Mazocarpon or the Structural Sigillariostrobus.

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With Plates XVII and XVIII and four Figures in the Text.

CONTENTS.

PART I. DESCRIPTION OF MAZOCARPON.

SECTION I. *Introduction.*

SPECIMENS of the megasporangia of this new type have been gradually accumulating for a long time. The large megaspores, showing a considerable range of sectional form and for the most part with a portion of their sporange-wall adhering to their base, are relatively frequent, especially in Shore nodules. Specimens are also in hand from those of Halifax, Stalybridge, Dulesgate, Hough Hill, and Bacup. Two broken but well-characterized sporangia of another species[1] have been obtained from a block of the calciferous sandstone material from Pettycur, Scotland.

A transverse section of a cone from an unrecorded locality, and probably specifically distinct, was most kindly contributed by Prof. Weiss from the

[1] Benson: N. Ph. vii, 1908, p. 143, Figs. 25 and 26.

Manchester Collections. I also wish to gratefully acknowledge his loan of an excellent preparation from a Shore ball, from which Fig. 1 is prepared.

In the spring of 1913, having exhausted my own supply of Shore balls in the search for more information of this structure, Prof. Oliver kindly allowed me to cut some of his supply. Almost immediately, by exceptional good fortune, a radial section of the megasporange (Fig. 5) was secured.

This enabled me to correlate a number of other sections. Shortly after, from three successive balls, were added not only a series of five sections tangential to a megasporange but a similar series of four through a well-preserved, large microsporange. Microsporangia had not previously been observed in the Upper Carboniferous rocks.

Other objects, bearing on this research, found at the same time, will be referred to later.[1]

For the present it is sufficient to add that Dr. Scott, with whom I had hoped to co-operate in the description of the new form, most generously handed over to me his specimens of *Mazocarpon*, including a fine series of three longitudinal sections through a mature megasporangial cone from Hough Hill, and suggested that I should give a short account of the work at the Australian Meeting of the British Association in 1914.[2] For many other tokens of kind interest in the research I owe Dr. Scott grateful acknowledgement.

Section II. *The Megasporange.*

The megasporange resembles in many respects that of *Lepidostrobus*. It is a bulky, radially extended body attached to a bract along its whole length. The wall is composed of a palisade and subjacent parenchyma. The sporogenous tissue is found lying over a well-developed subarchesporial pad.

The new characters are (1) the large amount of persistent, sterile tissue and its differentiation into various types, e.g. transfusion tissue, tapetal tissue, &c.

(2) The prolongation of the wall into a shovel-shaped distal lamella which fits into the concave upper surface of the bract to which the sporange is attached.

(3) The form and distribution of the spores and their limited number.

It was owing to the persistent, sterile tissue, which by enveloping the dark-coloured spores gives the sporange much the appearance of a sausage-roll, that the name *Mazocarpon* (μᾶζα = a loaf) was selected.

A mass of transfusion tissue consisting of scalariform tracheides is clearly to be seen at the base of the pad in the Manchester slide 472 A

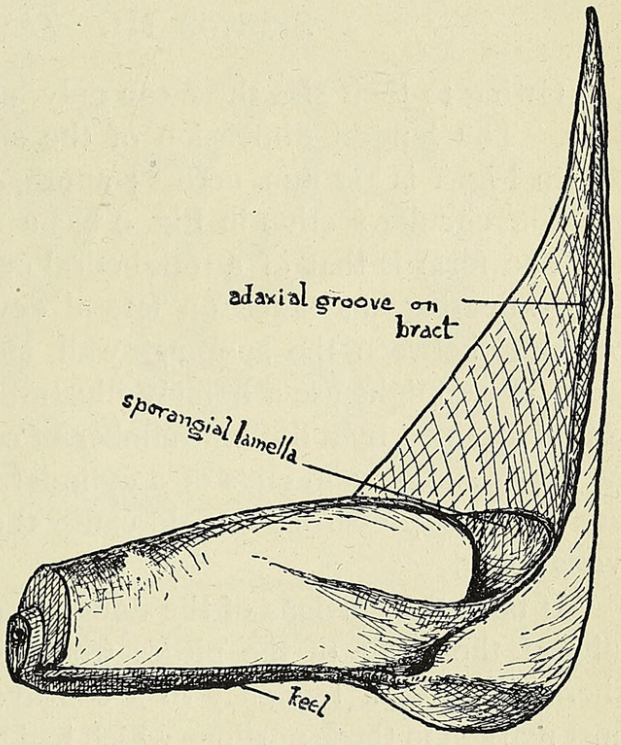
[1] See Part II of this paper.

[2] British Association Report, 1914, p. 584.

(Fig. 15), and strands of apparently lignified cells would appear to be present in others also, e.g. H. Cn. 519, 4 and 5, but are there cut transversely.

In immature sporangia, e.g. those in the Manchester slide (see Fig. 15), the germinating spores lie in tissue which markedly differs from the pad and certainly suggests barren sporogenous tissue. On this abut the tubular tapetal cells which grow centroscopically into the sporogenous region which they surround. A few of these can be seen in several figures (Fig. 16), but they reach an extraordinary development in an abortive sporange (Fig. 7) and in the microsporange (Figs. 13 and 13 *a*). In the latter the repeated serial divisions of the tapetal cells give a most unusual appearance to the sporange.

The mature sporange shown in Fig. 18 measures slightly over 5 mm. in length, and 2·6 mm. in height. These are approximately the dimensions, as we shall see later, of Dr. Kidston's incrustation specimen of the sporange of *Sigillariostrobus ciliatus*,[1] with which the new petrifactions agree also as respects the size, surface, and probably the form, of the spores. The sporangia occur occasionally in an almost intact condition free from the cone-axis—such are those of Figs. 1, 6, 13, 17, and 18. The abortive specimens, also, which are shown in Figs. 5 and 7, were lying free from any cone-axis. Thus we may regard the sporophyll as liable to fall off even in an immature condition of the gametophyte or 'spore' (Fig. 15). Not only did the sporophyte as a whole fall, but the sporange seems to have broken up very easily into pieces, each consisting of a 'spore' and a piece of the thick sporange-wall attached to its base (Fig. 9).



TEXT-FIG. 1. Explanation in the text. A diagram from a model of the megasporange of *Mazocarpon*.

The characteristic formation of a distal lamella, into which the convex base of the bract above must have fitted, was probably a contributory factor, as will be shown later, to the rupture of the sporange. Distally the lamella springs from the base of the sporange, but from a higher level at the sides (Text-fig. 1). In the third, or middle, member of a series of five

[1] See Kidston, loc. cit., Plate II, Figs. 3 and 3 *a* (or consult Scott's Studies in Fossil Botany, Fig. 96 B, p. 234).

sections tangential to the sporange (H. Cn. 518, 4–8) the lamella is very nearly level with the upper surface of the sporange.

The lamella is shown well in Figs. 6, 5, and 18, and is indicated in others.

Along the dorsal median line of the sporange a ridge is often seen which is doubtless due to the unusual degree of vegetative development the sporange has attained, which has made it capable of accommodating itself to the available space.

In no Upper Carboniferous specimen has the number of spores per sporange exceeded eight.

They will now be described.

Section III. *The 'Megaspore'.*

Owing to their size these can only be examined in section in petrifactions. The longest dimension of the spore shown in Fig. 3 is 1·94 mm. One in Fig. 1 is 1·7 mm. across; another in Fig. 1 is 1·52 mm. across.

The circular section in Fig. 9 has a 1·25 mm. diameter.

