VI.* *On the Structure and Affinities of Fossil Plants from the Palæozoic Rocks.*—IV. *The Seed-like Fructification of* Lepidocarpon, *a Genus of Lycopodiaceous Cones from the Carboniferous Formation.*

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Received February 19,—Read February 28, 1901.

(Plates 38–43.)

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Introduction.

In a Note, communicated to the Royal Society in August, 1900,* a short account has been given of *Lepidocarpon*, a new genus founded to receive certain Lycopodiaceous strobili, of Palæozoic age, which bore integumented megasporangia, identical with the "seeds" described by Williamson under the name of *Cardiocarpon*

* 'Roy. Soc. Proc.,' vol. 67, p. 306.

*anomalum.** In the present memoir it is proposed to give a further statement of the evidence on which this conclusion is based, to describe and illustrate the structure of the remarkable fructification in question, and finally to discuss its morphology, and its possible bearing on the line of evolution of the seed-bearing plants. The fact that an organ which has hitherto been accepted without question as a true seed, was borne on a typical Lycopodiaceous strobilus, is a somewhat surprising one, and demands very careful consideration, if we would avoid being led into too hasty conclusions.

The discovery of the strobilus of *Lepidocarpon* is due to Messrs. G. WILD and J. LOMAX, who, at my request, published a short joint note on their observations in the 'Annals of Botany' for March, 1900, under the title "On a New *Cardiocarpon*-bearing Strobilus." The relation of the new cone to *Lepidostrobus* was recognised by these authors, who deserve great credit for the discovery, and for their essentially correct interpretation of it. The sections were placed by the discoverers in my hands for further botanical investigation.

The first preparations which I received (those illustrated in Plate 38, phots. 5 and 6 of the present paper) were sent me by Mr. LOMAX as long ago as September, 1897. The specimen (derived from the Lower Coal-Measures, at Hough Hill, Lancashire) is a strobilus, of ordinary Lepidostroboid organisation, each sporophyll bearing a single large sporangium on its upper surface. The structure will be described fully below; here it will be sufficient to say that the only essential difference from known *Lepidostrobi* consists in the presence of a single large megaspore in each sporangium, nearly filling the cavity, but accompanied by the remains of its abortive sister-cells. A series of sections, cut from the same block, showed a number of seed-like specimens clearly referable to the *Cardiocarpon anomalum* of WILLIAMSON, associated with detached sporophylls and sporangia, identical with those of the new cone. The latter was itself regarded by Mr. LOMAX as belonging to *Cardiocarpon*. The sporangia borne on the strobilus, however, differed conspicuously from the "seeds" of WILLIAMSON'S *Cardiocarpon*, in the fact that they were without any integument, a character of essential importance, on which the identification of WILLIAMSON'S specimens as *seeds* to a great extent depends. Thus, in spite of the close agreement in detail between the nucellus of the one and the sporangium of the other, and though realising the possibility that an integument might grow up, at a later stage, around the sporangium, I was for a long time unwilling to draw the startling conclusion that a *Lepidostrobus* (for such the new cone essentially was) bore seeds, identical with a "*Cardiocarpon*." Other specimens, received during 1898–1899, did not remove this initial difficulty, and it was not till January 22nd, 1900, that I received what could be accepted as finally convincing evidence. This was afforded

* Quite different, however, as will be shown below, from the true *Cardiocarpon anomalum* of CARRUTHERS. See WILLIAMSON, "Organisation of Fossil Plants of Coal-Measures, Part VIII.," 'Phil. Trans.,' vol. 167, pt. 1, 1877, p. 255, figs. 116–120; Part X., 'Phil. Trans.,' vol. 171, pt. 2, 1880, p. 518, fig. 64.

by a specimen collected and sectioned by Mr. G. WILD, which showed perfectly typical "seeds" (WILLIAMSON'S *Cardiocarpon*) borne on a strobilus identical in structure with the sporangium-bearing cones previously examined. While sections from the lower part of Mr. WILD'S strobilus thus showed the integumented, mature condition of the reproductive bodies, the upper part of the same cone bore only Lepidostroboid sporangia, identical with those of Mr. LOMAX'S specimens (see Plate 39, phots. 10–13 and Plate 43, figs. 26 and 27). Mr. WILD'S cone therefore proves, on the one hand, that the "*Cardiocarpon anomalum*" of WILLIAMSON was borne on a Lepidostroboid strobilus, and on the other that the integumented and non-integumented forms of the megasporangium belonged to the same fructification.

As explained in the preliminary Note, WILLIAMSON'S *Cardiocarpon anomalum*, or at least those specimens of it which he figures, had nothing to do with the *Cardiocarpon anomalum* of CARRUTHERS,* or with any species of the true genus *Cardiocarpon* or *Cardiocarpus* of BRONGNIART. All these were undoubtedly true Gymnospermous seeds belonging to the Cordaiteæ or allied plants. The Lepidostroboid fructification described in the present paper, though bearing, when seen in certain planes of section, a resemblance to BRONGNIART'S *Cardiocarpon* sufficient to have deceived good palæobotanists, is totally different in minute structure from any Cordaitean or other Gymnospermous seeds, with which there is no reason to suppose it had any affinity. At the same time, the fructification, though closely allied to *Lepidostrobus*, is too distinct to be simply left in that genus. I have therefore founded a new genus for its reception under the name *Lepidocarpon*, the character of which was given in the preliminary Note, and is repeated, with some modifications, below (p. 325). The Coal-Measure species, which was first discovered, is distinguished as *Lepidocarpon Lomaxi*, while a similar fossil from the more ancient horizon of the Calciferous Sandstones of Burntisland, is named *L. Wildianum*. I have thus endeavoured to commemorate the two discoverers to whom we owe our present knowledge of these remarkable fossils.

Five specimens of the actual strobilus have been examined. Four of these (all received from Mr. LOMAX) are in the Lepidostroboid condition, having their megasporangia without integuments. These I refer to as Specimens I. to IV., numbering them in the order of their discovery.† The fifth is the important specimen dis-

* WILLIAMSON states (*loc. cit.*, Part VIII., p. 257): "Mr. CARRUTHERS, to whom I showed the original of fig. 116, considers it to be identical with his *C. anomalum*. Though far from certain, not having seen Mr. CARRUTHERS'S specimen, the seed which I have described may remain under that name, upon the authority of its author." The specimen in question (No. 1413 in the WILLIAMSON Collection) is a solid fragment, and no doubt belongs to our *Lepidocarpon Lomaxi*, and not to the true *Cardiocarpon anomalum* of CARRUTHERS. Its nature, however, could never have been determined without the comparative study of better specimens, by means of sections.

† Specimen II. has not been figured, as its preservation is less good than that of the others. [Two more specimens of the strobilus have since been found by Mr. LOMAX, and sections of them are now in the Botanical Museum of University College, London.—*June* 18, 1901.]

covered by Mr. WILD, which alone shows the seed-like stage of the fructification *in situ*. This specimen, as Mr. WILD informs me, was discovered fourteen or fifteen years ago, though I only became acquainted with it at the beginning of this year (1900). It will be referred to simply as WILD'S specimen.

Another strobilus, bearing microsporangia, and from the same block as Specimen I., probably belongs to the species *Lepidocarpon Lomaxi* (see p. 312). In addition to specimens of the cones, a very large number of detached sporophylls bearing sporangia, some with and others without integuments, have come under observation, and have proved quite as important as those *in situ*. It is only, however, the knowledge of the strobilus as a whole, which has rendered possible the correct interpretation of these isolated specimens.

The structure of the Coal-Measure species—*Lepidocarpon Lomaxi**—of which our knowledge is the more complete, will first be described; in certain points the one form supplements the other.

I. LEPIDOCARPON LOMAXI.

1. *Organisation of the Strobilus.*

For the present we will confine our attention to the megasporangiate cones, for the evidence indicates that the two kinds of sporangia were borne on separate strobili,† the specific identification of which is necessarily open to some doubt.

In the immature, Lepidostroboid condition, *i.e.*, before the development of integuments around the sporangia, the cone averages about 15 millims. in mean diameter. The specimen shown in transverse section in Plate 38, phot. 2, is of average size, and in its compressed condition measures about 20 × 10 millims. Specimen III. (phots. 1 and 3) is somewhat smaller, and perhaps younger. In the mature state, when the sporangia had assumed their final seed-like character, the dimensions are considerably greater; the lower part of WILD'S specimen is quite 3 centims. in diameter, while the upper end, where the sporangia are still immature, is less than 2 centims. (See Plate 39, phots. 10 and 11.) As regards the length, we know that Specimen IV. (phot. 2) was *not less* than an inch and a half long, but we cannot tell how much longer it may have been, as it is incomplete towards the base.

The general organisation of the strobilus is that of a typical *Lepidostrobus*, and requires no detailed description. The axis bears numerous, densely crowded sporophylls, the arrangement of which was evidently a spiral one, as shown especially clearly in the tangential section represented in phot. 3. The sporophylls are simple, and of the form usual in *Lepidostrobus*, *i.e.*, each sporophyll consists of a

* It is possible, as explained below, that more than one species may be included under this name.

† The probability of this arrangement occurring in Lepidodendreæ was recognised by Count SOLMS-LAUBACH in 1887. 'Introduction to Fossil Botany,' English ed., p. 236.

long narrow pedicel, almost horizontal in position or slightly inclined upwards, expanding at the distal end into a relatively broad and thick lamina, with its point directed vertically. The form of the sporophyll in its various parts will be best understood by comparing Plate 38, phots. 1–6, and Plate 40, figs. 1–4. The most characteristic points are the following :—

The pedicel has a well-marked dorsal rib, appearing as a tail-like appendage in tangential sections of the cone (phots. 3, 4, 5, and 6 ; fig. 1) ; at the proximal end this rib was decurrent on the axis (phot. 5), while at the distal end it became merged in the thickened lamina. The pedicel also has two lateral wings or cushions which helped to support the bulky sporangium. Near the axis, where the pedicel is a slender structure, these cushions are inclined upwards (phots. 3, 4, and 6). Further out, the whole pedicel becomes thicker, both the lateral wings and the dorsal rib increasing in bulk ; at the same time the cushions become flatter and broader (phots. 3 and 6 ; fig. 1). In this region a lateral groove appears on each side, marking off the cushion from the lower part of the wing (fig. 1). In Specimens I. and IV. these grooves are well marked, and appear to be continuous outwards with the lateral furrows of the lamina. They may correspond to the stomatiferous furrows of the vegetative leaf of *Lepidodendron.** In Specimen III., which is a smaller cone, the lateral furrows are scarcely indicated on the pedicel, though well marked in the lamina. The pedicel, as we trace it further outwards, becomes still broader and flatter on the top, until, in the region of the ligule, the cushions begin to slope downwards from the median line† (phot. 3 ; fig. 2).

Quite at the distal end the pedicel acquires a thin marginal wing (fig. 2, *l*), continuous with that of the upturned lamina. At the bend, where the horizontal pedicel is passing over into the vertical lamina, the sporophyll is a massive structure, having a somewhat triangular section when cut tangentially to the strobilus (phots. 3, 5, and 6 ; fig. 2). Though the bend is the thickest part of the sporophyll, there is no marked dorsal outgrowth here, so that the somewhat peltate form, often occurring in *Lepidostrobus*, is not attained (fig. 3). The upturned lamina reaches its greatest width a little above the bend, and then narrows out gradually, extending for a long distance in the vertical direction. Its sectional form often bears a considerable resemblance to that of the lamina of a vegetative leaf of *Lepidodendron* (fig. 4). The upper half of Specimen IV., about $\frac{3}{4}$ inch (19 millims.) long, was cut by Mr. LOMAX into thirteen consecutive transverse sections. The uppermost two or three sections show only the tips of the sporophylls, proving that they considerably overtopped the axis of the cone, as in an ordinary *Lepidostrobus*.

* *Cf.* fig. 59 in SCOTT, 'Studies in Fossil Botany,' 1900.

† It is this downward inclination of the lateral cushions which accounts for the curious form, like a double kite, which the sporophyll sometimes assumes, when seen in approximately horizontal sections of the cone (see phot. 2, *sph'*). As the flanks of the pedicel dip down towards the distal end, they may fall below the plane of section, giving the appearance of a sharp constriction of the sporophyll in this region.

A single large sporangium is seated on the upper surface of the pedicel of each sporophyll, to which it is attached along almost its whole length, from a point close to the axis as far as the ligule at the distal end (see phots. 3, 5, and 6 ; fig. 3). Although a longitudinal section is seldom so accurately radial as to follow the narrow line of attachment for any great distance, yet the comparison of tangential sections at varying distances from the axis demonstrates the mode of connection quite clearly. Along the whole length of the pedicel the narrow base of the sporangium is seated in a socket or groove, the sides of which are formed by the prominent lateral cushions (see phot. 4 ; fig. 1).

The ligule of the sporophyll is situated immediately beyond the distal end of the base of the sporangium, and lies in a pit, closed in on three sides by sporophyll-tissue, and on the fourth or proximal side by the sporangium itself (see phot. 3 ; figs. 2 and 3). It is thus in the normal position for the ligule in *Lepidostrobus*, as shown by Mr. MASLEN's investigations ;* as pointed out by that author, the position of the ligule shows that the whole of the long pedicel of the sporophyll is homologous with the short base of the vegetative leaf.

The general form of the sporangium is that of an elongated sac, with its long diameter radial to the strobilus, broad towards its base, and narrowing out to a sharp ridge along the top. It is supported below by the lateral cushions of the pedicel, and hence, in the proximal region, where the cushions slope upwards, its sectional form is somewhat rhomboidal, while as the cushions become flatter the sporangium assumes a more triangular section (see phots. 3, 5, and 6 ; figs. 1 and 2). The maximum vertical height of the sporangium in Specimens I. and IV. reaches 4·5 millims., and the maximum tangential width 2·5 millims. ; the radial length is about 6 to 7 millims. In Specimen III. all the dimensions are smaller, while, as we shall see, the mature specimens which had developed an integument reached a considerably greater size. Radial sections scarcely ever show the sporangium in its full height, for the upper ridge-like part is so narrow that it rarely happens to coincide with the plane of section (see fig. 3, in which the sporangia appear too low).

At the distal end, where the sporophyll becomes convex on its upper surface, the sporangium follows its curvature, and assumes what may be called the "saddle-bags" form when seen in tangential section (see phots. 3 and 6 ; fig. 2). As the sporophyll curves upwards towards the vertical lamina, the height of the sporangium correspondingly diminishes, and at the distal end its cavity is quite narrow, and its form, as seen in tangential section, three-lobed, consisting of the apical ridge and the two lateral flaps in contact with the sloping cushions. In fact, the distal end of the sporangium applies itself closely to the curvature of the sporophyll surface ; seen in horizontal section it shows two lateral processes following the surface of the lamina,

* MASLEN, "The Ligule in *Lepidostrobus*," 'Ann. of Bot.,' vol. 12, p. 257, 1898; "The Structure of *Lepidostrobus*," 'Trans. Linn. Soc. Lond.,' ser. 2, vol. 5, p. 371, 1899.

and giving a Y-shape to the sporangium in this aspect (see fig. 4). These peculiarities of form have proved of some importance as a means of identification with corresponding sections from the later, seed-like stage of the organ.

From the account just given of the general morphology of the cone, it follows that it is in all respects that of a *Lepidostrobus*, as shown by the arrangement and form of the sporophylls, the presence and position of the ligule, and the position and form of the sporangium. We have now to consider the organisation of the strobilus in its more mature condition. For this purpose we are dependent on Mr. WILD'S specimen, sections of which are represented in Plate 39, phots. 10–13, and details in Plate 43, figs. 26 and 27. Of this important specimen six sections exist: three transverse, two tangential, and one approximately radial. Two of the transverse sections are in the Manchester Museum, having been acquired from Mr. WILD a few years back. One of these, which, with other slides, was kindly entrusted to me for investigation by Mr. W. E. HOYLE, Director of the Museum, is represented in phot. 11; the other sections, originally in Mr. WILD'S private collection, are now in my possession. A short account of the specimen was given by Mr. WILD at a palæobotanic meeting at Shaw, Lancashire, early in 1899.

One of the transverse sections (see phot. 10), no doubt from the upper part of the strobilus, shows the same organisation as the immature specimens already described, as is shown on comparing phot. 10 with phots. 1 and 2. The form of the sporophylls and sporangia is the same, and the sporangia are of the ordinary kind, without any integument. Some of the sporophylls are cut obliquely, in a plane between transverse and tangential, and these show the lateral cushions supporting the sporangium just as in previous specimens (compare fig. 26 with fig. 1). A more detailed comparison must be postponed until the minute structure has been dealt with, but, as regards general morphology, it is evident that this end of WILD'S cone differs in no way from the other Lepidostroboid specimens already described. In this part the diameter of the strobilus is 19 millims.

The other sections show a different organisation. In the transverse section represented in phot. 11 (where the cone attains a diameter of 3 centims.), while the general arrangement of the parts is the same as before, we find that the sporangia are replaced by integumented, seed-like structures. One of these is shown more enlarged in fig. 27. The plane of section is similar in this case to that of fig. 26, but here, instead of the cushions at the base of the sporangium, we have a prolonged integument completely investing it, except for a narrow crevice at the top. The tangential sections, such as that represented in phot. 13, show the seed-like bodies very clearly, and demonstrate a close agreement with the *Cardiocarpon anomalum* of WILLIAMSON,* especially as shown in fig. 118 of his Part VIII. cited in the foot-note. The integument is clearly an additional structure, which has grown up from the pedicel of the sporophyll. WILD'S specimen is imperfectly preserved, especially in the part bearing

* 'Organisation of the Fossil Plants of the Coal-Measures,' Parts VIII. and X.

the seed-like organs, and the structure is shown far more clearly in many of the detached specimens, as, for example, those illustrated in Plates 38 and 39, phots. 7 and 14–16, and in Plate 41, figs. 10 and 12. To these we shall return; for our immediate purpose it is sufficient to point out that this specimen, while in one part identical with the Lepidostroboid fructifications just described, in another region bears integumented seed-like sporangia, agreeing with the *Cardiocarpon anomalum* of WILLIAMSON.

We have now to consider the exact relation between the ordinary Lepidostroboid sporangia and the seed-like organs, to examine the evidence for the development of the latter from the former, and to determine the nature of the changes which such a process involved. It will be most convenient to begin by describing fully the structure of the sporangium and its sporophyll in the simpler, non-integumented condition.

2. *Structure of the Sporangium and Sporophyll.*

A tangential section through a sporangium and sporophyll, passing about midway between the proximal and distal ends, is shown in fig. 1, from Specimen I. A general view of the section from which it is taken is given in phot. 6. The sporangial wall consists of two layers, an outer columnar or palisade layer, consisting of narrow prismatic cells set vertically to the surface, and an inner delicate tissue several cells thick, but incompletely preserved. The narrow apical ridge of the sporangium is filled up by the delicate internal tissue, except at the extreme apex, where only the palisade layer is represented. The opening at the top is inconstant and no doubt accidental; it is not present, for example, in the sporangium of which the apex is shown more highly magnified in Plate 41, fig. 8.

The columnar layer extends uniformly all round the sporangium, as shown in the various sections represented in figs. 1–5. The narrow base, by which the sporangium is attached to the sporophyll, is also coated by the columnar cells, which only die out where the tissues of sporangium and sporophyll become continuous (fig. 1, *a*).* The inner layer of the sporangial wall, owing to its delicacy, is unequally preserved. It is usually thickest at the base of the sporangium, where it is continuous with the tissue by which the latter is attached to the sporophyll. The cells of the inner layer are thin-walled, and usually somewhat elongated in the plane of the surface of the sporangium; in the section shown in fig. 4, where this layer is particularly well preserved, they appear nearly isodiametric, for, in a horizontal section such as this, these cells are cut transversely. They must be regarded as belonging to the wall itself, not to the tapetum, for they have none of the characters of a tapetal layer. They are no doubt homologous with the inner tissue of the sporangial wall in *Lepidostrobus Brownii.*†

* Exactly as in some Lepidostrobi. See MASLEN'S figures of *L. foliaceus*, 'Structure of Lepidostrobus,' Pl. 38, fig. 38.

† BOWER, "Studies in the Morphology of Spore-producing Members. Part 1. Equisetineæ and Lycopodineæ," 'Phil Trans.,' B, vol. 185 (1894), fig. 93.

In specimens of other species of *Lepidostrobus* the inner layer has very generally disappeared except at the base of the sporangium.

If there was a true tapetum it has left no trace, unless it be the dark structureless band, which in some cases forms the inner limit of the internal layer of wall (figs. 1 and 4).

The base (appearing as a short stalk in tangential section, fig. 1) by which the sporangium is attached to the horizontal pedicel of the sporophyll, consists internally of tissue like that of the inner parietal layer, but with some of its cells thicker-walled; externally, as already mentioned, it is coated by the columnar layer, which is almost in contact with the sides of the groove formed by the prominent lateral pads (fig. 1).

In the characters described up to this point we have met with a practically complete agreement with the familiar structure of a *Lepidostrobus*. It is only when we come to consider the spores contained within the sporangium that an important difference appears. In many cases, as shown in phots. 5 and 6 and fig. 1 (*mg*), we find, within the sporangial wall, a brown, structureless, or at least non-cellular membrane, enclosing the greater part of the cavity of the sporangium. In other instances the membrane has contracted considerably, so as to assume irregular shapes (phots. 1 and 2; figs. 4 and 5, *mg'*). Sometimes the membrane has split locally into two layers (fig. 1). Where seen in superficial view the membrane may show an irregularly honeycombed appearance (fig. 3, *mg*; fig. 4, *mg'*), but the sectional aspect proves that this is not the expression of cellular structure, though it may possibly in some cases be due to the impress of adjacent cells.

It is impossible to avoid the conclusion that this closed membrane, which in its natural condition clearly embraced the greater part of the sporangial cavity, represents the wall of an embryo-sac or megaspore. The discovery of the prothallus has proved that this conclusion is correct. In the earlier, non-integumented condition of the sporangium, such as we are now considering, the megaspore nearly always appears empty. In the mature integumented stage, however, to be described below, the prothallus has been observed (phot. 7; fig. 23) occupying the whole cavity of the large embryo-sac or megaspore. Its preservation is so rare that no negative conclusion can be drawn from its apparent absence at the earlier stage.

Many of the sections show smaller spore-like bodies accompanying the principal megaspore (figs. 4 and 5). From their frequency there is little doubt that they were present in every sporangium, though the plane of section is not always such as to show them. An interesting case is represented in phot. 1 and fig. 5, where four spores are shown in the same sporangium. One of these (fig. 5, *mg'*) is large, and in its natural condition would no doubt have occupied most of the cavity. The other three (*mg*) are much smaller, and of irregular, shrivelled form. These smaller spores usually appear to have thicker walls than the principal one (see fig. 4, *mg*). They

are most often found at the distal end of the sporangium.* Anticipating a little, it may be mentioned here that four spores—one large and three small—were also found in the large integumented specimen, of which three sections are shown in Plate 39, phots. 14–16. I have never found more than four in any sporangium, and believe that this was the full number. In one section from the distal end of a sporangium, three of the smaller spores are shown, arranged as if belonging to a tetrad; the fourth spore had, doubtless, developed into the principal megaspore, but was missed by the section. In all cases there is one megaspore large enough to occupy almost the whole of the sporangium, while any others there may be are very small in comparison,† and have a partially obliterated appearance. The obvious explanation of the facts appears to be that one tetrad was alone developed in each megasporangium, and that of the four sister-cells composing it one only came to perfection, constituting the single functional megaspore, in which, as will be shown below, the prothallus was formed; the other three were evidently abortive. This is a case hitherto unknown among Lepidodendreæ, or indeed among any Lycopodiales, in all of which, as at present known, four megaspores at least (often more) come to maturity in each megasporangium. A perfectly analogous case is, however, presented by the Rhizocarps among the Filicales. It need scarcely be pointed out that in the predominance of one megaspore, displacing its fellows and arresting their development, we have an approach to the condition usual in Flowering Plants.

