the original specimens may still be commemorated, I have selected the generic name *Spencerites*, so that the species in question will be called *Spencerites insignis*, for which *Lepidostrobus insignis*, WILLIAMSON, 1879, and *Lepidodendron Spenceri*, WILLIAMSON, 1889, are synonyms. To this species all the specimens described and figured by WILLIAMSON in the 'Phil. Trans.' Memoirs belong. There is, however, a second species, a specimen of which is referred to in his "General Index,"† but not discriminated. For the new species the name *Spencerites majusculus* is proposed. Generic and specific diagnoses will be given at the close of the paper, after the structure has been described.

* 'Fossil Botany,' 1887; English Edition, p. 239.

† Part 2, p. 24. This is the strobilus represented in the WILLIAMSON Collection by slides 624c and 624g.

I. SPENCERITES INSIGNIS (*Williamson*).1. *The Axis and Bracts.*

It makes little difference whether the structure of the axis be studied in the peduncle or in the cone itself; the characters are practically the same, and present similar variations in both. The diameter of the axis ranges from 3·5 to 5 millims. As the epidermis can usually be traced as a continuous and unbroken layer, there can be no question that the specimens are complete externally, and that no part of the outer cortex has been lost (see Plate 13, fig. 6). The specimens of the peduncle often show the remains of foliar appendages, which are sometimes reduced to mere shreds, and are never preserved entire. Fig. 6 shows the best specimens of one of these appendages which I have found. It has a somewhat conical form, and evidently represents the stalk only of the organ; whatever there may have been of the nature of a lamina has perished, except for some torn shreds. These appendages closely resemble the stalks of the sporophylls in the actual cone (*cf.* Plate 14, fig. 11); on the other hand, they are totally unlike the bases of vegetative leaves in any of the Lycopods; they are best regarded as sterile bracts. Their bases by no means cover the whole exterior of the stem, as is the case in the vegetative regions of *Lepidodendron*; a considerable part of the surface is left free.

The material does not allow of the phyllotaxis being determined from the leaves themselves, for they are only preserved occasionally. From the position of the leaf-traces, however, some idea of the arrangement can be gained. On carefully following the leaf-traces in transverse section, through a complete circuit (not an easy undertaking, as their oblique course renders them excessively obscure), it appears that the arrangement is a very flat spiral.* The same conclusion follows, perhaps more clearly, from the examination of a tangential section through the cortex, as shown in Plate 13, fig. 7. The divergence between two adjacent leaves was about one-ninth or one-tenth of the circumference, as shown by the position of the leaf-traces in transverse sections, confirmed by a single case in which the bases of two adjacent leaves are preserved.† It is not improbable that at some places the spiral arrangement may have passed over into a verticillate one, with crowded alternating whorls.

Passing on to the anatomy of the axis, we find that the parts usually preserved are the following:—First, in the middle is the central strand of wood; around this is usually a narrow empty space, from which the soft tissues (probably phloem and pericycle) have, as a rule, perished. Then we come to a zone which may be called the inner cortex, in which the sections of the leaf-trace bundles may often be seen. Beyond this is another space, more or less empty in most of the sections, and of considerable width, representing the middle cortex, which in some cases is partly preserved.

* C.N. 419B, for example, and other sections of the same group of peduncles.

† Slide No. 3 in my own collection.

To the outside of all is the zone of well-preserved, partly sclerotic, outer cortex, bounded externally by the epidermis, and bearing the foliar appendages, where these are preserved.* The chief variations in the structure of the central mass of wood have already been described by WILLIAMSON.† Sometimes the tracheæ occupy the whole area, extending quite to the centre; in other sections a few thin-walled cells occur in the middle of the strand; in others again, the central thin-walled tissue is more extensive, and appears to deserve the name of a medulla. These variations occur both in the sterile region, which I regard as peduncle, and in the strobilus itself.‡

Longitudinal sections show that the central thin-walled cells, when present, are prosenchymatous (Plate 13, fig. 8B, and WILLIAMSON, Mem. 16, Plate 7, fig. 22); they should perhaps be regarded in most cases rather as undifferentiated procambium than as constituting a true pith. This interpretation would agree well with WILLIAMSON'S observation that tracheæ with very delicate thickenings, apparently in course of development, occur in this central tissue,§ showing that the centripetal differentiation of the xylem was not yet complete near the centre, even when the organ was mature. Curiously enough, these central tracheæ are sometimes spirally thickened (fig. 8B), while those of the wood generally are scalariform, but they must not be confused with the narrow spiral tracheæ of the protoxylem, which here, as in Lycopods generally, lie at the extreme periphery of the wood (fig. 8A), and are usually somewhat disorganized.

In one of the strobili (C.N. 1922F *ter*, &c.), the central cells appear very thick-walled (see Plate 13, fig. 4). If this is really their natural condition, and not due to any process of infiltration, the medulla here differs from that of other specimens. There is no doubt from the other characters (spores, &c.), that this strobilus is of the same species with the rest.

Seen in transverse section, the protoxylem-angles (which correspond to the insertion of the leaf-trace bundles) are not very prominent—they are usually about 10 in number.

As a rule, the tissues immediately surrounding the wood have perished; in one case, however|| (see Plate 13, fig. 5), the whole of the tissue between wood and inner

* See Plate 13, fig. 4; also WILLIAMSON, 10th Mem., Plate 15, fig. 11, and 16th Mem., Plate 8, fig. 19.

† 'General Index,' Part 2, p. 25.

‡ Thus, of the four peduncles shown in C.N. 419B, and other sections of that block, some show solid wood, others a small medulla; the peduncle shown in C.N. 1922F *bis* has a considerable medulla. Similarly, the axis of the strobilus shown in Fig. 4 (C.N. 1922F *ter*), and that in C.N. 624, represented by WILLIAMSON (10th Mem., Plate 15, fig. 12), have a well-marked medulla, which appears to be entirely absent from the section C.N. 627, also of a strobilus.

§ "Organization," &c., 16th Mem., p. 199, Plate 7, fig. 22.

|| Section No. 4 in my own Collection. MR. SPENCER informs me that this was cut from the base of the same cone of which sections are figured by WILLIAMSON, in his 10th Mem., Plate 15, figs. 11 and 12 and 19th Mem., Plate 7, fig. 50.

cortex is preserved, though slightly crushed. This zone consists of small, thin-walled cells, no doubt representing the phloëm; slightly larger cells, which border on the coarser cortical tissue, may be regarded as pericyclic.

The inner cortex, which is constantly preserved, consists of a few layers of fairly thick-walled somewhat elongated cells (see Plate 14, fig. 9). The broader middle cortex beyond has often disappeared, rather on account of its loose texture than because its cells were specially delicate. Sometimes the more coherent sheaths, surrounding the leaf-trace bundles, are alone preserved, while in other cases the whole of the middle cortical tissue has remained fairly perfect (see fig. 9). It consists of curiously interwoven, long, sometimes branched cells, with rather thick walls, resembling the form of trabecular tissue found by BOWER in the cortex of various Lycopods, recent and fossil.* These cells are connected, sometimes with the inner or outer cortex, sometimes with the sheaths of the leaf-trace bundles. Single cells of this layer may recall the curious internal hairs found in the cortex of the root of *Pilularia*.†

The outer cortex forms a fairly thick zone, nearly always well preserved, and consists in its external portion of more or less well-defined radial bands or masses of sclerenchyma, surrounded by rather more delicate tissue (see fig. 4), while its inner zone is more uniform, and without special groups of sclerenchyma. The sclerenchyma appears to constitute a network, the meshes of which are occupied by the more delicate tissues, through which the leaf-trace bundles pass out. The distinction between the two kinds of tissue is not always equally well marked, for sometimes the cell-walls are considerably thickened throughout the external cortex, but, on the whole, the "Dictyoxylon" structure of the cortex is characteristic, and serves, among other features, to distinguish *Spencerites insignis* from such forms as *Lepidodendron mundum*, WILL. The elements of the outer cortex are generally prosenchymatous. The small-celled epidermis is often very distinct (see fig. 6, e).

The leaf-trace bundles, as they start from the central cylinder, diverge but little from the vertical, gradually curving so as to assume a nearly horizontal direction before entering the bracts. The vertical distance traversed by each leaf-trace is small—about 0·8 millim.—and scarcely equal to the length of an internode (*cf.* Plate 13, fig. 7). Hence, the number of these strands met with in transverse section is small, usually about nine or ten, approximately equal to the number of appendages in one circuit of the spiral. Thus the leaf-trace bundles, owing to their small number and obliquity, by no means form so conspicuous a feature in the transverse section, as is usually the case in the axis of the *Lepidostrobi*, a distinction noted long ago by WILLIAMSON.‡

* "On the Structure of the axis of *Lepidostrobus Brownii*." 'Annals of Botany,' vol. 7, p. 341, Plate 17, 1893.

† Russow, 'Vergl. Untersuchungen,' Plate 2, fig. 20.

‡ "Organization," Part X., 1880, p. 502.

Each bundle is surrounded by a strongly-developed sheath, which is especially evident where the lacunar middle cortex is traversed (Plate 14, fig. 9, *sh*). The structure of the bundles is best shown in tangential sections of the outer cortex (fig. 10). The phloem has almost wholly perished, but from the position of the parts it is most probable that the bundle was concentric; the smallest elements (protoxylem?) lie toward the middle of the woody strand.

The bract-like appendages, or rather their stalks, which are alone preserved, consist of an outer envelope of thick-walled, elongated cells, within which is a more delicate tissue surrounding the vascular bundle.

The anatomical description just given applies equally to the sterile specimens, which I interpret as peduncles, and to the axis of the cone itself (compare Plate 13, fig. 4 with WILLIAMSON'S figure in his 16th Memoir, Plate 8, fig. 19). So close is the agreement that the question arose whether the apparently barren specimens might not be simply withered fructifications, which had lost their sporangia, and partly lost their sporophylls, before fossilization. It is more probable, however, that the sterile portions really represent the peduncle of the cone, for in one specimen at any rate,* peduncle and cone were found in connection. The section (C.N. 624E) figured by WILLIAMSON in his 19th Memoir, Plate 7, figs. 41 and 42, was cut from the transitional region between the peduncle and the actual strobilus.

It also appears that the sporophylls of the cone itself were more crowded than the bracts of the sterile specimens. (Compare WILLIAMSON'S figure in his 9th Memoir Plate 22, fig. 54, with fig. 7 in the present paper.)

2. *Sporophylls and Sporangia.*

The general organization of the cone has been fully described and illustrated by WILLIAMSON in his 9th and 19th Memoirs above cited. The longitudinal section represented in the latter Memoir, Plate 7, fig. 50, is extraordinarily perfect, and gives a better idea of the whole structure than any other preparation. In this case the arrangement of the sporophylls may not improbably have been in alternating verticils. The section passes directly through an orthostichy of sporophylls on either side of the axis. It is instructive to compare the tangential section, figured by WILLIAMSON (from another specimen) in his 9th Memoir, Plate 22, figs. 54, 55, which show very clearly the alternation of the sporophylls in the adjacent orthostichies. The short sporophylls and spherical sporangia give the cone a very different habit from that of a *Lepidostrobus*.

The form of the individual sporophyll is peltate; the stalk is horizontal, resembling that of the bracts already described; at the distal end it expands into a lamina, of looser tissue, projecting both upwards and downwards, so as to cover in the sporangia lying between. A single sporangium belongs to each sporophyll, as is

* From which sections C.N. 624D, E, and F, and 1922F *bis*, in the WILLIAMSON Collection were cut.

evident from the comparison of sections in the three planes (see Plate 14, figs. 11 and 13, together with WILLIAMSON'S figures above cited).

The most important question relates to the point of insertion of the sporangia on the sporophylls. WILLIAMSON (19th Memoir, p. 25) determined this with perfect accuracy, though he expressed his opinion with some reserve. The sporangium is attached, by a narrow neck of tissue only, to the upper side of the sporophyll, near its distal end, where the lamina begins to expand. There is no attachment whatever to the horizontal pedicel of the supporting organ, and in this respect *Spencerites* differs entirely from any species of *Lepidostrobus*. The point of attachment is evident at several places in the radial section referred to. In Plate 14, fig. 11, which is taken from this preparation, the lower sporophyll is incomplete, but the insertion of the sporangium at α is unmistakable, though slightly obscured by a fragment of coal which overlies the connecting tissue. In the sporophyll next above, the connection with its sporangium is broken, but the point of attachment was no doubt at α . In fig. 12 from another preparation, a sporophyll is figured, which has been detached from its base, and is fortunately cut in the radial plane. The form of the lamina is well shown, and at α the remains of a sporangium, seated on its upper surface, near its junction with the pedicel, are evident. The points of sporangial insertion detected by WILLIAMSON, have been re-examined and his interpretation confirmed. A reference to WILLIAMSON'S figure (19th Memoir, Plate 7, fig. 50, e' and f'') will show that the place of insertion is on the upward slope of the peltate lamina, here incompletely preserved. Our fig. 13 is from a transverse section, and shows very clearly that the sporangium is connected at its distal end with the sporophyll-lamina. The connecting neck of tissue was evidently wider in the tangential than in the radial plane. The vascular bundle approached very closely to the base of the sporangium and may have been connected with it by a short branch (figs. 11 and 12).

The structure of the sporangial wall was described and figured by WILLIAMSON in his first account of the fossil.* In its present state of preservation it is one cell only in thickness (except sometimes near the point of attachment); the cells of which it consists are prosenchymatous, their elongation lying in the plane of the sporangial surface, and not at right angles to it. They thus differ entirely from the palisade-like cells which usually constitute the wall of the sporangium in *Lepidostrobus*. The lateral septa of the cells of the sporangial wall are considerably thickened, while their top and bottom membranes are much more delicate.

3. *The Spores.*

The spores themselves have been very fully described by WILLIAMSON, whose interpretation of their structure, however, is, I believe, mistaken. Each spore, in its

* "Organization," Part IX., p. 341, Plate 22, fig. 38.

mature state, has approximately the form of an oblate spheroid, with a broad hollow wing running round its equator (see Plate 14, figs. 11 and 14A).* The maximum diameter of the spore itself is on the average 0·14 millim., while the whole diameter, including the wing, reaches 0·28 millim. The membrane of the spore is thick; that of the wing is excessively delicate. The cavity of the wing is widest at a short distance from its insertion on the spore, and narrows off towards its outer edge. WILLIAMSON interpreted the wing as consisting of the abortive sister-cells of the spore. For this view there is, I think, no evidence. The cavity of the wing always appears empty, whereas that of the spore itself constantly shows some remains of cell-contents. Also, the wing appears to be perfectly continuous all round the spore, and not to be in any way sub-divided into compartments or cells. The fusion of the three abortive sister-cells of a macrospore into such a continuous ring, is entirely without precedent, and can hardly be assumed in the absence of any positive evidence. The fact that the winged spores of *Spencerites* are often found still grouped in their original tetrads (see fig. 14B) is also opposed to the interpretation of each spore as itself representing a group of four sister-cells. On the latter assumption, we should have tetrads of tetrads, an arrangement for which there seems to be no analogy.

There is, I think, no doubt that the interpretation of the wing suggested by Count SOLMS-LAUBACH is the right one,† namely, that it “represents an organ analogous with the air-sacs of the pollen of the Pine.” When seen in sectional view, the spore of *S. insignis* bears a considerable resemblance to the pollen grain of *Pinus* (see fig. 14), though, as the superficial aspect shows (see fig. 11; also, WILLIAMSON, 19th Mem., Plate 7, figs. 43 and 44), its real form is quite different, for in the fossil the air-sac forms a continuous rim all round the spore, a fact not recognised by Count SOLMS-LAUBACH. There is little doubt, however, that the wing agrees with the air-sacs of *Pinus* pollen in being formed by a dilation of the cuticle, and probably its function was the same.

The four spores of a tetrad are arranged tetrahedrally, as is shown with great clearness in some of the sporangia (see Plate 14, fig. 14B, and compare with WILLIAMSON, 9th Mem., Plate 22, fig. 57). At this stage, the tetrahedral form of the individual spores is still evident; when they become free their shape grows more spheroidal. The lines of junction of the three sister-cells are indicated on the spore by three sharp ridges, meeting each other at an angle of 120° (see WILLIAMSON, 19th Mem., Plate 9, fig. 49, and fig. 14A in the present paper).

The wings lie in the planes of the four free surfaces of the tetrahedral group (see fig. 14B). Hence the wing of each spore, as seen in surface view, has a somewhat triangular outline (see fig. 11).

The cell-contents of the spore are often represented merely by a dark carbonaceous mass in the middle of the cell. In other cases, however, the central body shows a

* Also WILLIAMSON, “Organization,” Part IX., Plate 22, figs. 46, &c., and Part XIX., Plate 7, figs. 43 and 44.

† ‘Fossil Botany,’ English edition, p. 239.

very definite structure, forming a regular reticulum, suggestive of a cellular tissue (fig. 14A, *cb.*). In other cases again, a number of small spherical spore-like bodies are contained within the large spore, a condition which has been repeatedly figured by WILLIAMSON.* These minute spore-like bodies have an average diameter of about 0·02 millim. They have a very distinct outline, and evidently possess a membrane of their own, which in some cases has split. Similar sporules, as we may provisionally call them, also occasionally occur free in the cavity of the sporangia; in one case where this was noticed, two large spores in their neighbourhood had manifestly burst, and there is little doubt that it was from them that the free sporules had been derived. In some cases appearances are met with within the larger spores, which indicate that the sporules may be developed from the central reticulum. The latter body has been interpreted as a prothallium, a very tempting idea, and probable enough if we consider the analogous case observed by M. RENAULT in the pollen grains of *Cordaites*. It is impossible to arrive at a certain conclusion, but the impression left on one's mind, after the examination of a great number of spores, is rather that the reticulum is the expression of some pathological or *post-mortem* change in the cell-contents. The definite cellular appearance seems to be only a particular case of a variable and inconstant frothy coagulation. How, then, are we to interpret the free sporules which occasionally appear, and which seem to have been sometimes set free by the bursting of the spores within which they were formed? Various possible views were discussed by WILLIAMSON, without his reaching any decisive conclusion.† The sporules are of comparatively rare occurrence, and I do not myself believe that they form part of the normal structure of the spores. That the large winged bodies really are the spores (whether microspores or macrospores) can no longer be doubted, and the production of spores within spores would be a phenomenon without analogy among Vascular Cryptogams.‡ I therefore incline to regard these sporules as foreign bodies, possibly the product of some low organism, parasitic or saprophytic, within the spore. Fungi living and fructifying within pollen grains and spores are well known at the present day.§

Another possibility which has been suggested to me is that the "sporules" may merely represent altered vesicular aggregations of the protoplasm of the spores. Such bodies have often been observed in the cells of recent plants, when rich in tannin, and may present a deceptive resemblance to Fungal or Myxomycetous spores. Structures, probably of the same nature, have also been detected in fossil

* "Organization," Part IX, Plate 22, figs. 42-44; Part XIX., Plate 9, fig. 48.