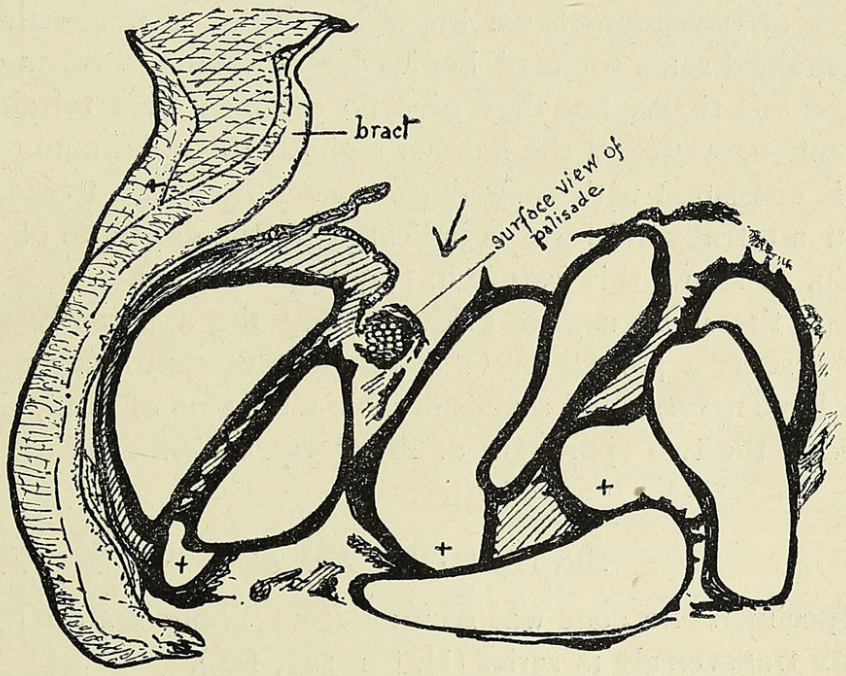
The form is that of a tetrahedral or radially-symmetrical spore which on germinating has taken on lateral development in the restricted space available between the sporange-wall and the cylindrical subarchesporial pad. If we might use a homely illustration we might compare their form to that attained by a limited number of equal pieces of dough disposed over the upper surface and ends of a cylinder, after they had been submitted to such external pressure as would cause them to cover the cylinder without overlapping.

If both the portions of the dough and the distribution of pressure were uniform the form of the pieces would show certain features in common. There would be a tendency to a concavo-convex form, and this would be most marked in those portions which had to 'round' the ends of the cylinder. The problem in *Mazocarpon* is not quite so simple, however, for the sporange narrows rapidly towards the cone-axis and there are occasional instances of the invasion of the pad by the advancing development of the 'spore'.

A remarkable feature in the orientation of the 'spores' is that the organic apex (triradiate scar) abuts directly upon the pad, i.e. is centroscopic with reference to the whole sporange. One can only correlate this fact with the observed character of the pad tissue. This tissue was the chief source of water and food, and one must conjecture that it was a nutritive stimulus which brought about the definite orientation. The megaspores geminated while still young and, growing in the residual sterile sporogenous tissue, became filled with a prothallial tissue which is often

extraordinarily well preserved (Fig. 4). The venters of the archegonia are to be seen beneath the scar in a large number of cases (Figs. 3 and 18). When the sporange breaks up the 'spore' apex invariably comes away from the pad, but the base of the 'spore' more frequently retains its connexion with the outer tissue of the sporange (see Fig. 9), a fact which may have been of biological advantage, as is the association of the embryo sac with the perisperm or nucellar tissue in the more typical 'seed'.

The spore-wall is obviously not rigid throughout development. Its base is covered with pointed processes which undoubtedly helped it to



TEXT-FIG. 2. A diagram constructed from two successive nearly horizontal sections through a megasporange on a bract (the keel of the bract is not shown in the section, as it appears in the third section of the series). The spores marked with + were cut in the middle section, and one has been slightly displaced by a stigmarian rootlet entering the sporange in the direction indicated by the arrow. H. Cn. 525, 2 and 3.

retain its hold on the surrounding tissue. When the prothallus has attained its maximum size the wall appears to have become rigid, as there are several cases of the prothallial tissue being separated from the spore-wall by shrinkage (Fig. 4).[1]

Owing to the permanent tissue uniting the pad to the pedicel of the sporange more spores occur in the upper than in the lower horizontal plane of the sporange. In Text-fig. 2 five spores are cut in the uppermost section (H. Cn. 525, 3), but only three in the lower (H. Cn. 525, 2). The latter three spores are marked with + in the text-figure. As the two planes of section were respectively near the upper and the lower surfaces of the sporange not a single 'spore' has been cut through its organic apex, so

[1] See also Scott's Studies, Fig. 78, p. 188.

that they offer a marked contrast in that respect with the 'spores' in Fig. 18.

If one compares the various figures of 'spores' in Pl. XVII and Text-fig. 2, one sees a wide range of form of sectional area, but one must be on one's guard against assuming that the uncut 'spores' were necessarily so varied in form. As already stated, they probably for the most part agreed in showing a convex base and a plane or concave upper surface. End members in a distal part of the sporange may have been like the radially cut spore in Fig. 3, i.e. of the shallow crucible form. Such 'spores' when cut tangentially show a circular area, as is shown in Fig. 9. As respects the early stages of development we know but little. An abortive sporange (Fig. 7) contained some rounded bodies larger than the other elements of the sporogenous tissue, but they give no evidence of a tetrahedral form. The frequent suggestion of the number eight as the maximum of spores per sporange is consistent with their development from two tetrads, and their origin from a tetrahedral form is indicated by the existence of a triradiate scar (H. Cn. 41 shows this feature in tangential section).

Perhaps the most cogent evidence that the apparently ripe 'spore' always represents a gametophyte is its definite centroscopic orientation. This must have necessitated a considerable alteration of form, which indeed is indicated in the two sporangia of *Mazocarpon Cashii* shown in Figs. 16 and 17.

Section IV. *The Cone.*

One specimen of a cone was secured from Shore material and cut by Mr. Lomax transversely in series (H. Cn. 527, 1–9).

Another cone from a Hough Hill ball, kindly lent by Dr. Scott, has yielded three longitudinal sections. The sporangia show mature prothallia, and some are cut tangentially, but one exceptionally perfect specimen is cut radially (S. Cn. 1925–7).

There is also a single transverse section of a cone from an unknown locality (? Halifax), M. Cn. 472 A, which has been lent by Prof. Weiss.

The transverse sections of these cones have rendered possible the identification of transverse sections of the peduncle, and denuded cone-axes, which now prove to be no uncommon objects in Coal Measure nodules (e.g. H. Cn. 530, 1–30). These cone-axes have hitherto proved rather enigmatic structures.

From the series 527, 1–9, it is obvious that the cone was pedunculate, and that both the peduncle and the sporophyll-bearing axis were hexagonal in transverse section.

The tangential sections of the cone (S. Cn. 1926) and the transverse sections in H. Cn. 527, and H. Cn. 530, 2–30, clearly demonstrate the arrangement of the cone-scales in a close spiral. The area of attachment of

the cone-scale, i.e. the cone-scale scar or bract scar, measures only one millemetre across. This small area is largely occupied by parichnos strands which accompany the trace and render the attachment very fragile. A great tendency existed for the cone-scales to separate from the cone-axis. Even the relatively perfect sporophyll cut radially (see Fig. 18) had become detached though scarcely displaced.

In the upper part of the cone where the cone-scales are barren or immature they are found attached. These facts point strongly to the conclusion that the sporophylls of *Mazocarpon* were exceptionally caducous. Mr. Lomax informed me, on inquiry soon after the delivery of the specimens, that the sections in the series 527, 1–9, 'may be taken as on an average half an inch apart'. As two of these are in the peduncular region (527, 1 and 2, see Fig. 10) this estimate, if correct, would justify us in regarding the cone as having measured between three and four inches in length. It may have been somewhat longer, as the stele, in the ninth and last available member of the series, is still giving off leaf-traces.

The width of the cone can be obtained approximately by doubling the radial length of the sporophyll and adding the diameter of axis. As the radial section (Fig. 18) measures a little over 5 mm. and the axis (Fig. 20) is 3 mm. we may regard 13 mm. as a little under the width of the cone before it broke up. The upturned and laterally expanded parts of the sporophyll, which appear to have extended to the third in rank above (triple layers being seen in the transverse sections (527, 5 and 7)), must have also added to the thickness of the cone, which we may safely conclude could not have been less than 13·5 mm. in diameter.

The anatomy of the Cone-axis, &c. All the tissues are primary. The cortex is differentiated into the usual mechanical outer region and the lacunar middle cortex, which is often fairly well preserved. The stele is circular in section, medullated, and shows projecting protoxylem groups. The sporophyll traces are mesarch and pass out through the outer cortex accompanied by a trough-shaped parichnos strand. The leaf-trace is undivided throughout and travels in the pedicel of the sporange and not in the keel or dorsal midrib of the sporophyll. It can be detected with difficulty in the distal upturned part of the lamina (see next section).

Section V. *The Sporophyll or Bract.*

The bract supporting the megasporange has been met with oftener and in better preservation than that of the microsporange, which appears in Figs. 12 and 13 as a curiously inadequate structure to support the bulky microsporange.

The following description is therefore based on the megasporangial bract.

The main features can be recognized from Text-fig. 1, but it is necessary to explain by what means the form of the bract has been arrived at.

Sections are available tangential to the bract throughout the radially extended portion—that is, the series from which Fig. 8 is obtained.