The form of the sporophyll bearing the sporangium has already been described; its structure need not detain us long. The pedicel, shown in transverse section (tangential to the whole cone) in phot. 4 and fig. 1, is traversed by a vascular bundle of collateral structure. There appears to be no important difference in this respect between the earlier and later stages. The bundle shown in detail in Plate 41, fig. 11, is taken from a specimen (fig. 10) in the mature, seed-like condition. The xylem has its smallest elements towards the middle, and its development was probably of the mesarch type; the delicate small-celled phloem is very evident, forming the lower half of the bundle, and is sharply distinguished from the adjacent parenchyma. I may add that longitudinal sections show quite clearly that the phloem is limited to the lower side of the strand, and that it consists of narrow, elongated, thin-walled elements; there is thus no reason to doubt that we have here to do with a perfectly normal phloem, though we cannot expect to be able to observe its detailed structure. The vascular bundle, as it passes into the lamina, acquires a well-developed tracheal sheath or transfusion-tissue, consisting of short tracheides of larger diameter than those of the xylem. A few of these transfusion-tracheides sometimes appear in the pedicel also. In the presence of this supplementary tracheal system the sporophylls

* The body *mg* in fig. 2 is probably one of these smaller spores, though it might be a portion of the membrane of the large one.

† In fig. 4, where the difference between the two spores shown is not so marked, the large spore *mg'* had doubtless contracted, and is not shown in anything like its full extent.

of *Lepidocarpon* agree exactly with the vegetative leaves of the Lepidodendreæ, and the same structure also occurs in the sporophylls of typical Lepidostrobi.* Returning to the pedicel, we find that the lateral pads, supporting the sporangium, are formed of a sclerotic tissue, with its cells often arranged somewhat regularly in series vertical to the surface (fig. 1). The rest of the pedicel consists of a delicate mesophyll, contrasting sharply with the thick-walled tissue of the pads (fig. 1). The tissue is most delicate towards the lower side of the pedicel; the whole is covered by a small-celled epidermis, and the hypodermal elements have somewhat thicker walls than those further to the interior. In the distal region the structure is much the same, but the differentiation rather less marked (fig. 2). In the upturned lamina the elements of the upper surface are thick-walled, and the mesophyll generally is more strongly constructed than in the pedicel (fig. 4). There seems to be some tissue more delicate than elsewhere next the lateral furrows of the lamina; I have not been able to determine whether these furrows are stomatiferous, as in the vegetative leaves of *Lepidodendron*.

The position of the ligule has been explained above. It has been observed in several cases, two of which are figured; in fig. 2 the ligule (*lg.*), no doubt incomplete at the top, is shown as it appears in tangential section, while in fig. 3 it is shown in approximately radial section. Judging from the most complete examples the ligule was about ·3 millim. or more in height, about ·12 millim. in tangential width, and about ·08 millim. in maximum thickness in the radial direction. It is clavate in form, but somewhat flattened. The cells of which it is composed are small and delicate, and imperfectly preserved, but it is noticeable that those of the apical part are full of carbonaceous contents, while the more basal cells appear clear and empty. There is a general agreement with the ligule of *Lepidostrobus Oldhamius*, as described by Mr. Maslen (*loc. cit.*).

Anatomical details have been passed over rather curtly, as they are not of essential importance for our present purpose. I hope to deal with the comparative anatomy of the Lepidodendreæ generally on another occasion.

In the structure both of the sporangium and sporophylls, we have found an agreement with *Lepidostrobus* so exact as to leave no doubt, when coupled with the other characters of the strobilus, of close affinity between the two genera. So far there is only a single point of difference to be recorded, though one of great importance, namely, that in *Lepidocarpon* a single megaspore in each megasporangium gained the upper hand over its fellows, and alone attained functional maturity.

We have next to examine the more advanced, seed-like condition of the fructification.

* Renault, "Bassin Houiller et Permien d'Autun et d'Épinac," 'Flore Fossile,' II., Pl 34, figs, 4–7 Maslen, 'Structure of *Lepidostrobus*,' Pl. 37, fig. 18.

3. *Structure of the Mature "Seed."*

The evidence of WILD'S specimen proves that integumented, seed-like structures, agreeing with the *Cardiocarpon anomalum* of WILLIAMSON (not of CARRUTHERS), were borne on a Lepidostroboid cone, which in other parts produced naked megasporangia. Each seed-like organ of the lower part of the strobilus evidently corresponds to a sporangium and sporophyll of the upper region (compare phots. 10 and 11, and also the tangential section in phot. 13 with the corresponding section in phot. 6 from a specimen without integuments). The more or less shrivelled megaspores can be recognised alike in the simple sporangia (phot. 10) and in the integumented bodies of WILD'S cone (phot. 11). The specimen further shows that in form and orientation the two organs agree (compare phots. 10 and 11, 6 and 13, fig. 3 and phot. 12). The matter of orientation is specially important, as it enables us to refer the detached specimens of the "seeds," such as are commonly met with, to their position relatively to the cone on which they were borne. Thus, the tangential section of WILD'S cone (phot. 13) shows the integumented bodies in their characteristic, seed-like aspect, with an open micropyle, as figured by WILLIAMSON (Part VIII., figs. 118, 119; Part X., fig. 64). Radial sections, parallel to the micropylar crevice, present quite a different appearance, much less obviously seed-like (compare phot. 12, from WILD'S cone, with fig. 14, from a detached specimen), while horizontal sections can also be recognised by comparison with the transverse section of the cone (phot. 11, s^2).* With a little consideration the various oblique sections so commonly met with can also, in most cases, be referred to their approximate planes, with reference to the parent strobilus. After these preliminary considerations we will go on to consider the structure of the *Lepidocarpon* "seed" in detail, as shown in the detached specimens, which are very numerous, and often beautifully preserved, and which, in the light of WILD'S specimen of the strobilus, can now be correctly interpreted.

The sections figured by WILLIAMSON of the seed which he named *Cardiocarpon anomalum* (*Lepidocarpon Lomaxi* of the present paper) were all cut approximately in the tangential plane (with reference to the parent cone), as shown by the fact that the micropyle appears at the apex as a narrow passage, as well as by the general form of the organ, and by the vascular bundle appearing in transverse section.†

* Where the micropyle appears in an approximately transverse section of the cone, as in the "seed" shown enlarged in Plate 43, fig. 27, this is because the plane of section is really oblique, forming an angle with the transverse and tangential planes.

† WILLIAMSON, it is true, was under the impression that fig. 64 in his Part X. represented a section in a plane vertical to that of his fig. 119 in Part VIII. from another specimen (see Part X., p. 518). An examination of the sections shows, however, that this is not the case. Both sections alike show all the features characteristic of the tangential aspect. The difference in form no doubt depends chiefly on the distance of the plane of section from the axis of the parent cone. The narrow section shown in fig. 64,

WILLIAMSON'S terminology is easily explained in terms of our own—

WILLIAMSON'S	exotesta	=	our integument.
,,	endotesta.	=	,, sporangium.
,,	chalaza	=	,, pedicel of sporophyll.
,,	funiculus.	=	,, dorsal rib of pedicel.
,,	perispermic membrane	=	,, membrane of megaspore.

WILLIAMSON'S "micropylar canal" may continue to be called a micropyle, though its form, as we shall see, was quite different from what he supposed, and from that of the micropyle in ordinary seeds.

Recently discovered specimens are in many respects better preserved than those with which WILLIAMSON worked, and our description will be based on the newer and more favourable material.

Great light has been thrown on the structure by a series of eight sections, cut by Mr. LOMAX from a single "seed," in parallel tangential planes. Of the eight sections no less than seven pass through the micropyle; the only one that misses it is cut at the extreme distal end, beyond the seed-cavity. Three sections from this series are shown in phots. 14–16. Phot. 14 is from the first section at the proximal end; phot. 15 represents the sixth from the proximal end, and shows the typical structure where the width of the seed is at its maximum. Phot. 16 is the seventh, and is from the distal extremity, being the last which shows the seed-cavity. The determination of the proximal and distal ends follows at once from the comparison with WILD'S cone (phot. 11), from which it is evident, as indeed must necessarily be the case, that the "seed" is narrowest at its proximal, and broadest at its distal extremity.

The most striking fact which comes out from the study of this series is the great radial length of the micropyle, which, from its appearing in practically all the sections, is shown to be a long narrow crevice, extending throughout the whole length of the seed from one end to the other. It is thus very different from the more or less tubular micropyle of the seeds of Phanerogams. WILLIAMSON, who had not the opportunity of examining a complete series of sections, was unaware of this fact, which appreciably weakens the resemblance to a true seed, for it is only when cut tangentially, at right angles to the micropylar crevice, that the characteristic seed-like appearance is presented. Sections in the other vertical plane (radial with reference to the parent cone) run parallel to the micropylar opening, and present quite a different appearance. (See phot. 12 and fig. 14.)

Returning to the tangential sections, phot. 15 shows the characteristic structure clearly, and corresponds very closely with WILLIAMSON'S fig. 119 in his Part VIII. Below, we see the sporophyll with its dorsal rib, which runs through most of the

Part X., was evidently cut near the proximal end, while the broad form represented in fig. 119, Part VIII., characterises the distal region (compare phots. 14 and 15). The difference may have been accentuated by the effects of compression.

sections. The sporophyll-pedicel is widened out laterally, in correspondence with the growth of the "seed" as a whole. The tissue towards the upper surface of the sporophyll is sclerotic, just as in the pads which support the sporangium in the non-integumented condition (*cf.* fig. 1). The integument springs directly from the margins of the sporophyll, and here has its greatest thickness, thinning out towards the top; together with the sporophyll, the integument forms a complete envelope to the "seed," leaving only the narrow micropylar crevice at the apex. Towards the micropyle the two sides of the integument are roughly parallel, enclosing a narrow passage.

The integumentary tissue is thick-walled towards its inner and outer surfaces, and more delicate in its middle region; in badly preserved specimens this internal tissue of the integument has sometimes perished, leaving an empty space, as in some of the "seeds" of WILD's specimen. (See fig. 27.)

Within the integument, and nearly filling the space which it encloses, is the sporangium, or nucellus, attached by its base to the median line of the sporophyll. The attachment is somewhat wider, and the socket less marked than in the non-integumented condition, changes no doubt correlated with the growth of the whole body in width. The structure of the sporangium is however the same, as in its naked condition. The wall has a superficial columnar layer, with a more delicate lining tissue within it. The cells of the columnar layer are often shorter and broader than in the non-integumented sporangium, owing no doubt to superficial extension of the wall; at other places, however, and especially at the apex, where the narrow ridge of the sporangium fits into the micropylar opening, the structure is quite unchanged. This is very evident on comparing fig. 8 with fig. 9 (Plate 41). Fig. 8 is from the apex of one of the non-integumented sporangia of Specimen III., shown in tangential section in phot. 3. Fig. 9 is from one of the serial sections of the large "seed" now under consideration. The structure of the sporangial wall is identical in both; in fig. 8 it is naked, as in an ordinary Lepidostroboid sporangium, while in fig. 9 it is enclosed within the thick, dense tissue of the integument which has grown up and walled it in. In all the numerous sections examined, the apex of the sporangiumhas the same structure as that represented in fig. 9. Sometimes, in the integumented as in the non-integumented condition, the sporangial wall has split open at the top (figs. 10 and 12), but this appears to be accidental; a similar splitting is often observed at the lower lateral angles (fig. 12, on right), where it could scarcely have any biological significance. Nothing of the nature of a pollen-chamber has been observed in any of the specimens.

In phot. 15 the shrivelled membrane of the large megaspore is seen in the lower part of the sporangial cavity. The smaller club-shaped body at the micropylar end is no doubt an abortive megaspore; its small lumen is clearly visible when more highly magnified. Two other similar bodies were found in other sections of this "seed," so that here also there were four megaspores in all, three abortive and one fully developed.

Various details are shown more clearly in other specimens, some of which are figured. Fig. 10 shows a very beautiful example, also in tangential section; its form is acutely conical, differing considerably from that of the seed shown in phots. 14–16. This is a rather extreme case, but a good deal of variation in form occurs among the specimens. These differences may be partly accounted for by position relative to other sporangia on the cone, and by their unequal growth, for there is much evidence that only a certain number of the sporangia on each strobilus ever developed into "seeds."* The form and structure of the sporangium, its attachment to the sporophyll, and its relation to the integument which encloses it, are all shown with great clearness in this example. The micropyle appears closed, just above the apex of the sporangium, and the passage is curved in an unusual manner—points, however, of no great importance.

A single large megaspore is alone visible, and its membrane is here but little contracted, still enclosing nearly the whole of the sporangial cavity.

The sporophyll is here very distinctly divided into an upper and lower lobe, by a deep furrow on either side. This character has already been mentioned (p. 295) as occurring in some of the sporophylls of the non-integumented form. It is curious that there is scarcely an indication of any such lobing in the specimen from which phots. 14 and 15 were taken. It will be remembered that it is also almost absent (so far as the horizontal pedicel of the sporophyll is concerned) from the non-integumented Specimen III. (phot. 3). I cannot explain these differences; they may indicate that under the name *Lepidocarpon Lomaxi* more than one species is included. This is perfectly possible, but at present it seems to me premature to attempt their discrimination.

The structure of the vascular bundle (fig. 11) has been already considered (p. 300). It is also well exhibited in the specimen from which phots. 14–16 are taken, and in others. The two gaps, one on either side of the bundle (*pa* in fig. 10), which recur in other specimens (phot. 16 and fig. 12), are strongly suggestive of the parichnos of the vegetative leaf-base in other Lepidodendreæ.† At earlier stages, however, the differentiation of the tissue in the corresponding region is not much marked (see figs. 1 and 2), though no doubt the tissue immediately flanking the bundle is specially delicate. A really sharp differentiation of parichnos-tissue is only found near the base of the sporophyll (fig. 15).

We have so far considered the structure of the "seed" as shown in its middle region. At the distal end it presents a different form, corresponding to that of the

* This evidence is afforded, not only by WILD'S cone, but also by the constant association, among the detached specimens, of integumented and non-integumented individuals. The height of the seed often appears exaggerated where the direction of the section is oblique, forming an angle with the tangential and transverse planes. This explanation may apply in some degree to fig. 10, where, however, the bundle of the sporophyll is seen in true transverse section (*cf.* fig. 11), so that the obliquity can scarcely be great.

† Compare, for example, the figure of *Lepidophloios* in my 'Studies in Fossil Botany,' fig. 57, p. 144.

original sporangium in the same region. Fig. 12 is instructive from this point of view, and should be compared with fig. 2, and with the more distal sections of sporangia shown in phots. 3 and 6. As its form indicates, fig. 12 is from a section taken just where the attachment between sporangium and sporophyll ceases, at the distal end. The sporangium has the curious triangular form noticed above as characteristic of this part (p. 296). The integument which has grown up around it closely follows its contour. The structure of the sporangium shows the same characters as before, unless it be that in this part the internal layers of the wall are better developed or better preserved than elsewhere. Two abortive megaspores are evident, and there is part of the membrane of a third, which may have been the functional one. The most interesting point is perhaps the form of the sporophyll, which here has a distinct wing or lamina (*l*) projecting beyond the base of the integument. This feature is shown still more clearly in fig. 13, which represents part of another "seed," in similar section. The presence of this laminar margin exactly agrees with what we found in the corresponding region of the non-integumented specimens. (Fig 2, *l*.) The fact is important, because it proves that the integument is not merely the incurved lamina of the sporophyll, folding round the sporangium, and forming a kind of false indusium, but is really a new formation growing up from the upper surface of the sporophyll. In the more proximal part of the pedicel, where the base of the integument corresponds with the margin of the sporophyll, either interpretation might hold good, but the structure in the distal region proves that integument and lamina are quite distinct organs. The section shown in phot. 16, from the series so often referred to, is no doubt in a somewhat more distal plane than that of fig. 12. The sporangium here appears as a three-rayed body, with an extremely narrow cavity. The apical limb of the sporangium is short, and so also is the micropylar passage of the integument. The sporophyll is very thick, and the integument is seated upon it with a broad base. The section appears to have been cut in the region of the ligule, which however is not seen. As regards the form of the sporophyll and sporangium there is a fair agreement with the non-integumented specimens as shown in the tangential sections through the corresponding distal region (*cf.* phots. 3 and 6; fig. 2). The sectional form of the sporophyll, however, is simpler than in some of the other specimens, and there is here no sign of the laminar margin. The wide gap between the bottom of the sporangium and the upper surface of the sporophyll is unusual, and probably due to *post-mortem* changes.

At the proximal end, as shown in tangential section in phot. 14, the whole "seed" is narrower than elsewhere, and the sporangium smaller, compared with the sporophyll and integument. The micropyle extends to this extremity, but the attachment between sporangium and sporophyll is missed.

The facts already detailed show that the integument of *Lepidocarpon Lomaxi* was a wall of tissue which grew up on either side of the sporangium from the upper part

of the sporophyll-pedicel. Along the greater part of the length of the pedicel the insertion of the integument was approximately marginal, but towards the distal extremity this was not the case, the margin of the sporophyll projecting far beyond the base of the integument. We have also found that the micropylar opening between the upper edges of the integument had the form of a long crevice, extending practically the whole length of the seed, in the radial direction. The question remains, whether the integument formed a mere trough, open at the ends, or was closed at the proximal and distal extremities. As regards the distal end there is no doubt that the integument abutted on, and was continuous with, the ascending lamina of the sporophyll, which itself formed the wall of the "seed" at that extremity. This is shown, for example, in the approximately radial section represented in fig. 14. The section is sufficiently radial to follow the narrow base (a) of the sporangium through almost its whole length, and to show the vascular bundle for some distance. That it is not, however, in a strictly vertical plane is proved by the too small height of the "seed," and by the fact that it is closed in above by the integument; a truly radial section would of course follow the micropylar opening in this region. As a matter of fact, the narrow ridge of the "seed," where the micropyle is situated, is missed (as is almost always the case) by the plane of section. The figure is, however, interesting, because it shows how, as the sporangium narrows out towards the distal extremity, the integument, roofing it in above, approaches the ascending lamina, and eventually meets and joins the latter. How far the union in this part was a congenital one cannot be determined. The integument, no doubt, grew out from the lower part of the ascending lamina, as well as from the horizontal pedicel, but towards the top the junction between integument and lamina may have been due to a subsequent adhesion.*

At the proximal end, on the other hand, it seems clear that the closure of the seed was effected by the integument itself. The transverse and radial sections of WILD'S specimen (phots. 11 and 12) indicate that this was the case, but are not by themselves conclusive, as we cannot distinguish with certainty between the proximal part of the integument and tissue belonging to the sporophyll or the axis. The radial section of a detached "seed" (fig. 14) is more convincing. At the proximal end the "seed" is completely inclosed by the integument, which is here of considerable thickness. As, however, we have seen that this section is not absolutely in the median radial plane it does not exclude the possibility of a narrow opening, comparable to the micropylar crevice, having existed at the proximal end.

Occasionally sections are met with showing the "seed" with a completely closed envelope. Such a section is represented in Plate 43, fig. 24; it is oblique, and not, at the first glance, easy to interpret, but I believe really settles the question. The basal attachment of the sporangium is shown at a, essentially as in the tangential aspect, but

* In some specimens the integument has separated from the ascending lamina, leaving a kind of distal micropyle, but it may be doubted whether this condition was natural.

drawn out longer, while the vascular bundle below is also cut obliquely, facts which indicate that the section was at an angle between the tangential and horizontal planes. At the opposite end the integument is completely closed, without the least indication of any crevice. It is obvious that at this closed end the section approaches either the distal or the proximal extremity of the "seed." The form of the section at the closed end is, however, far too narrow for the distal region (*cf.* phots. 14 and 16), and we thus arrive at the conclusion that it is the proximal end of the seed which is completely inclosed by the integument, a conclusion which agrees with all the rest of the evidence. It need scarcely be pointed out that the continuity of the integument at the proximal end, where it extends across the sporophyll, affords another proof that the former organ cannot be interpreted as the incurved margin of the latter.

We thus see that the protection of the sporangium in the mature condition of the "seed" was complete, for it was inclosed by the sporophyll itself below and at the distal end, by the integument at the sides and at the proximal end. Only along the top was there communication with the exterior by means of the narrow micropylar crevice. In these respects the conditions were essentially those which exist in a true seed. The fossil which WILLIAMSON described as a seed, and which has been erroneously referred to the *Cardiocarpon anomalum* of CARRUTHERS, thus proves to be a Lycopodiaceous megasporangium, seated on its sporophyll, and inclosed by an integument.

As a rule, only so much of the sporophyll was persistent in the ripe condition as was necessary for the complete investiture of the sporangium. The vertical tip of the sporophyll-lamina, above the top of the sporangium, seems to have been thrown off or to have died away, for this part is almost always absent in the mature seed-like stage. Some indications of it are, however, to be seen in the radial section of WILD'S specimen (phot. 12). As regards the lower part of the sporophyll, the condition of the specimens is variable. As a rule its depth below the sporangium is decidedly less in the integumented than in the non-integumented stage (compare fig. 10 with fig. 1, and fig. 12 with fig. 2). The loss may be accounted for in part by mere shrivelling of the delicate mesophyll (fig. 10); in other cases tissue seems to have been actually lost (see fig. 12 and the radial section, fig. 14).

In one specimen there were signs of periderm-formation in the tissue of the sporophyll below the vascular bundle, indicating that a definite abscission of the superfluous part of the organ sometimes took place. In WILD'S cone, the distal parts of the sporophylls are much reduced in the integumented as compared with the non-integumented condition (compare phot. 10 with phot. 11), but here the preservation is not sufficiently good to show how the reduction took place. In other specimens, however, the sporophyll (leaving its apex out of consideration) appears intact (see phots. 14-16). In the specimen represented in obliquely tangential section, in Plate 43, fig. 25, the whole of the sporophyll-tissue (evidently shown near the lobed distal end) remains attached to the "seed," though in a somewhat disorganised condition. This

section is of interest for comparison with specimens in the non-integumented stage (*cf.* phot. 2), and shows that there is no constant difference between the two conditions as regards the form of the sporophyll.

4. *The Prothallus.*

In the great majority of the specimens of *Lepidocarpon Lomaxi*, the membrane of the large megaspore is perfectly empty. At present I have only seen one specimen in which its cavity is filled with tissue, or, in other words, in which the prothallus is preserved. This interesting case is illustrated in Plate 38, phot. 7, and Plate 43, fig. 23, from a section cut by Mr. LOMAX. The specimen is an isolated "seed," seen in tangential section, and shows the same general structure as the examples already described, especially resembling such a section as that illustrated in phot. 15. The dorsal rib of the sporophyll is well marked, and the integument presents the usual features; the external parts, however, are not particularly well preserved. The wall of the sporangium is for the most part reduced to a thin layer, but the usual columnar structure is recognisable at some places, especially at the apical ridge which projects through the micropyle.* The megaspore or embryo-sac occupies practically the whole of the sporangial cavity, and is itself completely filled with tissue. Its membrane is indicated by a strongly marked contour (fig. 23). The prothallial tissue is preserved entire, though its preservation is not equally perfect in all parts. Towards the exterior, where the tissue is especially well shown, the cells are more or less isodiametric and attain a diameter of about ·12 millim., but the superficial layer consists of much smaller elements (fig. 23). The tissue in all this part has well-marked, brown cell-walls; the whole appearance agrees generally with that of a prothallus of *Isoetes* or *Selaginella*. Some remains of the cell-contents are often present in the prothallial cells. No archegonia are to be recognised with any certainty, but the cell marked *y* in fig. 23, which is filled with especially dense, carbonised contents, might possibly be the central cell of an archegonium, the neck of which lay in a different plane. Neither the prothallus nor the megaspore extends into the extreme apical ridge of the sporangium. The tissue in the middle of the prothallus is extremely delicate, and the cell-walls by no means conspicuous (phot. 7 and fig. 23, *c.s.*). In this region especially, a rounded, granular body, strongly suggestive of a nucleus, is commonly present in each cell. The central, delicate tissue forms a fairly definite vertical column, consisting of much elongated cells, and recalling a procambial strand (fig. 23, *c.s.*). This differentiation is sharpest in the upper part of the seed, shown in the figure cited. Lower down, the central strand broadens out, and its limits are not so definite, though it is clearly distinct from the ordinary prothallial tissue towards the base of the "seed" (phot. 7).