† "Organization," Part IX., p. 343.

‡ Spermatozoid mother-cells might be thought of in this connection, but such cells, as known to us among recent plants, are far too delicate to be preserved in so definite a form.

§ E.g., *Rhizophidium pollinis*, *Olpidium pendulum*, *Lagenidium pygmaeum*. See ZOPF, "Die Pilze," in SCHENK'S 'Handbuch der Botanik,' vol. 4, pp. 296, 297, and 556.

vegetable tissues.* The great definiteness of the membrane of the "sporules," which has sometimes split, with a perfectly sharp fissure, suggests however the cuticularized cell-wall of an actual spore, rather than a mere precipitation-membrane. In any case, it will be safer, in the present state of our knowledge, to leave the "sporules" out of consideration, in discussing the morphology of the spores of *Spencerites*.

We have at present, no means of determining whether *Spencerites insignis* was homosporous, or if heterosporous, whether the winged spores represent microspores or macrospores. In dimensions they are intermediate between the two, if we compare them with the spores of other Lycopods. The maximum diameter of the spore of *Spencerites insignis* (not counting the wing) is pretty constantly about 0·14 millim. The microspores of *Lepidostrobi* are very much smaller, usually about 0·02 to 0·03 millim., though those of *L. Brownii* Schp. reach a diameter of about 0·05 millim. On the other hand, the macrospores of the Carboniferous Lycopodiaceæ were usually of very large size. Of the numerous macrospores described by Mr. KIDSTON† (among which those of *Sigillariostrobus* as well as *Lepidostrobus* are probably included) the great majority are from 1 to 2 millims. in diameter; the smallest exceeds 0·5 millim. Macrospores belonging to *Lepidostrobi* from Oldham and from Burntisland, which I have measured, were about 0·8 millim. in diameter. The macrospores of *Sigillariostrobus* were very large, varying from 1·5 millim. to 2 millims. in different species.‡ The macrospores of recent heterosporous Lycopods (*Selaginella* and *Isoëtes*) range from about 0·2 to 0·5 millim.

On the whole then, it appears that the spores of *Spencerites insignis* are decidedly large for microspores, and decidedly small for macrospores. The comparatively small numbers in which they occur in each sporangium (see fig. 11) would suggest the latter rather than the former, but no conclusion can be drawn. So far as I can ascertain, only four distinct specimens of the actual cone are known. In these, all the sections (which in two of the specimens include the base of the cone) show spores of one kind only. A few minute spore-like bodies have occasionally been detected, but, as mentioned above, they appear to have escaped from the interior of large spores, and to be foreign or pathological products, and certainly not microspores.

4. Abortive Sporangia.

In one of the sections of the original specimen of the cone,§ some of the sporangia shown have a very different appearance from the ordinary ones, and offer, at first

* SEWARD, "On *Cycadeoidea gigantea*;" 'Quarterly Journal of the Geological Society,' Feb., 1897, vol. 53, p. 26.

† J. BENNIE and R. KIDSTON, "On the Occurrence of Spores in the Carboniferous Formation of Scotland." 'Proc. Roy. Phys. Soc.,' Edinburgh, vol. 9, p. 82, 1886.

‡ ZEILLER, "Cones de Fructification de *Sigillaria*;" 'Ann. des Sci. Nat. (Bot.),' Ser. 6, vol. 19, 1885.

§ See WILLIAMSON, "Organization," Part IX., Pl. 22, fig. 53e, C.N. 626.

sight, a startling resemblance to seeds. One of these sporangia is shown in detail in Plate 15, fig. 15. In this case the section evidently passes medianly through the sporangium, so WILLIAMSON'S interpretation "sporangial wall," which would imply that it is cut tangentially, will not hold good here. The anomalous sporangia, which are much smaller than the normal organs, are evidently attached, as usual, at their distal ends, but the sporophylls in this part are crowded and apparently somewhat displaced. WILLIAMSON supposed, no doubt with good reason, that this section was cut near one end of the strobilus.*

The wall of the anomalous sporangia appears to have been several cells in thickness. The cavity is partly filled by a carbonized mass, showing some traces of a cellular structure, and seated on a pad of tissue at the end where the sporangium is itself attached to its sporophyll. From the black mass delicate fibrils radiate, connecting it in places with the sporangial wall, from which it appears to have contracted away, before fossilization.

None of the other sections, either of the same or of different specimens, show these anomalous sporangia, which, in all probability, are simply abortive organs, the development of which had been arrested at a rather early stage. If so, they afford evidence that the inner layers of the wall were absorbed as the sporangium became ripe.

The consideration of the affinities of *Spencerites insignis* will be postponed until the next species has been described.

II. SPENCERITES MAJUSCULUS, *sp. nov.*

1. *General Characters.*

This form was not described or distinguished from the previous species by WILLIAMSON, though two sections of it are cited in his "General Index,"† under the head of "*Lepidodendron Spenceri*." So far as I know, only one specimen of the new species has ever been found. This was discovered by Mr. J. SPENCER, who prepared a number of sections from it. Only two of these (both transverse) are in the WILLIAMSON collection. I have examined numerous other preparations, including four longitudinal sections, two of which, one radial and the other tangential, are figured in the present paper, in addition to a transverse section (Plates 12 and 13, figs. 1, 2, and 3). The comparison of all the sections examined has completely cleared up the important points in the structure of the strobilus, and has shown that it is nearly allied to, though quite distinct from, the former species.

The specimen consists of the strobilus only; all the sections show the sporophylls borne upon the axis. The diameter of the whole cone, including the sporophylls is

* *Loc. cit.*, Part IX., p. 341.

† Part II., p. 25. The sections are 624c and 624g.

about 15 millims., while that of the axis is quite 9 millims., much larger than that of *S. insignis*, which does not exceed 5 millims. The short sporophylls and thick axis give a characteristic habit to the fruit. The diameter of the central cylinder is about 1·7 millims., quite double that in the former species (see Plate 12, fig. 1, and Plate 15, fig. 17). The state of preservation is similar to that of most specimens of *S. insignis*; the wood is perfectly preserved; only slight remains of the phloem are present; the inner zone of cortex immediately surrounding the central cylinder is in good preservation; beyond this is a wide empty space, from which the middle cortical tissue has entirely disappeared, except that in some cases the leaf-trace bundles, enclosed in their sheaths, are seen crossing the gap (fig. 17). Lastly, the dense layer of outer cortex is perfect and bounded by a definite epidermis.

The arrangement of the sporophylls cannot be determined with certainty from the transverse sections, but the tangential section (represented in Plate 13, fig. 3) leaves little doubt that, in this part of the cone, at any rate, they were placed in alternating verticils. Judging from the position of the sporophyll-bases, as shown in transverse section, the number of members in each verticil must have been fourteen or fifteen. The form of the sporophylls and their relation to the sporangia will be considered below.

2. *The Axis.*

Taking the structure more in detail, and beginning with the stele of the axis, we find that the wood extends to the centre, without any indication of a pith or of conjunctive parenchyma (Plate 12, fig. 2, and Plate 15, fig. 17). At the periphery of the wood are a large number (about thirty) of prominent groups of very small tracheæ, which the radial section shows to be spiral. Elsewhere, the elements of the wood are of the usual scalariform type. The large number of protoxylem-groups is a marked difference from *S. insignis*, where their number is usually about ten, and has not been found to exceed fourteen. Their number in the present species appears to correspond to that of the orthostichies of sporophylls, and is therefore double the number of the members in each verticil. There are some slight remnants of the soft tissue (no doubt phloem), immediately surrounding the xylem (fig. 17, *ph.*).

The inner cortex consists of several layers of rather delicate, elongated cells (figs. 1, 2, and 17). The broad zone of middle cortex has entirely disappeared, leaving an empty gap, crossed in some places by the leaf-trace strands (fig. 17). The outer cortex consists of almost uniform sclerotic tissue, the elements of which are prosenchymatous (figs. 1 and 2). There is no differentiation into radial bands of diverse structure, and this uniformity of the outer cortex forms another distinction from *S. insignis*, in which the corresponding zone has the "Dictyoxylon" character.

The leaf-trace bundles are met with at all points of their outward course, and are best seen in transverse sections through the inner cortex (fig. 17). Both in their direction and structure they agree closely with those of *S. insignis*, but, they appear in greater numbers in transverse section.

3. *The Sporophylls and Sporangia.*

The form of the sporophylls is a complex and peculiar one. Each sporophyll consists of a petiole and a lamina. The former is inserted, with a somewhat broad base, on the axis, and tapers towards the distal end (compare Plate 12, figs. 1 and 2; Plate 13, fig. 3, and Plate 15, fig. 16). The sectional form of the petiole is that of an ellipse, with its main axis horizontal (fig. 3). In general appearance this part of the sporophyll is similar to that of *S. insignis*. As in that plant the outer tissue of the petiole is prosenchymatous and thick-walled; within this, is a more delicate strand of parenchyma, enclosing the vascular bundle.

The laminae are extremely conspicuous objects in all the preparations (see Plate 12, figs. 1 and 2; Plate 13, fig. 3), though in the transverse sections their connection with the rest of the specimen is not usually evident (fig. 1). The point of connection between petiole and lamina was evidently a weak place in the tissue, and has generally broken down, but in several cases, as in the sporophyll figured, in radial section, in Plate 15, fig. 16, the continuity is perfect, though there is a bend or kink at the weak spot.

The lamina widens and broadens out suddenly, in every direction, from its point of attachment to the petiole. Its greatest dimension is in the tangential direction, in which its width is about 3 millims. (figs. 1 and 3). In the radial plane the lamina reaches a length of about 2·5 millims. (figs. 2 and 16). The extreme vertical height or thickness is about 2 millims., as best shown in the tangential section (fig. 3). This section, which passes rather obliquely through the laminae towards the left hand side, gives an excellent idea of the way they were packed together in alternating rows, each lamina thus acquiring a somewhat diamond-shaped outline. At its outer margin the lamina thins out into a narrow horizontal ridge, shown in figs. 2, 3, and 16.

The laminae must have had a fleshy character during life; they consist almost wholly of a very large-celled parenchyma, bounded externally by an epidermis of smaller cells, with thickened external walls (fig. 16). The small vascular bundle runs near the upper surface. The thick fleshy laminae form a most characteristic feature of the species.

Fragments of the sporangia, with their contained spores, occur everywhere in the space between the laminae and the axis (figs. 1, 2, and 3). In their shattered condition, the form of the sporangia cannot be determined with any exactness, but judging from the better preserved specimens, it would seem to have been approximately spherical, as in *S. insignis* (Plate 15, fig. 16). The important question of the insertion of the sporangia on the sporophylls could only be determined by the comparison of a number of instances. The sporophyll shown in radial section, in fig. 16, gives a good idea of the relative positions. The sporangium is certainly free from the petiole. It appears to have been attached on the upper surface exactly at

the point (*a*) where the petiole passes over into the lamina. From this case alone, one could not be certain that the sporangium might not also have been adherent to the upper face of the lamina itself, but other sporophylls show clearly that the two organs were free from each other in this region, and that the only attachment was at the point indicated. In particular, the tangential section, shown in Plate 13, fig. 3, is conclusive as to the absence of any adhesion between lamina and sporangium. At *a* the plane of section passes through the junction of the lamina and petiole of one of the sporophylls, and here the remains of a sporangium attached to the upper surface at this point are clearly seen. It appears then that the place of insertion of the sporangium in this species is essentially the same as in *S. insignis*, though relatively nearer the axis, owing to the great development of the laminar portion of the sporophyll in *S. majusculus*.

The membrane of the sporangium, in its present condition, consists of a single layer of prosenchymatous cells, and is much like that of *S. insignis* (see Plate 15, figs. 18 and 19). Seen in transverse section, the cells appear triangular, their thick lateral walls forming a regular zigzag, more definite here than in *S. insignis*. The inner and outer cell-walls are delicate, the outer usually the better preserved of the two (fig. 19A).

4. *The Spores.*

The spores, sometimes found within the sporangium, and sometimes scattered about outside, are very characteristic, and afford, perhaps, the best diagnostic character of the species. The spores of *S. majusculus* are not tetrahedral like those of *S. insignis*, but have the form of quadrants of a sphere (see Plate 15, fig. 19B-E). They are winged, but in quite a different way from those of the former species, for in *S. majusculus* each spore has three wings running along the three angles of the quadrant (fig. 19B and E). The wings themselves are thin, and not obviously hollow like those of *S. insignis*. The dimensions are smaller, the extreme length of the spore without wings varying from 0.09 to 0.12 millim., and inclusive of the wings reaching 0.15 millim. Thus the wings are narrower, and the dimensions of the winged spore, as a whole, little more than half those of *S. insignis*. Remains of the contracted cell-contents are often found, and occasionally distinct, cell-like bodies, comparable, perhaps, to the similar structures in the former species, occur within the spores. In one preparation (C.N., 624c) a few minute spore-like bodies were found free, but their connection with the specimen is altogether doubtful.

The spores are occasionally found grouped together, as if in their original tetrads (figs. 19D and E). They are arranged, as might be expected from their form, like the quadrants of a sphere, and not in tetrahedrons. The spores are, on the whole, less perfectly preserved than in *S. insignis*, but the difference between those of the two species is evident at the first glance. (Compare Plate 14, figs. 11 and 14 with Plate 15, fig. 19.)

CONCLUSIONS.

There are two questions to be considered in conclusion: the relation between the two forms which have been described, and the relation of both together to other plants. The smaller question will be taken first.

No one who has compared the specimens which I have referred to *Spencerites majusculus* and *S. insignis*, or the drawings of their structure accompanying the present paper, is likely to doubt that the two forms are specifically quite distinct. The great difference in absolute dimensions (the axis of *S. majusculus* being about twice as thick as that of *S. insignis*), though striking enough, would go for little if it stood alone. It is accompanied, however, by a considerable difference in the relative dimensions of axis and sporophylls, and by marked structural distinctions, in the outline of the wood, the arrangement of the leaf-trace bundles, and the details of the outer cortex. The sporophylls are not only much larger in *S. majusculus* than in *S. insignis*, while relatively shorter in the former as compared with the size of the axis, but have a somewhat different form, though the superior preservation of these organs in the former renders exact comparison difficult. The great tangential width of the lamina is characteristic of *S. majusculus*, while the peltate form, as seen in radial section, is more marked in *S. insignis*. The sporangia are similar in both, but the spores are quite different, those of *S. insignis* being decidedly the larger, of tetrahedral or spheroidal form, with a broad equatorial wing, while those of *S. majusculus* are smaller, with the form of quadrants of a sphere, each spore having three narrow wings running along its angles. The difference in the dimensions of the spores is not sufficient to justify us in regarding them as microspores and macrospores of the same species, nor would such a suggestion be consistent with the other marked distinctions between the strobili.

On the other hand, the two species, distinct as they are, have much in common. The general anatomy is similar; in this respect the two forms resemble each other more closely than they resemble any other known strobilus. The sporophylls, with their broad laminæ, sharply marked off from the almost cylindrical petiole, are characteristic of both forms jointly. The insertion of the sporangium, by a narrow attachment, to the upper surface of the sporophyll, where it begins to expand into the lamina, is as I have shown, essentially the same in both. The spores also have something in common, at least in the fact that they are winged, while the form and structure of the sporangium are alike in both.

These various points of agreement and difference find, I believe, their best expression, if we regard the two forms as two species of the same genus.

We now come to the more important question of the relation of these forms to other plants, and especially to other members of the Palæozoic Flora.

That the strobili are Lycopodiaceous can scarcely be questioned, for this conclusion

follows at once from the position of the sporangia, seated singly on the upper surface of each sporophyll, and from the whole anatomical structure.

It is natural to place any Palæozoic Lycopodiaceous cone, in the first instance, in the genus *Lepidostrobus*, and this is the position hitherto assigned to *Spencerites insignis*, though WILLIAMSON, as already mentioned, thought it might ultimately be necessary to make it the type of a new genus.* I think the results of the renewed examination of this fossil, and the discovery of a second allied species, indicate that the time has come when WILLIAMSON'S suggestion should be carried into effect.

We may take the generic character of *Lepidostrobus*, given by M. ZEILLER, as fairly representing the modern conception of the genus. In the following literal translation the italics are M. ZEILLER'S OWN: "*Cones of fructification cylindrical, oblong, or ovoid; composed of a woody axis bearing sporangiferous bracts arranged in a spiral, and somewhat crowded. Bracts formed of a narrow pedicel, usually normal to the axis, and of a uni-nervate limb, lanceolate or linear-lanceolate in outline, generally erect, and often even applied to the surface of the cone. Sporangia ovoid, solitary, fixed upon the superior face of the pedicel of the bracts.*"† Of these characters the spiral arrangement of the sporophylls is, perhaps, the least constant, for M. ZEILLER himself points out in the same work that in his *Lepidostrobus Olryi* the phyllotaxis is verticillate. I therefore attach no importance to the fact that in *Spencerites* the arrangement appears to have been variable in this respect.