Horizontal sections are available in the transverse sections of two cones and from fallen sporangia (see Figs. 2 and 20).

Sections approximately radial, together with a series of three sections in a plane at an angle of about 45° with the horizontal and radial planes (H. Cn. 530, 14–16), have all been brought into requisition.

In harmony with all these sections we find there was a narrow lamina with a keeled midrib on the horizontal part to which the sporange was attached. In spite of the well-marked keel, the vascular bundle and parichnos did not run in the bract, but, as already stated, in the pedicel or radially extended stalk of the sporange.[1]

The bract thickened considerably just at the distal end of the sporangial attachment, the under surface sinking to form a convex cushion which might be 8 mm. below the plane of the keel. Thus the convex base is not shown in Fig. 2. In this region there was no projecting ridge nor keel.

The free lamina was hood-like in form and measured 6 mm. in the widest part.

As the distal part overlapped the sporophylls above it on the cone we are able to determine that the width increased from 1 mm. to 2 mm., and then to 6 mm., tapering again to a point a little over 6 mm. above the bend.

The erect part had an adaxial groove, so that, as there was no dorsal ridge, the middle line is the thinnest part of the bract. The merest trace of a vascular bundle has been detected near the adaxial surface in the groove.

The whole of the abaxial surface of the bract is strengthened by a layer of thick-walled cells. The wide erect free part of the distal lamina thins out to the margin, but the narrow free part, in the transition region where the bract thickens, has the sclerized layer duplicated like a hem. The upper surface in the concavity (upon which lies the sporangial lamella) is covered with a delicate layer of cells with small lumen under which the tissue usually perishes. Traces of a ligule are seen (H. Cn. 530, 16) in a groove immediately distal to the sporange and beneath its lamella. At this level the bract is still narrow, so that the ligule may be regarded as occupying the distal end of the keel. It may be of interest to point out that the structure of the bract was such that any hygroscopic contraction of the outer surface would have tended to straighten or bend back the structure. If this took place in the cone where the convex surface fitted into the

[1] Dr. Scott has pointed out to me that a similar route of the vascular bundle is shown in *Lepidostrobus Brownii*, as was demonstrated by Zeiller, Étude sur le *Lepidostrobus Brownii*, 1911, and in *Lepidostrobus Fischeri* (now *L. Kentuckiensis*). See Scott and Jeffrey : On Fossil Plants . . . of Kentucky. Trans. Roy. Soc., vol. ccv, 1914, p. 358.

hollow of the sporophyll below in which the sporangial lamella lay, rupture of the sporange and its attachments would necessarily ensue. It has already been pointed out that these were quite unusually fragile.

Section VI. *The Microsporange.*

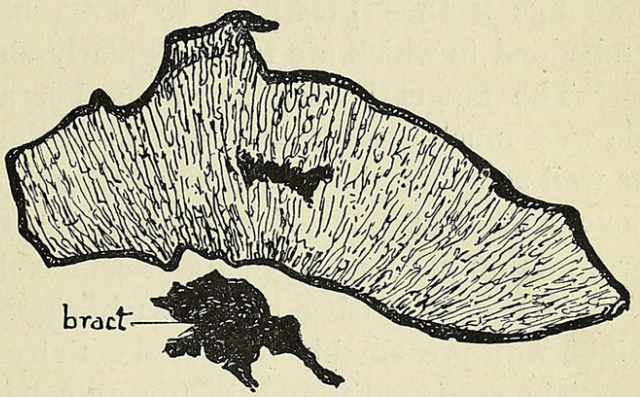
In June, 1913, a series of four tangential sections from a microsporange on a bract, but separate from the cone-axis, was secured from a Shore coal ball (H. Cn. 526, 12–15).

That in 526, 12, is proximal and is injured at the point of attachment to the bract, but shows the tetrads well (Fig. 11).

That in 526, 13, is the most perfect of the series (see Fig. 12).

That in 526, 14, is injured very slightly on the dorsal ridge of the sporange, but shows the position in the pedicel of the vascular bundle. On the left is seen a lateral lamella (Fig. 13).

That in 526, 15, is cut through the wedge-shaped sterile distal part of the sporange beyond the attachment to the bract, which is also cut through (see Text-fig. 3).



Text-fig. 3. *Mazocarpon* microsporange. A vertical section through the distal part of the sporange-wall where it is free from the bract. H. Cn. 526, 15.

Though unattached, the body is identified as *Mazocarpon* by its structure throughout, and especially its lateral lamella, which is so thin at the margin that it is turned back on itself. The tissue, which seems to correspond with the tapetal tabular cells of the megasporange, is here divided up into series of short cells.

The spores are formed not merely in one uniform layer over a sub-archesporial pad, but in several supplementary masses, with sterile tissue between them, so that the sporange bears some resemblance to the microsporange of *Isoëtes*. The structure suggests that parenchyma has been formed from potential sporogenous tissue. The spores are still arranged in tetrads, as is so frequently the case in *Lepidostrobus*. They measure 55 μ by 65 μ and are thus larger than those of *Lepidostrobus* and smaller than those of *Spencerites*.

There is nothing to indicate how the sporophyll was borne, but 526, 11, has a part of a megasporange and megaspores occurring in the same section as the microsporange. This, however, is not surprising, as the sections are rich with *Sigillaria* leaves, so that if it can be shown (see Part II) that *Mazocarpon* is *Sigillariostrobus* it would be quite consistent for both kinds

of sporangia to be present even if they were not formed on the same cone. No distal erect part of the lamina of the bract was secured.

Section VII. *Abortive and Semi-abortive Sporangia.*

More or less abortive sporangia have been met with. In one block two were lying at right angles to each other. One was cut tangentially and the other radially (Figs. 5 and 7).

In the upper part of the transversely-cut cone (H. Cn. 527, 1–9) sections pass through cone-scales which are possibly abortive microsporophylls since only megasporangia occur in the fertile part.

In the radial section shown in Fig. 5 the form and length of a normal fertile megasporange has been attained, but only two megaspores have gone on with their development, though the sporogenous tissue is well defined in area. Covering the subarchesporial pad is a palisade to which I have referred as 'tapetal tissue'. A very unusual condition for a full-sized sporange is thus presented to us—a body filled with continuous tissue, embedded in which are two irregularly-shaped 'spores'.

The tangential section of another abortive sporange seen in Fig. 7 shows a much greater development of the 'tapetal' tissue. It occurs above as well as below the sporogenous tissue, and, possibly owing to the arrested development of 'spores', has grown into the sporogenous tissue till it meets or abuts on one or two enlarged cells which show no sign of tetrad formation. It is surprising to see such vigorous growth of the tapetum combined with presumably restricted activity in the sporogenous layer.

The sections through the upper cone-scales in H. Cn. 527, 8 and 9, are interesting because of their form. The vestigial sporange has flattened down upon the bract, and thus the cone-scale is convex above and below, but is provided with a lamellar margin. The contents appear glandular and the vascular bundle takes a median position comparable to that in a foliage leaf. Reference will be made to these later (see p. 585).

Section VIII. *The Problem of Species.*

Three species are recognized: *Mazocarpon Pettycurense*, *Mazocarpon Shorense*, *Mazocarpon Cashii.*

Mazocarpon Pettycurense. Two specimens have been secured from the Calciferous Sandstone Series of Pettycur, Scotland, and are thus of Lower Carboniferous age. These show distinctive characters, although not fully know

More megaspores are seen in a tangential section of the sporange than have been seen in any similar section in the Upper Carboniferous forms. The microsporange is smaller than the Upper Carboniferous specimen. It is about 4 mm. across, while the latter is 5 mm. across (Figs. 10 and 11). There is a layer of small cells beneath the palisade in the Pettycur micro-

sporange which is sharply defined. In fact we may note that with the exception of this single layer the rest of the persistent sterile tissue is not differentiated into tapetal tissue and parenchyma, but largely partakes of the character of the former.[1] There is as yet no evidence of the existence of a sporangial lamella.

Owing to these distinctive characters, which mark it as a less specialized type, and the great antiquity of these specimens it is desirable to give them specific rank, and the name *Mazocarpon Pettycurense* is proposed until they are more fully known.

Mazocarpon Shorense. The great bulk of the specimens of *Mazocarpon* described in this paper have been secured from coal balls from many localities in the Yorkshire Lower Coal Measure beds. One cone, the microsporange, and the megasporange from which Text-fig. 2 is taken, were obtained from Shore balls. Those which agree with these specimens I propose to refer to as *Mazocarpon Shorense.* The diagnosis will be found as a summary of the characters given in the next section (Section IX).