* That the sporangium overtops one side of the integument is no doubt due merely to incomplete preservation of the latter.

It occurred to me as a possible hypothesis that the delicate central mass of tissue might represent an embryo, for the cells in this part are very different from those of the surrounding prothallial tissue, and the form and position of the whole mass are such as we should expect in the case of an embryo. The central strand tapers towards the upper end, and terminates above in an irregular gap in the tissue, which might be interpreted as having some relation to the archegonium which had given rise to the embryo.

It seems worth while to place this suggestion on record, though there are strong arguments against it, the chief being the absence of a definite boundary between the central and peripheral tissue. On the whole, perhaps, the probability is in favour of the central mass representing merely a younger portion of the prothallial tissue, development having advanced, as in other endosporic prothalli, from the periphery inwards. The form of the cells in the central strand appears, however, to be exceptional in prothalli of this type, though familiar in the case of the free prothalli of homosporous Pteridophyta.

The presence of the prothallus or endosperm, filling the whole cavity within the integument, and only separated from it by the megaspore-membrane and the extremely reduced sporangium or nucellus, gives the whole organ, as seen in this section, a most striking resemblance to a Gymnospermous seed.* We must not, however, forget that there are important differences in detail, which may be sufficient to invalidate the general similarity.

As will be shown below, a good case of preservation of the prothallus has also been observed in the Burntisland species, *Lepidocarpon Wildianum*. Among the Coal-Measure specimens I have seen no other satisfactory instance.† In one case some remains of tissue were found within the megaspore, but its nature was doubtful. In another specimen the megaspore-membrane was lined by a thick layer of brown carbonaceous substance, which may either have represented a parietal layer of protoplasm or the products of decay of the prothallus; here also no definite conclusion could be drawn.

There is a section in the WILLIAMSON Collection (C. N. 1933) labelled "*Cardiocarpon*, endospermic cells," showing a seed in which the whole cavity is completely filled by a rather large-celled uniform tissue, no doubt prothallial but without any

* The mere dimensions of the megaspore containing the prothallus are unprecedented in a Cryptogam. The megaspore shown in phot. 7 measures about 4 millims. in transverse, by about 3 millims. in vertical diameter. Its length in the direction of the radius of the parent cone would probably have approached 8 millims. (*cf.* the radial section of WILD'S specimen, phot. 12). In other "seeds," such as that shown in phots. 14–16, the dimensions of the functional megaspore in its natural condition were considerably greater.

† WILLIAMSON found some remains of "perispermic tissue" (= endosperm) in the solid specimen of his *Cardiocarpon anomalum* (*loc. cit.*, Part VIII., p. 255, figs. 117, 120). As stated above, this "seed," like the others figured by WILLIAMSON under the same name, is no doubt our *Lepidocarpon Lomaxi*, but from the nature of the specimen the evidence as to the presence of endosperm is inconclusive.

signs of archegonia. I could not, however, satisfy myself that this specimen is really a *Lepidocarpon*, though the fact that the nucellus or sporangium is free from the integument down to its base is in favour of this attribution. From WILLIAMSON'S remarks,* it appears that he referred this specimen to his *Cardiocarpon Butterworthi*, which, from its cylindrical stalk, must have been of quite a different nature from a *Lepidocarpon*, and may rather have been related to the true *Cardiocarpon* of BRONGNIART and CARRUTHERS. In any case, the nature of WILLIAMSON'S prothallus-containing seed must for the present be left an open question.

Some general considerations as to the prothallus of *Lepidocarpon* will be postponed to the conclusion of the paper, after the other species, *L. Wildianum*, has been described.†

5. *Anatomy of the Axis of the Strobilus.*

It is proposed to deal with this part of the subject somewhat briefly, giving only so much detail as is necessary for comparison with the structure of *Lepidostrobus*. The anatomy of the axis is best shown in Specimen III., one of the immature strobili, and in WILD'S specimen, which is the only known example of the fully developed cone. The structure of the former, as seen in an obliquely transverse section of the stelar region, is illustrated in Plate 40, fig. 6, while for a more general view phot. 1 may be consulted. The single stele which occupies the middle of the axis shows a narrow zone of wood, limited in places to a single layer of elements (fig. 6, *x*). Those tracheides of which the structure can be made out have scalariform or densely spiral sculpturing. The interior of the stele is occupied by a parenchymatous pith, but the thin-walled elements immediately within the ring of tracheides are narrower and more delicate than the pith-cells and are probably procambial, representing undifferentiated wood. The evidence thus indicates that the stele was a medullate one with a zone of centripetal wood, as in *Lepidostrobus*. The slight development of the xylem suggests that the strobilus was immature; this suggestion is confirmed by comparison with WILD'S specimen, which was evidently in a more advanced condition. The transverse section shown in Plate 42, fig. 15, is from that part of WILD'S cone where the sporangia are in the mature, integumented condition (phot. 11), and thus shows the structure fully developed. The stele is somewhat damaged, but parts of it are well preserved. The large-celled pith, partly destroyed, is surrounded by a zone of wood (*x*), three or four elements in thickness, in which the smallest tracheæ are evidently at the periphery. The narrow xylem-zone of the immature axis (fig. 6) has here attained its full development, and the differentiation has clearly been in the centripetal direction. The leaf-traces, seen in oblique section

* 'Organisation,' &c., Part VIII., p. 260. A part of the endosperm, probably from this specimen, is shown in fig. 131 of that memoir. For *C. Butterworthi*, *cf.* figs. 129 and 130.

† The prothallus within the megaspore of a *Lepidodendron* has been figured by M. RENAULT, "Bassin Houiller et Permien d'Autun et d'Épinac," 'Flore Fossile,' Pt. 2, 1896, fig. 36, p. 182.

in fig. 6, are much better shown in the older specimen (fig. 15), of which the section is more accurately transverse. They are seen in various positions on their outward course through the cortex. The bundles are not so well preserved as in the sporophylls (*cf.* fig. 11), but are of the same type of structure, and agree very closely with the leaf traces of *Lepidostrobus Oldhamius* as figured by Mr. MASLEN.* At *sph* the base of a sporophyll is shown, and here the structure of the vascular bundle is especially clear. A band of parenchyma (preserved) intervenes between the xylem and the gap representing the phloem. Precisely the same condition was found by Mr. MASLEN in the vascular bundles of his *Lepidostrobus.*† On the outer side of the bundle in the sporophyll is a strand of large-celled tissue, also recognisable in other places and recurring in other specimens (*cf.* phot. 2). This strand probably represents the parichnos of the vegetative leaf-base of Lepidodendreæ.

The important point as to the anatomy is that it is altogether of the Lepidodendroid type, and agrees closely, in particular with that of the axis of a *Lepidostrobus*. The inner cortex is well preserved in *Lepidocarpon*, and was evidently a firm, resistant tissue (fig. 15), whereas the corresponding zone in *Lepidostrobus* was more delicate, and has usually perished. This difference is no doubt correlated with the greater mechanical strength required in the former, where the axis was destined to bear the large and heavy seed-like organs, and must also have been of longer duration.

All the specimens showing the internal structure of the axis (Specimens II., III., and IV.) in the strobili with naked sporangia have the xylem little developed. This indicates that complete anatomical differentiation was only attained later, as the naked sporangia became converted into the integumented, seed-like organs, a condition shown only in WILD'S specimen of the strobilus. The tracheides of the axis, as shown by longitudinal sections, were for the most part of scalariform structure, and agree in all respects with those of the Lepidodendreæ.

6. *A possible Male Cone of* Lepidocarpon Lomaxi.

In my preliminary note (*loc. cit.*, p. 308) I stated that "in a strobilus associated with the seed-like specimens, and bearing microsporangia, it was found that the latter, like the megasporangia of the female cone, are provided with integuments." Further investigation has thrown new light on the structure of this strobilus, and has shown that the organs interpreted as microsporangial integuments differ more widely than at first appeared from the integuments of the female *Lepidocarpon*.

The specimen in question is a small Lepidostroboid cone, contained in the same block in which Specimen I. of *Lepidocarpon Lomaxi* occurs, together with many detached "seeds" and sporangia of that species. The specimen was referred by Mr. MASLEN to his variety γ of *Lepidostrobus Oldhamius*, though possibly, as he

* "Structure of *Lepidostrobus*," *loc. cit.*, Pl. 36, figs. 2 and 12; Pl. 37, fig. 23.

† *Loc. cit.*, p. 365, Pl. 36, fig. 2; Pl. 37, fig. 14.

suggests, deserving specific rank;* he figures the axis in transverse section (*loc. cit.*, Plate 37, fig. 21), and mentions that the ligule is seen in a radial section of the specimen. In the present paper a transverse and a tangential section of the cone are shown in phots. 8 and 9. The transverse section presents all the characters of a small *Lepidostrobus* of the *Oldhamius* type. One of the sporophylls shows the ligule, seated in the ligular pit. The sporangia here are crushed and nearly empty, containing but few microspores. The tangential section (phot. 9) shows at the top the overlapping bracts at the apex of the strobilus. A little lower down, a large microsporangium is seen, seated on its sporophyll (*sph'*), and placed somewhat obliquely with reference to the axis of the cone. This sporangium (represented, on a larger scale, in Plate 41, fig. 7) is invested by a well-marked integument springing from the margins of the sporophyll. The integument, which consists of dense fibrous tissue, as in the "seed" of *Lepidocarpon Lomaxi*, is of equal length with the sporangium on one side, but on the other is only about half as long. The sporangial wall, which is beautifully preserved, has the structure usual in *Lepidostrobus* or *Lepidocarpon*, consisting of an external columnar layer, lined by a more delicate tissue. The sporangium contains numerous microspores about ·02 millim. in diameter, and of tetrahedral form. At the base the sporangium is attached, in the usual way, to the middle of the sporophyll. The sporophyll is imperfectly preserved, but its vascular bundle is seen, in oblique section.

If the section of this sporangium were a truly tangential one, it would follow that the integument reached to its apex, as in the female *Lepidocarpon*. This, however, proves not to be the case. Comparison with other sporophylls and sporangia, shown in various sections of the strobilus,† proves that the sporangium represented in fig. 7 is cut in an oblique direction, intermediate between the tangential and transverse planes. At the base this section passes through the distal end of the sporophyll; comparison with radial sections shows that in this strobilus the line of attachment between sporangium and sporophyll extended for a short distance onto the ascending lamina. A number of other sporangia show something of the integument; in the radial section of the cone, for example, the integuments appear here and there in surface-view, partially covering the lateral walls of the sporangia. In the crushed condition of the strobilus it is difficult to make out the exact form of the integumentary envelope. It appears, however, to have been an incomplete one, both as regards its vertical and horizontal extent. In the vertical direction the evidence indicates that it extended about half-way up the sporangium, while, traced horizontally, it evidently died out towards the proximal end of the sporophyll; for a tangential section, cut near the axis, shows only the usual lateral cushions of the

* "Structure of *Lepidostrobus*," *loc. cit.*, p. 371. The sections in which the integument is clearly shown were not among those which passed through Mr. MASLEN'S hands.

† There are seven sections of the specimen—four transverse and three longitudinal. The numbers in my collection are 610–613 and 615–617.

pedicel, with no indications of an integument. The latter, in fact, seems to have had the shape of a coal-scoop, forming a sheath in which the distal end of the sporangium was seated but not completely inclosed.*

The word "integument" has been used in speaking of the sheaths of the microsporangia, because these envelopes, though comparatively little developed, appear to be homologous, as indicated by structure and position, with the complete integument of the mature megasporangium in the female *Lepidocarpon*. It is a point of considerable interest to find, in a microsporangiate strobilus, so clear an indication of the same structure, which, in the case of the megasporangia of *Lepidocarpon*, had developed further, and led to the formation of the seed-like organ.

The presence of rudimentary integuments, together with agreement in details of structure and the evidence of association, renders it highly probable that the microsporangiate strobilus just described may be of the same species with the female cones of *Lepidocarpon Lomaxi*.

II. Lepidocarpon Wildianum.

1. *Structure of the "Seed."*

In the calcified material from the well-known Burntisland beds, belonging to the Calciferous Sandstone Series, "seeds" are not uncommonly met with, agreeing in all important respects with those of *Lepidocarpon Lomaxi*. Some sections of these Burntisland specimens are in the Williamson Collection,† and were catalogued by Williamson under the same name, *Cardiocarpon anomalum*, as the Coal-Measure form. There is, in fact, very little to distinguish them, but the horizons are so widely apart that a separate specific designation seems called for. I have therefore named the Burntisland form *Lepidocarpon Wildianum*, associating it with the name of Mr. George Wild, who has borne so important a part in the elucidation of these fossils. It is a fact of some interest that this curious seed-like form of Lycopodiaceous fructification should have already appeared at so ancient a period as that of the Calciferous Sandstone deposits, which belong to the lowest strata of the Carboniferous Formation. At present, *Lepidocarpon Wildianum* has only been found in the form of detached specimens, in the mature, seed-like condition. Further search in the rich material from this locality will no doubt reveal other stages of this fructification. In the meantime, the specimens at present available are of value, as supplementing our knowledge of the closely similar Coal-Measure form.

In Plate 42, fig. 16, a small specimen of *Lepidocarpon Wildianum* is represented in tangential section. From its narrow proportions the section appears to have been cut

* The incompleteness of the integuments accounts for the fact that they are not always to be found in the transverse sections of the strobilus.

† *E.g.*, sections 1419–1421.

near the proximal end, especially as the sporangium is here scarcely if at all attached to the sporophyll beneath. The sporangium has the same organisation as in the Coal-Measure species; the outer layer of its wall has the customary columnar structure, and is lined by a delicate tissue, several cells in thickness. The integument, which just overtops the sporangium, is formed of dense fibrous tissue, and the sporophyll-pedicel is also, for the most part, of firm construction. This section corresponds very nearly with one through the proximal region of *L. Lomaxi*, cut a little further out than that shown in phot. 14. Other tangential sections of *L. Wildianum*, cut no doubt in planes further from the axis of the parent cone, are of much greater breadth, show the attachment of the sporangium clearly, and, in fact, present the same features as the corresponding sections of *L. Lomaxi*.

A series of four sections from one "seed," cut in parallel, nearly horizontal* planes, is of interest, especially as this aspect has not been illustrated in the former species. Three of the sections are represented in figs. 17, 18, and 20. The proximal end (with reference to the parent cone) is to the left, and the distal to the right, in all the figures. Fig. 17 is from the lowest of the series. The plane of section throughout the series is not strictly horizontal, but somewhat inclined, the distal end of the section being at a lower level than the proximal. Thus, in fig. 17 the distal extremity is missed, the plane of section here passing below the sporophyll. The vascular bundle of the sporophyll appears at three places, twice at the proximal and once at the distal end. On entering the sporophyll it made a sharp curve, which is clearly shown in some of the radial sections.† The fact that the attachment of the sporangium is seen near the distal end, and that the bundle reappears in this region, indicates that the pedicel of the sporophyll was curved, with its convexity downwards, an inference confirmed by the radial sections. The sporangium shows the usual structure and contains a large megaspore, much contracted. It may be mentioned that the membrane of the megaspore in this species shows an irregularly reticulated structure. Fig. 18, representing the third section from below (the intermediate one not being figured), is of greater interest. The marked narrowing of the "seed" towards the proximal end is due to the fact that the plane of section here passes through the micropylar region. The contracted megaspore is still visible; the sporangium is free from the sporophyll; between the two at the distal end, and seated in a depression of the sporophyll-tissue, is a delicate crescent-shaped body (*lg*), which from its position, form, and structure is evidently the ligule. It is shown, more highly magnified, in fig. 19, from which we see that the ligule consists of an extremely delicate tissue, a dark body in each cell no doubt representing the contracted and carbonised cell-contents. The ligule is cut transversely, as must necessarily be the case in an approximately horizontal section of the sporophyll.

* By *horizontal* I mean in a plane parallel to the sporophyll-pedicel, and transverse with reference to the axis of the parent strobilus. Compare above, p. 302.

† *Cf.* Plate 40, fig. 3, *l.t.*, from *L. Lomaxi*.

This is the only case, so far, in which the ligule has been detected in the mature, seed-like condition of the fructification of *Lepidocarpon*, and is no doubt the first instance in which a ligule has been seen in an organ commonly regarded as a seed.

Another point of interest, shown in fig. 18, is the presence of a recurved laminar margin (*l*) on one side of the sporophyll; on the other side it is almost torn away.

Fig. 20, from a section cut at a still higher level, shows the narrow top of the sporangium, which contains an abortive megaspore and is flanked on either side by the integument. The sporangium in this aspect has the same Y-form so often seen in corresponding sections of *L. Lomaxi* and may be compared with Plate 40, fig. 4, representing a sporangium of that species in the non-integumented condition. The sporophyll shown in fig. 20 is incompletely preserved, and detached from the integument.

This specimen has been described somewhat fully, both on account of its interest in showing the ligule, and because it helps us to gain a more complete idea than before of the form of the seed-like organ as a whole. There is no important difference between the two species in any of the characters at present available for comparison, so we may use the one form to supplement the other.

In dimensions *L. Wildianum* agrees with the smaller specimens of the "seeds" of *L. Lomaxi*, but has not yet been found to attain the maximum size reached by the latter. (*Cf.* p. 325.)

2. *The Prothallus.*

The most important of the Burntisland specimens is one in which the prothallus is well preserved. This was the first example of an undoubted *Lepidocarpon* prothallus found, and is shortly described in my preliminary note.* The "seed" in question is seen in approximately tangential section, probably, as indicated by its narrow form, cut near the proximal end (fig. 21). The micropyle is widely open, but this is probably due to accident, for the opening is asymmetrical and may have been caused or enlarged by the intrusion of foreign bodies into the crevice. The sporangium is attached to the sporophyll at the base, and is complete, ending above in a narrow ridge almost equal in height to the integument. The sporangial wall has the usual structure, and is somewhat more perfect than in the corresponding specimen of *L. Lomaxi*, for here the delicate lining tissue is for the most part preserved, as well as the outer columnar layer, from which it has sometimes contracted away. (See fig. 22.) The megaspore-membrane is well marked, and incloses nearly the whole of the sporangial cavity, having a narrow prolongation which stretches up into the apical ridge of the sporangium.

The megaspore contains the prothallus, which, though not completely preserved, fills a great part of the cavity. It consists of a large-celled tissue, the more internal cells attaining a diameter of ·1 millim. Where the peripheral layer is preserved, its

* 'Roy. Soc. Proc.,' vol. 67, p. 309.

cells are smaller than the rest, but the difference is not so well marked as in *L. Lomaxi*. (*Cf.* fig. 23.) Some remains of the cell-contents can be traced. There are no satisfactory indications of archegonia; the apical part of the prothallus, where they would be most likely to occur, is not preserved. The structure of the prothallus is thus simple in the extreme, and agrees most nearly with that of *Isoetes* among recent plants, but of course the basis for comparison is scanty in the case of such simple structures. It would not be safe to conclude that the prothallus of *L. Wildianum* had a simpler organisation than that of *L. Lomaxi*, for the sections of the two are not strictly comparable; the prothallus of *L. Wildianum* is seen in the narrow proximal region of the "seed," while the corresponding section of *L. Lomaxi* is through the broader and more distal portion. (*Cf.* figs. 21 and 23.) It is a fortunate circumstance that we are enabled to give at any rate some account of this important stage in the life-history, in the case of both species.

Summary.

In summing up our conclusions as to the nature of *Lepidocarpon*, the two species may be considered together. The strobilus and the earlier stages of the sporangia are only known, at present, in the case of *L. Lomaxi*. *L. Wildianum*, though hitherto only observed in the mature state, is so exactly similar to the corresponding stage of the former species, that what is true of the one is no doubt in essentials true of the other also.

The main result of our investigation is to show that the seed-like fructification which we have named *Lepidocarpon*, but which has hitherto been erroneously referred to the *Cardiocarpon anomalum* of Carruthers, was borne on a Lycopodiaceous strobilus, agreeing so closely both in morphology and anatomy with a *Lepidostrobus* that in its earlier stage it would be referred without doubt to that genus. The direct proof of this is afforded by Wild's specimen, which in one part retains the ordinary *Lepidostrobus* structure, while in another part it bears the seed-like organs of Williamson's *Cardiocarpon anomalum*.

The comparison of specimens in the two conditions has shown the relation of the seed-like organ of *Lepidocarpon* to the ordinary megasporangium of a *Lepidostrobus*. The former differs from the latter in two principal respects:—

(1.) It contains only one functional megaspore, which, like the embryo-sac of an ovule or seed, occupies almost the whole interior of the megasporangium, but is accompanied by the three other spores of the tetrad in an abortive condition.

(2.) When mature, the megasporangium of *Lepidocarpon* is inclosed by an integument, which is a new formation, growing up from the tissue of the sporophyll, and forming, together with the latter, a complete envelope to the sporangium, only open by a narrow micropylar crevice along the top.

The mature seed-like organ thus consists of the sporophyll and integument, inclosing the megasporangium; the latter is occupied by a single functional megaspore, or embryo-sac, which, in certain cases, is filled by the prothallus. This conclusion is proved by the identical structure of the sporangium in the integumented, and in the naked, Lepidostroboid condition, and by the identity of the sporophyll in both, modified only by minor changes such as might be expected to occur during maturation. The evidence, derived partly from WILD'S cone, and partly from the comparison of other specimens, is conclusive, but one kind of evidence which we might naturally have looked for is absent. No transitional stages between the naked and the integumented condition of the megasporangium have yet been observed. This negative result is somewhat remarkable. Five specimens of the strobilus have come under investigation; four of these show only the non-integumented condition; in one case (Specimen IV.) the part of the strobilus sectioned was an inch and a half in length, but all the sporangia shown were in the same state. In the fifth specimen (WILD'S cone) both the integumented and non-integumented sporangia are present, but here too no intermediate stages occur.

Detached specimens are very numerous; some have integuments, some have not, but in no single instance has a partly developed integument been found. All known megasporangia of *Lepidocarpon* are either in the naked or in the completely integumented condition.

Further, the non-integumented specimens have the tissues of their sporophylls fully developed, and to a great extent sclerotic (see photographs 3–6; figs. 1–3, and 26). It is difficult to believe that they could subsequently have become the seat of the active growth necessary to form the integument. It is also noticeable that among the detached examples, integumented and non-integumented specimens are always associated together, and in about equal numbers. This is not easy to explain if the latter were simply a young stage of development of the former. The explanation which suggests itself is that the condition with naked sporangia, as shown in the specimens before us, is an arrested one, and that the sporangia actually observed in this state would not themselves have developed any further. We may take these arrested specimens as representing in essentials the young condition,* but their tissues had to a certain extent matured and hardened, rendering them better fitted for preservation than specimens in the normal course of development. Why so many sporangia should have been abortive, or at least arrested before developing an integument, is not easy to understand. It is common enough to find, among the Spermophyta, arrested or abortive ovules side by side with ripe seeds; here the arrest of the development is due to the absence of fertilisation; it is not likely that this was the explanation in *Lepidocarpon*, though we have at present no evidence as to the stage at which pollination and fertilisation respectively occurred.