In several points, however, the strobili described above diverge from the character of *Lepidostrobus*. The form of the limb or lamina is totally unlike, and its preservation, especially in *S. majusculus*, is sometimes sufficiently perfect for us to be sure that the difference is a real one. The sporangia are not ovoid, but approximately spherical, and, which is the chief point, they are not fixed upon the superior surface of the pedicel, but are altogether free from this part of the sporophyll, and only attached, by a narrow base, to the lamina where it begins to expand. It is instructive to compare such a species of *Lepidostrobus* as *L. Olryi*, ZEILL. with our strobili. In dimensions and general form *L. Olryi* appears to be not unlike our *Spencerites insignis*, but, in the former, the attachment of the elongated sporangium to the whole upper surface of the pedicel is evident from M. ZEILLER'S detailed figure, and at once distinguishes this species as a true *Lepidostrobus*.‡

The attachment of the sporangium, either by the whole length of its lower surface, or by a considerable part of it, to the upper side of the pedicel, appears to be constant in all species of *Lepidostrobus* where the preservation is sufficiently good for such points to be determined, and must, in my opinion be regarded as an essential character of the genus.§ It is chiefly on this ground, then, that I base the generic

* 'General Index,' Part II., p. 24, 1893.

† ZEILLER, "Bassin Houiller de Valenciennes." 'Flora Fossile,' 1888, p. 496.

‡ ZEILLER, *loc. cit.*, Atlas, Plate 77, figs. 1 and 1A.

§ Any of the published figures of well-preserved *Lepidostrobi* will serve to illustrate this character

separation of *Spencerites* from *Lepidostrobus*, but the character derived from the insertion of the sporangia is supported by several others, namely the form of the sporophylls and sporangia, the structure of the sporangial wall, and of the spores, the arrangement of the leaf-traces, and the whole habit of the strobilus.

The resemblance of *Spencerites insignis* to a cone described by M. ZEILLER under the name of *Sigillariostrobus Crepini** is rather striking, and for some time led me to suppose that both our species might belong to the genus *Sigillariostrobus*, in which case they would have been of special interest as the first known fructifications of *Sigillaria* with their structure preserved.† M. ZEILLER most kindly sent me the type specimen of *S. Crepini* for examination, so I was able to compare it directly with the preparations of our strobili. M. ZEILLER'S fossil is preserved in the form of impressions, of which there are two on the same fragment of rock. As M. ZEILLER pointed out in a letter to me, the dark colour of the matrix somewhat obscures the details of the fossil, but I was able to satisfy myself as to all the important points shown in the author's figures. *Sigillariostrobus Crepini* agrees with *Spencerites insignis* in the dimensions of the axis, the arrangement of the sporophylls, and to some extent in their form. So far as can be ascertained, the two plants also agree in the position of the sporangia, which in *Sigillariostrobus Crepini* appear to be free from the pedicel and attached at the distal end to the spoon-shaped lamina of the sporophyll. The point is, of course, comparatively obscure in the French fossil, owing to its mode of preservation, but I believe M. ZEILLER'S interpretation to be the correct one.

Up to this time nothing whatever was known of the sporangia (as distinguished from the spores) of *Sigillariostrobus*, with the solitary exception of *S. Crepini*, so it was permissible to suppose that their insertion at the distal end of the sporophyll might be characteristic of the genus.

Since then, however, owing to the kindness of my friend, Mr. R. KIDSTON, F.G.S., I have had the opportunity of examining a fine specimen of his *Sigillariostrobus ciliatus*, in which the sporangia containing the macrospores are well preserved. Mr. KIDSTON is about to publish a full account of the fossil in the 'Transactions of the Royal Society of Edinburgh,'‡ so I will only say that the examination of the specimen in question appears to leave no doubt that in this *Sigillariostrobus* the

The diagram by WILLIAMSON, "Organization," Part XIX., Plate 6, fig. 62, is quite true to nature for *Lepidostrobus Oldhamius*, and contrasts sharply with *Spencerites insignis*, as shown in Plate 7, fig. 50 of the same memoir. HOOKER'S figure, from *L. ornatus* ('Mem. Geol. Survey of Great Britain,' vol. 2, Part II., Plate 8, fig. 11, 1848), reproduced in various text-books, e.g., SOLMS-LAUBACH, 'Fossil Bot.,' fig. 25c, may illustrate another type, which would approach rather nearer to *Spencerites*, though still quite distinct.

* ZEILLER, "Bassin Houiller de Valenciennes." 'Flore Fossile,' Plate 77, fig. 3.

† See 'British Association Report,' 1896, p. 1024.

‡ This has now appeared: "On the Fossil Flora of the Yorkshire Coal-field; Second Paper." *Loc. cit.*, vol. 39, Part I., No. 5, 1897.—Jan. 26, 1898.

sporangium is attached along the whole of its lower surface to the horizontal pedicel of the sporophyll, and that it is partly roofed in above by a kind of indusium, arising from the upturned lamina, as in *Isoëtes*. In these points (to which Mr. KIDSTON first called my attention) *Sigillariostrobus ciliatus* differs entirely from *Spencerites*, and apparently from *Sigillariostrobus Crepini* also.

In the face of these facts it is impossible to unite *Spencerites* with *Sigillariostrobus*, any more than with *Lepidostrobus*; our two species are best regarded as the representatives of a distinct Lycopodiaceous genus.

This conclusion leaves us in doubt as to the true nature of M. ZEILLER's *Sigillariostrobus Crepini*. As that author points out, it seems to be quite distinct from *Lepidostrobus*, and to bear a considerable likeness to some undoubted *Sigillariostrobus*, especially *S. Goldenbergi*, ZEILLER.*

Possibly *Sigillariostrobus*, as at present constituted, may have to be broken up into two or more genera, in which case it may be that *S. Crepini* and our *Spencerites* may still be brought together. Until, however, we are acquainted with the internal structure of the Sigillarian fructifications, no definitive re-arrangement can be carried out.

In the insertion of the sporangium, by a narrow base, on the distal portion of the sporophyll, *Spencerites* differs from all other known Lycopods. It is at the opposite extreme from *Selaginella*, where the sporangia are axillary. There is a certain analogy with the insertion of the synangium in Psilotaceæ, especially *Tmesipteris*, but this comparison is of doubtful value, so long as the homologies of the Psilotaceous synangium remain uncertain.† If Professor BOWER is right in believing that the synangium represents a single, elaborated sporangium, then the comparison with *Spencerites* may hold good. But if, as GOEBEL‡ supposed, the synangium corresponds to a fertile branch, or if, as I have ventured to suggest in a previous paper,§ it represents the sporangiferous pedicel in Sphenophylleæ, then the structure is no longer comparable with that of our fossil. However this may be, the Psilotaceæ appear to be too remote from the strobiloid Lycopods to throw much light on a fructification like that of *Spencerites*.

In the fact that the insertion of the sporangium is broader in the tangential than in the radial direction, the new genus differs conspicuously from *Lepidostrobus*, and resembles some living species of *Lycopodium*, such as *L. clavatum* and *L. Selago*.||

The distal insertion of the sporangium—reminding us of *Cheirostrobus* and the Sphenophylleæ, otherwise so remote—may perhaps be an indication that *Spencerites*

* *Loc. cit.*, Plate 89, fig. 1.

† See BOWER, "Studies in the Morphology of Spore-producing Members," Part I., 'Phil. Trans., B, vol. 185, 1894, p. 539, where the various interpretations are stated.

‡ 'Bot. Zeitung,' 1881.

§ "On *Cheirostrobus*," &c., 'Phil. Trans.,' B, vol. 189, p. 1, 1897.

|| BOWER, *loc. cit.*, Plate 47, fig. 92.

represents a somewhat more archaic type of Lycopodiaceous strobilus than that of *Lepidostrobus*.

DIAGNOSIS.

Spencerites, gen. nov.

Cone consisting of a cylindrical axis, bearing numerous simple sporophylls, arranged spirally, or in crowded alternating verticils.

Sporophylls short, formed of a sub-cylindrical pedicel expanding into a large peltate lamina.

Sporangia, solitary on each sporophyll, inserted, by a narrow base, on the upper surface of the lamina, but free from the pedicel.

Sporangial wall, formed of a single layer of prosenchymatous cells.

Spores winged.

1. *Spencerites insignis* (WILL.).

Lepidostrobus, sp., WILLIAMSON, "Organization of the Fossil Plants of the Coal-Measures," Part IX., 'Phil. Trans.,' 1878, p. 340, figs. 39 to 47 and 52 to 57. *Lepidostrobus insignis*, WILL., *loc. cit.*, Part X., 'Phil. Trans.,' 1880, p. 502, figs. 11 and 12. *Lepidodendron Spencersi*, WILL., *loc. cit.*, Part XVI., 'Phil. Trans.,' 1889, p. 199, figs. 19 to 22. *Loc. cit.*, Part XIX., 'Phil. Trans.,' 1893, p. 24, figs. 41 to 50.

Cone pedunculate. Peduncle bractigerous.

Whole cone, 8 to 10 millims. in diameter.

Axis, 3·5 to 5 millims. in diameter.

Sporophylls, 2 to 2·5 millims. long; lamina distinctly peltate, vertically elongated.

Sporangia approximately spherical.

Spores tetrahedral, becoming spheroidal when free, with a hollow equatorial wing.

Maximum diameter of spore without wing, about 0·14 millim.; with wing, about 0·28 millim.

Wood of axis, 10-arch to 14-arch, without prominent angles; with or without pith. Outer cortex containing distinct bands of sclerenchyma.

Locality, near Halifax and Huddersfield.

Horizon, Lower Coal-Measures.

2. *Spencerites majusculus*, sp. nov.

Whole cone, about 15 millims. in diameter.

Axis, about 9 millims. in diameter.

Sporophylls, about 3 millims. long; lamina obscurely peltate, as seen in radial section, but greatly expanded tangentially, attaining a breadth of 3 millims.

Sporangia approximately spherical.

Spores, having the form of quadrants of a sphere, with three narrow wings.

Maximum diameter of spore without wings, on the average about 0·11 millim.; with wings, about 0·15 millim.

Wood of axis, with about thirty somewhat prominent angles; without pith.

Outer cortex uniformly sclerotic.

Locality, near Halifax.

Horizon, Lower Coal-Measures.

It must be remembered that *S. majusculus* is described from a single specimen, so it is to be expected that the specific character will require modification in the future. The specimens of *S. insignis* are more numerous, but so far as the actual strobilus is concerned, I am only acquainted with four distinct examples.

In addition to the slides in the WILLIAMSON Collection and in my own, I have had the use of two sections lent by Mr. SPENCER, and of preparations from the HICK, WILD, and CASH Collections in the Manchester Museum. For the loan of the latter I am indebted to Professor F. E. WEISS, of the Owens College.

Of the illustrations to this paper, six, namely, figs. 1, 2, 3, 4, 5, and 12, were drawn for me by Mr. G. T. GWILLIAM, and the remainder by Mr. W. C. WORSDELL.

EXPLANATION OF PLATES, 12–15.

PLATE 12.

Spencerites majusculus.

Fig. 1. Transverse section of strobilus. *x.*, wood of axis; *i.c.*, inner cortex; the middle cortex has perished, leaving a space into which Stigmarian rootlets have penetrated; *o.c.*, outer cortex, in which the leaf-trace bundles can be seen at several places; *sm.*, remains of sporangia, containing spores; *sph.*, bases of sporophylls; *sph'*, laminae of sporophylls. $\times 10$. S., 7* (from Mr. J. SPENCER) (see pp. 95 and 96).

* Slides in my own Collection are indicated by the letter *S* before the number; those in the WILLIAMSON Collection are marked C.N. (Cabinet number) as heretofore. Slides from other Collections are specially referred to.

- Fig. 2. Radial section of strobilus. *x.*, wood of axis; *i.c.*, inner cortex; the middle cortex only shows fragments of leaf-trace bundles, and an intruding Stigmarian rootlet; *o.c.*, outer cortex; *sm.*, sporangia, containing spores; *sph.*, bases of sporophylls; *sph'*, their laminae. $\times 9$. From a slide in Mr. J. SPENCER'S Collection (see pp. 95 and 96).

PLATE 13.

Fig. 3, *Spencerites majusculus*; figs. 4 to 8B, *S. insignis*.

- Fig. 3. *S. majusculus*. Tangential section of strobilus. The section is slightly oblique, passing through the cortex of the axis above, and through the sporophyll-pedicels, below. On either side the laminae are shown, best preserved on the left hand. *ax.*, axis with bases of sporophylls; *sph.*, pedicels of sporophylls; *sph'*, their laminae. Note the regular alternate verticils. *sm.*, remains of sporangia, containing spores; *a.*, insertion of a sporangium. $\times 6$. From a slide in Mr. J. SPENCER'S Collection (see p. 96). For other figures of *S. majusculus* see Plate 15.
- Fig. 4. *S. insignis*. Transverse section of a strobilus. *x.*, wood of axis, enclosing a thick-walled pith; *i.c.*, inner cortex; middle cortex penetrated by Stigmarian rootlets; *o.c.*, outer cortex, with "Dictyoxylon" structure; the leaf-trace bundles are seen both here and in the inner cortex: *sph.*, sporophylls, imperfectly preserved; *sm.*, sporangia, containing the winged spores; *s.r.*, Stigmarian rootlet. $\times 10$. From a slide by Mr. J. LOMAX in the WILD Collection (No. 159), Manchester Museum. Other sections of the same cone are in the WILLIAMSON* and HICK Collections, and in my own (see pp. 86-90).
- Fig. 5. Transverse section (from the base of a strobilus) of the stele and inner cortex. The large central mass, *x.*, is the wood; *p.h.*, phloem-zone, somewhat crushed; *i.c.*, inner cortex. $\times 50$. S., 4 (from Mr. J. SPENCER). Other sections of the same cone are in the WILLIAMSON† and CASH Collections (see p. 87).
- Fig. 6. Part of a transverse section from a peduncle, to show bract. *e.*, epidermis; *c.*, outer cortex, the external layers of which are very thick-walled; *l.t.*, leaf-trace bundle, passing out to bract.; *b.r.*, bract. C.N., 419G (from Mr. J. SPENCER). $\times 45$ (see p. 86).
- Fig. 7. Tangential section through the cortex of a peduncle to show the arrangement of the leaf-trace bundles, which appear to form a flat spiral with a

* C.N. 1922F, *ter.*

† C.N. 624, 624A and B 625.

small divergence; slightly diagrammatic; *l.t.*, leaf-trace bundles. In many of them the group of tracheæ can be seen, and also the bundle-sheath; *b.r.*, base of a bract. $\times 18$. C.N., 419D (from Mr. J. SPENCER) (see p. 86).

- Fig. 8A. Tracheæ from the extreme outer edge of the wood, seen in radial section. *px.*, *px.*, small spiral tracheæ of the protoxylem, somewhat disorganized. The larger element to the right (*i.e.*, towards the interior) is also partly spiral.
- Fig. 8B. From the same section, showing a spiral trachea (*tr.*) imbedded in the middle of the pith; *p.*, elongated pith-cells. Both figures $\times 165$. C.N., 419E (from Mr. J. LOMAX) (see p. 87).

PLATE 14.

Spencerites insignis.

- Fig. 9. Part of a radial section of a peduncle, to show the middle cortex. *sh.*, sheath of elongated cells surrounding a leaf-trace bundle; *l.c.*, lacunar middle cortex, consisting of irregular interwoven trabeculæ. $\times 70$. C.N., 419E (from Mr. J. LOMAX) (see p. 88).
- Fig. 10. Part of tangential section of an axis to show a leaf-trace bundle passing through the outer cortex. *x.*, xylem of bundle; *sh.*, bundle-sheath. The larger surrounding cells are cortical. $\times 165$. C.N., 624D (from Mr. J. LOMAX) (see p. 89).
- Fig. 11. Part of the radial section of a strobilus, figured as a whole by WILLIAMSON, "Organization," Part XIX., Plate 7, fig. 50. The sporangium shown here is the lowest on the left. *c.*, cortex of axis. Two sporophylls (*sph.*) are shown, the lower incomplete. Each contains a vascular bundle; *sm.*, sporangia; the lower is shown complete and is filled with winged spores; *a.*, point of attachment of the sporangium to the distal part of the sporophyll. The rest of the sporangial wall is perfectly free. $\times 45$. C.N., 624B (from Mr. J. SPENCER) (see p. 89).
- Fig. 12. Detached sporophyll, seen in radial section. In the tissue of the large lamina, the vascular bundle, *v.b.*, is seen at two places. *sm.*, base of the sporangium, inserted on the upper surface of the lamina at *a.*; *s.t.*, torn fragment of the pedicel, bent upwards. Compare WILLIAMSON'S figure, in "Organization," Part XIX., Plate 7, fig. 50. The sporophyll lies close to the cone to which it belongs. \times about 50. From a slide in the CASH Collection (*Lepidodendron Spencersi*, II.) by Mr. J. SPENCER. The section is from the cone shown in WILLIAMSON'S figure above cited (see p. 90).

- Fig. 13. Part of transverse section of a strobilus to show sporophyll and sporangium. *ax.*, outer limit of the cortex of the axis; *sph.*, sporophyll, shown both in its proximal and distal part; *sm.*, sporangium, containing winged spores; *a.*, attachment of sporangium to distal end, *sph.'*, of sporophyll. $\times 45$. C.N. 626 (from Mr. J. BINNS) (see p. 90).
- Fig. 14A. A single spore, seen in section. *w.w.*, the wing; *r.*, one of the radiating ridges, marking the line of junction with the sister-spores; *c.b.*, cellular or vacuolated body in the interior of the spore. $\times 265$ (see pp. 91 and 92).
- Fig. 14B. A tetrad of spores seen in section, showing the position of the wings. As the arrangement is tetrahedral, only three spores are seen in one plane. $\times 150$. Both Figs. from C.N. 624B (see p. 91).

PLATE 15.

Fig. 15. *Spencerites insignis*. Figs. 16–19. *S. majusculus*.