Mazocarpon Cashii. Specimens of this species occur in one slide, M. Cn. 472 A, which must be regarded as the type slide. The specimen is given specific rank because of two characters by which it may be distinguished from *M. Shorense.* The leaf-traces as seen in a transverse section of the cone-axis are surrounded by a sheath as they pass out through the lacunar middle cortex. The transfusion tissue of the base of sporange (see Fig. 15) is more highly differentiated than that observed in *M. Shorense.*

Other specimens show slight deviations from *M. Shorense.* Thus the sporange from Dulesgate (Fig. 6) has a wider lamina than would be seen in a tangential section through sporange and keel in *M. Shorense*, but there are not sufficient data for distinguishing a new species. The sporange of *M. Shorense* differs so much with its age and place on the cone that a considerable range of variation in detached sporangia must be expected. It is, therefore, inadvisable to multiply species, more especially as it is the aim of the Palaeobotanist to avoid as far as possible leaving a fossil long in a mere form genus such as *Mazocarpon.* If we can show that *Mazocarpon* is *Sigillariostrobus*, the probability is very high that some at least of the specimens of *M. Shorense* are the fructifications of *Sigillaria mamillaris* with which many of them occur.

Section IX. *Summary of Part I.*

Mazocarpon is a provisional term used for a form genus of the structural remains of a sporangial apparatus of a Lycopsid type.

The cone bore, in a close spiral, cone-scales of the *Lepidostrobus*

[1] See Benson, loc. cit., p. 144, Fig. 25, *a* and *a'*, where *a'* is magnified thirty-nine times and *a* only thirty times.

ground-plan, but differing in showing a constriction at the plane of attachment to the axis. The cone-scales are exceptionally caducous.

There is no free lamella directed downwards, but a convex thicker portion without a ridge may extend to about 0·8 mm. below the plane of the keel of the proximal part of the bract (cone-scale). The distal erect part tapers from 6 mm. in width to a point at not less than 6 mm. above. The sporangia are characterized by the possession of much sterile persistent tissue and the proliferation of the distal wall beyond the limit of the attachment of the sporange to the brac

In the megasporange this lamella is shovel-shaped and fits into the adaxial concave surface of the upturned part of the bract.

The megaspores are limited in number (the maximum so far found in any species of Upper Carboniferous age being eight) and germinate *in situ*, while the spore-wall is plastic. The organic apex of each so-called 'spore' is directed centroscopically with reference to the sporange.

There is a considerable range of form, determined by the position which the germinating 'spore' occupies in the space between the sporange-wall and the subarchesporial pad. The form of those occupying the wider distal end of the sporange in *M. Shorense* tends to be that of a shallow crucible with the organic apex in the hollow, but many asymmetric forms occur. The spore-wall bears pointed prong-like teeth over its convex base, i. e. the surface directed towards the wall of the sporange.

The cone is pedunculate.

The sectional area of cone-axis and peduncle is so far found to be hexagonal.

The cone may be several inches in length and half an inch in diameter. Denuded axes are far commoner than those with cone-scales still attached, only three of which have so far been recorded.

One detached microsporange has been described and is shown to resemble certain incrustation specimens from the same horizon described by Dr. Kidston.

Part II. The Evidence for the Attribution of Mazocarpon to Sigillaria.

Section X. *Introduction to Part II.*

Although *Mazocarpon* has been recognized since 1902, full data were not to hand respecting its form and dimensions. Without sections in recognizable planes or in series, the sporangial lamella was a very puzzling feature, nor was it possible to determine the number of megaspores and their relative position in the sporange. It was in the course of a special search for more material (see Section I) that the association of *Mazocarpon* with Sigillarian leaves was observed. This first clue was obtained in May, 1913, and, being confirmed by Dr. Scott's observations independently, it was

followed up by a thorough examination of the blocks from which *Mazocarpon* had been obtained. Striking association with denuded cone-axes and with the bark of *Sigillaria mamillaris* was found.[1]

More reliable evidence was next obtained by a comparison of the structural material with the incrustation fossils already admitted to be *Sigillariostrobus*. The history of our slowly accumulated knowledge of the cones of *Sigillaria* has been related by Zeiller[2] and Kidston.[3] Goldenberg[4] had previously published diagnoses of Sigillarian cones. Kidston's material, collected by Mr. Hemingway from the Middle Coal Measure Strata of Yorkshire, included for the first time a portion of the cone with sporangia giving some indication of the form, number, and distribution of the megaspores in a species he named *Sigillariostrobus ciliatus*.[5] Another cone of Lower Coal Measure age with larger sporangia was regarded by Dr. Kidston as bearing microsporangia. The features of resemblance shown by *Mazocarpon* with these specimens are very numerous and will be dealt with in the next section (Section XI).

Incrustations of complete cones were also figured in natural size and cone-axes from which the cone-scales had fallen.

Mr. Hemingway was able to provide further specimens of these denuded cone-axes (R. H. C. Bot. Museum 2, 95), so that material has been available for comparison with surface sections of the *Mazocarpon* cone-axis, and it is found that the scars on each are similar in form and size (set Fig. 19).

Dr. Kidston says (loc. cit., p. 51): 'The shedding of the bracts at maturity seems to be a characteristic of Sigillarian cones and one of the distinguishing points between them and *Lepidostrobus*.' This tendency to fall to pieces is one of the causes in the delay in the interpretation of *Mazocarpon*, but is now shown to be one of the strongest proofs of its Sigillarian nature.

Section XI. *Detailed comparison of the Structural Material of Mazocarpon with the Incrustation Remains of Sigillariostrobus.*

1. *The Megasporange.*

If one compares Fig. 18, which is a single radial section of a megasporange of *Mazocarpon*, or, still better, Text-fig. 2, which is constructed by superposing two tracings of photographs of successive horizontal sections

[1] The bark of *S. mamillaris* was found in such a good state of preservation that not only were the twin bundles of the leaf-trace shown, but the ligule was found *in situ* for the first time (H. Cn. 531, 8). Cf. Arber and Thomas: Ann. Bot., xxiii, p. 514.

[2] Zeiller: Ann. d. Sc. Nat., Bot., 6e sér., vol. xix, p. 256, 1884.

[3] Kidston: On the Fossil Flora of the Yorkshire Coal Field (second paper). Trans. Roy. Soc. Ed., vol. xxxix, Part 1, 1897.

[4] Goldenberg: Flora Saraepont. foss., Heft I (1855) and Heft II (1857).

[5] For convenience of reference, see Scott's Studies, Fig. 96, A and B, but the original figure more closely corresponds with *Mazocarpon*.

through a megasporange and thus exhibits the total number of spores in the sporange, with Kidston's drawings (reproduced in Scott's Studies, Fig. 96 B), the resemblance is obvious.

It must of course be borne in mind that one is dealing with thin slices of spores in *Mazocarpon*, but with their compressed entire body in Kidston's material.

The dimensions of the sporangia correspond. Text-fig. 2 shows eight spores, and this number is that suggested in *Sigillariostrobus ciliatus*. The size and surface markings of the spores correspond and, so far as sections can be compared with solid bodies, the form is surprisingly similar. In certain cases it can be seen they are distributed peripherally as is shown in *Mazocarpon*, Fig. 18, but there is of course in an incrustation no indication of the actual tissue of the pad, though spaces occur between the spores. The spores in *S. ciliatus* were thought to owe their irregular form to distortion under pressure, and were regarded by Dr. Kidston as probably normally spherical. This interpretation was natural, as some of the bodies show a circular outline. It has been shown, however, in the description of the *Mazocarpon* megaspore that in several cases when a spore is cut tangentially the outline is circular (see Fig. 9). The spores of the French species described by Zeiller appeared to him to be derived from forms 'à peu près sphériques', although he added in a communication he kindly sent me on the subject (May 4, 1914), 'On ne peut, sur des spores aplaties comme on les observe presque toujours, juger avec certitude de la forme primitive'. In *Mazocarpon* the somewhat flattened form is the 'forme primitive'.

It is of course not impossible that some species of *Sigillaria* retained the ancestral form of the megaspore, for the *Mazocarpon* forms described in this paper are undoubtedly due to the germination of the spores while still in the sporange, and we are perhaps hardly justified in calling the body a mere spore.

In *Lepidocarpon* there is evidence that the original form of the spore was tetrahedral, but, with the abortion of three members of the tetrad and the germination *in situ* of the fourth, the whole sporange lumen was eventually occupied. *Mazocarpon* is exactly intermediate between *Lepidostrobus* and *Lepidocarpon*. It allots but one-eighth of the available space to each prothallus, and as these, when mature, are surrounded by a rigid spore-wall with characteristic appendages we incline to call them 'spores'.