The wall of the megasporangium of *Lepidocarpon* is, as a rule, thicker in the

* As shown especially by the immature state of the stelar tissue in the axis.

naked than in the integumented condition (compare fig. 1 with fig. 10, and fig. 26 with fig. 27). The loss of thickness during maturation no doubt depended partly on stretching, partly on absorption of the inner layers of the sporangial wall. This reduction is most extreme in the case of the specimen of *Lepidocarpon Lomaxi* with prothallus (fig. 23). It is common to find abortive sporangia in cones of *Lepidostrobus*, especially near the apex; these also are distinguished from the mature ones by their thicker walls. The same thing occurs in *Spencerites*,* and in the microsporangiate cone provisionally referred to *Lepidocarpon Lomaxi*. These abortive sporangia sometimes bear a considerable resemblance to the non-integumented stage of the megasporangiate *Lepidocarpon*.

On the whole of the evidence we may conclude that the naked megasporangia of *Lepidocarpon* represent an early stage of development of the integumented, seed-like organs, in an arrested condition.

This arrest of development took place after the differentiation of the megaspores, for in the non-integumented as in the integumented condition, we find the one large functional megaspore or embryo-sac accompanied by its abortive sister-cells.

The only example of a prothallus in *L. Lomaxi*, among the very numerous sporangia examined, is in an integumented specimen. One might naturally suppose that its absence in other examples is due simply to imperfect preservation, but it is not quite certain that this is the real explanation. The one prothallus-containing specimen is not so well preserved in other respects as some of those with the megaspore empty. In many of the latter (integumented as well as non-integumented) the large megaspore is much contracted (*e.g.*, phot. 15), which would perhaps have been less likely to happen if it had ever been filled with tissue. Further, the sporangial wall in the prothallus-containing "seed" is more reduced in thickness than in other specimens, suggesting that the former may really represent a more advanced stage of development. There is thus a certain probability, though only a weak one, that the prothallus may have developed late, after the integument was formed. If the central tissue within the prothallus (fig. 23) were really an embryo, it would follow that the prothallus itself had been developed at a considerably earlier stage; the probability, however, is in favour of the tissue in question being merely part of the prothallus.

Morphology.

We have now to consider the question of the morphological nature of the seed-like organ of *Lepidocarpon*—is it to be regarded as a true seed?† The idea of its being a seed is suggested, in the first instance, by the presence of an integument, inclosing

* Scott, "Structure and Affinities, &c. Part II., on *Spencerites*," p. 93, Plate 15, fig. 15, 'Phil. Trans.,' B, vol. 189 (1897).

† We must not allow our minds to be influenced by the fact that the body was accepted without doubt as a true seed before its relation to *Lepidostrobus* was known. The question must now be considered *de novo*.

the sporangium or nucellus, so as to leave only a narrow opening or micropyle, at the top. The fact that only a single megaspore or embryo-sac, occupying almost the whole of the sporangial cavity, comes to perfection, much heightens the resemblance to a true seed, especially when we find the embryo-sac filled with the prothallus or endosperm. The presence of an integument is in itself far from conclusive; the indusium of the megasporangium in *Azolla* is at least equally like an integument, yet it does not constitute the organ a seed, for it does not permanently inclose the megaspore.* Neither is the single megaspore in itself a crucial character, for this, though unknown in Lycopods, is common to all the Rhizocarps.

In *Lepidocarpon*, however, the "retention of the megaspore,"† one of the great characters of the Spermophytes, appears to hold good; at no stage is there any indication of dehiscence, or of the envelopes of the seed-like organ in any way breaking down. The megaspore has a comparatively thin wall, like an embryo-sac, and differs conspicuously in this respect from a spore destined to be set free. All the evidence goes to show that the integumented megasporangium, with its contents, was shed, *as a whole*, just as a true seed is.

The definite points of agreement with a true seed appear, then, to be the following—

(1.) The integument and micropyle.
(2.) The single functional megaspore.
(3.) The "retention of the megaspore," involving,
(4.) The detachment of the seed-like organ as a whole, and its indehiscent character.

Against the interpretation of the envelope as an integument it may be urged that this structure in *Lepidocarpon*, springs from the sporophyll and not from the sporangium. That however is an objection of little or no weight. Many morphologists have regarded the integument as a leaflet or a ligule, others as an indusium; on any of these views it would be an organ originally springing from the leaf and free from the sporangium. That an organ at first merely surrounding the sporangium should eventually come to be inserted upon it is perfectly intelligible; floral morphology abounds in parallel cases of "congenital adhesion." In fact it is unlikely, *à priori*, that the integument at its first origin formed part of the sporangium; in that case we should have to regard it not merely as a new formation, but as a structure absolutely without homologue among Cryptogams, whereas protective outgrowths from the leaf are common enough among them.

* In *Isoetes* also, a genus more closely allied to our fossil, the velum forms a kind of integument, though not much like that of a seed. The narrow opening of the velum in such species as *Isoetes Hystrix* was even termed by ALEX. BRAUN the "micropyle."

† I take this phrase from Professor COULTER'S judicious essay on the "Origin of the Gymnosperms and the Seed-habit," 'Bot. Gazette,' vol. 26, 1898.

A much more real difference from any known seed is the peculiar shape of the micropyle, forming a long narrow slit, extending the whole length of the seed, instead of a more or less tubular canal. This is a striking difference, but is no doubt correlated with the form of the sporangium. An ordinary sporangium or nucellus usually begins as a rounded papilla; the integument as it grows up around it leaves a tubular opening at the top; but in the Lepidodendreæ, where the sporangium is elongated in the radial direction, it is intelligible that when it became integumented, its envelope should have had a correspondingly elongated opening. The fact that in *Lepidocarpon* the whole sporophyll, or at least the greater part of it, takes part in the formation of the seed-like organ is again a marked difference from the typical seeds of the higher plants. This fact is connected with the foliar origin of the integument, which necessitates the participation of the sporophyll in order to complete the inclosure of the sporangium. From the point of view of formal morphology we might hence be led to speak of the seed-like organ as a "fruit"; it seems more profitable, however, to regard the participation of the sporophyll as a probable characteristic of a very primitive type of seed.

A seed, however, according to current definitions, should contain an embryo; that is to say, in typical seeds, the fertilised ovum develops to a certain, very variable extent, while still inclosed in the seed-coats. This criterion is of very little practical value; no satisfactory indication of an embryo has yet been found in *Lepidocarpon*, but this applies equally to the fossil Gymnospermous seeds, in none of which (until we come to the Mesozoic *Bennettites*) has an embryo ever been observed, although the archegonia are often recognisable. We know that in recent Cycads the embryo often does not begin to develop until after the seed has been shed, so that it is a matter of chance whether, in a given seed, we find an embryo or not.

We may reasonably regard a true seed as necessarily the result of an act of fertilisation, but this again is of no use as a practical test, for in many Cycads, for example, the unfertilised are scarcely distinguishable from the fertilised seeds.

It has been suggested to me that it would be more correct to call the integumented megasporangium of *Lepidocarpon* an ovule, rather than a seed, as this would avoid the difficulty as to the presence of an embryo. I have not adopted the suggestion, because an ovule is essentially a young and immature organ, whereas the seed-like organs of *Lepidocarpon* have all the indications of maturity, and were doubtless shed in the condition in which we find them. No one calls BRONGNIART'S Gymnospermous seeds "ovules," though we have not yet found an embryo in any of them.

The really essential distinction between Seed-plants and the Higher Cryptogams seem to be that in the former, fertilisation, or at least pollination, takes place on the parent plant. This is the important point physiologically, and on this the morphological differences ultimately depend. A megaspore set free before pollination, as in the Higher Cryptogams, is dependent on chance for its meeting with the microspores

(the first preliminary to fertilisation).* Where this meeting takes place on the parent plant, as in Phanerogams, arrangements become possible for insuring its occurrence, and when once pollination is effected, fertilisation follows with a considerable degree of certainty. The development of the new generation having once been started within the megasporangium, seed-formation became possible.

Unfortunately we are at present unable to decide whether pollination, in *Lepidocarpon*, took place on the parent plant or not. Microspores have not been observed within the integument of the megasporangium, nor is there anything of the nature of a pollen-chamber to receive them. We must therefore take into account the possibility that the seed-like organs of *Lepidocarpon* may have served merely for the protection of the megaspore and prothallus; that they were shed first and received the microspores afterwards. On this supposition it is possible that all the specimens observed, including those with prothalli, were still unfertilised or even unpollinated. If this were so, the organs in question were certainly not true seeds, though it is possible that the evolution of true seeds may have started in the same way.

I do not regard the presence of an incomplete integument in connection with the microsporangium, as any argument against the seed-homologies of the integumented megasporangium. On any hypothesis, the "seed" of *Lepidocarpon* was in an early stage of its evolution, as shown by the obviously sporangial structure of the nucellus, the late development of the integument, and the persistence of the abortive megaspores. The integument in the first instance may well have been a merely protective or supporting organ, common to both kinds of sporangia. On the male side its functions could only have been temporary and unessential, while in the case of the female it would have proved far more important, as affording a means of pollination on the parent plant, and ultimately enabling the embryo to be launched on the world in a well-equipped condition. So it may well have been retained and further developed under the influence of selection, on the female side, while in the male it remained rudimentary or was lost altogether. In *Lepidocarpon* the integument of the megasporangium was already by far the more important of the two (if only to protect the megaspore during the development of the prothallus), but all its possibilities may not yet have been realised.

On the whole, the analogy between the integumented megasporangium of *Lepidocarpon* and a true seed seems an important one, though probably we can only regard the former as, at most, a seed in a nascent stage of evolution. Such an organ, however, might well have formed the starting-point for the development of true seeds, such as those of the Gymnosperms. Whether this is likely to have actually been the case as regards *Lepidocarpon*, depends on general questions of affinity, which we shall shortly consider in the next section.

* The difficulty must have been greatest in the case of heterosporous trees, such as the Lepidodendreæ, for the chances must have been much against the light microspores and the heavy megaspores falling in the same spot.

In discussing the morphology of a Palæozoic plant, we must bear in mind that our current morphological conceptions are derived entirely from the study of the recent flora, and that we cannot expect them to apply rigidly to plants at a far earlier stage of evolution. On the whole, no doubt, the Palæozoic vascular plants were less different from their recent allies, both in morphology and anatomy, than we might expect. But we must be prepared to find, as we actually do find in numerous instances, combinations of characters which no longer exist. It is exactly from such cases, where our text-book definitions break down, that we may hope for new light on the evolution of organs hitherto known to us only in their more modern forms.

Affinities.

The affinities of *Lepidocarpon* on the Cryptogamic side need no discussion. The cone is beyond any question that of a Lycopod, with the closest relationship to *Lepidostrobus*, from which it only differs in the integumented megasporangium, and the presence within it of a single functional megaspore.

The important question for us to consider is, whether these latter characters indicate any affinity with higher classes of plants. First, it is desirable finally to clear the ground of a misconception which might arise from nomenclature.

Lepidocarpon, as has been shown in these pages, is identical with the *Cardiocarpon anomalum* of Williamson. It has, however, nothing whatever to do with the true *Cardiocarpon anomalum* of Carruthers, or with the seeds on which Brongniart originally founded the genus. In the true *Cardiocarpons* the seed is flattened, and the flat side somewhat heart-shaped. In *Lepidocarpon* the seed-like organ is a long sac, like an ordinary hand-bag in shape; it is the *end*, not the side, which has a cordate or triangular form. Consequently, the apparent resemblance in form between *Lepidocarpon* and the true *Cardiocarpon* is entirely illusory. The mistake arose from Williamson confining his attention to sections in the tangential plane, *i.e.*, at right angles to the long axis of the "seed." When seen in other aspects, all resemblance to Brongniart's *Cardiocarpon* vanishes.

In the true *Cardiocarpon anomalum* of Carruthers, each seed is borne at the end of a long stalk, the whole group forming a lax inflorescence absolutely different from the dense strobilus of *Lepidocarpon*.* In structure, also, *Lepidocarpon* and the *Cardiocarpon* of Brongniart are entirely distinct.† The characteristic pollen-chamber of *Cardiocarpon* is unrepresented in *Lepidocarpon*, while, on the other hand, the columnar layer of the sporangial wall in the latter is quite absent in the former. The integument is a complex structure with its own vascular system in *Cardiocarpon*, while in *Lepidocarpon* the integument shows little differentiation, and has no

* Carruthers, "Notes on some Fossil Plants," 'Geol. Mag.,' vol. 9, 1872.

† For illustrations of the *Cardiocarpus* or *Cardiocarpon* of Brongniart, see the magnificent posthumous work by that author, 'Recherches sur les Graines Fossiles Silicifiées,' Paris, 1881, Plates I.–III. and V.

vascular supply. The micropyle is tubular to the one, slit-shaped in the other. In fact, the two things are in every respect different, the true *Cardiocarpon* being a typical Gymnospermous seed, while the fructification of *Lepidocarpon* is, as we have seen, the integumented megasporangium of a Lycopod. CARRUTHERS' *C. anomalum*, like BRONGNIART'S specimens, doubtless belonged to the Cordaiteæ. WILLIAMSON'S *Cardiocarpon anomalum*, our *Lepidocarpon*, belongs to the Lycopodiaceæ, and has no affinity with BRONGNIART'S genus.

At present, *Lepidocarpon* stands isolated. Its reproductive bodies, as I have endeavoured to show, present important analogies with true seeds, but there is nothing to indicate affinity with any of the existing groups of Spermophytes. Those who hold to the belief that the Gymnosperms, or a part of them, sprang from Lycopods, may find in the discovery of *Lepidocarpon* some support for their views. In spite of its seed-like organ, however, the new genus was a true Lycopod, and shows no indication of transition to any other group. The mere fact that these plants produced a reproductive body agreeing in many respects with a true seed, is no proof that they belonged to the line of descent of any of the known types of seed-bearing plants. *Lepidocarpon* is of great interest as demonstrating to us one way in which seeds may have originated, but we have no right to assume that it presents to us the actual origin of the seeds of Phanerogams. To take an analogous case: *Bennettites* affords the earliest known instance of an angiospermous fructification; yet botanists are agreed that it has no affinity with the Class Angiospermæ.

I have recently discussed, on another occasion,* the question of the probable origin of the Gymnosperms; it is unnecessary to repeat the arguments here, but the conclusion which appears best justified in the present state of our knowledge, is that the Cycads were almost certainly derived from Ferns (using the word in the widest sense), and that there is a strong probability that the Gymnosperms generally had a similar origin. The existence of the Palæozoic family Cordaiteæ, combining Cycadean with Coniferous characters, is sufficient to establish a strong presumption that the two latter groups belong to the same stock.

I do not consider that the discovery of *Lepidocarpon* in any way shakes the conclusion that the Gymnosperms were of Filicinean origin. It shows indeed that a Lycopod was capable of producing organs having much in common with true seeds, but these organs differ too much in detail from the seeds of Gymnosperms to afford any evidence of affinity.

We are still without any light whatever on the origin of the Angiosperms, and I see no indication that *Lepidocarpon* is likely to have led in that direction.

The balance of probability is in favour of the new genus representing merely a short branch of the phylogenetic tree, parallel, perhaps, or even convergent with the great Spermophytic phylum, but without genetic connection with it.

* 'Studies in Fossil Botany,' 1900, p. 513.

Diagnosis.

The generic character, given in my preliminary Note (*loc. cit.*, p. 309), is reproduced here, with certain emendations. I have thought it best to omit the microsporangiate cone from the diagnosis, until its relation to the female strobili is completely established.

Lepidocarpon, gen. nov.

Strobili, with the characters of *Lepidostrobus*,* but each megasporangium inclosed, when mature, in an integument, growing up from the superior face of the sporophyll-pedicel.

Integument, together with the lamina of the sporophyll, completely enveloping the megasporangium, or nucellus, leaving only an elongated, slit-like micropyle above. A single functional megaspore or embryo-sac developed in each megasporangium and occupying almost the whole of its cavity.

Megaspore ultimately filled by the prothallus or endosperm.

Sporophyll, together with the integumented megasporangium and its contents, detached entire from the axis of the strobilus, the whole forming a closed, seed-like, reproductive body.

Seed-like organ horizontally elongated, in the direction of the sporophyll-pedicel, to which the micropylar crevice is parallel.

Our knowledge of the Burntisland form, *Lepidocarpon Wildianum*, is at present limited to the mature seed-like organs, which agree so closely with those of the Coal-Measure species, *L. Lomaxi*, that I have so far failed to find any constant diagnostic characters. The two species are provisionally separated on account of their very different horizons. It is highly probable that when *L. Wildianum* comes to be known with the same degree of completeness as *L. Lomaxi*, good distinctive characters will reveal themselves. In the meantime I confine myself to giving a few comparative measurements, which are necessarily rough, as the "seeds" vary much in size, and have often undergone deformation, owing to pressure and other causes.

Lepidocarpon Lomaxi, sp. nov.

Length of seed-like organ, parallel to sporophyll-pedicel (radial with reference to parent-cone)	8–14 millims.†
Height, vertical to pedicel, and parallel to axis of cone	5–11 millims.
Width, at distal end (horizontal, and tangential to cone) . . .	5–12 millims.

* See Zeiller, "Bassin Houiller de Valenciennes," 'Flore Fossile,' 1888, p. 496.

† Actually measured. The largest specimens, such as that illustrated in phots. 14–16, may have been longer.

Locality: near Stalybridge, Oldham, and other places in Lancashire and Yorkshire.

Horizon: Lower Coal-Measures.

Lepidocarpon Wildianum, sp. nov.

Length of "seed"	about	10 millims.
Height	,,	5 ,,
Width, at distal end	,,	5 ,,

Locality: Pettycur, near Burntisland, Scotland.

Horizon: Calciferous Sandstone Series (Base of Carboniferous Formation).

Both species are included under *Cardiocarpon anomalum*, WILL. (*non* CARRUTHERS). WILLIAMSON's descriptions and figures, cited below,* relate to the Coal-Measure form, *Lepidocarpon Lomaxi*. I have mentioned above the possibility that more than one species may turn out to be included under the name *L. Lomaxi*.†

The nature of the other forms of "*Cardiocarpon*" described by WILLIAMSON must remain an open question until new material has come to light.

EXPLANATION OF THE PLATES.

Of the sixteen photographs, taken direct from the sections and reproduced in Plates 38 and 39, Nos. 1, 3, and 7 are by Mr. J. LOMAX, and all the rest by Mr. L. A. BOODLE. The photographs generally need to be examined with a hand-lens.

(Phots. 1–16, *Lepidocarpon Lomaxi*.)

Plate 38.

Phot. 1. Approximately transverse section of strobilus (Specimen III.), showing the axis, surrounded by the sporophylls with their sporangia. *sph*, sporophyll showing ligule; *sm*, sporangium containing four megaspores, shown enlarged in Plate 40, fig. 5.
× 7. S. 944.‡

Phot. 2. Transverse section of a larger strobilus (Specimen IV.), *ax*, axis; the stele is not shown; the patches of large-celled tissue are the parichnos-strands of the sporophyll-bases. *sph'*, sporophyll referred to on p. 295; it shows

* WILLIAMSON, "Organisation of Fossil Plants of Coal-Measures," Part VIII. ('Phil. Trans.,' vol. 167, pt. 1, 1877), p. 255, figs. 116–120; Part X., 'Phil. Trans.,' vol. 171, pt. 2, 1880, p. 518, fig. 64.

† [I have lately received from Mr. LOMAX sections of a large "seed" from the Coal-Measures, which appears to be new and quite distinct from *Lepidocarpon Lomaxi*, though allied.—*June* 22, 1901.]

‡ Numbers preceded by the letter S refer to slides in the author's collection.

base of sporangium towards distal end; *sph*^{2}, ascending lamina of a sporophyll, cut transversely.

× 4½. S. 1131.

Phot. 3. Tangential section of a strobilus (Specimen III.) showing numerous sporangia seated on their sporophylls; those near the bottom are cut towards the distal end. *sph'*, sporophyll with ligule, shown enlarged in Plate 40, fig. 2. *sph*^{2}, sporophyll cut further in, showing attachment of sporangium. Note the overlapping laminæ towards the apex of the strobilus.

× 7. S. 947.

Phot. 4. Detached sporophyll and sporangium, in tangential section through proximal region. *sm*, sporangial wall. *cu*, lateral cushions of sporophyll-pedicel; *d.r.*, its dorsal rib. *Cf.* Plate 40, fig. 1.

× about 8. From a slide in Mr. WILD'S private collection.

Phot. 5. Part of strobilus (Specimen I.) in longitudinal section. The right-hand side is approximately radial; on the left-hand side the sporophylls are bent so as to appear in nearly tangential section. *ax*, axis; the light bands of tissue seen in the lower part are parichnos-strands. *sph*, sporophyll in radial section showing its decurrent base. *sph*^{2}, sporophyll in nearly tangential section, bearing the sporangium, *sm*, in which the contracted membrane of the megaspore is seen.

× 5. S. 608.

Phot. 6. Tangential section of the same strobilus (Specimen I.) showing a number of sporangia seated on their sporophylls. The plane of section is somewhat inclined, so that the lower sporophylls are shown in more distal section than the upper. At the sides the ascending laminæ are seen. *sm*, *sph*, sporangium and sporophyll shown, enlarged, in Plate 40, fig 1.

× 5. S. 607.

Phot. 7. Mature "seed," containing the prothallus, seen in tangential section. *d. r.* dorsal rib of sporophyll-pedicel. *i*, integument. *m*, micropyle, within which the pointed apical ridge of the sporangium or nucellus is seen. *pr*, prothallial tissue, which completely fills the functional megaspore or embryo-sac. For details see Plate 43, fig. 23, which represents the upper half of this specimen on a larger scale.

× 12. S. 1073.

Phot. 8. Transverse section of a microsporangiate strobilus, perhaps referable to *L. Lomaxi*. *ax*, axis of strobilus, in which the stele and leaf-trace bundles are clearly seen. Surrounding the axis are the sporophylls and crushed microsporangia. *lg*, ligule, seated in the ligular chamber of a sporophyll-lamina. *sph*, detached sporophyll and megasporangium of *L. Lomaxi*, represented in detail in Plate 40, fig. 4.

× 4½. S. 613.

Plate 39.

Phot. 9. Tangential section of the same microsporangiate strobilus, showing the sporophyll-laminæ converging over the apex. *sph'*, integumented microsporangium in oblique section; represented on a larger scale in Plate 41, fig. 7. sph^2, another integumented microsporangium, cut still more obliquely.

× 4½. S. 617.

Phot. 10. Transverse section of the upper part of WILD'S specimen, showing the megasporangia in the naked condition. *ax*, axis of strobilus. *sph*, lamina of a sporophyll. *sm'*, a sporangium; *mg*, contracted membrane of principal megaspore. sm^2, sporangium and sporophyll in oblique section, shown enlarged in Plate 43, fig. 26.

× 4½. From a section acquired from Mr. WILD'S private collection.

Phot. 11. Transverse section from the lower part of the same specimen, showing the megasporangia in the integumented, seed-like condition. *ax*, axis of cone shown in detail in Plate 42, fig. 15. *s'*, a "seed" in oblique section, shown in detail in Plate 43, fig. 27. s^2, another "seed," in approximately horizontal section, attached to the axis, and showing the integument, sporangial wall, and large, contracted megaspore (*mg*) very clearly.

× about 3. Manchester Museum, WILD Collection, No. 139.

Phot. 12. Approximately radial section of the same specimen. *ax*, axis of strobilus. *s'*, large "seed" in radial section. The sporophyll, which forms the base of the "seed," is attached to the axis, and the integument is closed at the proximal end. *mg*, much-contracted membrane of the large megaspore. Towards the top the section becomes more tangential. s^2, a small "seed" in tangential aspect.