- Fig. 15. *S. insignis*. Abortive sporangium. *sph.*, part of sporophyll to which sporangium is attached; *sm.w.*, sporangial wall. The interior is occupied by a dark, contracted mass, showing some traces of cellular structure. $\times 110$. C.N. 626 (see p. 93).
- Fig. 16. *S. majusculus*. Sporophyll in radial section. This is from the left hand side of the section shown entire in Plate 12, fig. 2. *ax.*, external tissue of axis; *sph.*, pedicel of sporophyll; *sph.'*, its lamina; *v.b.*, vascular bundle; *sm.*, sporangium (containing spores) inserted on the sporophyll at *a.* \times about 40 (see p. 96).
- Fig. 17. Part of a transverse section of the strobilus, showing stele and inner cortex. *px.*, *px.*, protoxylem-groups, of which there are about thirty in all; all the tissue to the inside is wood; *ph.*, remains of phloem; *lt.*, leaf-trace bundles passing through inner cortex; *sh.*, sheaths surrounding the bundles, where they traverse the decayed middle cortex. \times about 40. C.N. 624C (from Mr. J. SPENCER). This section is practically identical with that shown in Plate 12, fig. 1 (see p. 95).
- Fig. 18. Part of sporangial wall, seen in surface view. \times about 70. C.N. 624C (see p. 97).
- Fig. 19. A. Part of sporangial wall, seen in section. $\times 150$. C.N. 624C.
 B. Spore seen from the side. *w.*, wing. $\times 150$. C.N. 624C.
 C. Spore seen in oblique section, *w.*, wing. $\times 150$. C.N. 624C.
 D. Tetrad in side view; only two spores visible. $\times 150$. C.N. 624C.
 E. Tetrad in end view, showing all four spores. $\times 150$. C.N. 624C.

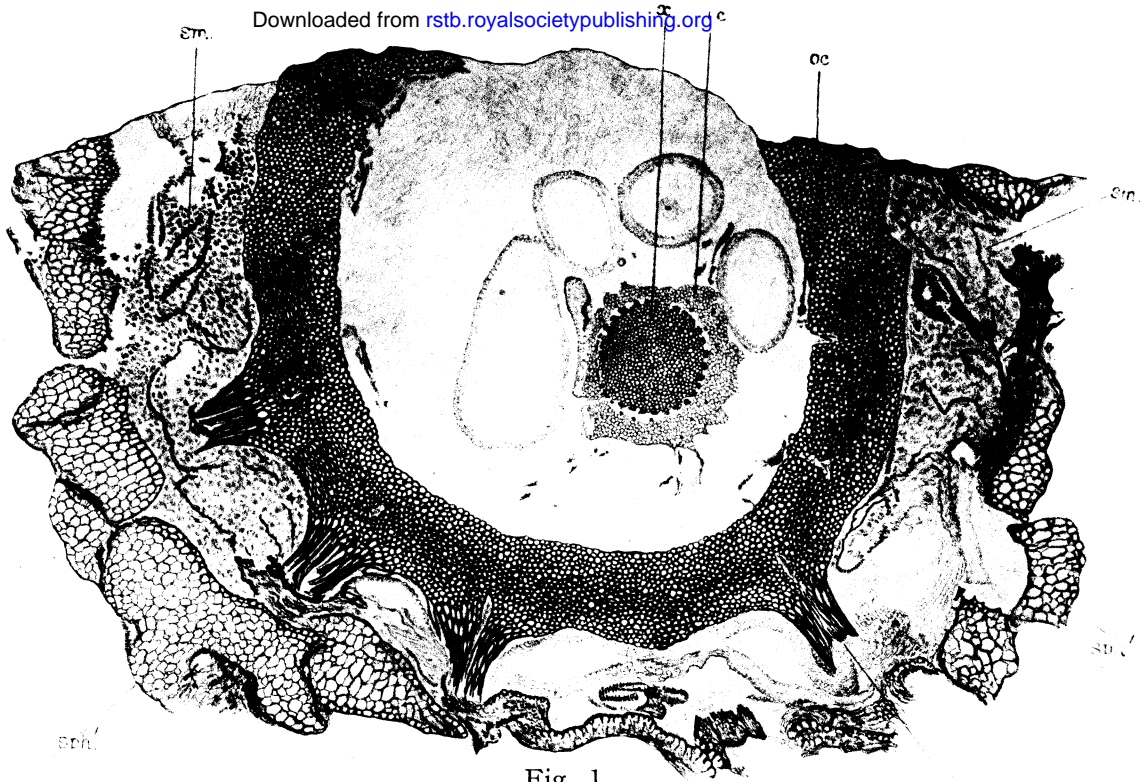


Fig. 1.

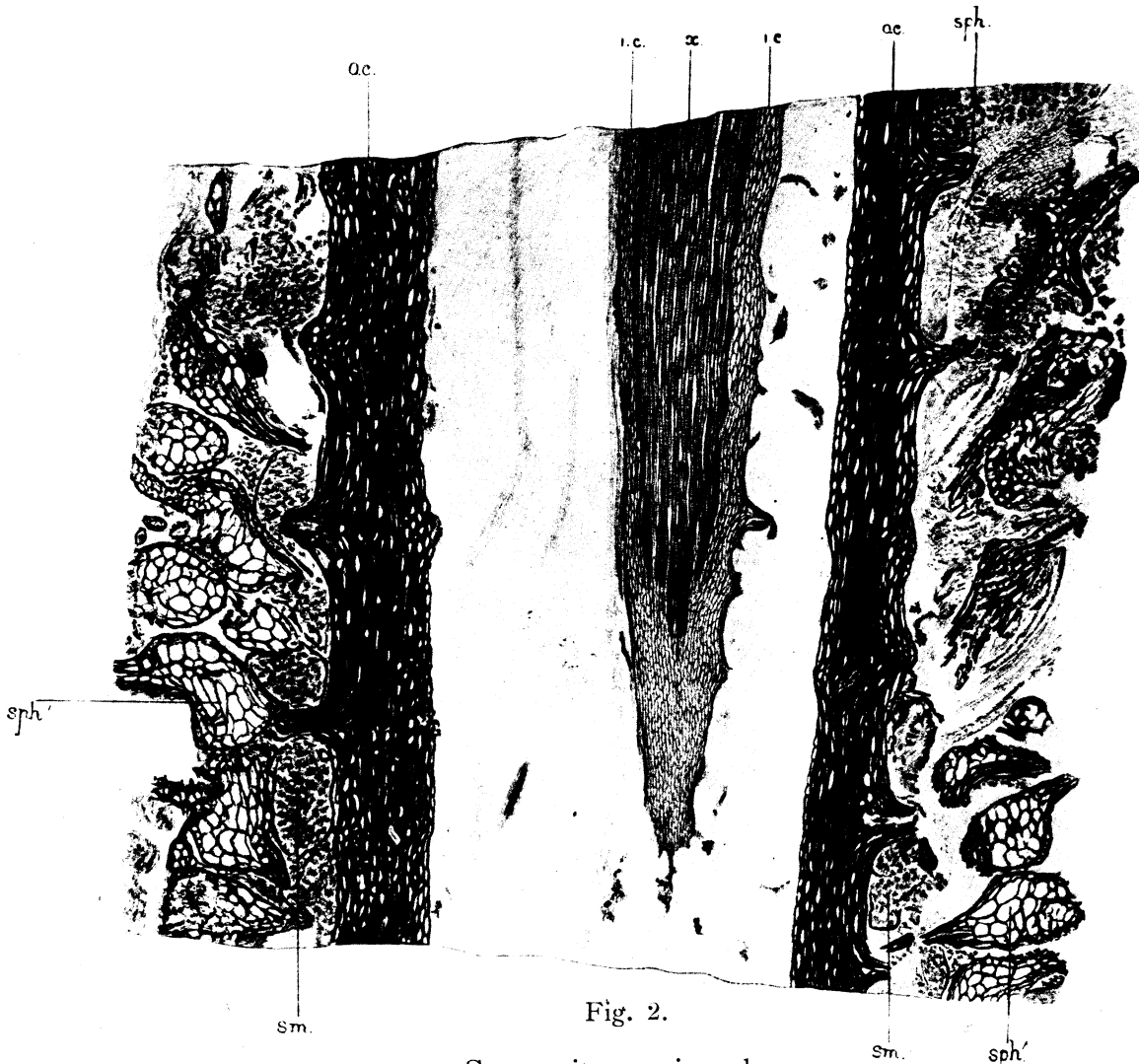


Fig. 2.

Spencerites majusculus.

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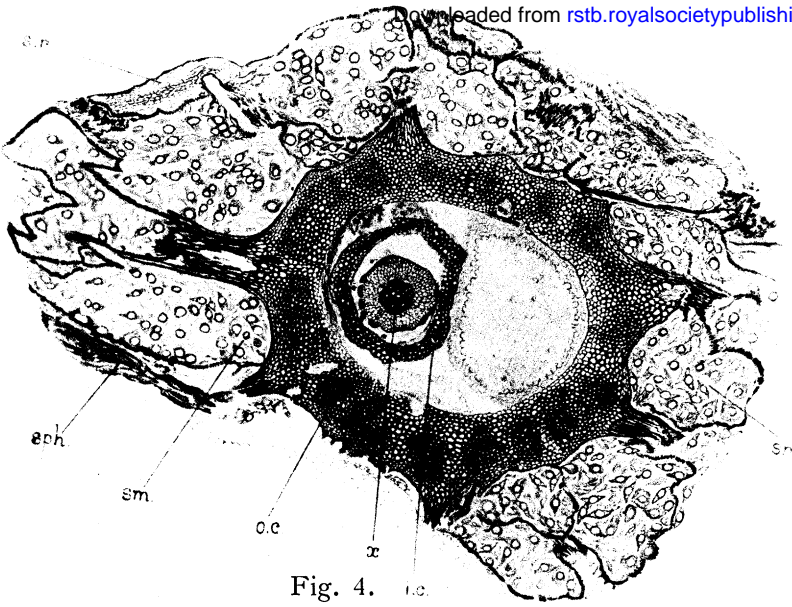


Fig. 4.

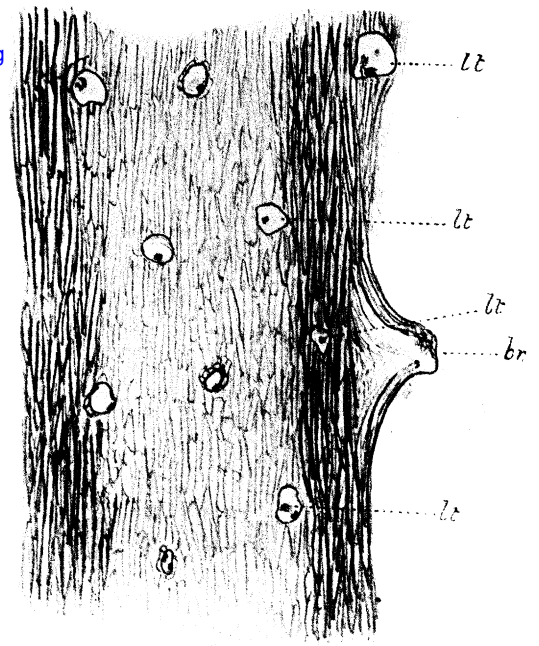


Fig. 7.

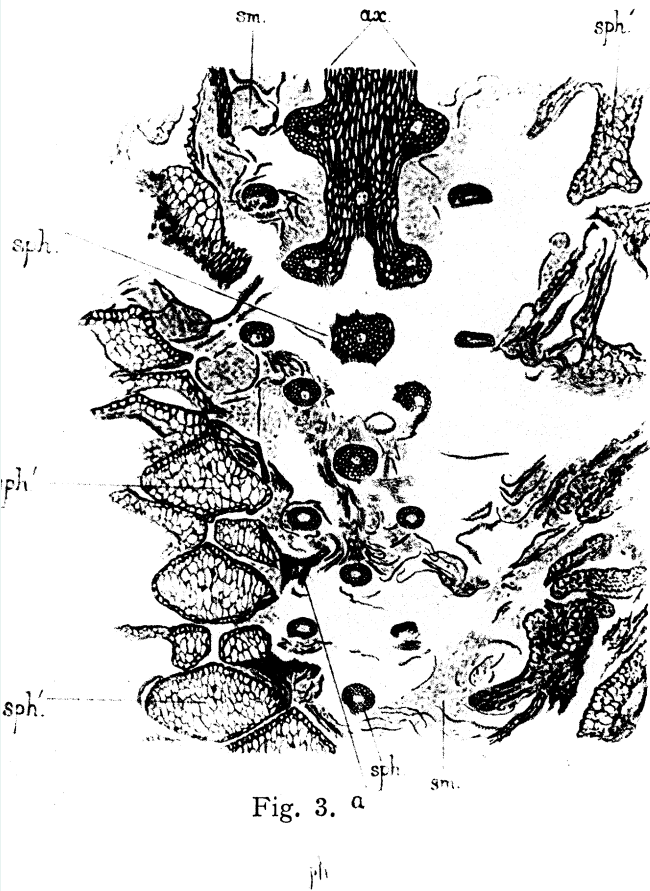


Fig. 3. a



Fig. 6.

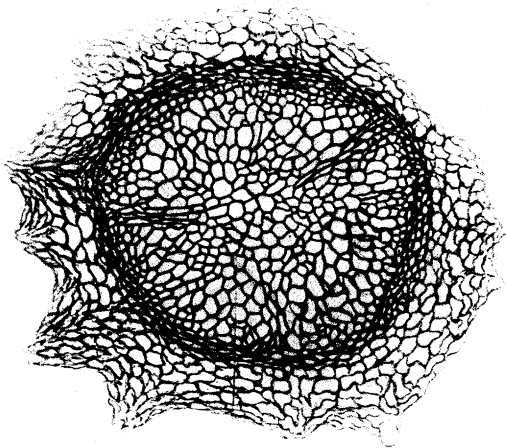


Fig. 5.



Fig. 8A.



Fig. 8B.

Fig. 3. *Spencerites majusculus*.

Figs. 4—8B. *S. insignis*.

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Fig. 9.

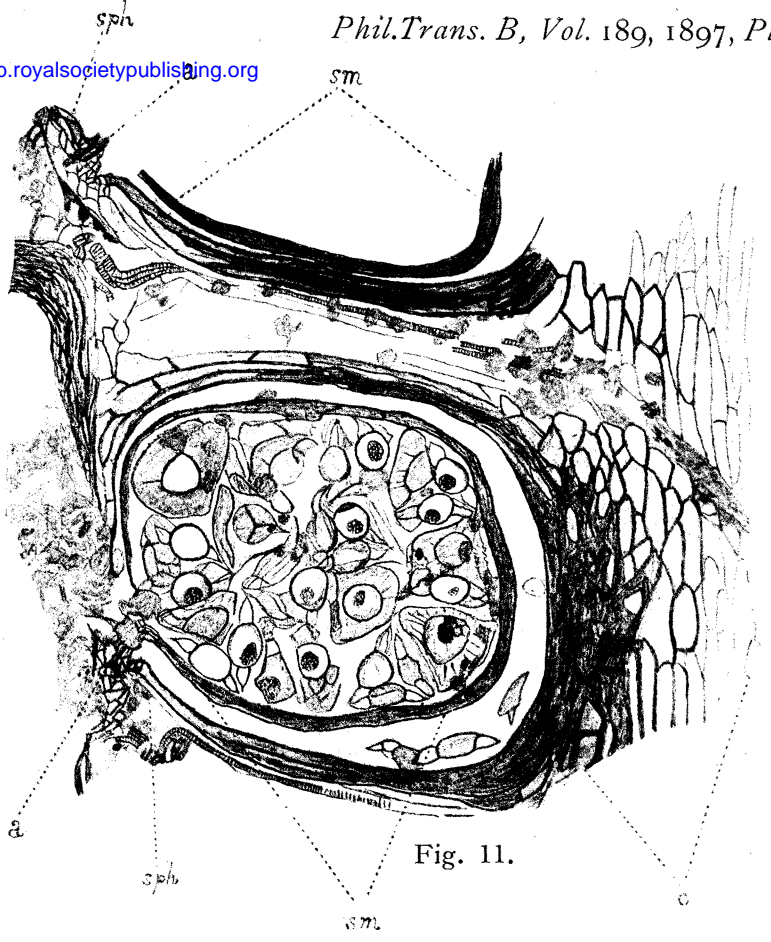


Fig. 11.

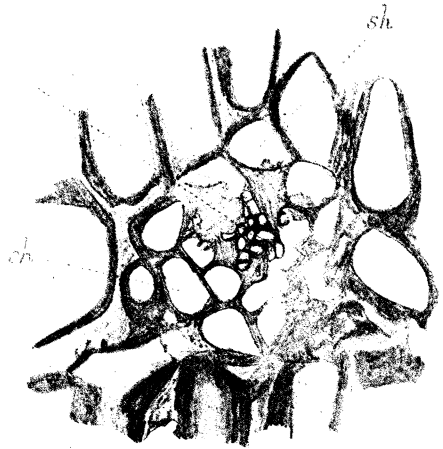


Fig. 10.

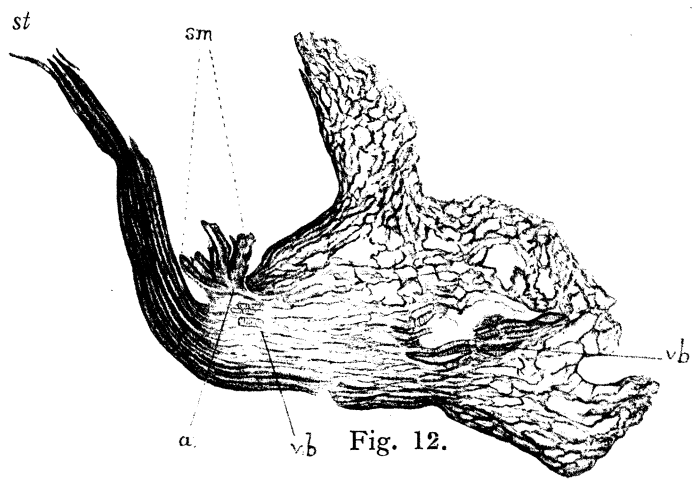


Fig. 12.