If it should be shown that distantly allied species retained the tetrahedral form of the spore it is probable that the number per sporange would be greater, as they would then not have had the space to extend much beyond the normal limit in *Lepidostrobus*.

The spores in Zeiller's[1] restoration of *Sigillariostrobus Tieghemii* in his

[1] Zeiller, loc cit., Fig. 4.

text-book 'Éléments de Paléobotanique', Fig. 138, are shown as little groups on each cone-scale, which certainly suggest a maximum of eight per sporange, but in an incrustation the sporange-wall has naturally perished, so that we can lay no stress on this specimen.

The fragile nature of the sporange-wall has prevented it being demonstrated in any of Zeiller's and Kidston's specimens, while in *Mazocarpon* no single radial section shows the wall unbroken; the sporange in Text-fig. 2 shows only vestiges of the wall.

The sporange in Fig. 18 is the most complete on the cone in S. Cn. 1595–7, and the wall can be seen to be broken in two places. All the sporangia in the cone are mature, but owing to the broken condition of the sporange-wall it is often difficult to be clear as to the limits of the respective sporangia. This is the usual condition in *Sigillariostrobus* and led one observer [1] to suggest that the spores were formed in the bract without a sporangial wall.

2. *The Cones.*

The characters of agreement between the structural specimens of the cone and the incrustation specimens of the cone of *Sigillariostrobus* both in Zeiller's and Kidston's material extend to the following:

a. Dimensions.
b. Phyllotaxy.
c. Form of bract.
d. Pedunculate character of the cone.
e. Agreement between the hexagonal form of section of cone-axis and the dimensions and form of the scar in the incrustations of *Sigillaria mamillaris.*
f. Cone-scale scar on the cone-axis.
g. Caducous nature of the cone-scales.

a. Dimensions. In Part I, p. 575, we estimated the cone in 527, 1–9, to be between three and four inches in length and a little over 13 mm. or half an inch in diameter. If these measurements are compared with Kidston's figures [2] of *Sigillariostrobus rhombibracteatus*, Plate I, Fig. 3, and Plate II, Fig. 10, they will be seen to correspond very closely with the dimensions of that species.

We cannot of course expect to determine the length of the peduncle, nor is there any reason to consider that all *Sigillaria* cones were of the same size, but the general agreement indicated above in the dimensions of the available material is sufficiently striking.

b. Phyllotaxy. Both show a close spiral phyllotaxy.

c. Form of bract. The description given in Part I, Section V, not

[1] Kidston: 'Les Végétaux houillers recueillis dans le Hainault Belge,' 1911, p. 184, Fig. 32.
[2] Kidston, loc. cit.

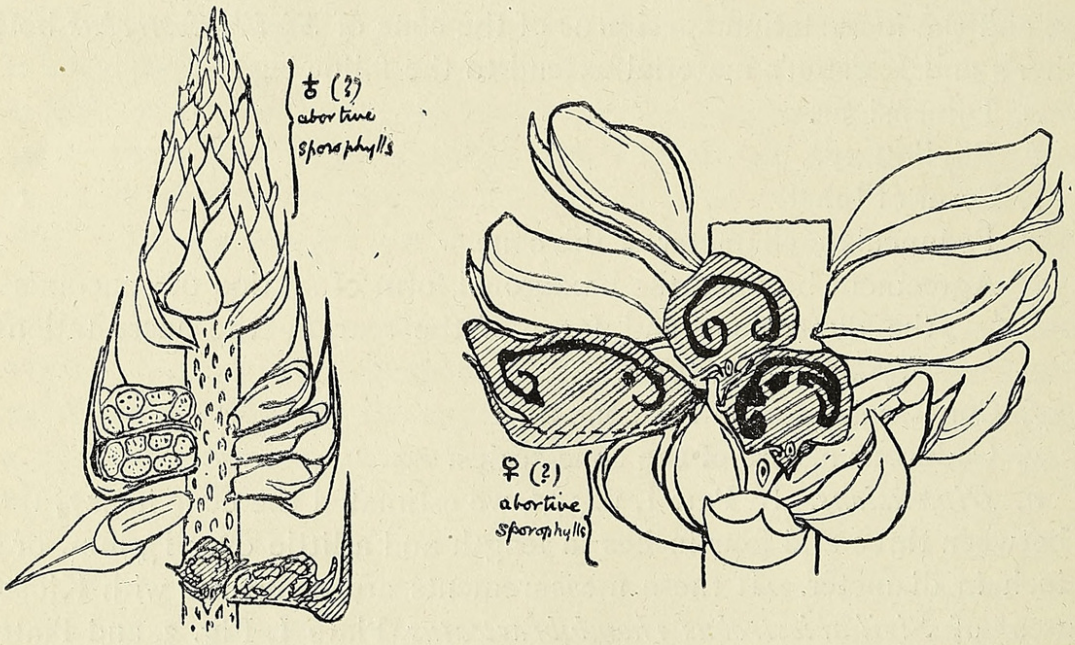
only tallies with the figures given by Zeiller[1] and by Kidston,[2] but it explains the fact of a line like a midrib appearing on the adaxial and not on the abaxial surface. It is shown that in *Mazocarpon* a deep groove occurs on the adaxial surface, but that the abaxial surface is uniformly smooth and shows no rib.

It is unexpected agreement in peculiarities such as this that makes one feel confident one is describing the same thing.

d and *e*. *Peduncle and its sectional form.* Both *Mazocarpon* and the various species of *Sigillariostrobus* described are pedunculate (Fig. 10). The peduncles, moreover, are deciduous, and Kidston remarks[3] that this seems to be the normal condition in *Sigillaria*. The section area of the peduncle and cone-axis in *Mazocarpon* is hexagonal, and those of *M. Shorense* have the form and size of the scar which has been attributed to the cone in *Sigillaria mamillaris*.

3. *The Microsporange.*

It is of especial interest to refer here to a specimen of *Sigillariostrobus* from the Lower Coal Measures of Yorkshire, which has been figured and



A B

TEXT-FIG. 4, A and B. Reconstruction of parts of the mega- and microsporangial cones of *Mazocarpon* (*Sigillaria*) showing the relative size and form of the sporangia. The presence of abortive sporophylls is indicated above the megasporophylls in A, and below the microsporophylls in B. Some of the sporophylls on each cone are represented in section, the cut surface being hatched. Both structural and incrustation material has been utilized in this diagram. For complete incrustations of cones of *Sigillaria* the works of Zeiller and Kidston should be consulted. A represents the upper part of a megasporangial cone; B represents the lower part of a microsporangial cone.

described by Kidston[4] in his above-mentioned work. The cone is of the same geological age as *Mazocarpon*. The sporangia, regarded by Kidston

[1] Zeiller, loc. cit., Fig. 5, Plate XII.
[2] Kidston, loc. cit.
[3] Kidston, loc. cit., p. 56.
[4] Kidston, loc. cit., Plate II, Fig. 1.

as microsporangia, are split away from the cone-axis, but are still in the same relative position in which they were when attached. The sporange seen laterally (*d'*) is very like the microsporange of *Mazocarpon*. As to the dimensions, the large bodies (*b*, *c*, and *e* in the Fig. 1) given by Kidston[1] agree in every particular with that of the microsporange of *Mazocarpon*, which was nearly 5 mm. across (Figs. 10 and 11) and formed a lateral lamella.

The lower cone-scales which show unusual spore contents are possibly abortive megasporangia at the lower part of the cone and are analogous with the abortive (?) microsporangia at the apex of the megasporangial cone in *Mazocarpon* (H. Cn. 527, 8 and 9).

This remarkable specimen so happily interpreted by Kidston goes far to indicate that the fertile mega- and microsporangia of *Sigillaria* were at least sometimes borne on different cones, but showed vestiges, respectively above or below, of the cone-scales of the other type (cf. Text-fig. 4). This agreement with a very difficult specimen strengthens the evidence that *Mazocarpon* is *Sigillaria*, since the exceptionally bulky microsporange of *Mazocarpon* agrees in both form and size with specimens already regarded as microsporangia of *Sigillariostrobus* by Dr. Kidston.

Part III. General Discussion of Results.

a. Biological aspects of the new structure.

b. Possible bearing of the work on the affinity of *Pleuromoia* and *Isoëtes* and of genera of Lepidodendraceae.

c. General conclusions.