× 4½. From a section acquired from Mr. WILD'S private collection.

Phot. 13. Tangential section of the same specimen, showing several "seeds." *sph*, sporophyll forming the base of a "seed"; *i*, integument, within which the sporangial wall is seen; *m*, micropyle; *mg*, large megaspore, much contracted.

× 4. From a section acquired from Mr. WILD'S private collection.

Phots. 14–16, from a series of eight sections cut in parallel tangential planes from one large "seed."

Phot. 14. Section at proximal end. *v.b.* vascular bundle of sporophyll, which forms the massive base of the "seed." *i*, integument. *m*, micropyle. *sm*, wall of sporangium. The dark body below the sporangium appears to be a fragment from the proximal end of the integument.

× 5. S. 866.

Phot. 15. Section from broadest part of "seed" towards distal end. *sph*, sporophyll, with dorsal rib. *i*, integument. *m*, micropyle. *sm*, sporangial wall,

mg, an abortive megaspore; *mg'*, contracted membrane of the functional megaspore.

× 4½. S. 861.

Phot. 16. Section from distal extremity of "seed." *v.b.*, vascular bundle of the sporophyll, which is here of great thickness. *i*, integument; *m*, micropyle, apparently widely open. *sm*, sporangium (perhaps collapsed) forming a three-rayed body with almost obliterated cavity.

× 4. S. 860.

Plates 40–43, figs. 1–27, were all drawn for me, from the original sections, by Mr. G. T. GWILLIAM.

(Figs. 1–15, *Lepidocarpon Lomaxi.*)

Plate 40.

Fig. 1. Sporangium and sporophyll from Specimen I. (shown in Plate 38, phot. 5, *sm*, *sph*) in tangential section, cut about midway between the proximal and distal ends of the horizontal pedicel. *cu*, lateral cushions of the sporophyll-pedicel; *v.b.*, vascular bundle; *a*, attachment of sporangium to sporophyll; *w.p.*, outer, columnar layer of sporangial wall; *w.i.*, internal layer of wall; *mg.*, membrane of functional megaspore, occupying practically the whole cavity of the sporangium.

× 19. S. 607.

Fig. 2. Sporangium and sporophyll from Specimen III. (shown in Plate 38, phot. 3, *sph'*) in tangential section near distal extremity. *l*, laminar margin of sporophyll; *v.b.*, vascular bundle; *lg*, ligule, not quite complete, seated in ligular pit below sporangium; *w.p.*, columnar layer, *w.i.*, inner layer of sporangial wall; *mg*, megaspore.

× 25. S. 947.

Fig. 3. Approximately radial section of part of a strobilus (Specimen III.). *st*, stele of axis, in oblique section; *l.t.*, leaf-trace bundle; *sph*, sporophylls, of which three are shown, each with a horizontal pedicel and ascending lamina. *sm'*, *sm*^{2}, *sm*^{3}, sporangia belonging to the three sporophylls; *lg*, ligule; *mg*, remains of megaspores.

× 21. S. 945.

Fig. 4. Detached sporophyll and sporangium shown in Plate 38, phot. 8, in section transverse to parent strobilus. The ascending lamina of the sporophyll is seen in transverse section. *v.b.*, vascular bundle; *w.p.*, columnar layer, *w.i.*, inner layer of sporangial wall; *mg'*, membrane of functional megaspore (contracted); *mg*, an abortive megaspore.

× 32. S. 613.

Fig. 5. Sporangium from Specimen III. (shown in Plate 38, phot. 1, *sm*), in which all four megaspores are seen. *w.p.*, columnar layer, *w.i.*, inner layer of sporangial wall; *mg'*, contracted membrane of the functional megaspore; *mg*, the three abortive megaspores.

× 22. S. 944.

Fig. 6. Central part of axis of strobilus (Specimen III.) in oblique section, showing stele. *x*, narrow ring of xylem, consisting of spiral and scalariform tracheides; *l.t.*, leaf-trace bundles.

× 67. S. 943.

Plate 41.

Fig. 7. Microsporangium and sporophyll from supposed male strobilus (shown in Plate 39, phot. 9, *sph'*), in oblique section between the tangential and transverse planes. *sph*, sporophyll; *a*, attachment of sporangium to sporophyll; *i*, integument, springing from the sporophyll, and partly inclosing the sporangium; *w.p.*, *w.i.*, columnar and inner layers of sporangial wall; *mi*, the microspores.

× 31. S. 617.

Fig. 8. Apex of sporangium in non-integumented condition, from Specimen III., seen in tangential section. *w.p.*, columnar, *w.i.*, inner layer of sporangial wall.

× 150. S. 947.

Fig. 9. Apex of sporangium in integumented condition, to compare with fig. 8. The section is a tangential one, passing through the micropyle of the large "seed" shown in Plate 39, phots. 14–16. *i*, integument enclosing the sporangium; *w.p.*, columnar, *w.i.*, inner layer of sporangial wall.

× about 100. S. 865.

Fig. 10. Detached "seed" in approximately tangential section. The sporophyll, which forms the base of the "seed," is much lobed at the sides. *v.b.*, vascular bundle (*cf.* fig. 11); *pa*, lateral gaps, perhaps representing the parichnos; *i*, integument (the shading is partly diagrammatic); *m*, micropyle; *sm*, wall of sporangium or nucellus, showing the columnar layer; *a*, attachment of sporangium to sporophyll; *mg*, membrane of the functional megaspore, filling the sporangial cavity.

× 19. S. 621.

Fig. 11. Vascular bundle from fig. 10 more highly magnified, seen in transverse section. *x*, xylem; *px*, small elements, probably the protoxylem, in a central position; *ph*, phloem.

× 300. S. 621.

Fig. 12. Detached "seed" in tangential section near the distal end. *l*, laminar margin of sporophyll; *v.b.*, vascular bundle; *pa*, parichnos(?)-gaps; *i*, integument; *m*, micropyle; *sm*, wall of sporangium, showing columnar

layer very clearly; in this region the sporangium is free from the sporophyll; *mg*, megaspores; two are abortive; the third is probably a fragment of the functional one.

× 19. S. 610.

Fig. 13. Part of another "seed" in a similar plane of section to fig. 12. *l*, laminar margin of sporophyll, projecting far beyond the base of the integument *i*; *sm*, sporangial wall; *mg*, part of the membrane of functional megaspore.

× about 30. S. 1119.

Fig. 14. Detached "seed" in longitudinal section, approximately radial to parent strobilus. *sph*, sporophyll, forming base and distal extremity of "seed" (*cf.* Plate 40, fig. 3, for the corresponding view in the non-integumented condition). *v.b.*, vascular bundle of sporophyll-pedicel; *a*—*a*, attachment of sporangium to sporophyll; *i*, integument, closed at proximal end (to the right), and abutting on the sporophyll-lamina at the distal end. (The integument appears also above the sporangium because the plane of section misses the micropylar crevice.) *sm*, wall of sporangium; *mg*, membrane of functional megaspore.

× 15. S. 929.

Plate 42.

Fig. 15. Axis of WILD'S cone in transverse section (represented as a whole in Plate 39, phot. 11). *p*, pith, most of which has perished; *x*, parts of xylem-ring, showing the small protoxylem-elements towards the periphery; *l.t.*, leaf-trace bundles passing through the cortex; *sph*, base of a sporophyll; *v.b.*, its vascular bundle.

× about 30. Manchester Museum, WILD Collection, No. 139.

(Figs. 16–22, *Lepidocarpon Wildianum*.)

Fig. 16. Small "seed" in tangential section, near proximal end. *v.b.*, vascular bundle of sporophyll; *i*, integument; *m*, micropyle; *sm*, wall of sporangium.

× 19. S. 1105.

Fig. 17. "Seed" in horizontal section, approximately transverse with reference to parent strobilus. This section is the lowest of a series of four, of which three are figured (figs. 17–20). *v.b.*, vascular bundle of sporophyll-pedicel, which appears at three places—twice at the proximal end (to the left) and once towards the distal end; *i*, integument; *a*, attachment of sporangium to sporophyll; *sm*, wall of sporangium; *mg*, membrane of functional megaspore.

× about 12. S. 1104.

Fig. 18. Third section from below, same series. *l*, ascending lamina of sporophyll, seen in transverse section; *v.b.*, vascular bundle; *i*, integument; *lg*, ligule, seated between lamina and sporangium (see fig. 19); *sm*, wall of sporangium; *mg*, contracted membrane of functional megaspore.

× 12. S. 1106.

Fig. 19. Ligule from fig. 18, more highly magnified. *sph*, tissue of sporophyll; *sm*, wall of sporangium; *lg*, ligule, cut transversely.

× about 100. S. 1106.

Fig. 20. Uppermost section of same series. *sph*, lamina of sporophyll, incomplete and detached from integument, *i*; *sm*, sporangium, here assuming Y-shape (*cf.* Plate 40, fig. 4, for non-integumented condition); *mg*, abortive megaspore.

× 12. S. 1107.

Fig. 21. "Seed" in tangential section, near proximal end, to show prothallus. *sph*, sporophyll-pedicel; *v.b.*, vascular bundle; *i*, integument; *sm*, wall of sporangium or nucellus; *mg*, membrane of functional megaspore or embryo-sac, containing the large-celled prothallus, *pr*.

× 15. S. 1070.

Fig. 22. Part of the same section, more highly magnified, showing the upper part of the prothallus and surrounding tissues. *i*, integument; *w.p.*, columnar, *w.i.*, inner layer of sporangial wall; *mg*, membrane of megaspore; *pr*, tissue of prothallus.

× 70. S. 1070.

(Figs. 23–27, *L. Lomaxi.*)

Plate 43.

Fig. 23. Upper half of the "seed" with prothallus (shown in Plate 38, phot. 7) more highly magnified. *i*, integument; *sm*, wall of sporangium, or nucellus, much reduced in thickness; *mg*, membrane of functional megaspore; *pr*, ordinary tissue of prothallus; *y*, *possibly* the central cell of an archegonium; *c.s.*, central strand of elongated, thin-walled cells, containing nucleus-like bodies.

× 30. S. 1073.

Fig. 24. Detached "seed," in oblique section, cut at an angle with the transverse and tangential planes, showing the integument closed at the proximal end. *sph*, sporophyll; *v.b.*, vascular bundle, obliquely cut; *a*, attachment of sporangium; *i*, integument; *sm*, wall of sporangium.

× 20. S. 1117.

Fig. 25. Another "seed"; the plane of section is similar to that of fig. 24, but passes through the distal region of the sporophyll, *sph*, which is much lobed and preserved entire. *i*, integument (the plane of section passes obliquely through the micropyle); *a*, attachment of sporangium; *sm*, sporangial wall; *mg*, membrane of functional megaspore.

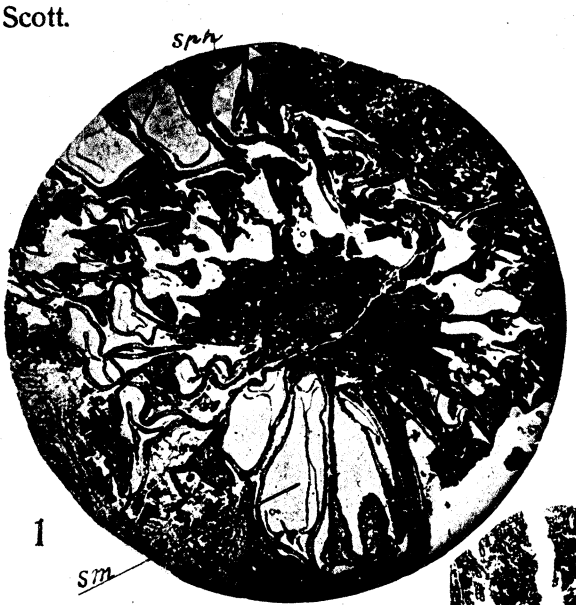
× 15. S. 1123.

Fig. 26. Sporophyll and sporangium (sm^2 in Plate 39, phot. 10) from upper part of WILD'S cone, to show non-integumented condition. *sph*, pedicel of sporophyll showing cushions; *a*, attachment of sporangium; *sm*, sporangial wall.

× 19. From Mr. WILD'S private collection.

Fig. 27. "Seed" (*s'* in Phot. 11) from lower part of WILD'S cone, to show integumented condition, agreeing with WILLIAMSON'S "*Cardiocarpon anomalum.*" *sph*, sporophyll with dorsal rib; *v.b.*, vascular bundle; *i*, integument; *m*, micropyle; *a*, attachment of sporangium; *sm*, sporangial wall.

× 12. Manchester Museum, WILD Collection, No. 139.



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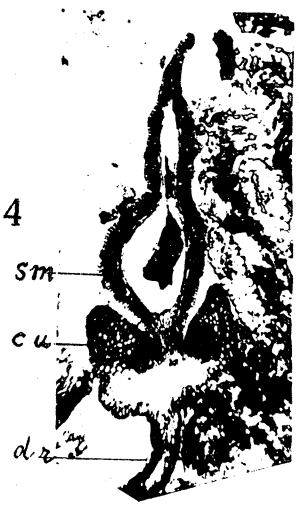

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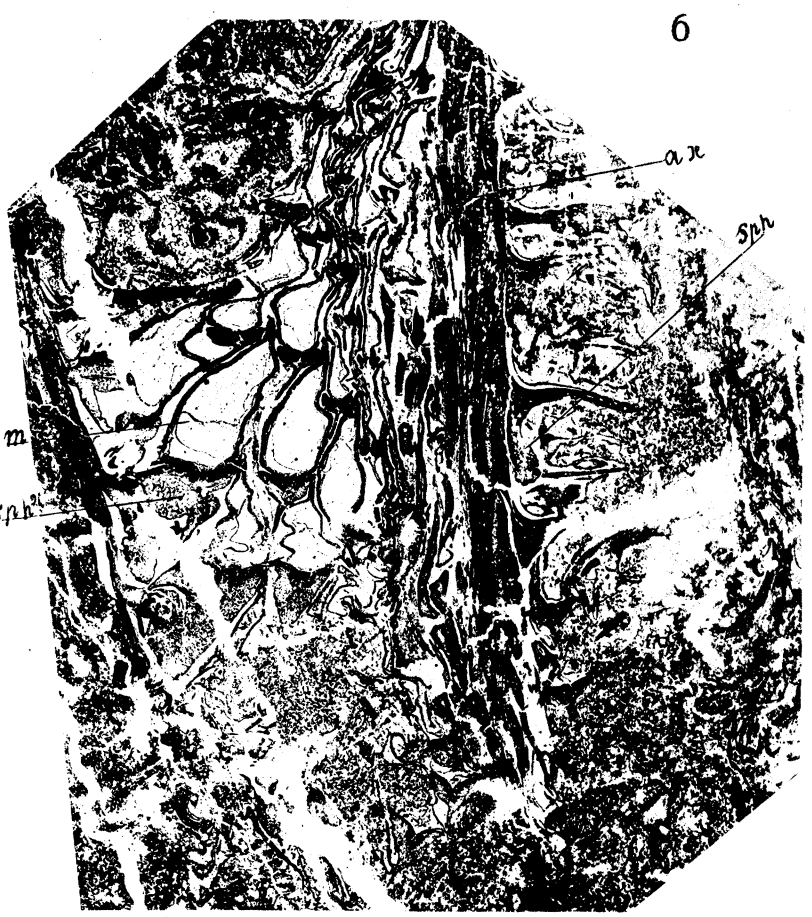

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L. A. Boodle phot.

Lepidocarpon Lomaxi.

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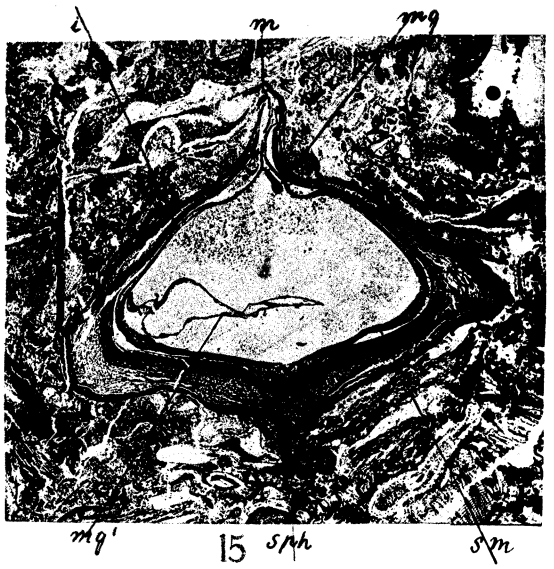

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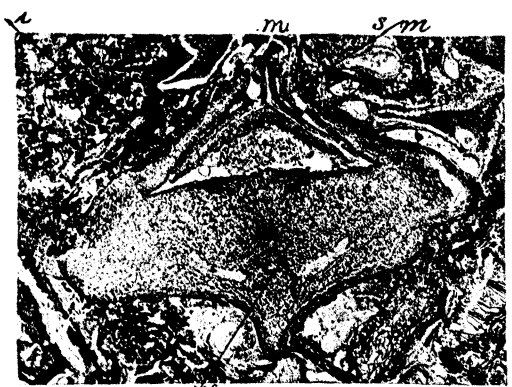

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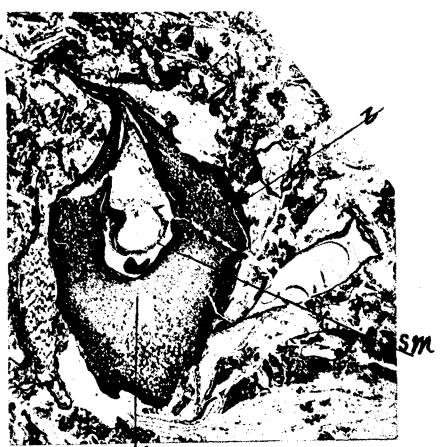

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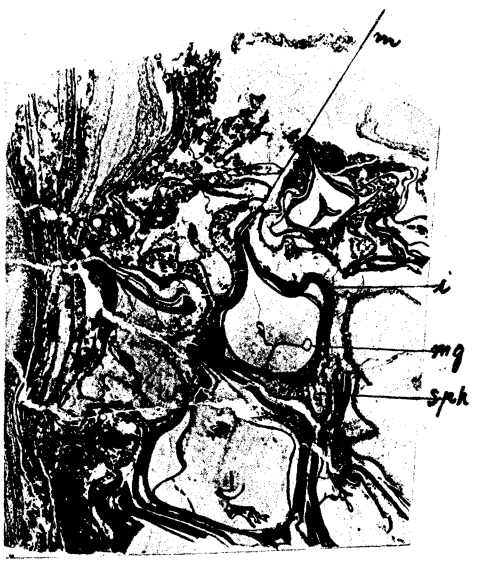

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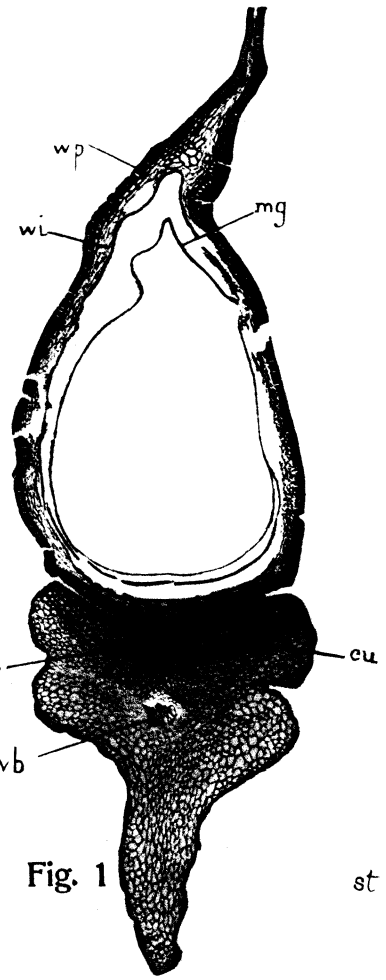