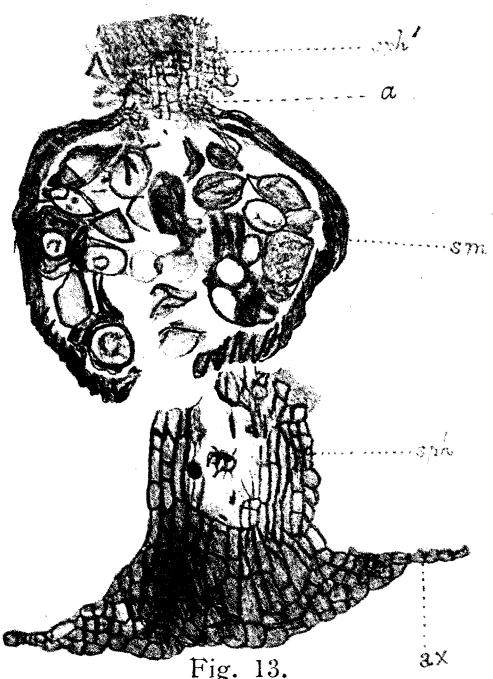


Fig. 13.

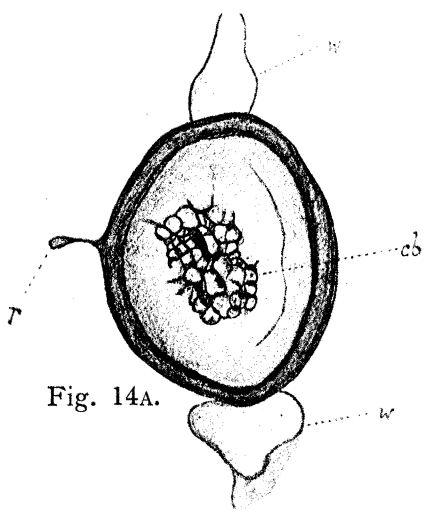


Fig. 14A.

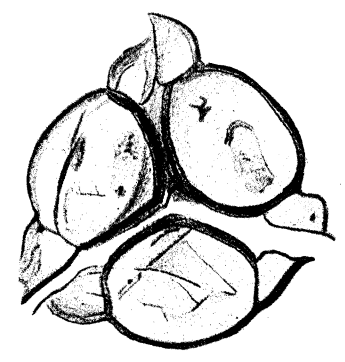


Fig. 14B.

Spencerites insignis.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY OF BIOLOGICAL SCIENCES

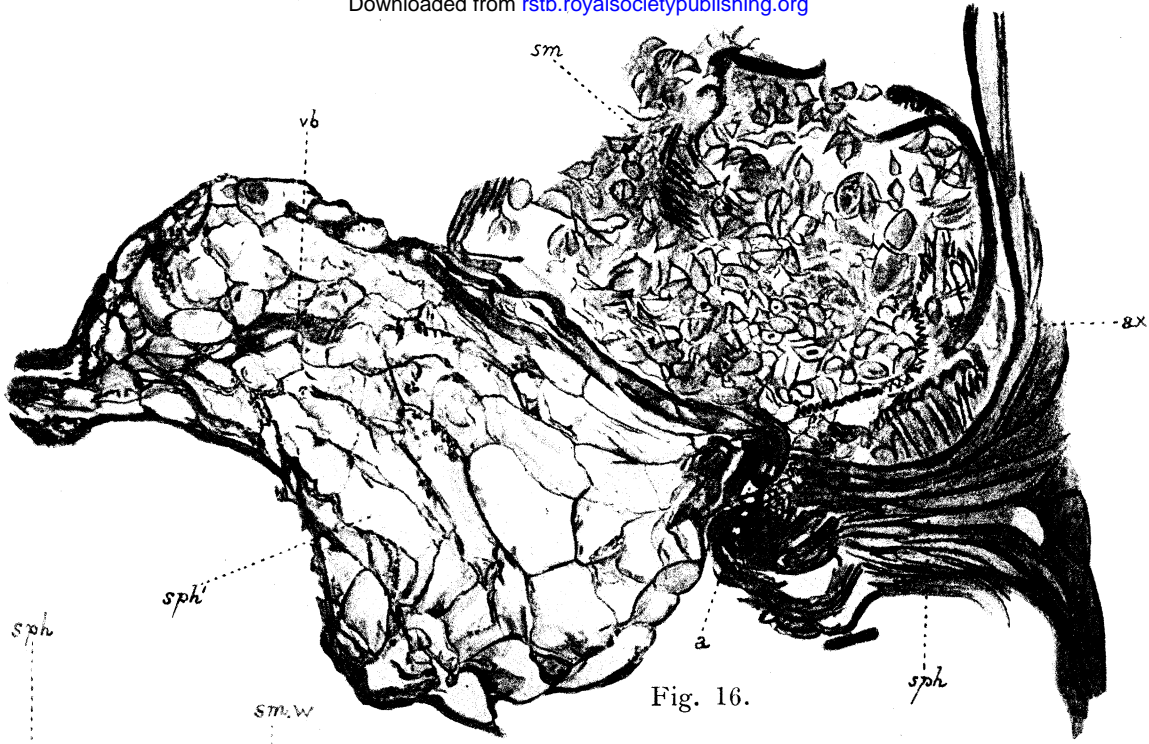


Fig. 16.

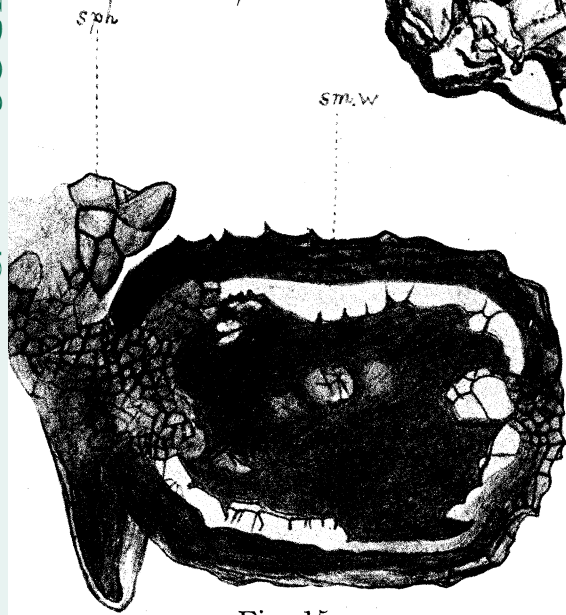


Fig. 15.

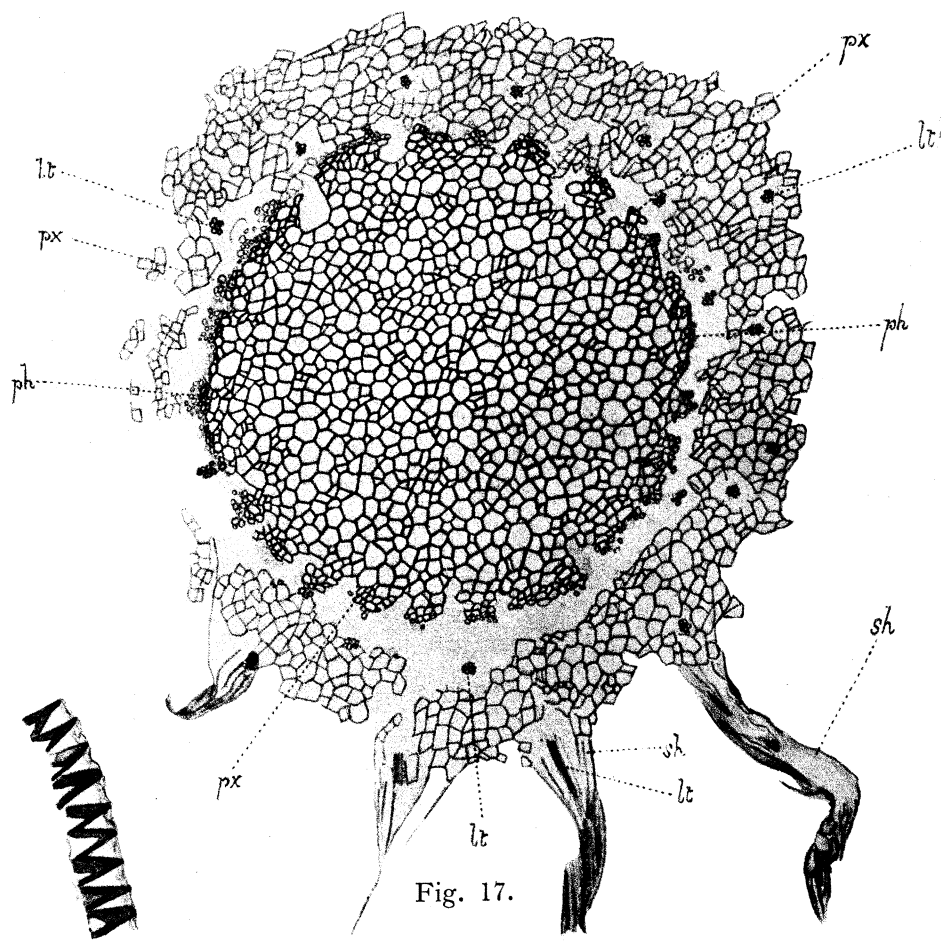


Fig. 17.

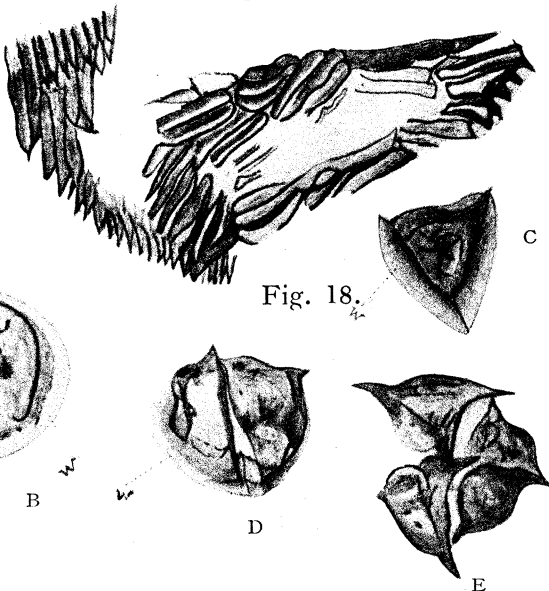


Fig. 18.



Fig. 19.

Fig. 15. *Spencerites insignis*.

Fig. 16—19. *S. majusculus*.

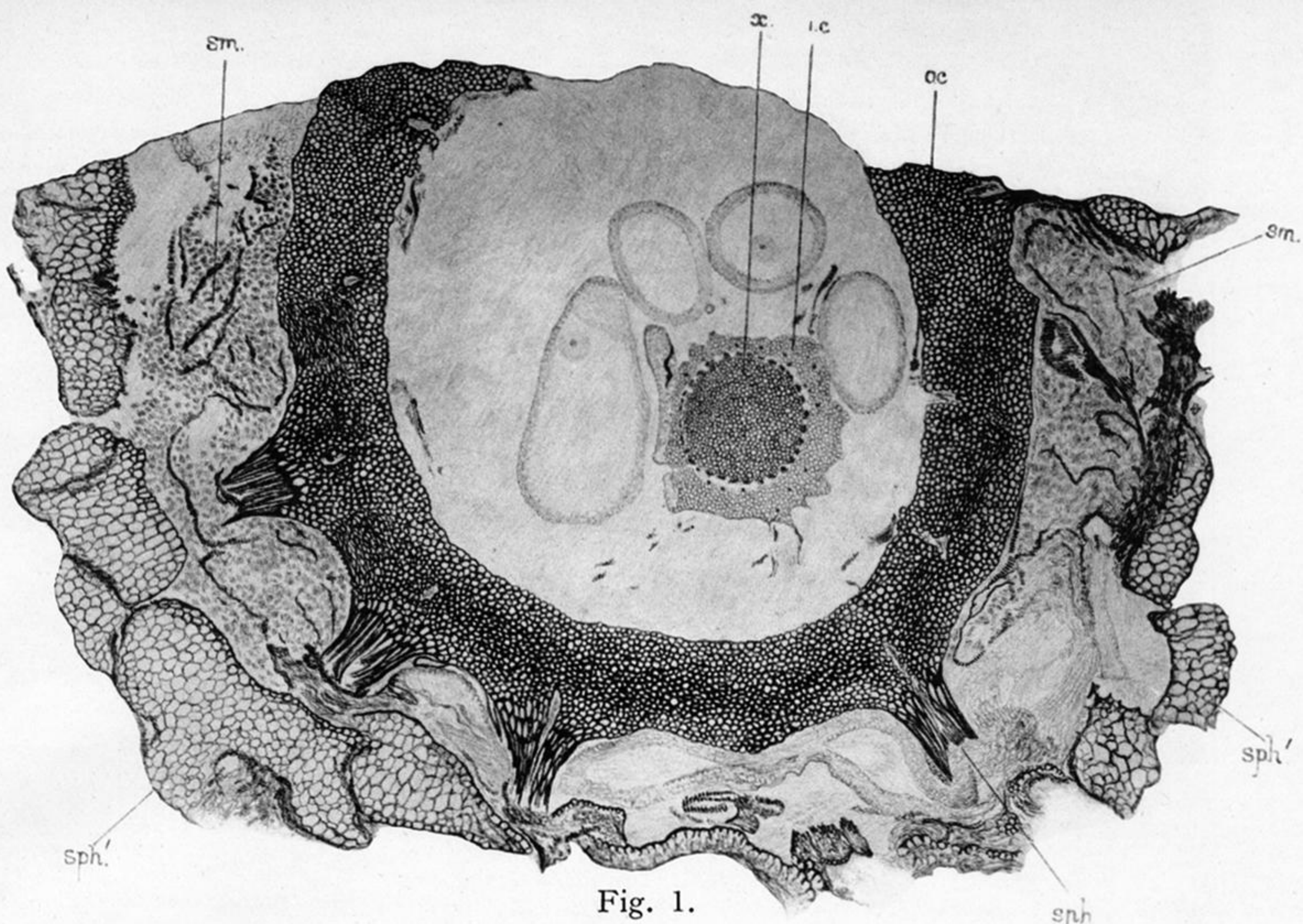


Fig. 1.

sph

sph'

sph'

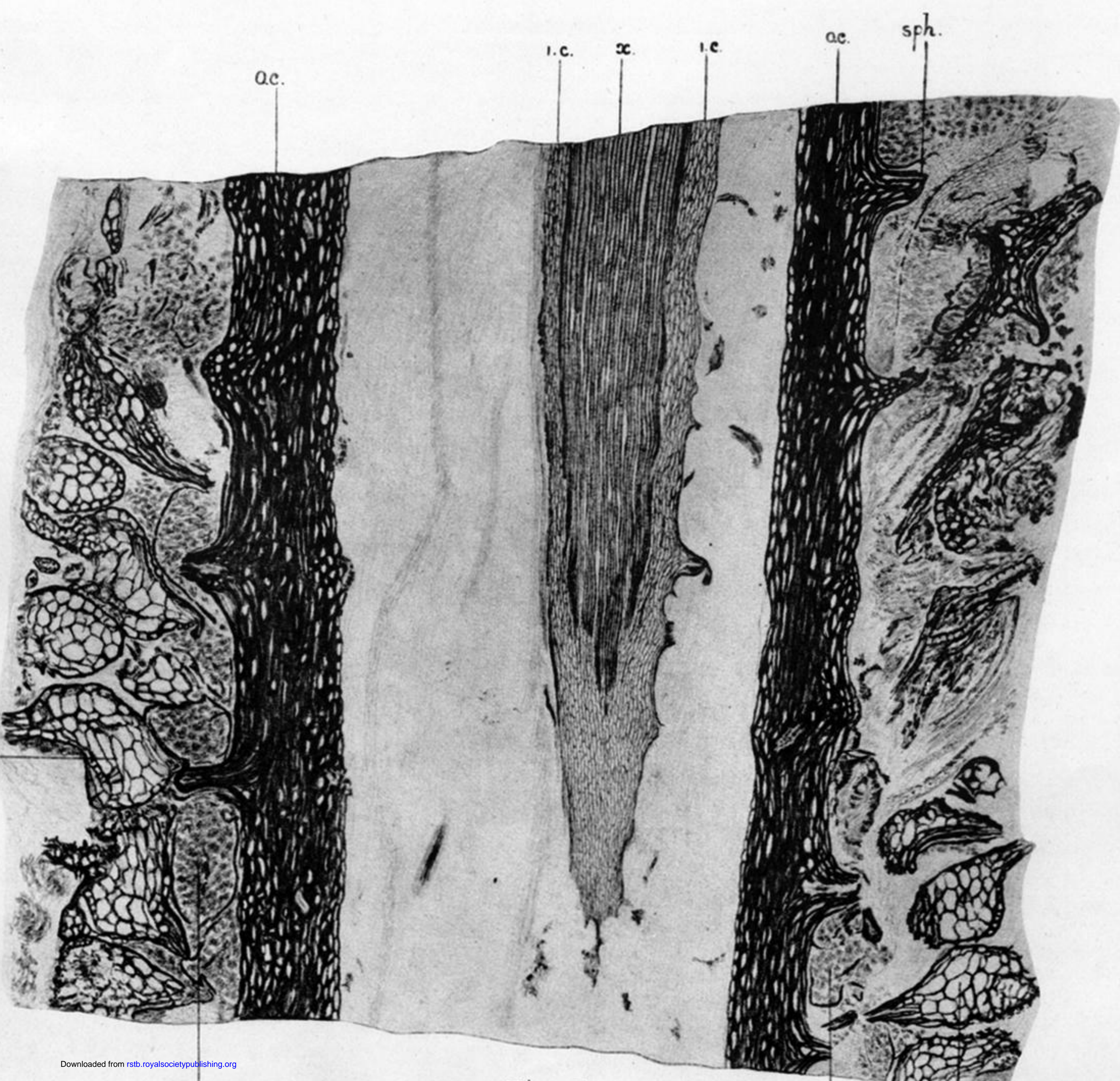


Fig. 2.