Section XII.

a. *Biological aspects of the new structure.*

A few words might be devoted to the biological aspect of the *Mazocarpon* type of megasporange. The presence in some sporangia of ruminating 'spores' which lie in a relatively large mass of sporogenous tissue (Fig. 15) would seem to indicate that the sporange is derived from an ancestral form with a larger number of functional spores. The decrease in the number appears to have been correlated with a limited special increase in the size of the prothallus, for when only one is developed in a sporange it has only attained the normal size (Fig. 5) found in an eight-spored sporange. The seed habit is approached in two ways: (*a*) the megaspores germinate within the sporange and (*b*) the sporange undergoes a certain amount of vegetative development. Fertilization is, however, impossible until fragmentation of the sporange has taken place, owing to the centroscopically directed archegonia. Thus a new factor is introduced and the lamella

[1] Kidston, loc. cit., Plate II, Fig. 1.

seems to have been framed so as to act as the fulcrum when the bract above straightens. Each prothallus would normally secure, by means of its toothed wall, a portion of the sterile sporangial (nucellar) tissue when the sporange broke up, and thus theoretically we find eight seed-like bodies produced from one sporange. Both the type and the adjustments are new to botanical literature.

b. *Possible bearing of the facts ascertained on the problem of the Affinity of the Pleuromoia and Isoëtes, and of genera of Lepidodendreae.*

Throughout the discussion on the incrustation specimens of *Sigillariostrobus*, whether by Goldenberg, Zeiller, or Kidston, mention has been made of the resemblance the genus *Sigillaria* shows to *Isoëtes*.

It may be worth while to inquire whether our new knowledge of the structure of the cones we must now attribute to *Sigillaria* gives us any corroboration of this view.

Potonié summarized [1] the resemblances as respects vegetative organs and accepts *Pleuromoia* as an intermediate form occurring rather happily in an intermediate epoch.

The character in which the sporangia of *Isoëtes* agree with *Mazocarpon*, besides the Lepidostroboid characters of radial extension, &c., is the persistence and relative abundance of sterile tissue. *Isoëtes* shows trabeculae in both mega- and microsporangia which may be suggestively compared with the large trabeculae of the *Mazocarpon* microsporange (Fig. 13). It is possible also that the *Mazocarpon* type of sporange may afford some clue to the better interpretation of the unusual features of the cone of the Mesozoic incrustation, *Pleuromoia*. The wedge-shaped distal part (Text-fig. 3) of the *Mazocarpon* microsporange is not unlike the projecting (i. e. distal) part of the sporange in *Pleuromoia*, as seen in Potonié's Fig. 453 B in the above-mentioned treatise. Moreover, some of the apparent irregularity of the cone of *Pleuromoia* may be due to the difficulty of distinguishing the wedge-like expansion of the sporange from the bract which appears similar to it in outline.

It is even possible that such an expansion may, in an incrustation, have adhered to the bract above and thus given rise to an appearance of a sporange growing on the lower surface; but the figures given by Solms-Laubach [2] are more suggestive of the sporange being partly inserted in a fovea, as in *Isoëtes*. In fact the regular striations of the *Pleuromoia* sporangia are more reminiscent of the trabeculae of *Isoëtes* than of the bulky irregular trabeculae of *Mazocarpon*. From these considerations it becomes possible to accept freely the suggestion of affinity between the genera if judged solely on the characters of their vegetative organs. Prof. Lang's

[1] Engler: Pflanzenfamilien, Teil I, Abt. 4, p. 752.

[2] Solms-Laubach: Bot. Zeit., Heft xii, 1899, p. 227, Fig. 7, Taf. VIII.

recent contribution[1] to the anatomy of *Isoëtes* does not essentially affect the problem. With reference to the relationship of *Sigillaria* to the other Lepidodendreae it might be useful to point out that the anatomy of the cone of *Mazocarpon* tends to prevent any great phylogenetic significance being attached to the presence of a double leaf-trace in some species of *Sigillaria*. *Mazocarpon* has but a single trace in its cone-scale, although there can be but little doubt that some of the Shore specimens belonged to *Sigillaria mamillaris*, as that is the species which was prevalent in the Shore balls yielding the bulk of the material, and *S. mamillaris* is one of the two species of *Sigillaria* in which the double leaf-trace has been identified. It is a well-recognized fact in morphology that the cone-scale is likely to retain ancestral characters longer than the foliage leaf, so that the division of the leaf-trace may be regarded as a recent character.

Again, we may ask if the more detailed knowledge of the sporangia throws any new light on the interrelationships of the genera of Lepidodendraceae. It has contributed to the removal of the view that was held by some botanists[2] that the sporange of *Sigillaria* had relatively lessr adial extension than that of *Lepidodendron*. Bearing in mind the distal extension of the sporange and the large mass of sporogenous tissue which is only partially fertile, we find no grounds for rejecting the very cogent theory that *Sigillaria* was an offshoot from some early Lepidodendroid stock. Though comparatively rare in the Lower Carboniferous rocks, a relatively unspecialized type of *Mazocarpon* (*M. Pettycurense*) was already evolved, and with very little change the type persists to the Upper Coal Measures, where it is recognizable as incrustations. It is increasingly probable that it survived as *Pleuromoia* in the Mesozoic and as *Isoëtes* to the present day.

c. *General Conclusion.*

In conclusion we may point out that when Zeiller made his discovery of the characteristic leaf-scars in vertical series on the peduncle of *Sigillariostrobus Tieghemii*, in 1884, he really laid the foundation for the diagnosis of *Mazocarpon* as *Sigillaria*. As Dr. Scott says:[3] 'This correlation having once been effected it became possible to identify various other specimens as cogeneric, and the genus *Sigillariostrobus* now includes several species.' Among these species, those of the structural remains, *Mazocarpon*, as now described, may well claim a place. Moreover, if we take into account that we can trace *Mazocarpon* from the Coal Measures back to a period when *Sigillaria* was comparatively rare it is even probable that it is the characteristic type of sporangial fructification of the whole genus.

[1] Lang: Studies in the Morphology of *Isoëtes*, I and II. Mem. and Proc. of the Manchester Lit. and Phil. Soc., vol. lix, Part II, 1915.

[2] Lady Isabel Browne: N. Ph., vi, pp. 153–6.

[3] Scott: Studies in Fossil Botany, p. 232.

DESCRIPTION OF PLATES XVII–XVIII.

Illustrating Professor Margaret J. Benson's paper on *Mazocarpon* or the Structural *Sigillariostrobus*.

(All the figures are micrographs.)

H. = R. H. C. Collection.
M. = Manchester ,,
S. = Dr. Scott's ,,

a. = archegonium; *b.* = bract; *b.l.* = adaxial groove on distal part of the bract; *b.s.* = bract scar; *d l.* = distal lamella of the megasporange; *s.* = spore; *s.t.* = sporogenous tissue; *t.* = tapetum; *tr.* = transfusion tissue; *v.b.* = vascular bundle.

PLATE XVII.

Fig. 1. Obliquely cut megasporange showing four to five megaspores and the persistent parenchyma of wall and subarchesporial pad. M. Cn. R. 758; Shore. × 12.

Fig. 2. Horizontal section of the bract showing the distal part and the narrow keel beneath the pedicel of the sporange. H. Cn. 37; Dulesgate. × 30.

Fig. 3. A nearly radial section of a megaspore from the same cone as Fig. 18. The venters of two archegonia, *a*, are clearly shown in the prothallus. The spore-wall shows the characteristic dentate apiculi. S. Cn. 1927. × 47.

Fig. 4. Approximately radial section through a spore with the prothallial tissue well preserved. The ring at the base is not an archegonium. H. Cn. 41; Dulesgate. × 25.

Fig. 5. A nearly radial section of a partially abortive megasporange showing only two spores. The distal lamella, *d.l.*, looks in section like a rhinoceros tusk. H. Cn. 519, 4; Shore. × 12.

Fig. 6. Tangentially-cut megasporange on bract near distal end of sporogenous region. The internal tissue has perished. The relation of the lateral parts of the sporangial lamella to the wide bract is shown. H. Cn. 22; Dulesgate. × about 20.

Fig. 7. A tangential section of an abortive sporange showing the extraordinary development of tapetal tissue and a few rounded cells which suggest (?) abortive spores. They are not in tetrads. The vascular bundle, *v.b.*, in the pedicel is well shown. H. Cn. 519, 6; Shore. × 22.

Fig. 8. Tangential section of a megasporange attached to a bract. It is one of a series of five sections through the sporange. It shows the vascular bundle, *v.b.*, in the pedicel and the parichnos. The character of the pedicel explains the easy detachment of the sporange from the bract. H. Cn. 518, 7; Shore. × 24.