Fig. 1

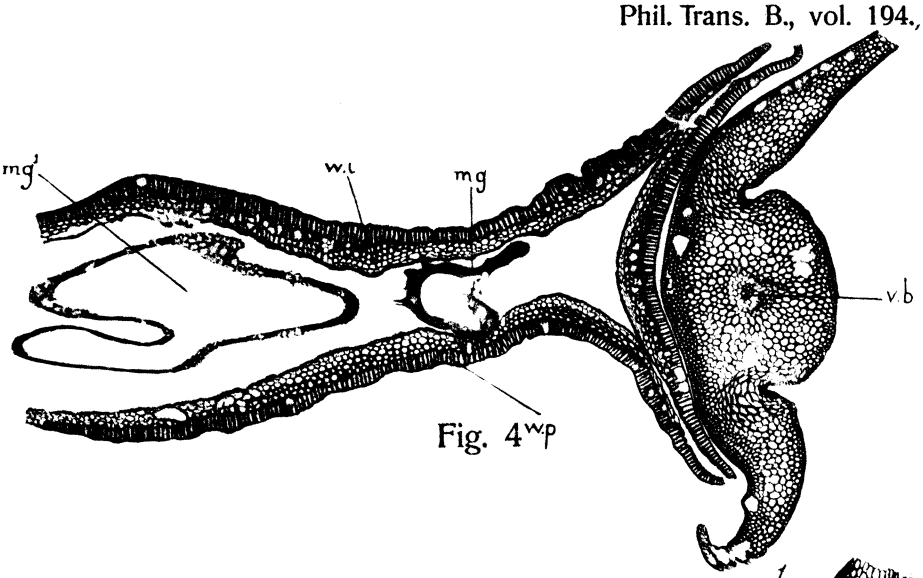

Fig. 4

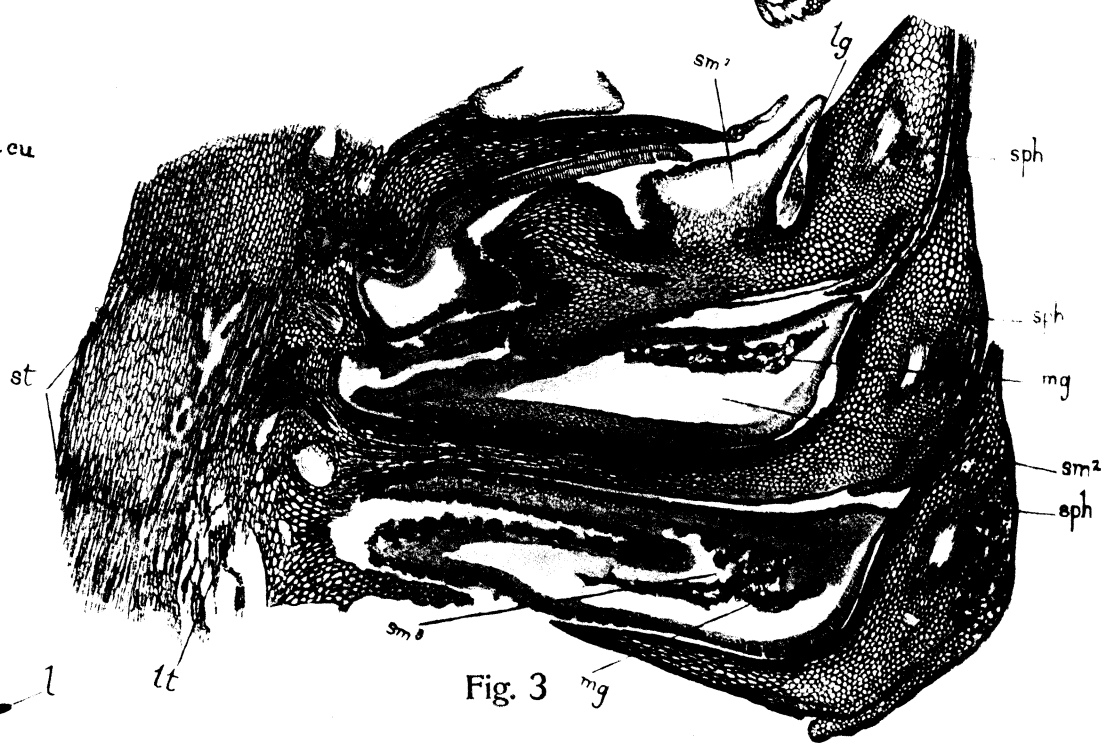

Fig. 3

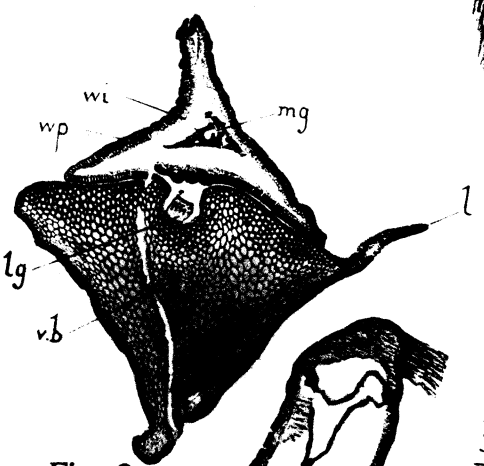

Fig. 2

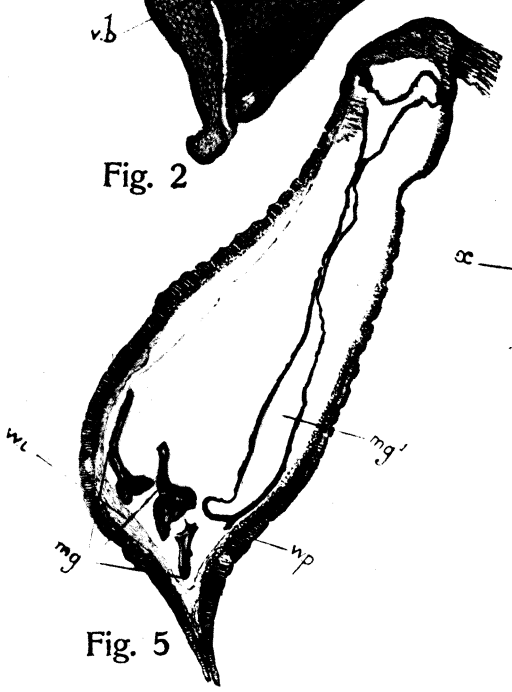

Fig. 5

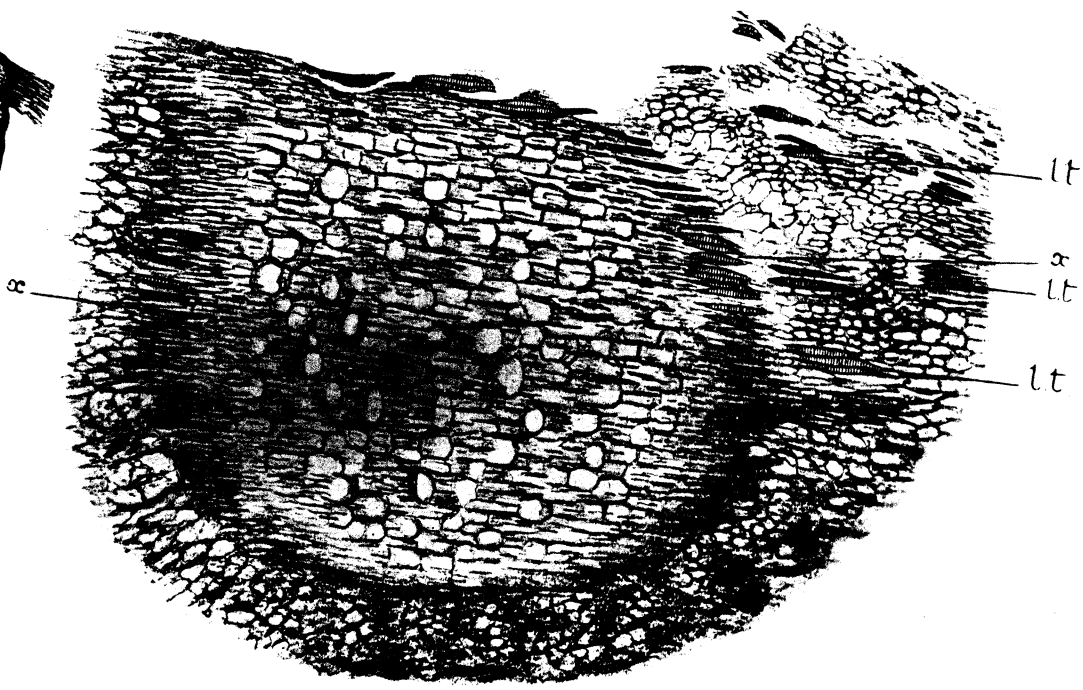

Fig. 6

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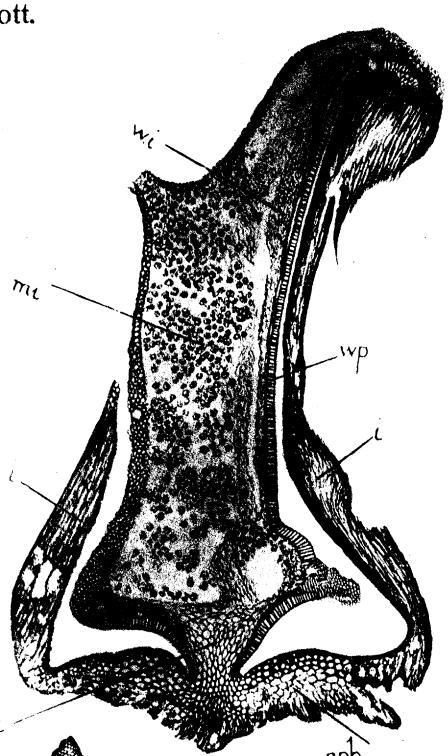

Fig. 7

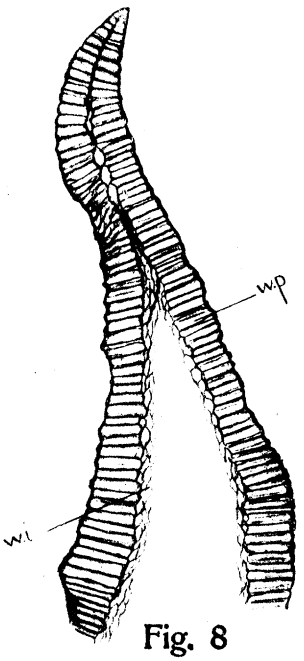

Fig. 8

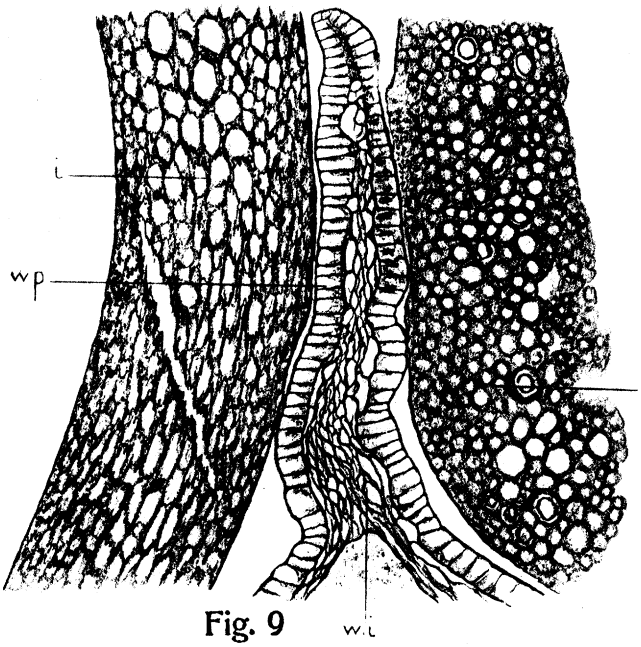

Fig. 9

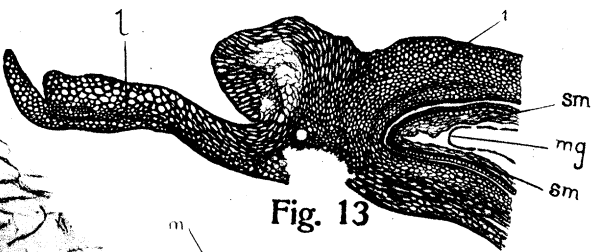

Fig. 13

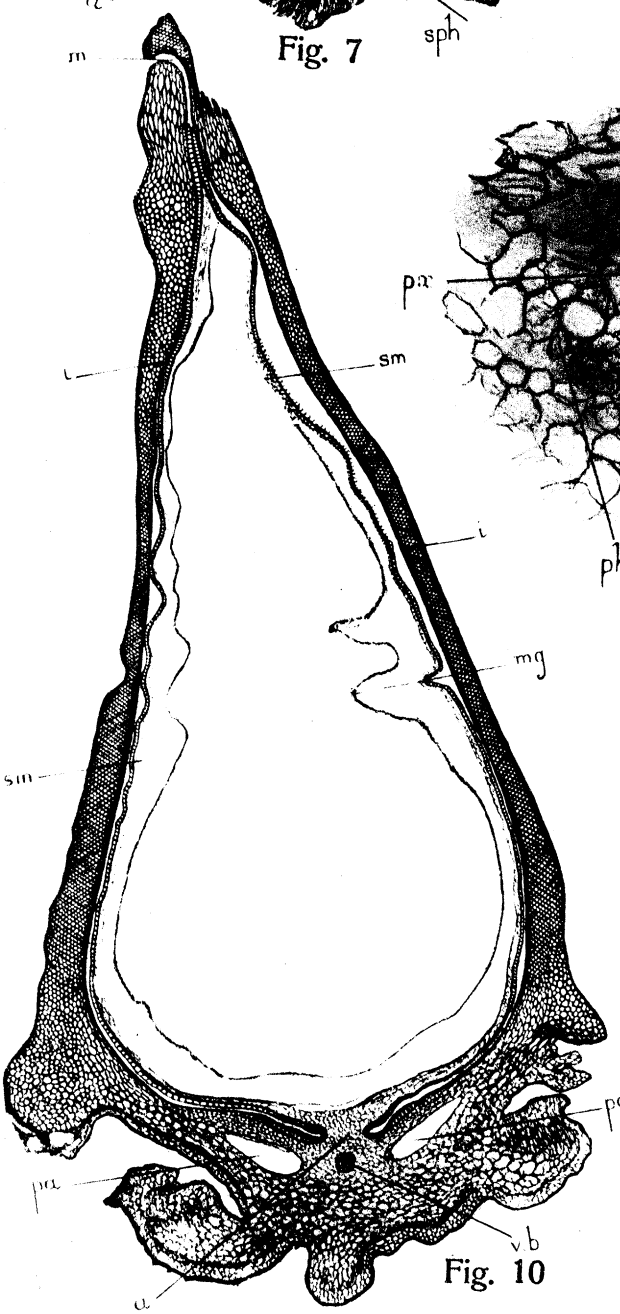

Fig. 10

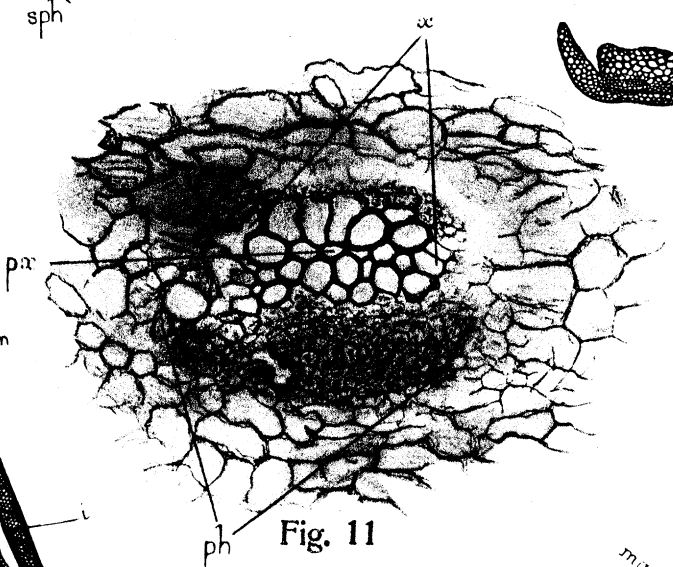

Fig. 11

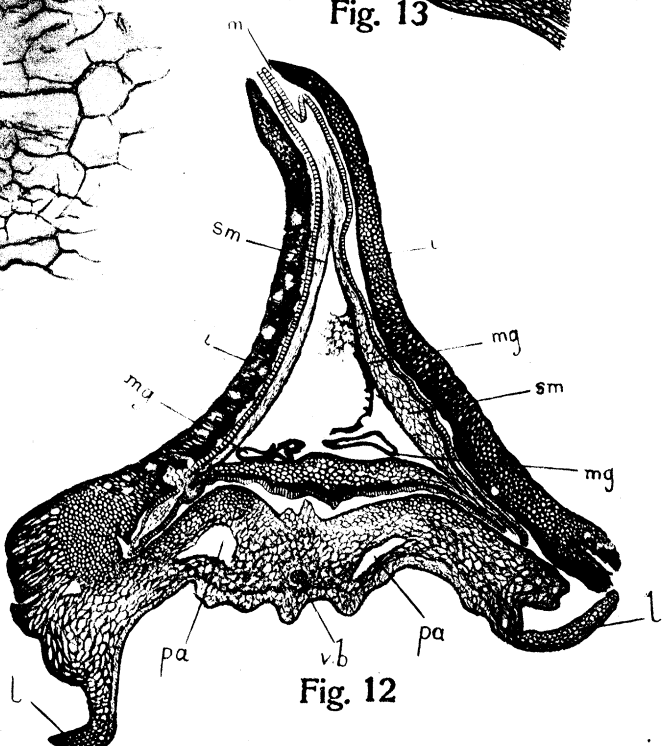

Fig. 12

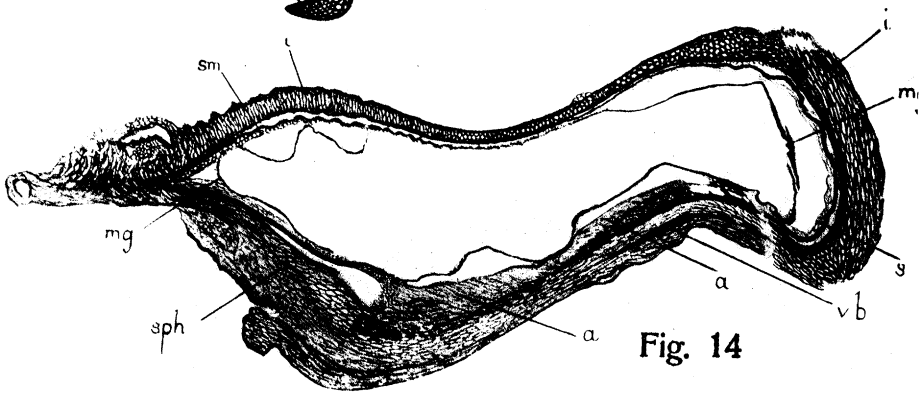

Fig. 14

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Lepidocarpon Lomaxi.

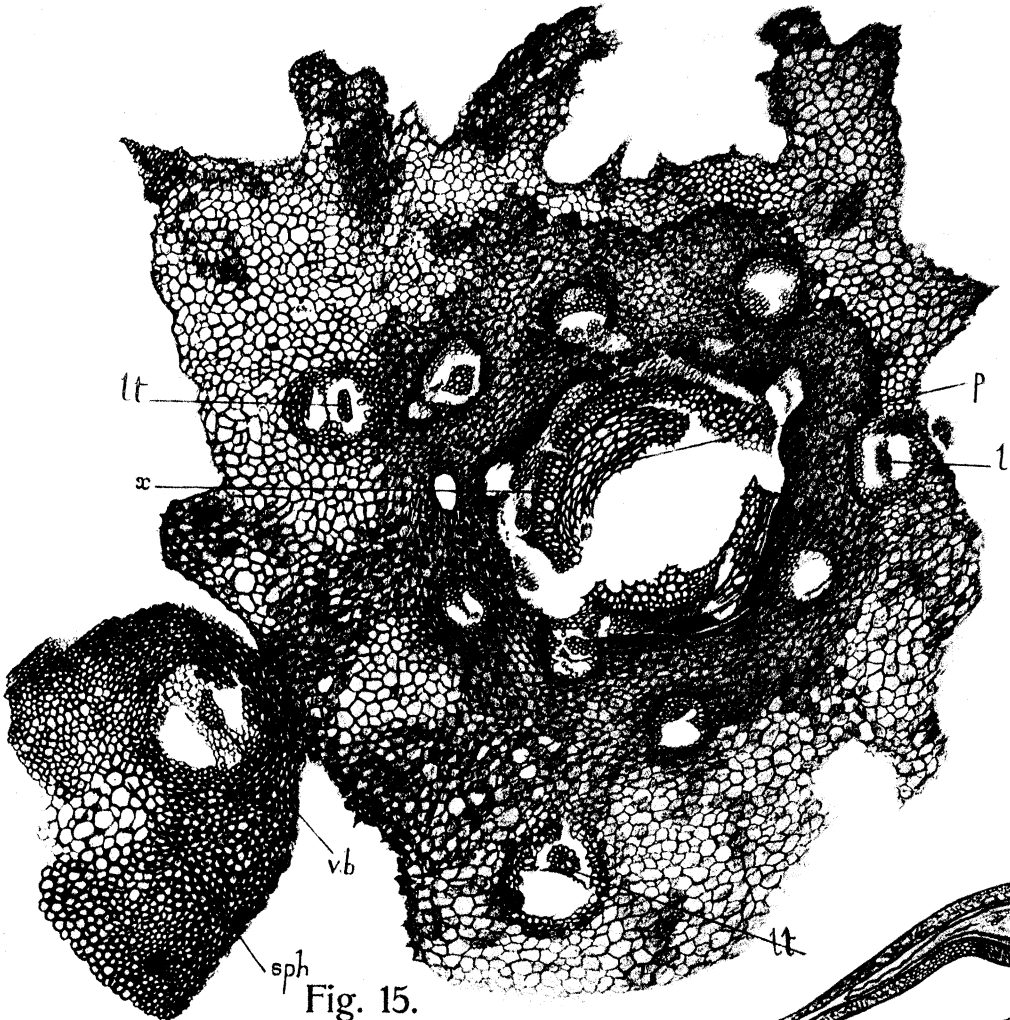


Fig. 15.