Spencerites majusculus.

sm.

sph'

sm.

sph'

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PLATE 12.

Spencerites majusculus.

Fig. 1. Transverse section of strobilus. *x.*, wood of axis; *i.c.*, inner cortex; the middle cortex has perished, leaving a space into which Stigmarian rootlets have penetrated; *o.c.*, outer cortex, in which the leaf-trace bundles can be seen at several places; *sm.*, remains of sporangia, containing spores; *sph.*, bases of sporophylls; *sph'*, laminae of sporophylls. $\times 10$. S., 7* (from Mr. J. SPENCER) (see pp. 95 and 96).

Fig. 2. Radial section of strobilus. *x.*, wood of axis; *i.c.*, inner cortex; the middle cortex only shows fragments of leaf-trace bundles, and an intruding Stigmarian rootlet; *o.c.*, outer cortex; *sm.*, sporangia, containing spores; *sph.*, bases of sporophylls; *sph'*, their laminae. $\times 9$. From a slide in Mr. J. SPENCER'S Collection (see pp. 95 and 96).

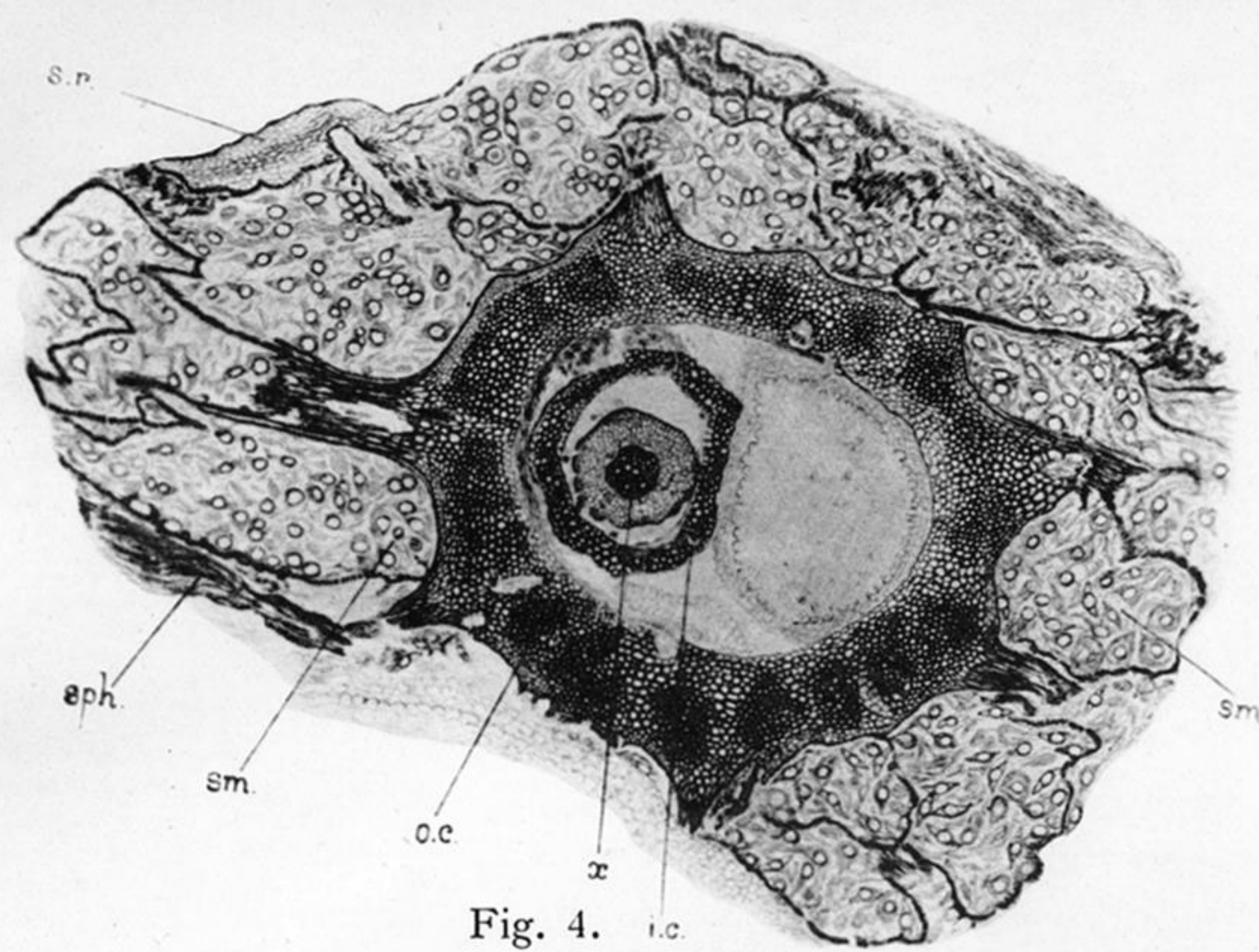


Fig. 4.

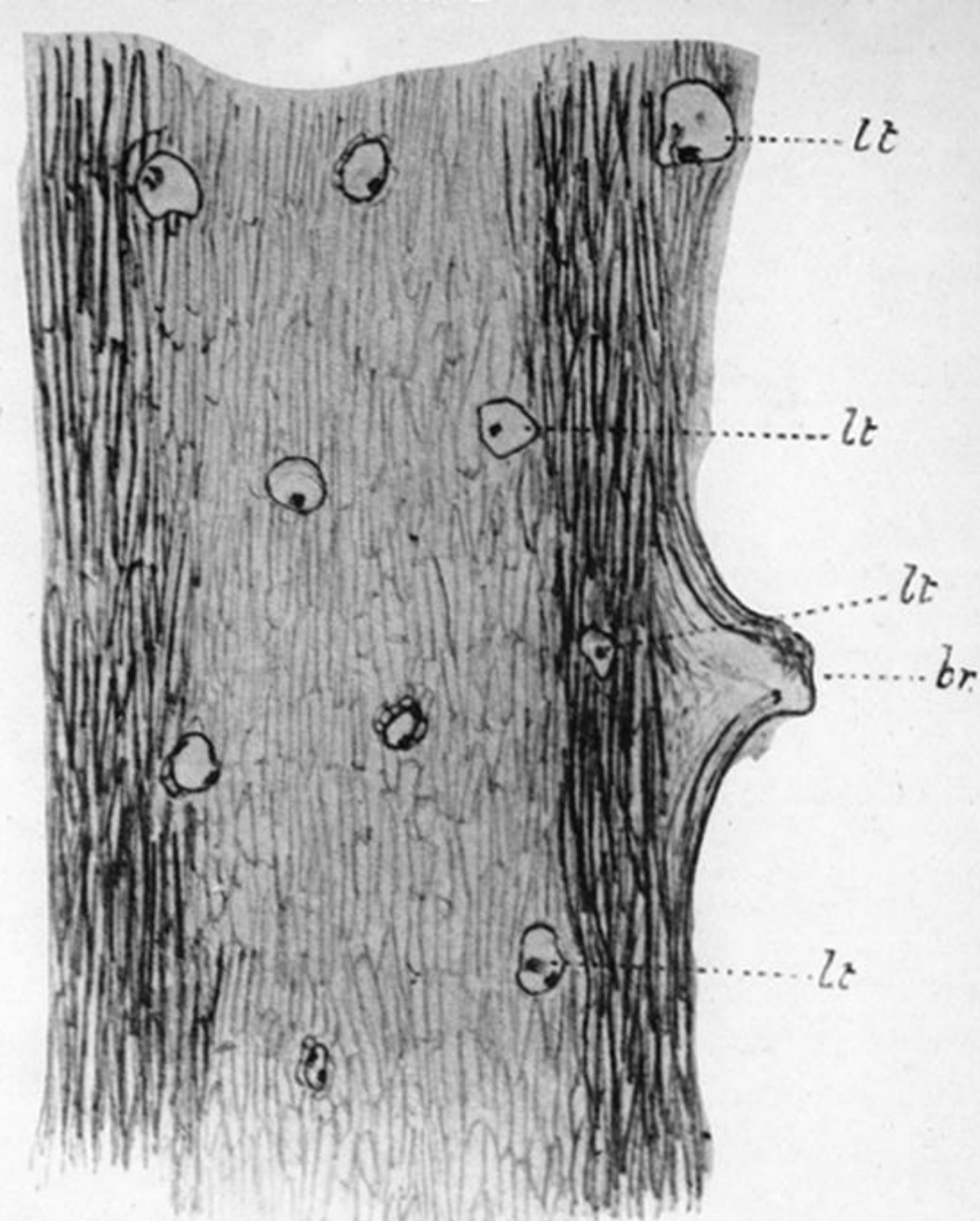


Fig. 7.

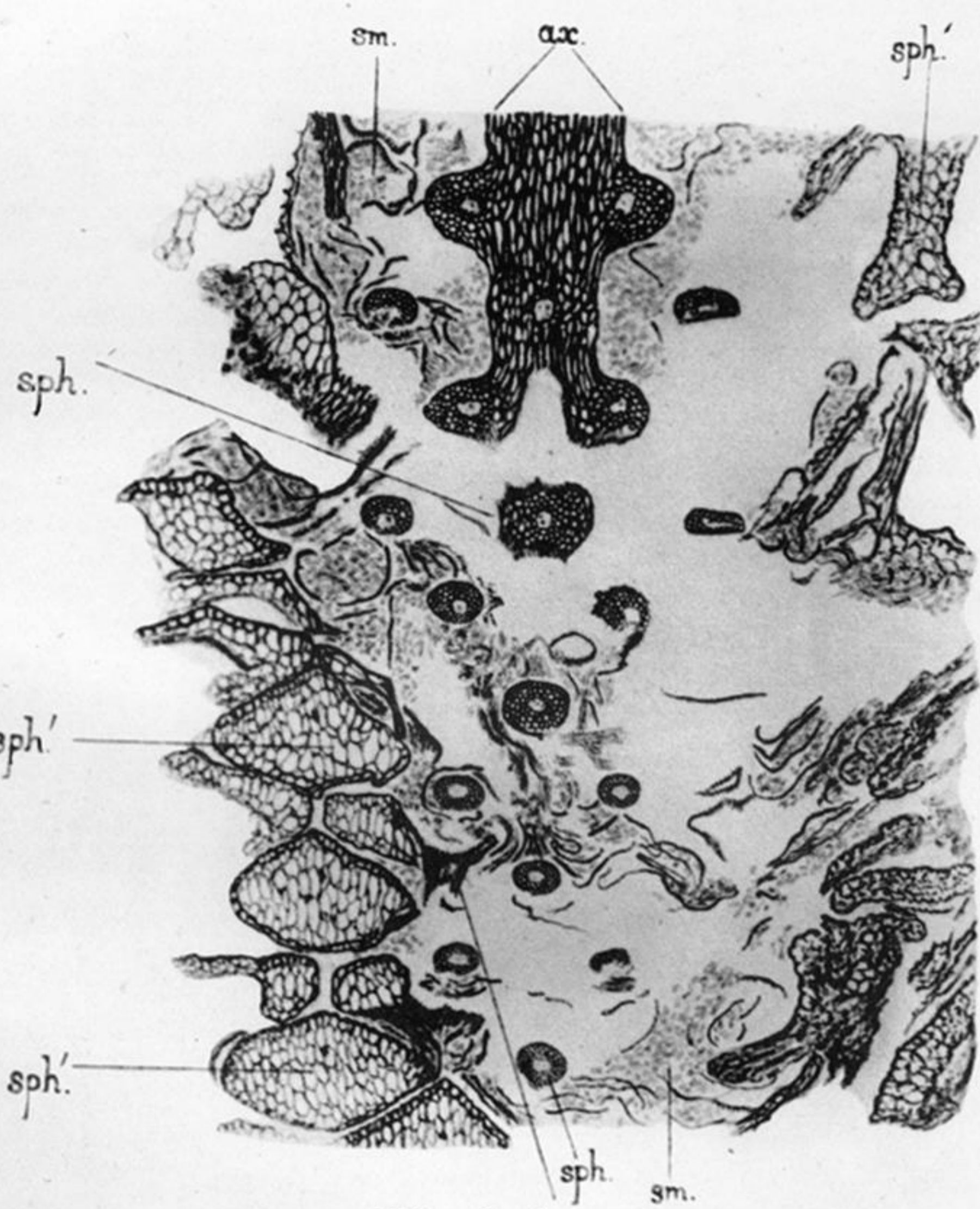


Fig. 3. a

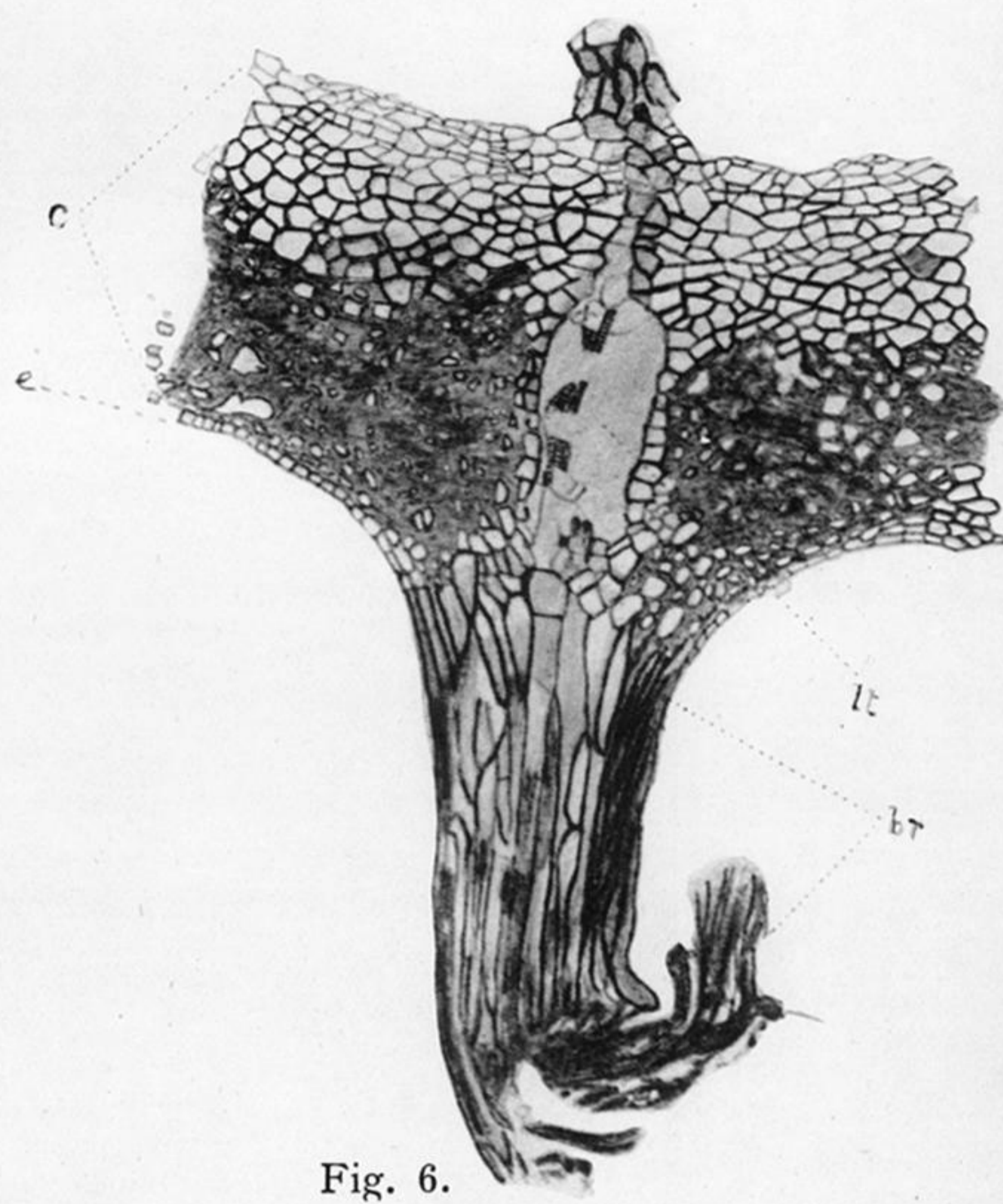


Fig. 6.