Fig. 9. Oblique section through the distal end of a sporange cutting a megaspore tangentially. The spore shows in this plane a circular sectional area. This section explains the occasionally circular form of megaspores in incrustation specimens. S. Cn. 1546; Halifax. × 26.

Fig. 10. A transverse section of the peduncle of a cone shown in Fig. 20 and described in the text. H. Cn. 527, 2; Shore. × 13.

Fig. 11. A high-power photograph of the spore-bearing region and upper wall of a microsporange. The spores are grouped in tetrads. H. Cn. 526, 12. × about 100.

Figs. 12 and 13. The two median members of a series of four tangential sections through a microsporange (the fourth or most distal in the series is shown in Text-fig. 3). The relative size of sporange and bract is very striking; also the large amount of sterile tissue in the sporange and the approximation in Fig. 13 to the construction of trabeculae, as in *Isoëtes*. There is no sharp distinction, as in the megasporange, between the subarchesporial tissue and tapetum (cf. Fig. 7). H. Cn. 526, 13 and 14; Shore. × 23.

Fig. 13 *a*. A part of section 13 showing the details of the tapetum. *v.b.* indicates the position of the vascular bundle. As Fig. 13.

Fig. 14. An obliquely-cut section of a sporange showing the lamella exactly fitting into the concavity of the bract. H. Cn. 35; Dulesgate. × 9.

PLATE XVIII.

Fig. 15. *Mazocarpon Cashii.* Part of the transverse section of a cone from the axis of which the sporangia of Fig. 17 had become detached. The hexagonal form of the axis and the details of the leaf-traces are well shown. M. Cn. 472 A. × 25.

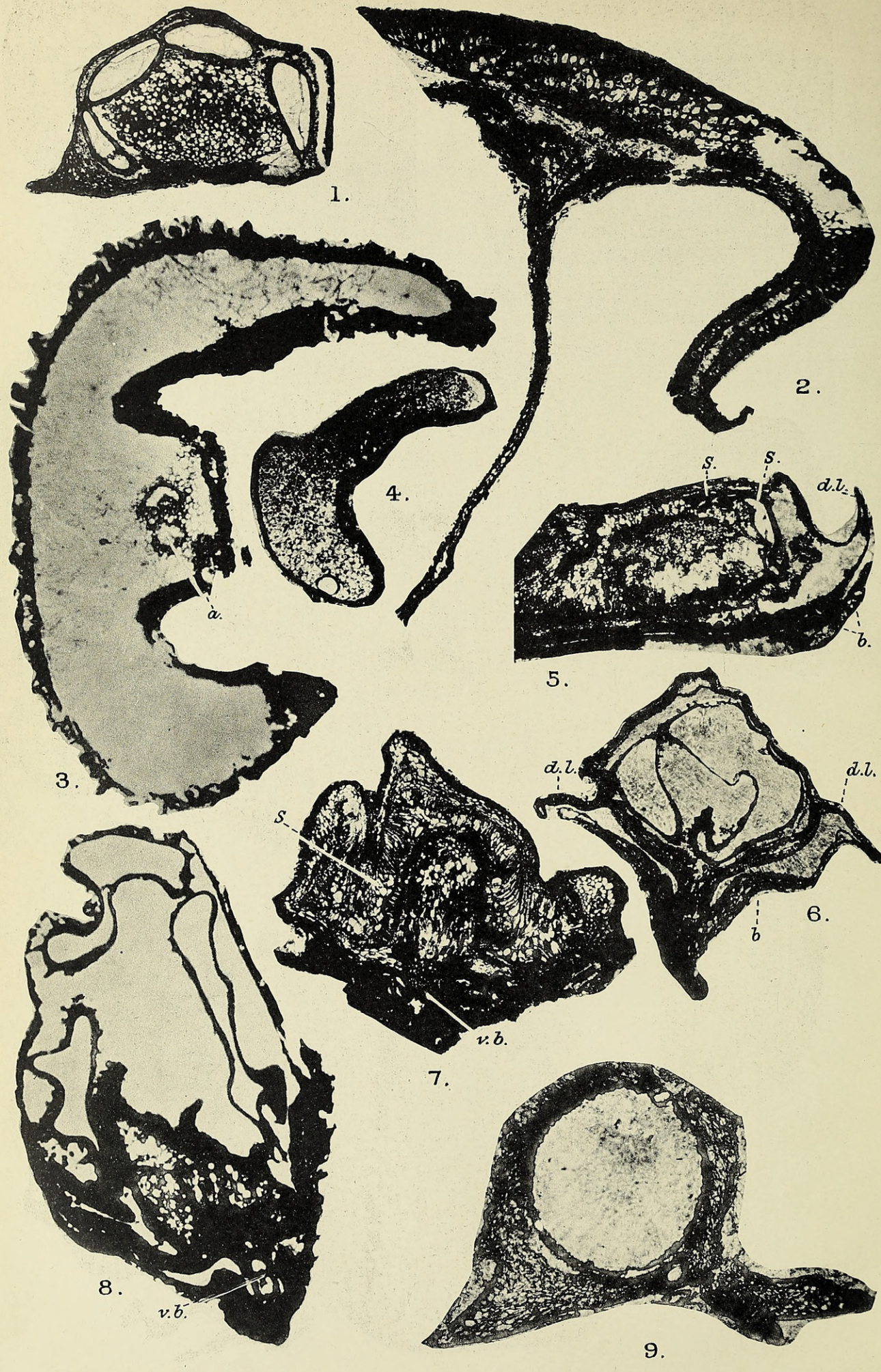
Fig. 16. *M. Cashii.* Obliquely tangential section through a sporange in which the germinating spores have not yet reached their final form. The spore on the right can be seen to have already established its centroscopic position, for its organic apex is directed towards the tapetal covering of the subarchesporial pad. The space occupied by the sporogenous tissue, *s.t.*, would eventually have been occupied by the convex base of the 'spore', as in Figs. 1 and 18. A large mass of transfusion tissue is seen at *tr.* As Fig. 15.

Fig. 17. A low-power photograph of part of the fragmented cone, parts of which are shown in the two previous figures. The section passes through several overlapping bracts, *b.*, one of which shows the adaxial groove, *b.g.* As Fig. 15. × 12.

Fig. 18. Part of the middle section of a series of three through a fine megasporangial cone. It shows a radial section through a sporange on its bract, *b.*, and the bract, *b'.*, of the sporange above fitting into the groove between the distal lamella, *d.l.*, and the fertile part of the sporange. Unfortunately the coal ball had been cut away too close to the cone, so that the distal ends of the lamella and bract are incomplete. Six spores can be counted in this section of a sporange, three of which are cut radially through the organic apex. The spore on the right shows prothallial tissue and an archegonium, *a.*, but the prothallus has been invaded by a stigmarian rootlet. In the original the vascular bundle, *v.b.*, can be detected in the pedicel. S. Cn. 1926; Hough Hill; Stalybridge. × 15.

Fig. 19. A surface section of the axis of the above cone showing the form and small size of the cone-scale scars (bract scars), *b.s.* S. Cn. 1925; Hough Hill. × 15.

Fig. 20. A transverse section of the upper part of another megasporangial cone. The hexagonal form of the axis and inner cortex is well shown, while the stele is circular in section. Note also the constriction of the bases of the bracts, which is a Sigillarian character. H. Cn. 527, 7; Shore. × 13.



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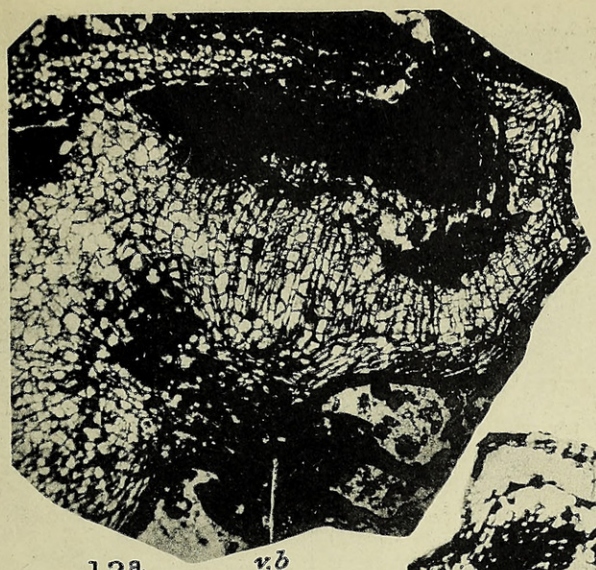