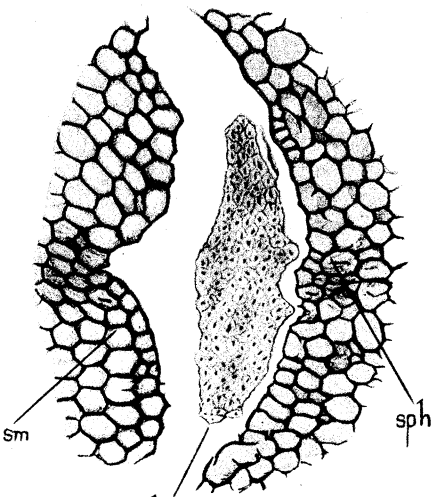


Fig. 19

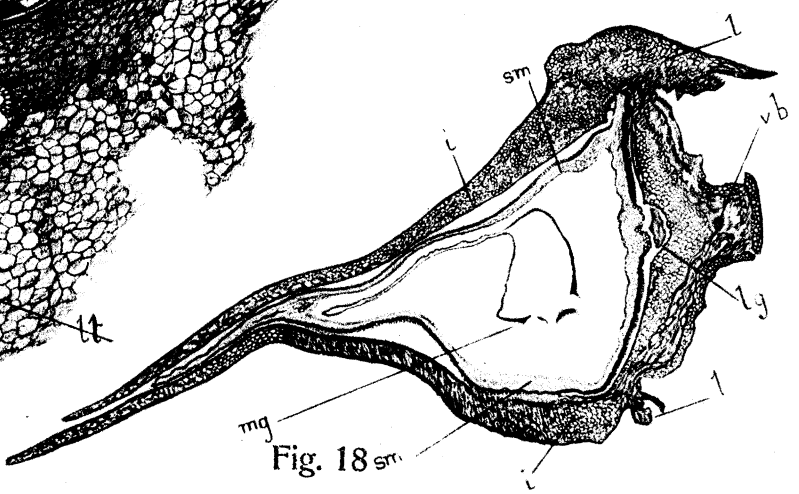


Fig. 18

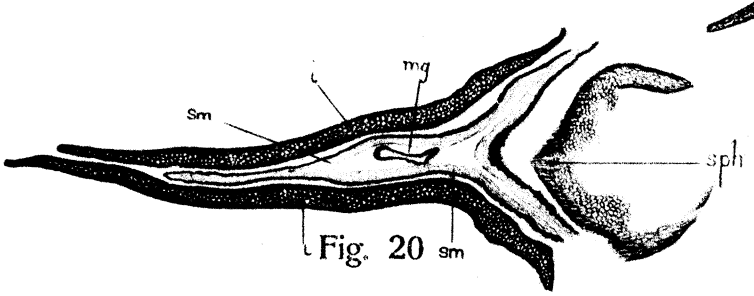


Fig. 20

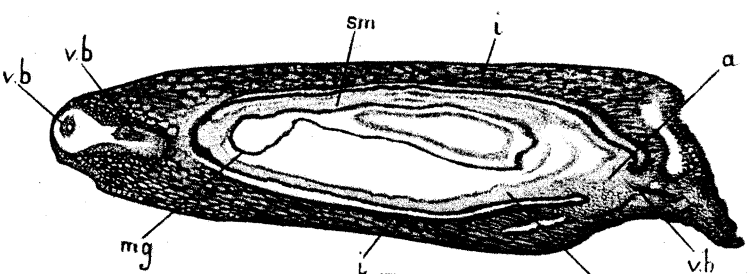


Fig. 17

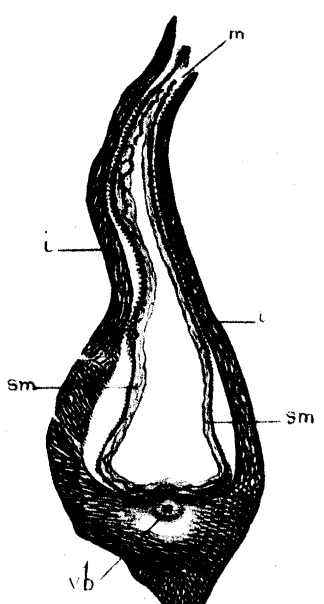


Fig. 16

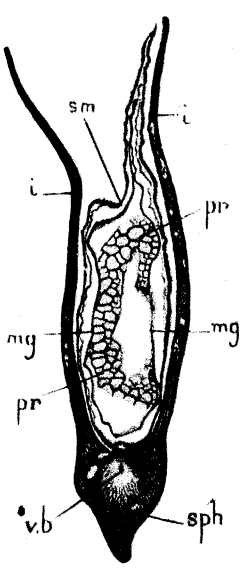


Fig. 21

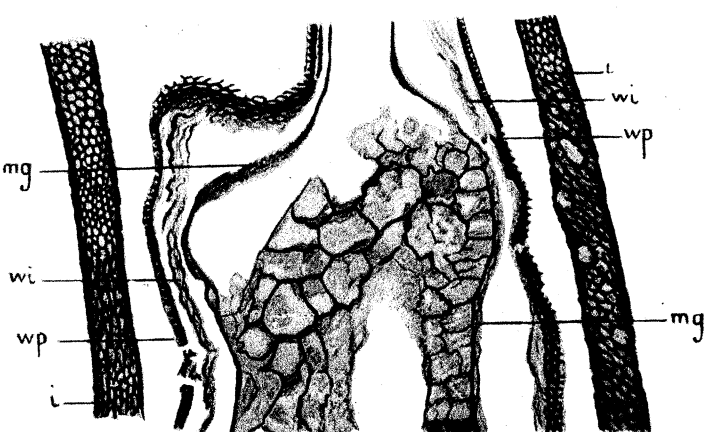


Fig. 22

G. T. Gwilliam del. Fig. 15. Lepidocarpon Lomaxi. Figs. 16—22. L. Wildianum.

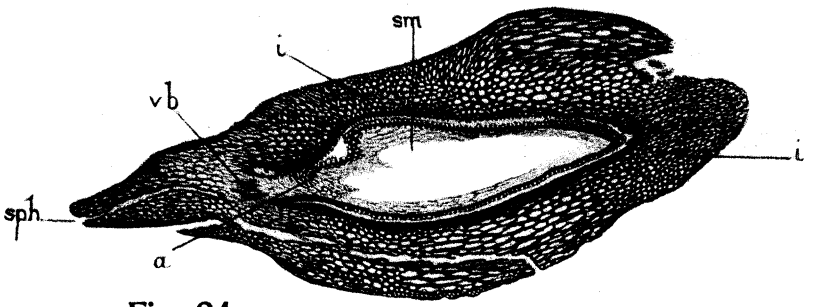


Fig. 24

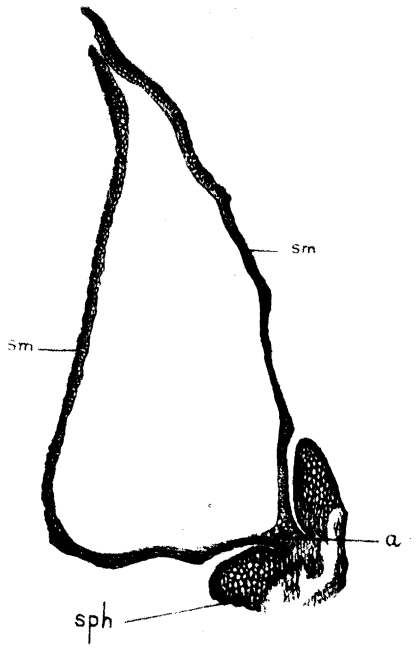


Fig. 26

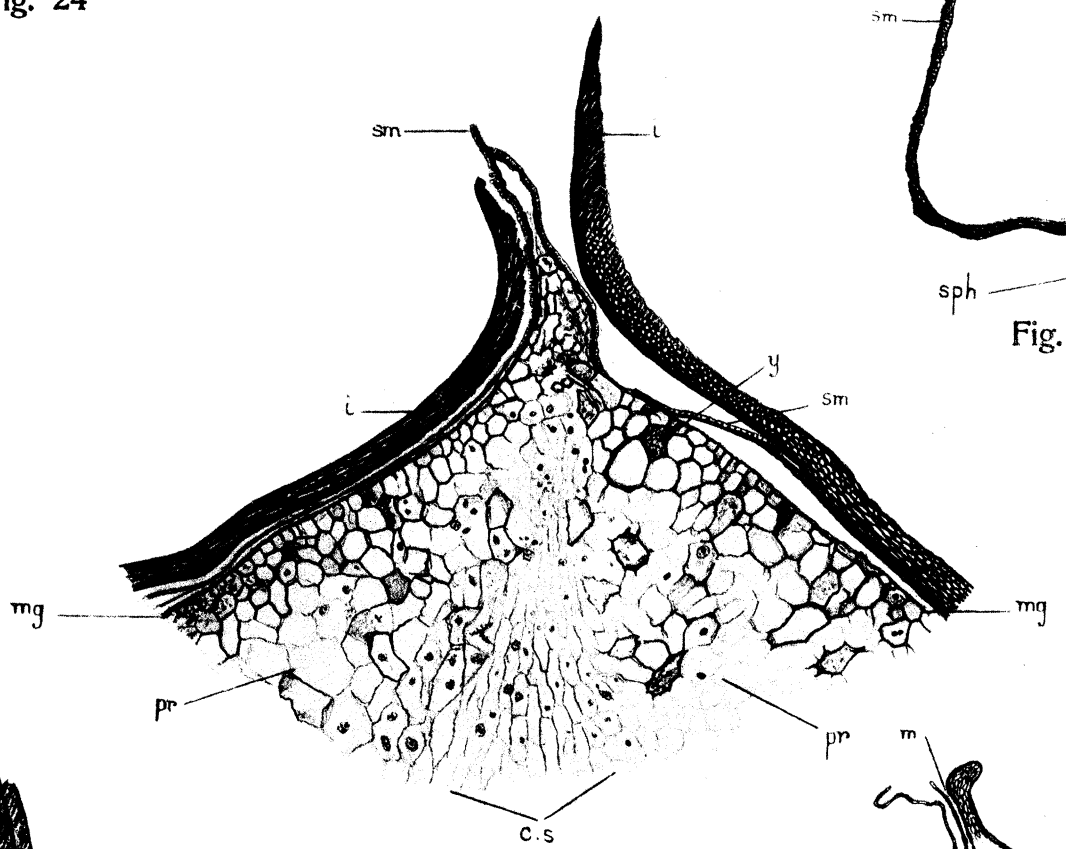


Fig. 23

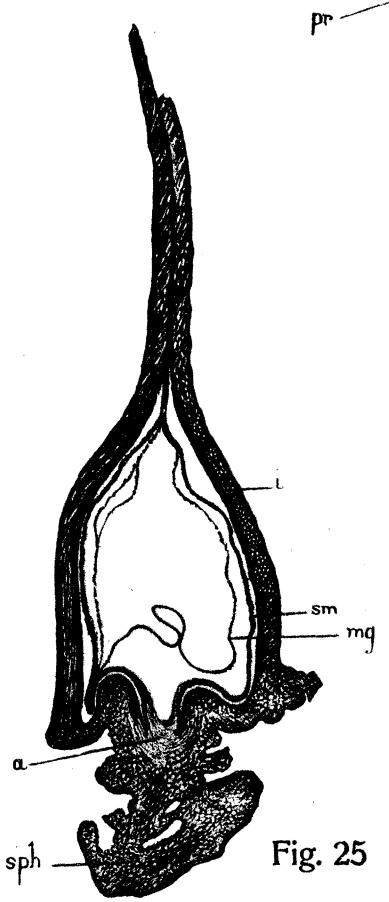


Fig. 25

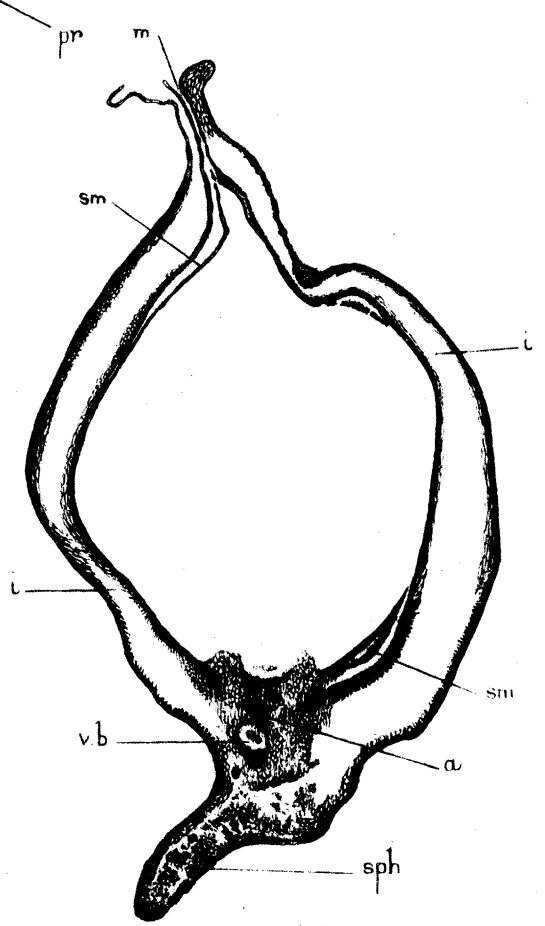
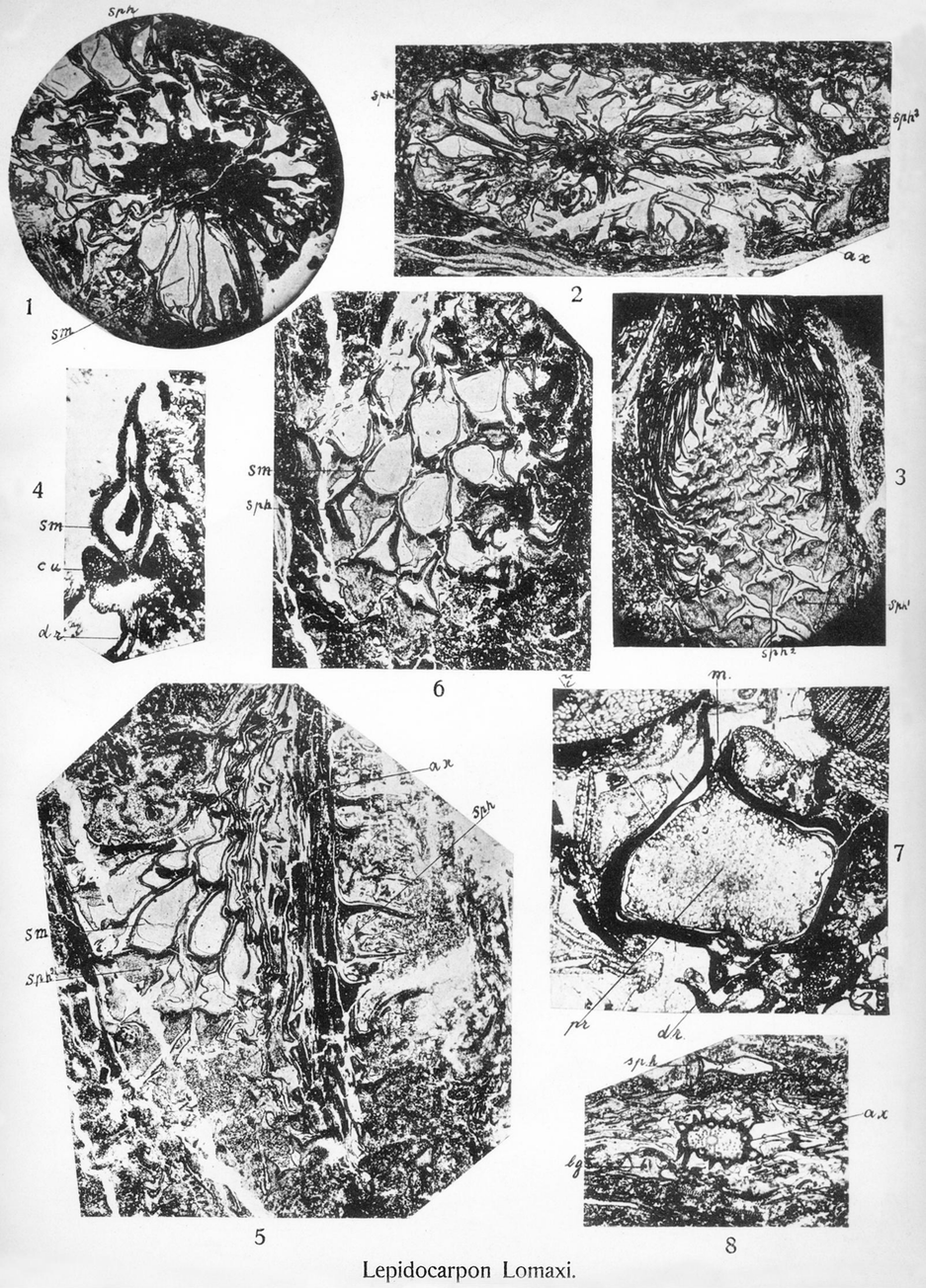


Fig. 27



Lepidocarpon Lomaxi.

Plate 38.

Phot. 1. Approximately transverse section of strobilus (Specimen III.), showing the axis, surrounded by the sporophylls with their sporangia. *sph*, sporophyll showing ligule; *sm*, sporangium containing four megaspores, shown enlarged in Plate 40, fig. 5.

× 7. S. 944.‡

Phot. 2. Transverse section of a larger strobilus (Specimen IV.), *ax*, axis; the stele is not shown; the patches of large-celled tissue are the parichnos-strands of the sporophyll-bases. *sph′*, sporophyll referred to on p. 295; it shows base of sporangium towards distal end; *sph²*, ascending lamina of a sporophyll, cut transversely.

× 4½. S. 1131.

Phot. 3. Tangential section of a strobilus (Specimen III.) showing numerous sporangia seated on their sporophylls; those near the bottom are cut towards the distal end. *sph′*, sporophyll with ligule, shown enlarged in Plate 40, fig. 2. *sph²*, sporophyll cut further in, showing attachment of sporangium. Note the overlapping laminæ towards the apex of the strobilus.

× 7. S. 947.

Phot. 4. Detached sporophyll and sporangium, in tangential section through proximal region. *sm*, sporangial wall. *cu*, lateral cushions of sporophyll-pedicel; *d.r.*, its dorsal rib. *Cf.* Plate 40, fig. 1.

× about 8. From a slide in Mr. WILD's private collection.

Phot. 5. Part of strobilus (Specimen I.) in longitudinal section. The right-hand side is approximately radial; on the left-hand side the sporophylls are bent so as to appear in nearly tangential section. *ax*, axis; the light bands of tissue seen in the lower part are parichnos-strands. *sph*, sporophyll in radial section showing its decurrent base. *sph²*, sporophyll in nearly tangential section, bearing the sporangium, *sm*, in which the contracted membrane of the megaspore is seen.

× 5. S. 608.

Phot. 6. Tangential section of the same strobilus (Specimen I.) showing a number of sporangia seated on their sporophylls. The plane of section is somewhat inclined, so that the lower sporophylls are shown in more distal section than the upper. At the sides the ascending laminæ are seen. *sm*, *sph*, sporangium and sporophyll shown, enlarged, in Plate 40, fig 1.

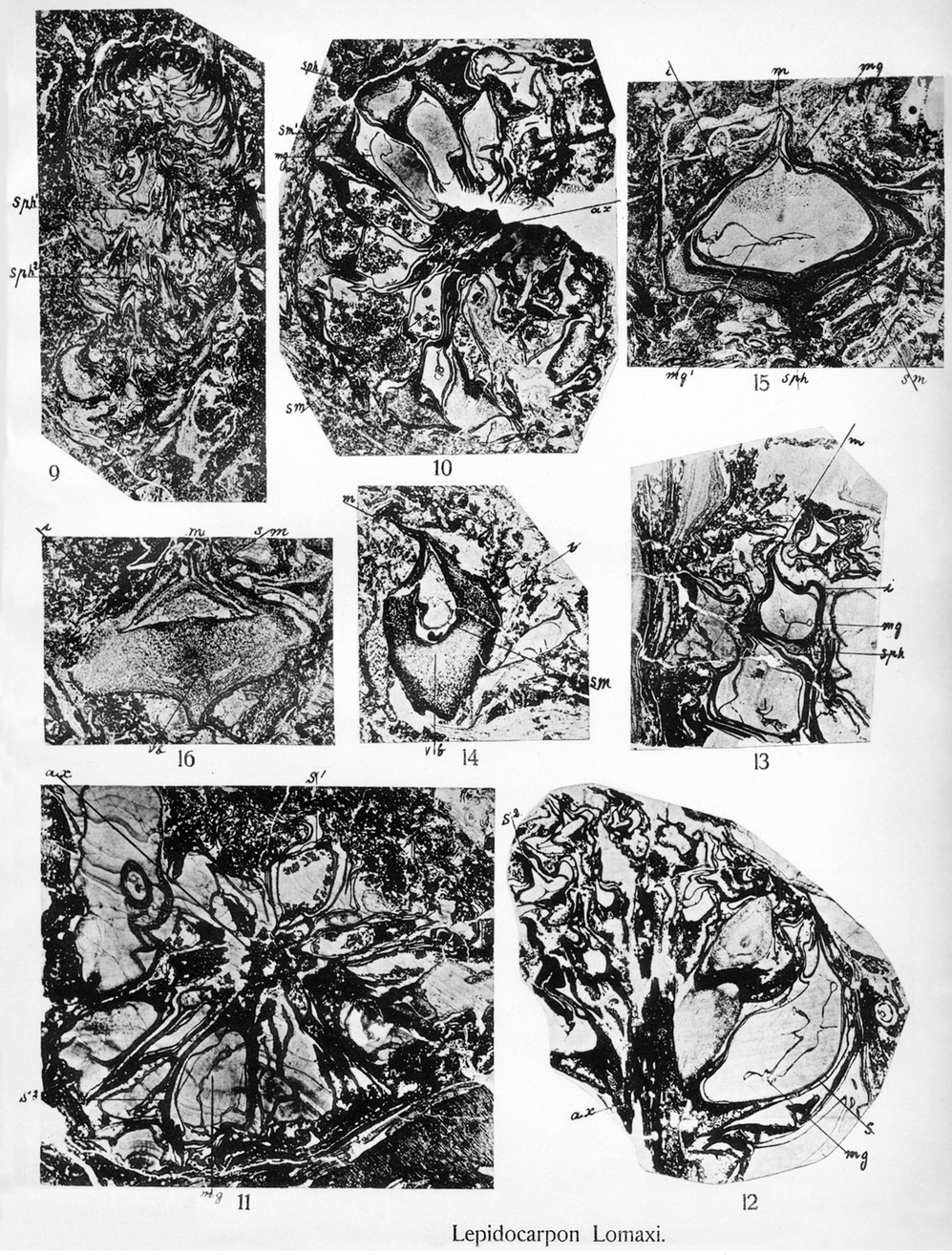
× 5. S. 607.

Phot. 7. Mature "seed," containing the prothallus, seen in tangential section. *d. r.* dorsal rib of sporophyll-pedicel. *i*, integument. *m*, micropyle, within which the pointed apical ridge of the sporangium or nucellus is seen. *pr*, prothallial tissue, which completely fills the functional megaspore or embryo-sac. For details see Plate 43, fig. 23, which represents the upper half of this specimen on a larger scale.

× 12. S. 1073.

Phot. 8. Transverse section of a microsporangiate strobilus, perhaps referable to *L. Lomaxi*. *ax*, axis of strobilus, in which the stele and leaf-trace bundles are clearly seen. Surrounding the axis are the sporophylls and crushed microsporangia. *lg*, ligule, seated in the ligular chamber of a sporophyll-lamina. *sph*, detached sporophyll and megasporangium of *L. Lomaxi*, represented in detail in Plate 40, fig. 4.

× 4½. S. 613.



Lepidocarpon Lomaxi.

Plate 39.

Phot. 9. Tangential section of the same microsporangiate strobilus, showing the sporophyll-laminæ converging over the apex. *sph'*, integumented microsporangium in oblique section; represented on a larger scale in Plate 41, fig. 7. *sph*³, another integumented microsporangium, cut still more obliquely.

× 4½. S. 617.

Phot. 10. Transverse section of the upper part of Wild's specimen, showing the megasporangia in the naked condition. *ax*, axis of strobilus. *sph*, lamina of a sporophyll. *sm'*, a sporangium; *mg*, contracted membrane of principal megaspore. *sm*², sporangium and sporophyll in oblique section, shown enlarged in Plate 43, fig. 26.

× 4½. From a section acquired from Mr. Wild's private collection.

Phot. 11. Transverse section from the lower part of the same specimen, showing the megasporangia in the integumented, seed-like condition. *ax*, axis of cone shown in detail in Plate 42, fig. 15. *s'*, a "seed" in oblique section, shown in detail in Plate 43, fig. 27. *s*², another "seed," in approximately horizontal section, attached to the axis, and showing the integument, sporangial wall, and large, contracted megaspore (*mg*) very clearly.

× about 3. Manchester Museum, Wild Collection, No. 139.

Phot. 12. Approximately radial section of the same specimen. *ax*, axis of strobilus. *s'*, large "seed" in radial section. The sporophyll, which forms the base of the "seed," is attached to the axis, and the integument is closed at the proximal end. *mg*, much-contracted membrane of the large megaspore. Towards the top the section becomes more tangential. *s*², a small "seed" in tangential aspect.

× 4½. From a section acquired from Mr. Wild's private collection.

Phot. 13. Tangential section of the same specimen, showing several "seeds." *sph*, sporophyll forming the base of a "seed"; *i*, integument, within which the sporangial wall is seen; *m*, micropyle; *mg*, large megaspore, much contracted.

× 4. From a section acquired from Mr. Wild's private collection.

Phots. 14–16, from a series of eight sections cut in parallel tangential planes from one large "seed."

Phot. 14. Section at proximal end. *v.b.* vascular bundle of sporophyll, which forms the massive base of the "seed." *i*, integument. *m*, micropyle. *sm*, wall of sporangium. The dark body below the sporangium appears to be a fragment from the proximal end of the integument.

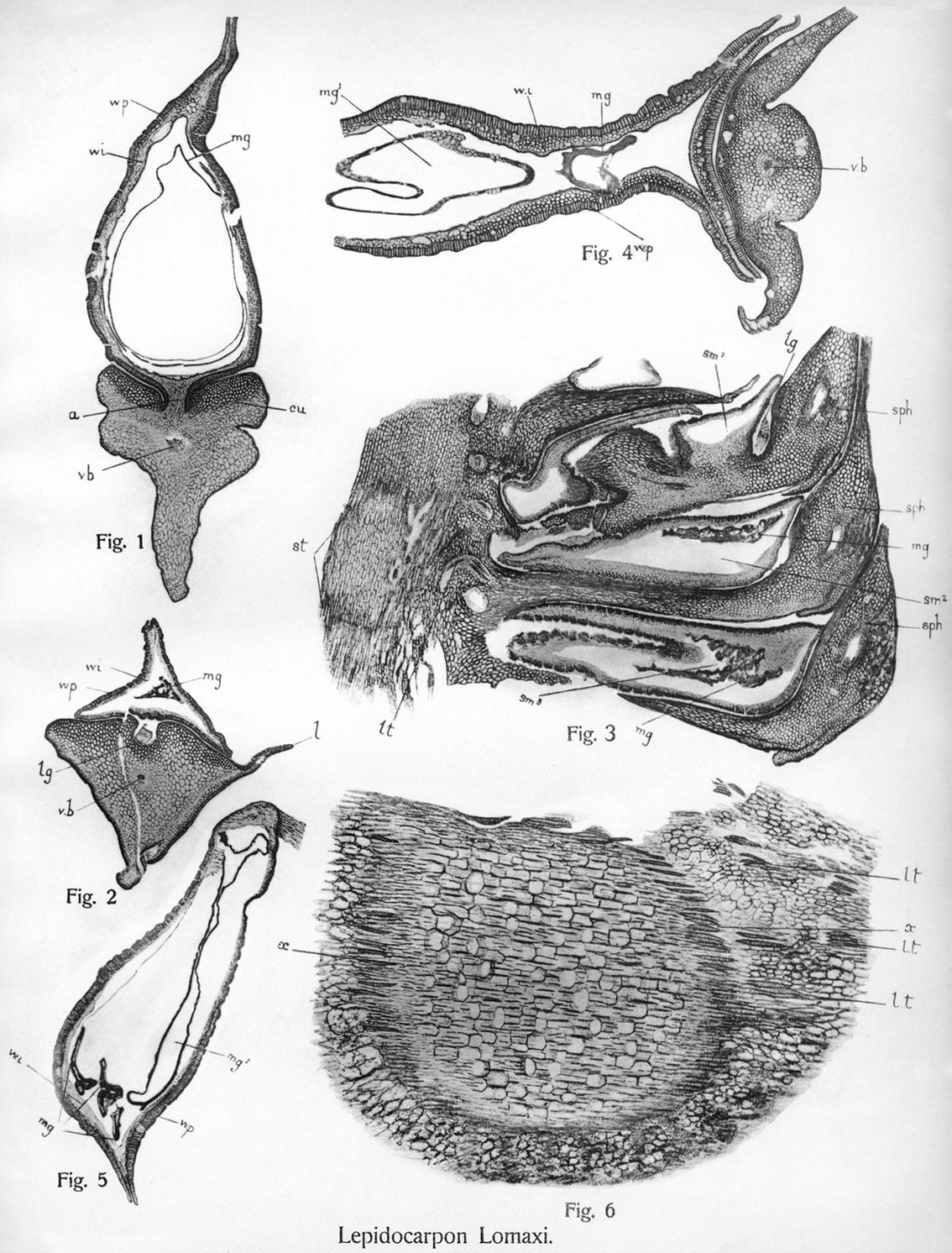
× 5. S. 866.