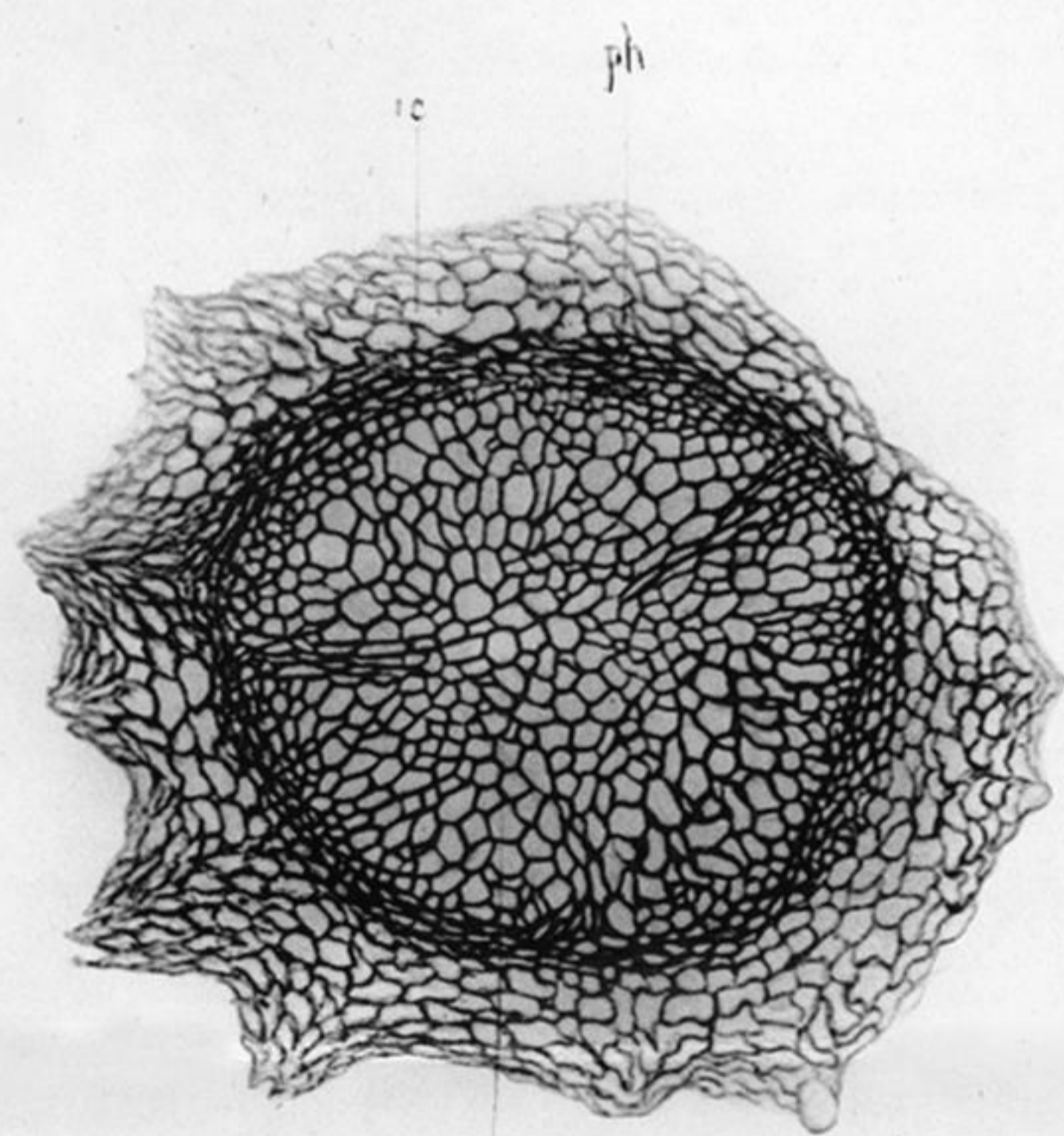


Fig. 5.



Fig. 8A.



Fig. 8B.

Fig. 3. *Spencerites majusculus*. Figs. 4—8B. *S. insignis*.

PLATE 13.

Fig. 3, *Spencerites majusculus*; figs. 4 to 8B, *S. insignis*.

Fig. 3. *S. majusculus*. Tangential section of strobilus. The section is slightly oblique, passing through the cortex of the axis above, and through the sporophyll-pedicels, below. On either side the laminæ are shown, best preserved on the left hand. *ax.*, axis with bases of sporophylls; *sph.*, pedicels of sporophylls; *sph'*, their laminæ. Note the regular alternate verticils. *sm.*, remains of sporangia, containing spores; *a.*, insertion of a sporangium. $\times 6$. From a slide in Mr. J. SPENCER'S Collection (see p. 96). For other figures of *S. majusculus* see Plate 15.

Fig. 4. *S. insignis*. Transverse section of a strobilus. *x.*, wood of axis, enclosing a thick-walled pith; *i.c.*, inner cortex; middle cortex penetrated by Stigmarian rootlets; *o.c.*, outer cortex, with "Dictyoxylon" structure; the leaf-trace bundles are seen both here and in the inner cortex: *sph.*, sporophylls, imperfectly preserved; *sm.*, sporangia, containing the winged spores; *s.r.*, Stigmarian rootlet. $\times 10$. From a slide by Mr. J. LOMAX in the WILD Collection (No. 159), Manchester Museum. Other sections of the same cone are in the WILLIAMSON* and HICK Collections, and in my own (see pp. 86-90).

Fig. 5. Transverse section (from the base of a strobilus) of the stele and inner cortex. The large central mass, *x.*, is the wood; *ph.*, phloem-zone, somewhat crushed; *i.c.*, inner cortex. $\times 50$. S., 4 (from Mr. J. SPENCER). Other sections of the same cone are in the WILLIAMSON† and CASH Collections (see p. 87).

Fig. 6. Part of a transverse section from a peduncle, to show bract. *e.*, epidermis; *c.*, outer cortex, the external layers of which are very thick-walled; *lt.*, leaf-trace bundle, passing out to bract; *br.*, bract. C.N., 419G (from Mr. J. SPENCER). $\times 45$ (see p. 86).

Fig. 7. Tangential section through the cortex of a peduncle to show the arrangement of the leaf-trace bundles, which appear to form a flat spiral with a small divergence; slightly diagrammatic; *lt.*, leaf-trace bundles. In many of them the group of tracheæ can be seen, and also the bundle-sheath; *br.*, base of a bract. $\times 18$. C.N., 419D (from Mr. J. SPENCER) (see p. 86).

Fig. 8A. Tracheæ from the extreme outer edge of the wood, seen in radial section. *px.*, *px.*, small spiral tracheæ of the protoxylem, somewhat disorganized. The larger element to the right (*i.e.*, towards the interior) is also partly spiral.

Fig. 8B. From the same section, showing a spiral trachea (*tr.*) imbedded in the middle of the pith; *p.*, elongated pith-cells. Both figures $\times 165$. C.N., 419E (from Mr. J. LOMAX) (see p. 87).



Fig. 9.

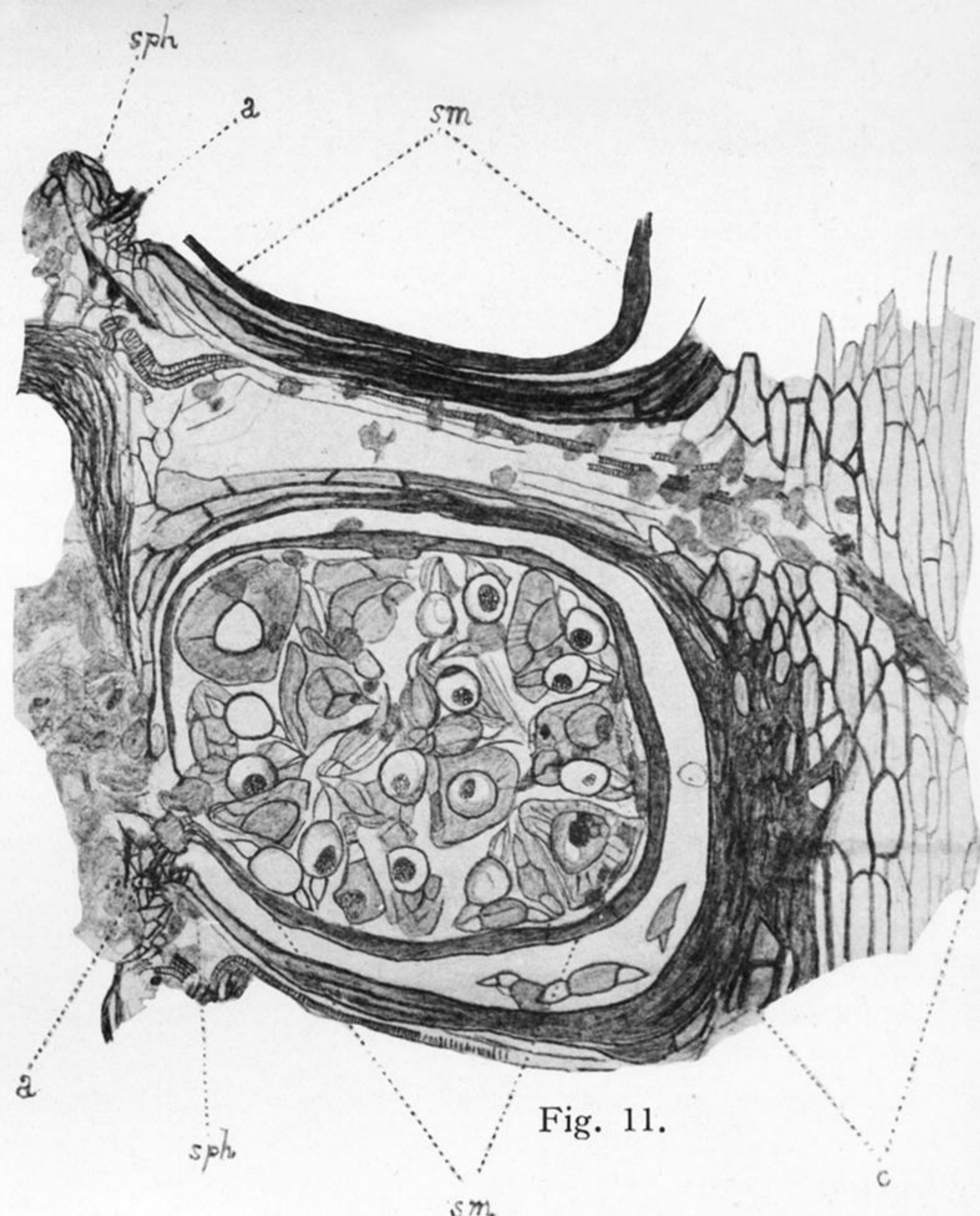


Fig. 11.

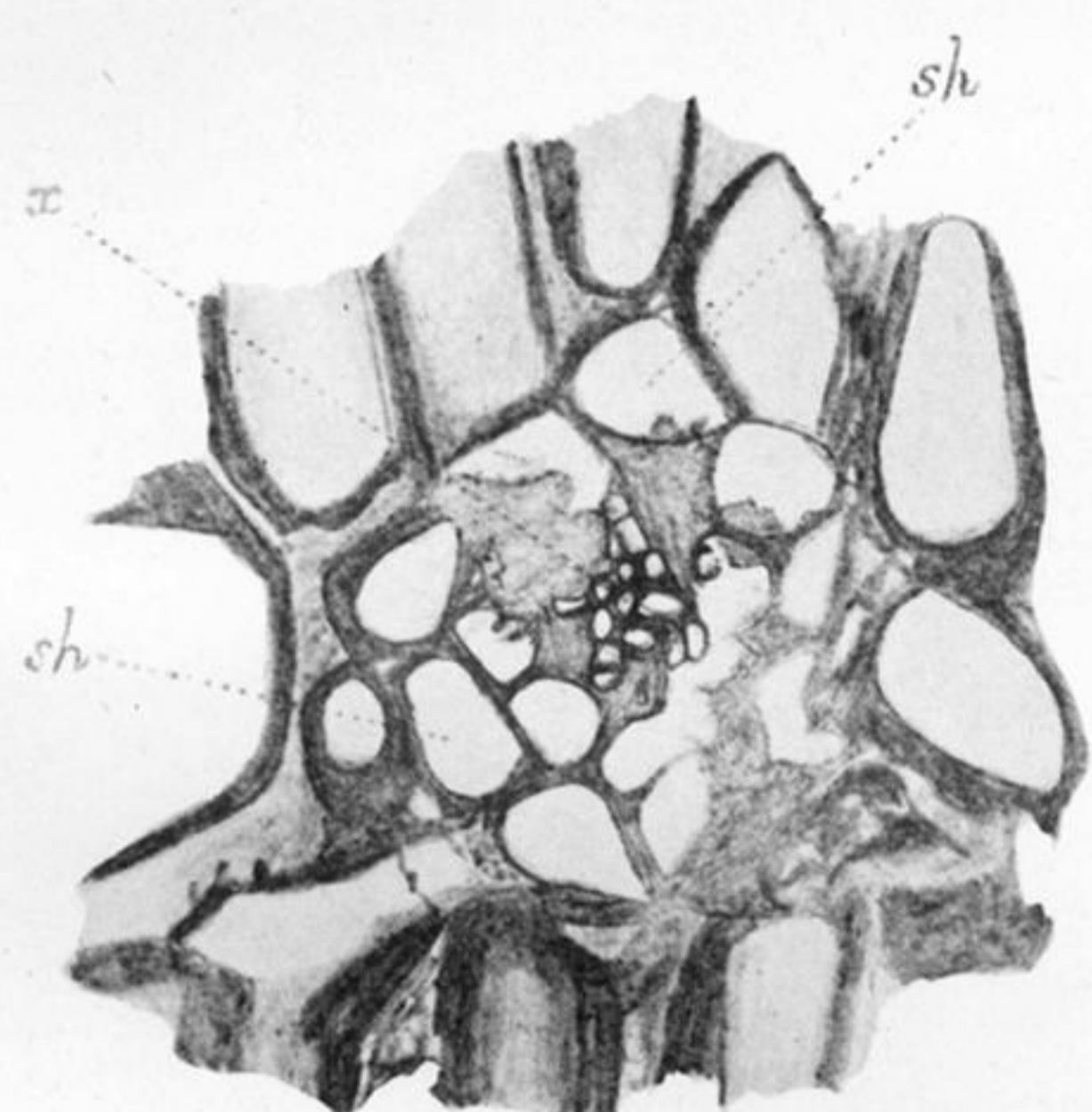


Fig. 10.

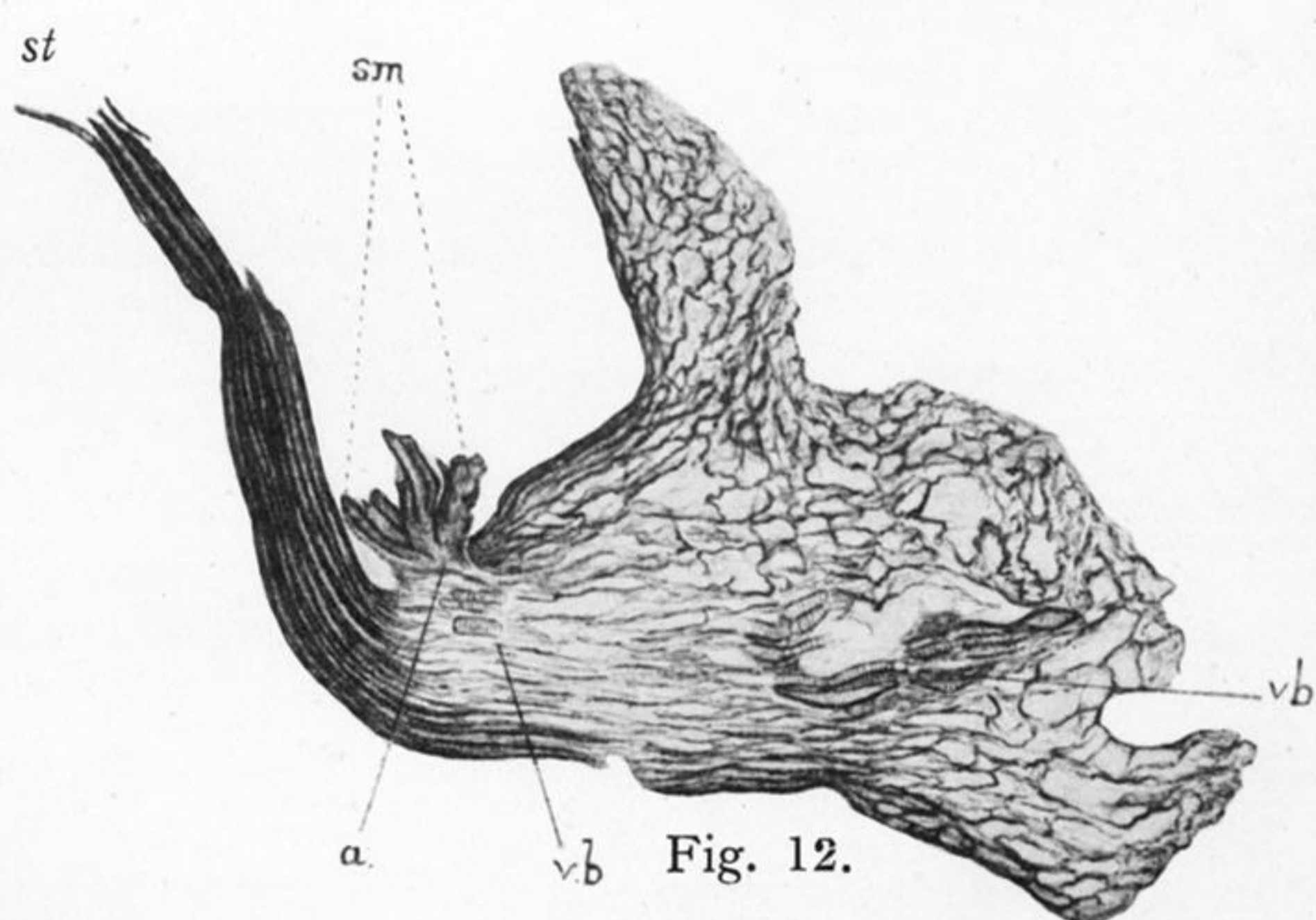


Fig. 12.

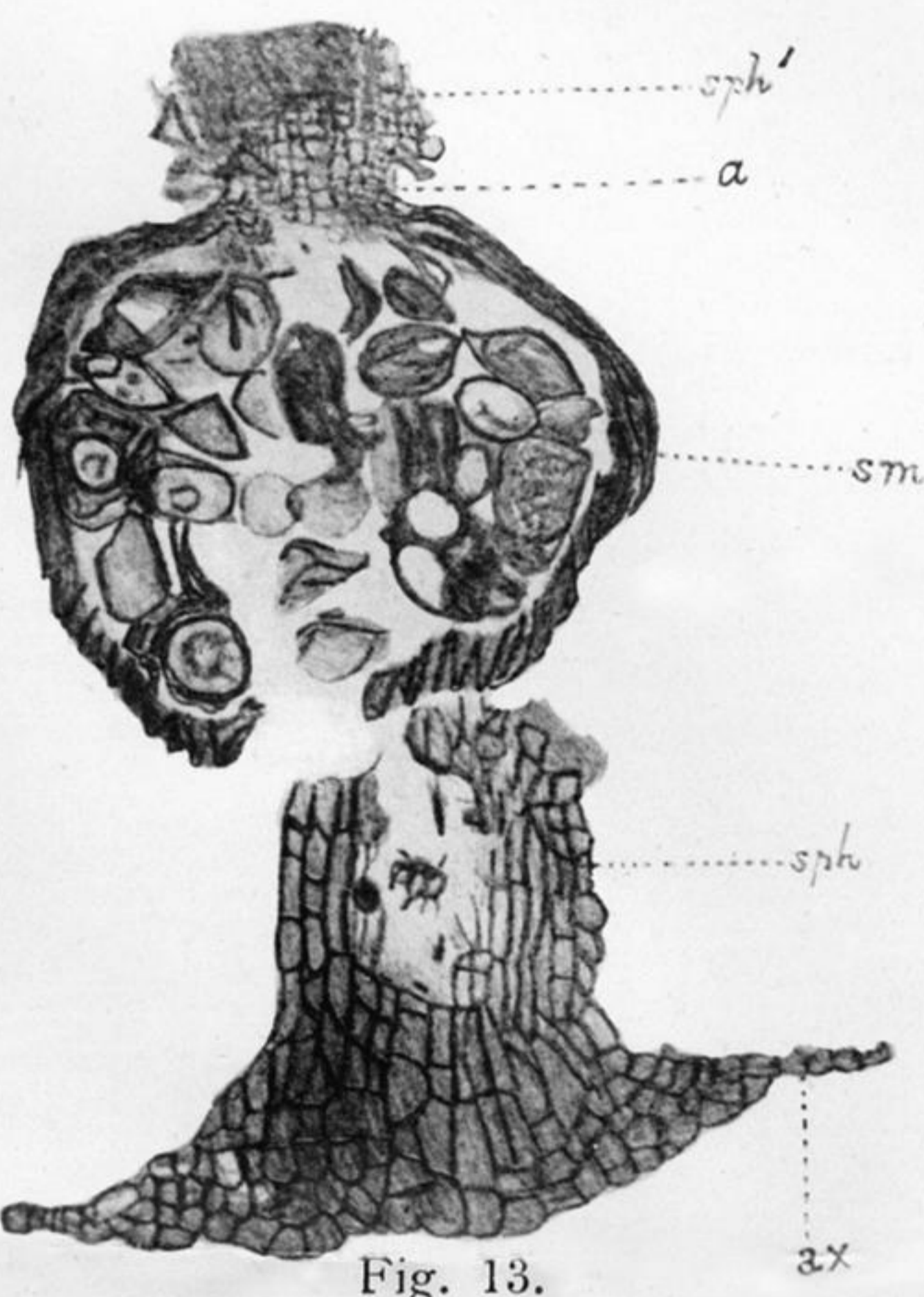


Fig. 13.

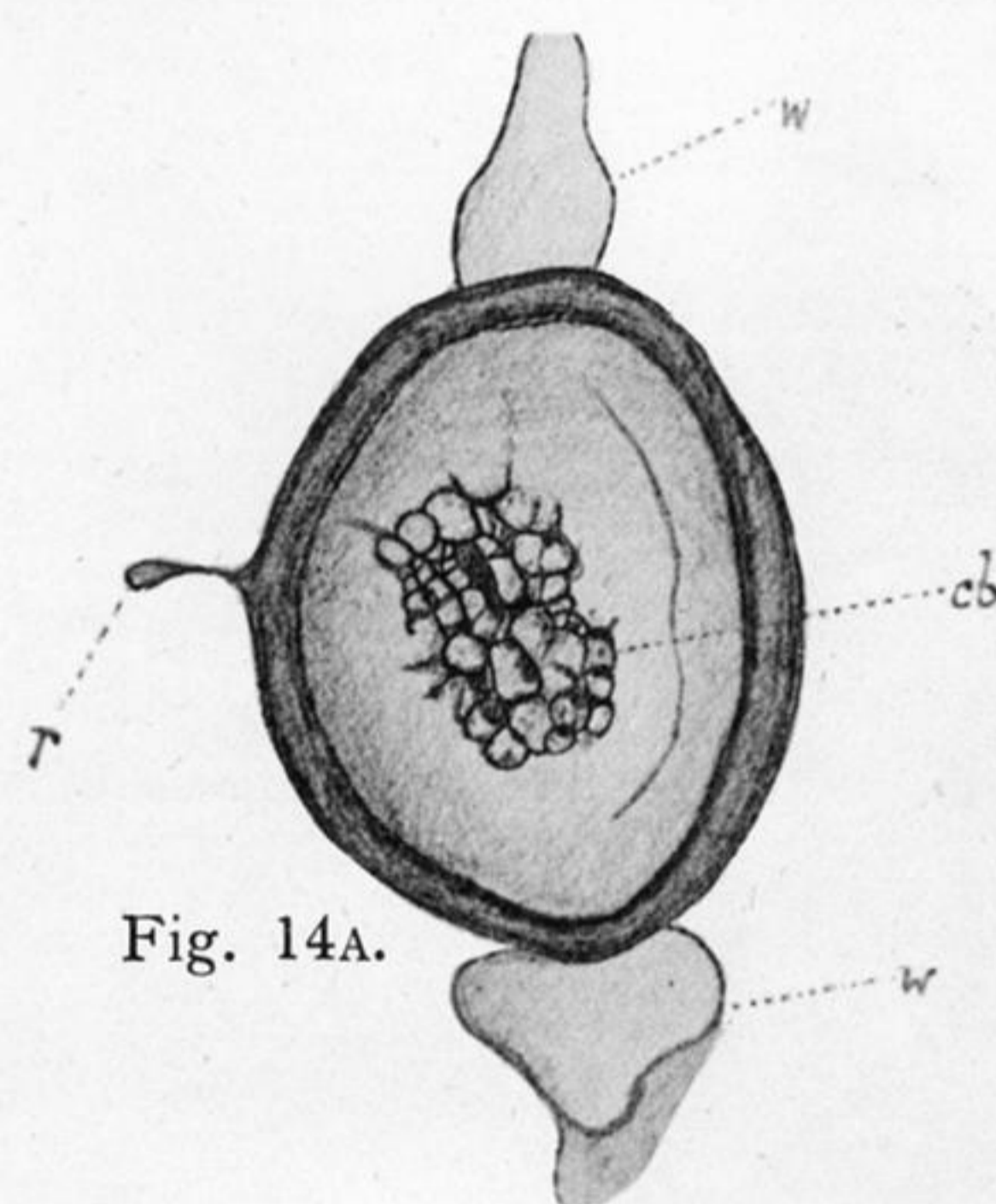


Fig. 14A.

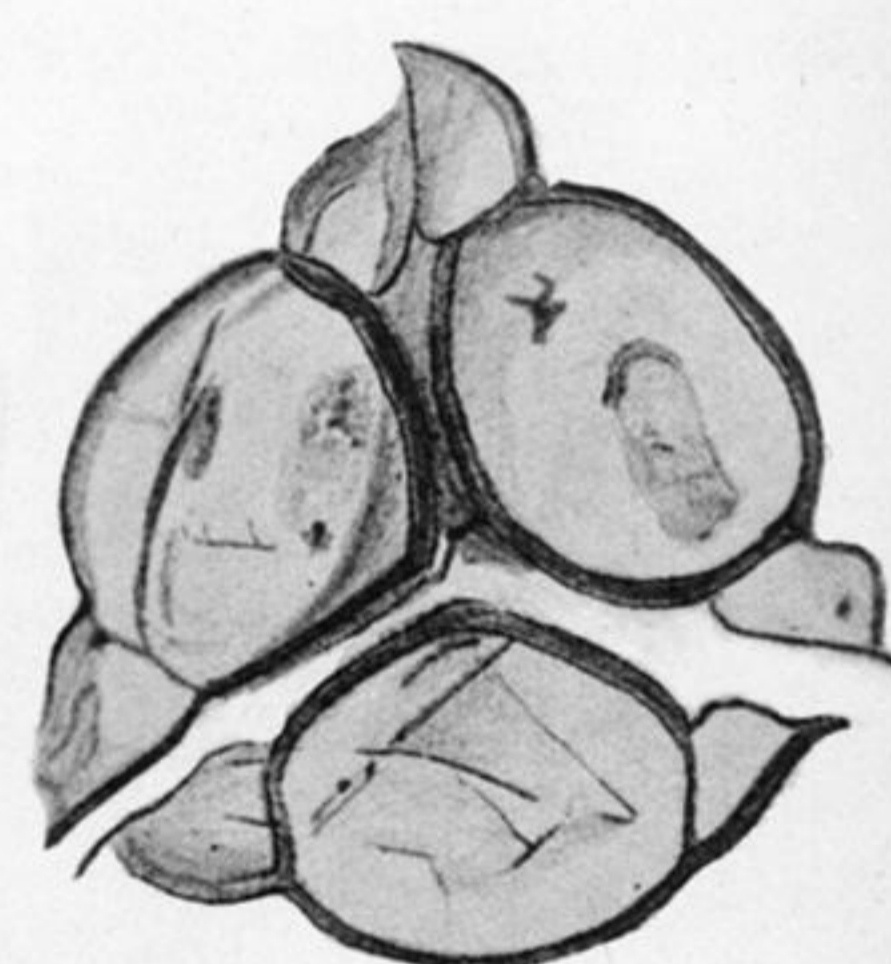


Fig. 14B.

Spencerites insignis.

PLATE 14.

Spencerites insignis.

Fig. 9. Part of a radial section of a peduncle, to show the middle cortex. *sh.*, sheath of elongated cells surrounding a leaf-trace bundle; *lc.*, lacunar middle cortex, consisting of irregular interwoven trabeculae. $\times 70$. C.N., 419E (from Mr. J. LOMAX) (see p. 88).

Fig. 10. Part of tangential section of an axis to show a leaf-trace bundle passing through the outer cortex. *x.*, xylem of bundle; *sh.*, bundle-sheath. The larger surrounding cells are cortical. $\times 165$. C.N., 624D (from Mr. J. LOMAX) (see p. 89).

Fig. 11. Part of the radial section of a strobilus, figured as a whole by WILLIAMSON, "Organization," Part XIX., Plate 7, fig. 50. The sporangium shown here is the lowest on the left. *c.*, cortex of axis. Two sporophylls (*sph.*) are shown, the lower incomplete. Each contains a vascular bundle; *sm.*, sporangia; the lower is shown complete and is filled with winged spores; *a.*, point of attachment of the sporangium to the distal part of the sporophyll. The rest of the sporangial wall is perfectly free. $\times 45$. C.N., 624B (from Mr. J. SPENCER) (see p. 89).

Fig. 12. Detached sporophyll, seen in radial section. In the tissue of the large lamina, the vascular bundle, *v.b.*, is seen at two places. *sm.*, base of the sporangium, inserted on the upper surface of the lamina at *a.*; *s.t.*, torn fragment of the pedicel, bent upwards. Compare WILLIAMSON'S figure, in "Organization," Part XIX., Plate 7, fig. 50. The sporophyll lies close to the cone to which it belongs. \times about 50. From a slide in the CASH Collection (*Lepidodendron Spenceri*, II.) by Mr. J. SPENCER. The section is from the cone shown in WILLIAMSON'S figure above cited (see p. 90).

Fig. 13. Part of transverse section of a strobilus to show sporophyll and sporangium *ax.*, outer limit of the cortex of the axis; *sph.*, sporophyll, shown both in its proximal and distal part; *sm.*, sporangium, containing winged spores; *a.*, attachment of sporangium to distal end, *sph'*, of sporophyll. $\times 45$. C.N. 626 (from Mr. J. BINNS) (see p. 90).

Fig. 14A. A single spore, seen in section. *w.w.*, the wing; *r.*, one of the radiating ridges, marking the line of junction with the sister-spores; *c.b.*, cellular or vacuolated body in the interior of the spore. $\times 265$ (see pp. 91 and 92).

Fig. 14B. A tetrad of spores seen in section, showing the position of the wings. As the arrangement is tetrahedral, only three spores are seen in one plane. $\times 150$. Both Figs. from C.N. 624B (see p. 91).

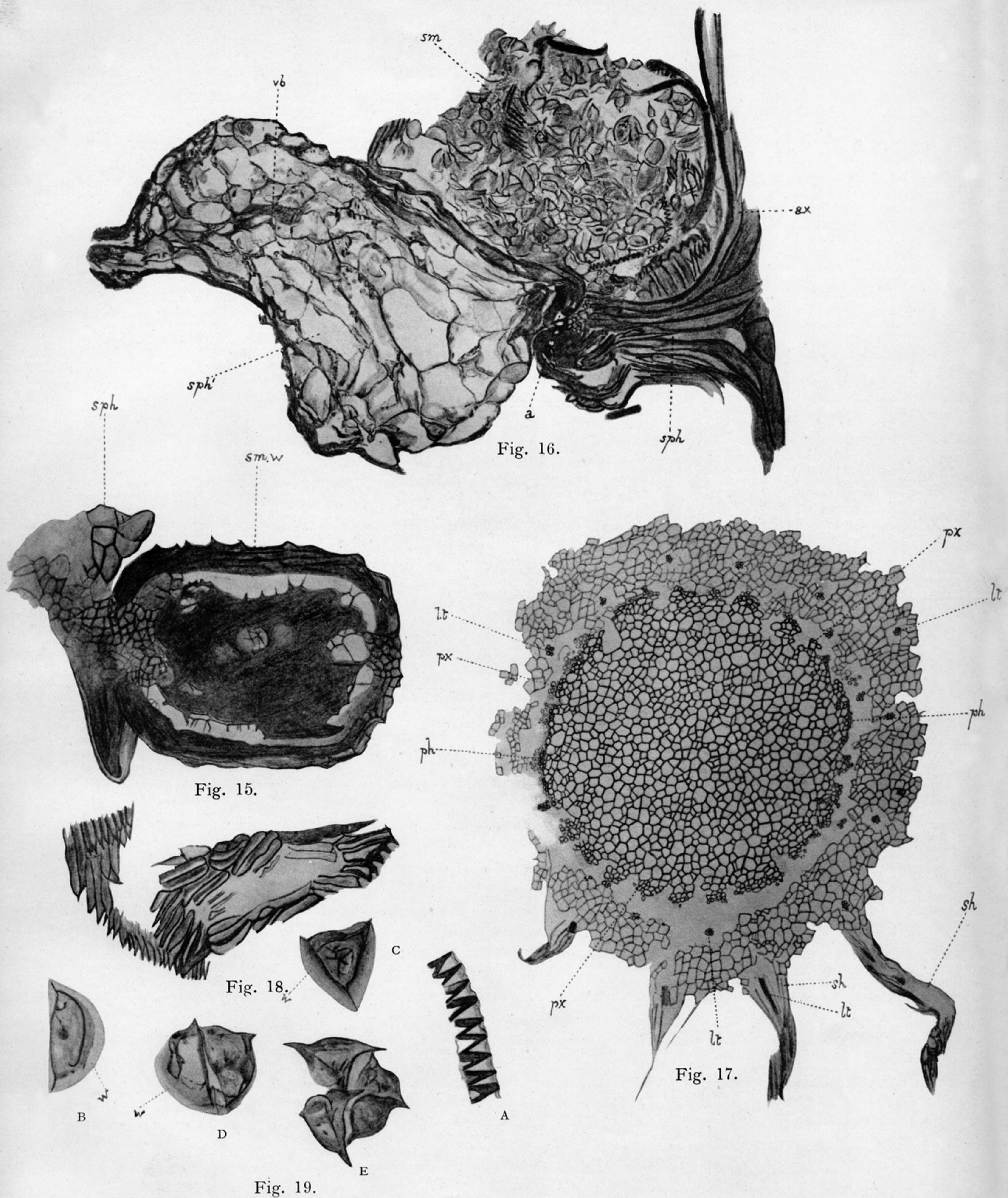


Fig. 15.

Fig. 16.

Fig. 17.

Fig. 18.

Fig. 19.

Fig. 15. *Spencerites insignis*.

Fig. 16—19. *S. majusculus*.

PLATE 15.

Fig. 15. *Spencerites insignis*. Figs. 16—19. *S. majusculus*.

Fig. 15. *S. insignis*. Abortive sporangium. *sph.*, part of sporophyll to which sporangium is attached; *sm.w.*, sporangial wall. The interior is occupied by a dark, contracted mass, showing some traces of cellular structure. $\times 110$. C.N. 626 (see p. 93).

Fig. 16. *S. majusculus*. Sporophyll in radial section. This is from the left hand side of the section shown entire in Plate 12, fig. 2. *ax.*, external tissue of axis; *sph.*, pedicel of sporophyll; *sph'*, its lamina; *v.b.*, vascular bundle; *sm.*, sporangium (containing spores) inserted on the sporophyll at *a*. \times about 40 (see p. 96).

Fig. 17. Part of a transverse section of the strobilus, showing stele and inner cortex. *px.*, *px.*, protoxylem-groups, of which there are about thirty in all; all the tissue to the inside is wood; *ph.*, remains of phloem; *lt.*, leaf-trace bundles passing through inner cortex; *sh.*, sheaths surrounding the bundles, where they traverse the decayed middle cortex. \times about 40. C.N. 624c (from Mr. J. SPENCER). This section is practically identical with that shown in Plate 12, fig. 1 (see p. 95).

Fig. 18. Part of sporangial wall, seen in surface view. \times about 70. C.N. 624c (see p. 97).

Fig. 19. A. Part of sporangial wall, seen in section. $\times 150$. C.N. 624g.

B. Spore seen from the side. *w.*, wing. $\times 150$. C.N. 624g.

C. Spore seen in oblique section, *w.*, wing. $\times 150$. C.N. 624c.

D. Tetrad in side view; only two spores visible. $\times 150$. C.N. 624c.

E. Tetrad in end view, showing all four spores. $\times 150$, C.N. 624c.