Phot. 15. Section from broadest part of "seed" towards distal end. *sph*, sporophyll, with dorsal rib. *i*, integument. *m*, micropyle. *sm*, sporangial wall, *mg*, an abortive megaspore; *mg'*, contracted membrane of the functional megaspore.

× 4½. S. 861.

Phot. 16. Section from distal extremity of "seed." *v.b.*, vascular bundle of the sporophyll, which is here of great thickness. *i*, integument; *m*, micropyle, apparently widely open. *sm*, sporangium (perhaps collapsed) forming a three-rayed body with almost obliterated cavity.

× 4. S. 860.



Lepidocarpon Lomaxi.

Plate 40.

Fig. 1. Sporangium and sporophyll from Specimen I. (shown in Plate 38, phot. 5, *sm*, *sph*) in tangential section, cut about midway between the proximal and distal ends of the horizontal pedicel. *cu*, lateral cushions of the sporophyll-pedicel; *v.b.*, vascular bundle; *a*, attachment of sporangium to sporophyll; *w.p.*, outer, columnar layer of sporangial wall; *w.i.*, internal layer of wall; *mg.*, membrane of functional megaspore, occupying practically the whole cavity of the sporangium.

× 19. S. 607.

Fig. 2. Sporangium and sporophyll from Specimen III. (shown in Plate 38, phot. 3, *sph'*) in tangential section near distal extremity. *l*, laminar margin of sporophyll; *v.b.*, vascular bundle; *lg*, ligule, not quite complete, seated in ligular pit below sporangium; *w.p.*, columnar layer, *w.i.*, inner layer of sporangial wall; *mg*, megaspore.

× 25. S. 947.

Fig. 3. Approximately radial section of part of a strobilus (Specimen III.). *st*, stele of axis, in oblique section; *l.t.*, leaf-trace bundle; *sph*, sporophylls, of which three are shown, each with a horizontal pedicel and ascending lamina. *sm'*, *sm²*, *sm³*, sporangia belonging to the three sporophylls; *lg*, ligule; *mg*, remains of megaspores.

× 21. S. 945.

Fig. 4. Detached sporophyll and sporangium shown in Plate 38, phot. 8, in section transverse to parent strobilus. The ascending lamina of the sporophyll is seen in transverse section. *v.b.*, vascular bundle; *w.p.*, columnar layer, *w.i.*, inner layer of sporangial wall; *mg'*, membrane of functional megaspore (contracted); *mg*, an abortive megaspore.

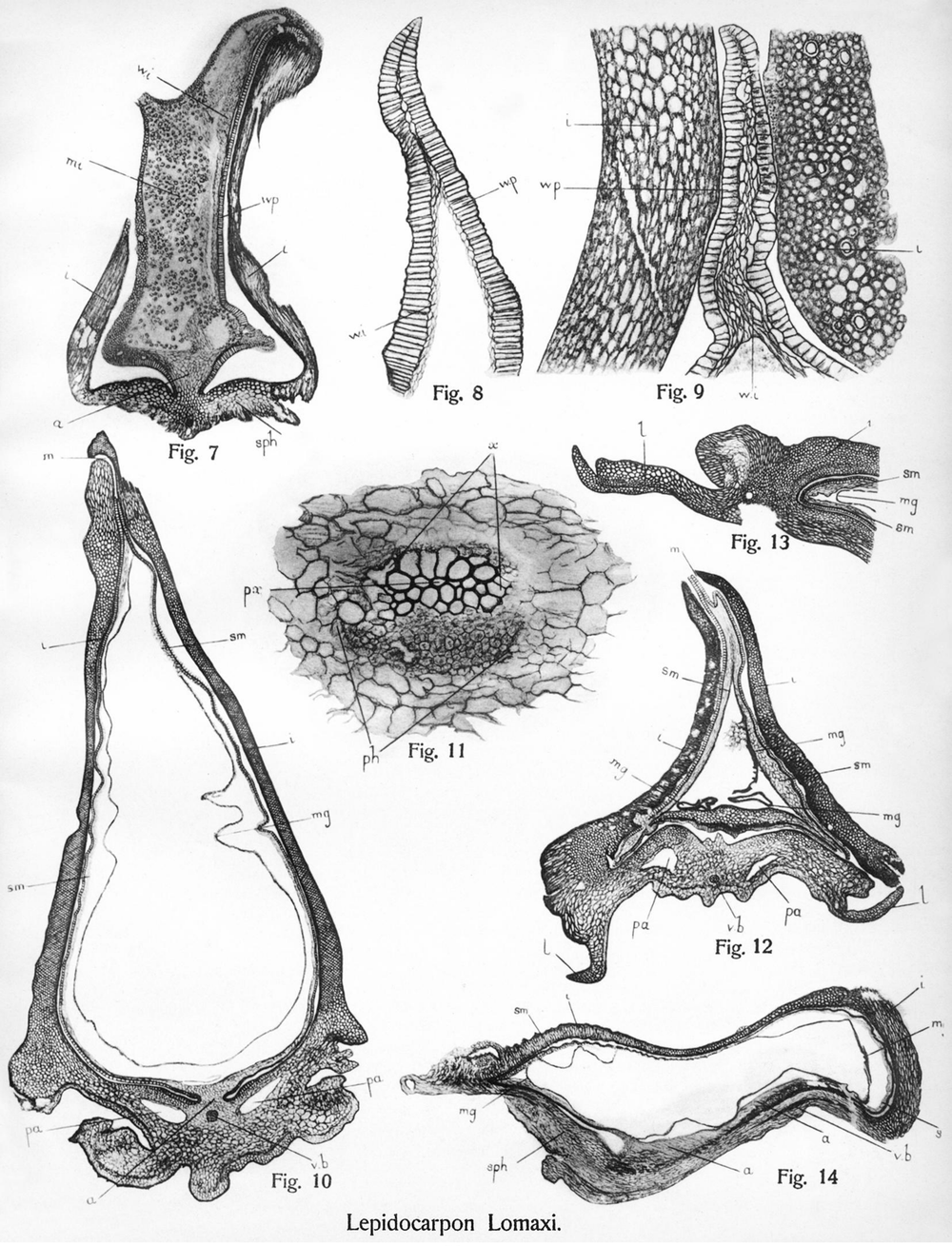
× 32. S. 613.

Fig. 5. Sporangium from Specimen III. (shown in Plate 38, phot. 1, *sm*), in which all four megaspores are seen. *w.p.*, columnar layer, *w.i.*, inner layer of sporangial wall; *mg'*, contracted membrane of the functional megaspore; *mg*, the three abortive megaspores.

× 22. S. 944.

Fig. 6. Central part of axis of strobilus (Specimen III.) in oblique section, showing stele. *x*, narrow ring of xylem, consisting of spiral and scalariform tracheides; *l.t.*, leaf-trace bundles.

× 67. S. 943.



Lepidocarpon Lomaxi.

Plate 41.

Fig. 7. Microsporangium and sporophyll from supposed male strobilus (shown in Plate 39, phot. 9, *sph'*), in oblique section between the tangential and transverse planes. *sph*, sporophyll; *a*, attachment of sporangium to sporophyll; *i*, integument, springing from the sporophyll, and partly inclosing the sporangium; *w.p.*, *w.i.*, columnar and inner layers of sporangial wall; *mi*, the microspores.
× 31. S. 617.

Fig. 8. Apex of sporangium in non-integumented condition, from Specimen III., seen in tangential section. *w.p.*, columnar, *w.i.*, inner layer of sporangial wall.
× 150. S. 947.

Fig. 9. Apex of sporangium in integumented condition, to compare with fig. 8. The section is a tangential one, passing through the micropyle of the large "seed" shown in Plate 39, phots. 14–16. *i*, integument enclosing the sporangium; *w.p.*, columnar, *w.i.*, inner layer of sporangial wall.
× about 100. S. 865.

Fig. 10. Detached "seed" in approximately tangential section. The sporophyll, which forms the base of the "seed," is much lobed at the sides. *v.b.*, vascular bundle (*cf.* fig. 11); *pa*, lateral gaps, perhaps representing the parichnos; *i*, integument (the shading is partly diagrammatic); *m*, micropyle; *sm*, wall of sporangium or nucellus, showing the columnar layer; *a*, attachment of sporangium to sporophyll; *mg*, membrane of the functional megaspore, filling the sporangial cavity.
× 19. S. 621.

Fig. 11. Vascular bundle from fig. 10 more highly magnified, seen in transverse section. *x*, xylem; *px*, small elements, probably the protoxylem, in a central position; *ph*, phloem.
× 300. S. 621.

Fig. 12. Detached "seed" in tangential section near the distal end. *l*, laminar margin of sporophyll; *v.b.*, vascular bundle; *pa*, parichnos(?)-gaps; *i*, integument; *m*, micropyle; *sm*, wall of sporangium, showing columnar layer very clearly; in this region the sporangium is free from the sporophyll; *mg*, megaspores; two are abortive; the third is probably a fragment of the functional one.
× 19. S. 610.

Fig. 13. Part of another "seed" in a similar plane of section to fig. 12. *l*, laminar margin of sporophyll, projecting far beyond the base of the integument *i*; *sm*, sporangial wall; *mg*, part of the membrane of functional megaspore.
× about 30. S. 1119.

Fig. 14. Detached "seed" in longitudinal section, approximately radial to parent strobilus. *sph*, sporophyll, forming base and distal extremity of "seed" (*cf.* Plate 40, fig. 3, for the corresponding view in the non-integumented condition). *v.b.*, vascular bundle of sporophyll-pedicel; *a*—*a*, attachment of sporangium to sporophyll; *i*, integument, closed at proximal end (to the right), and abutting on the sporophyll-lamina at the distal end. (The integument appears also above the sporangium because the plane of section misses the micropylar crevice.) *sm*, wall of sporangium; *mg*, membrane of functional megaspore.
× 15. S. 929.

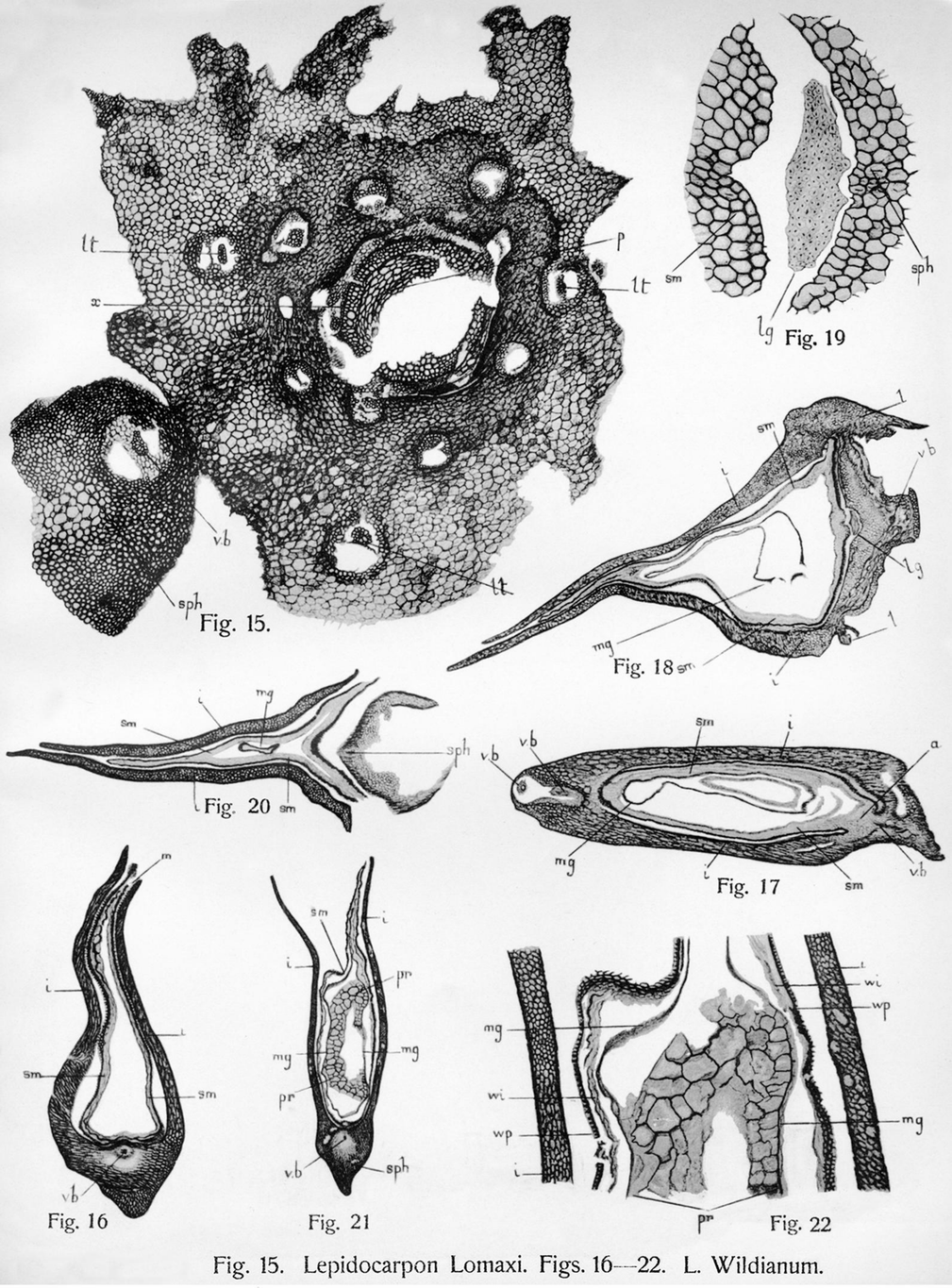


Fig. 15. Lepidocarpon Lomaxi. Figs. 16—22. L. Wildianum.

Plate 42.

Fig. 15. Axis of WILD'S cone in transverse section (represented as a whole in Plate 39, phot. 11). *p*, pith, most of which has perished; *x*, parts of xylem-ring, showing the small protoxylem-elements towards the periphery; *l.t.*, leaf-trace bundles passing through the cortex; *sph*, base of a sporophyll; *v.b.*, its vascular bundle.

× about 30. Manchester Museum, WILD Collection, No. 139.

(Figs. 16–22, *Lepidocarpon Wildianum*.)

Fig. 16. Small "seed" in tangential section, near proximal end. *v.b.*, vascular bundle of sporophyll; *i*, integument; *m*, micropyle; *sm*, wall of sporangium.

× 19. S. 1105.

Fig. 17. "Seed" in horizontal section, approximately transverse with reference to parent strobilus. This section is the lowest of a series of four, of which three are figured (figs. 17–20). *v.b.*, vascular bundle of sporophyll-pedicel, which appears at three places—twice at the proximal end (to the left) and once towards the distal end; *i*, integument; *a*, attachment of sporangium to sporophyll; *sm*, wall of sporangium; *mg*, membrane of functional megaspore.

× about 12. S. 1104.

Fig. 18. Third section from below, same series. *l*, ascending lamina of sporophyll, seen in transverse section; *v.b.*, vascular bundle; *i*, integument; *lg*, ligule, seated between lamina and sporangium (see fig. 19); *sm*, wall of sporangium; *mg*, contracted membrane of functional megaspore.

× 12. S. 1106.

Fig. 19. Ligule from fig. 18, more highly magnified. *sph*, tissue of sporophyll; *sm*, wall of sporangium; *lg*, ligule, cut transversely.

× about 100. S. 1106.

Fig. 20. Uppermost section of same series. *sph*, lamina of sporophyll, incomplete and detached from integument, *i*; *sm*, sporangium, here assuming Y-shape (*cf.* Plate 40, fig. 4, for non-integumented condition); *mg*, abortive megaspore.

× 12. S. 1107.

Fig. 21. "Seed" in tangential section, near proximal end, to show prothallus. *sph*, sporophyll-pedicel; *v.b.*, vascular bundle; *i*, integument; *sm*, wall of sporangium or nucellus; *mg*, membrane of functional megaspore or embryo-sac, containing the large-celled prothallus, *pr*.

× 15. S. 1070.

Fig. 22. Part of the same section, more highly magnified, showing the upper part of the prothallus and surrounding tissues. *i*, integument; *w.p.*, columnar, *w.i.*, inner layer of sporangial wall; *mg*, membrane of megaspore; *pr*, tissue of prothallus.

× 70. S. 1070.

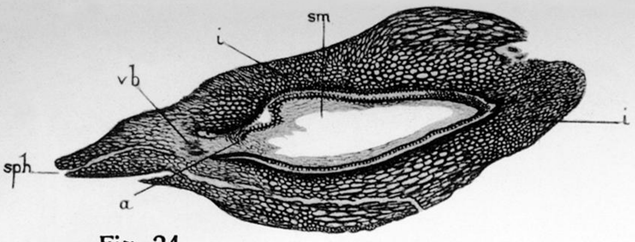


Fig. 24

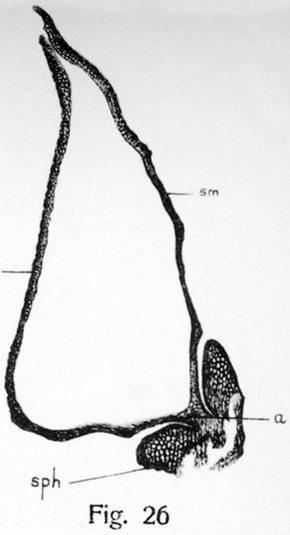


Fig. 26

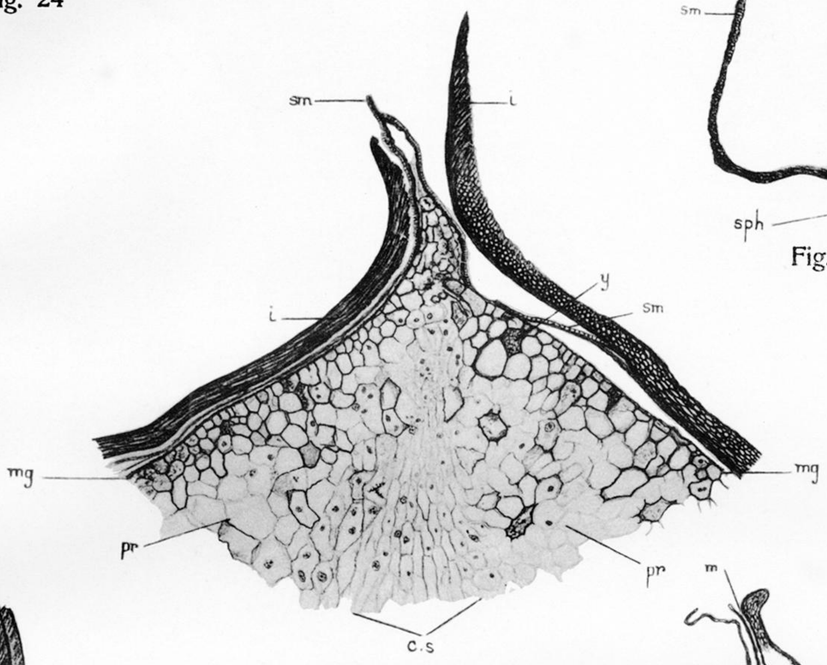


Fig. 23

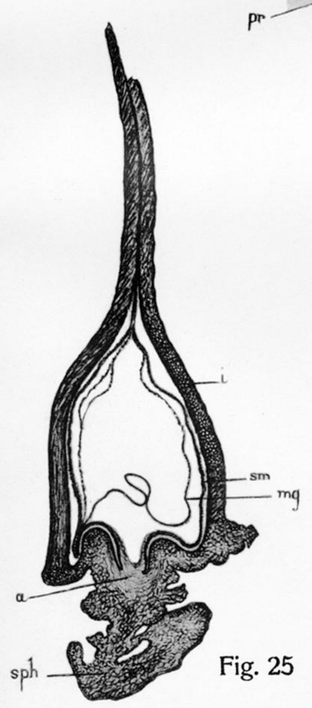


Fig. 25

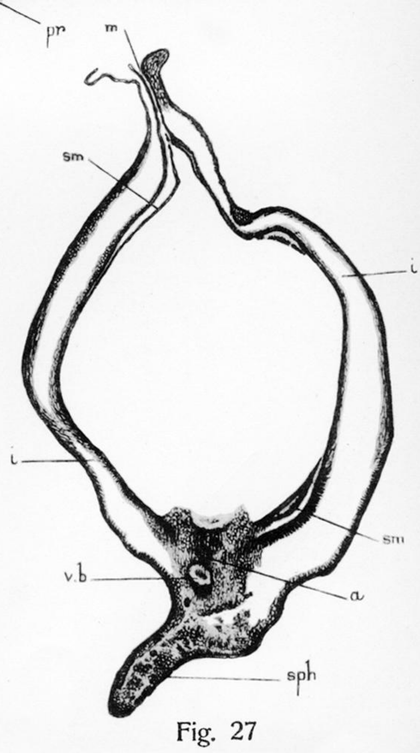


Fig. 27

Lepidocarpon Lomaxi.

Plate 43.

Fig. 23. Upper half of the "seed" with prothallus (shown in Plate 38, phot. 7) more highly magnified. *i*, integument; *sm*, wall of sporangium, or nucellus, much reduced in thickness; *mg*, membrane of functional megaspore; *pr*, ordinary tissue of prothallus; *y*, *possibly* the central cell of an archegonium; *c.s.*, central strand of elongated, thin-walled cells, containing nucleus-like bodies.

× 30. S. 1073.

Fig. 24. Detached "seed," in oblique section, cut at an angle with the transverse and tangential planes, showing the integument closed at the proximal end. *sph*, sporophyll; *v.b.*, vascular bundle, obliquely cut; *a*, attachment of sporangium; *i*, integument; *sm*, wall of sporangium.

× 20. S. 1117.

Fig. 25. Another "seed"; the plane of section is similar to that of fig. 24, but passes through the distal region of the sporophyll, *sph*, which is much lobed and preserved entire. *i*, integument (the plane of section passes obliquely through the micropyle); *a*, attachment of sporangium; *sm*, sporangial wall; *mg*, membrane of functional megaspore.

× 15. S. 1123.

Fig. 26. Sporophyll and sporangium (sm^2 in Plate 39, phot. 10) from upper part of WILD's cone, to show non-integumented condition. *sph*, pedicel of sporophyll showing cushions; *a*, attachment of sporangium; *sm*, sporangial wall.

× 19. From Mr. WILD's private collection.

Fig. 27. "Seed" (*s'* in Phot. 11) from lower part of WILD's cone, to show integumented condition, agreeing with WILLIAMSON's "*Cardiocarpon anomalum.*" *sph*, sporophyll with dorsal rib; *v.b.*, vascular bundle; *i*, integument; *m*, micropyle; *a*, attachment of sporangium; *sm*, sporangial wall.

× 12. Manchester Museum, WILD Collection, No. 139.