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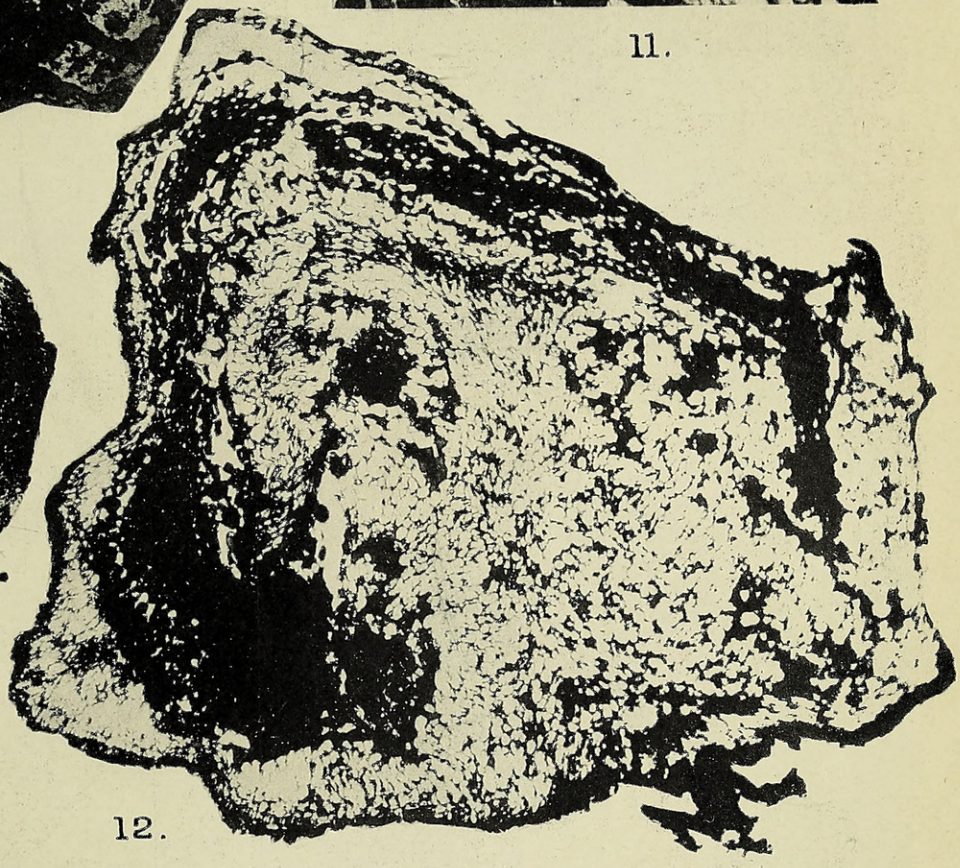

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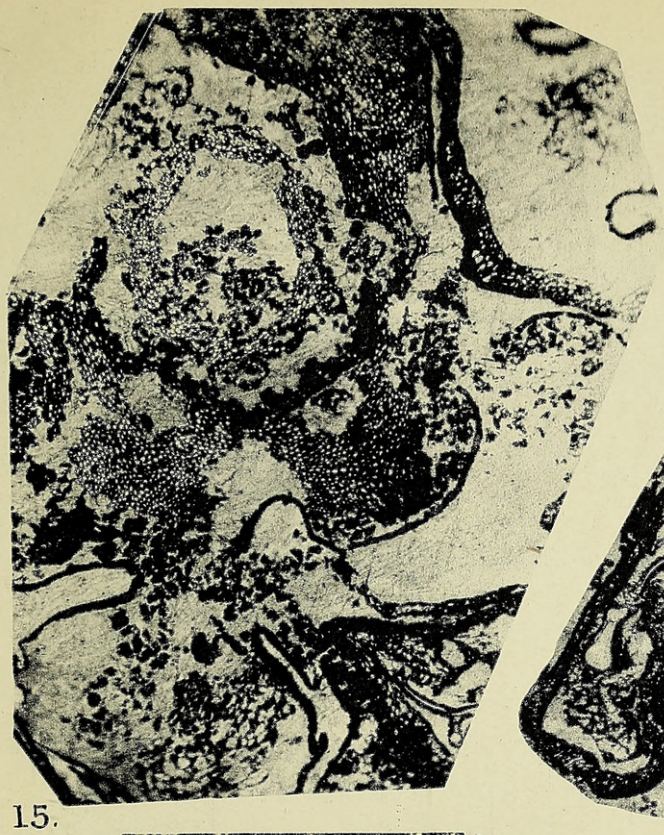

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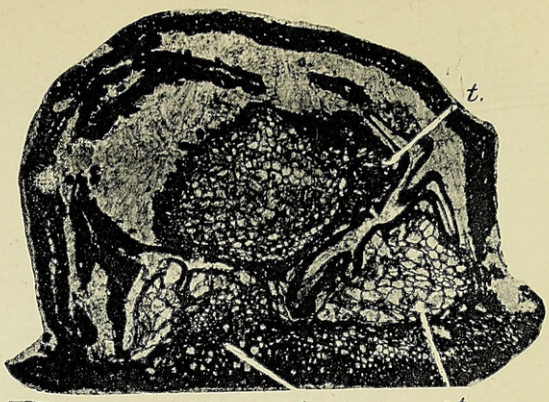

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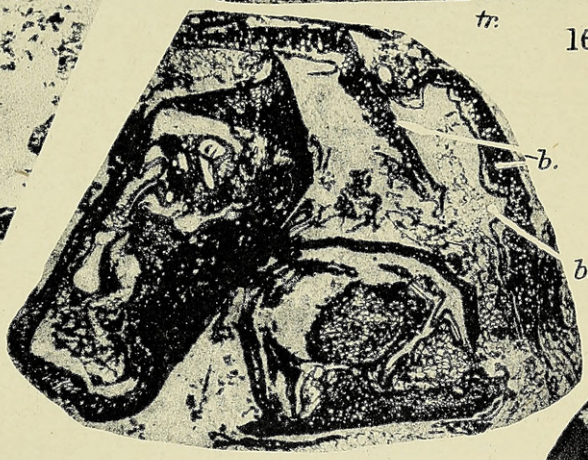

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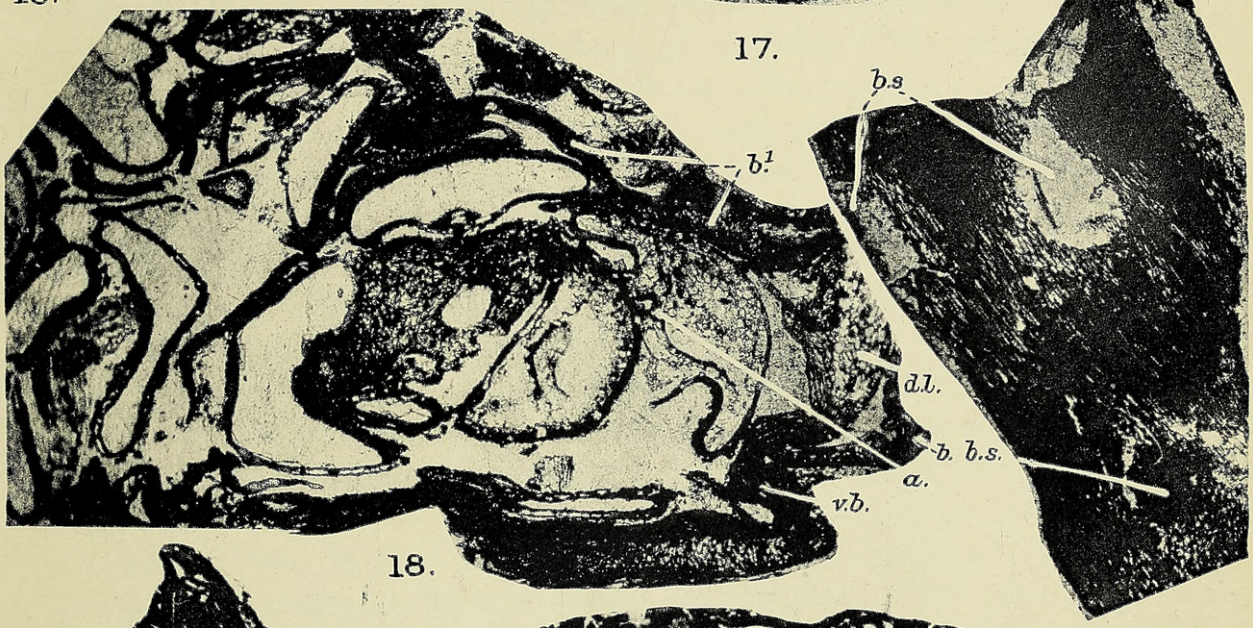

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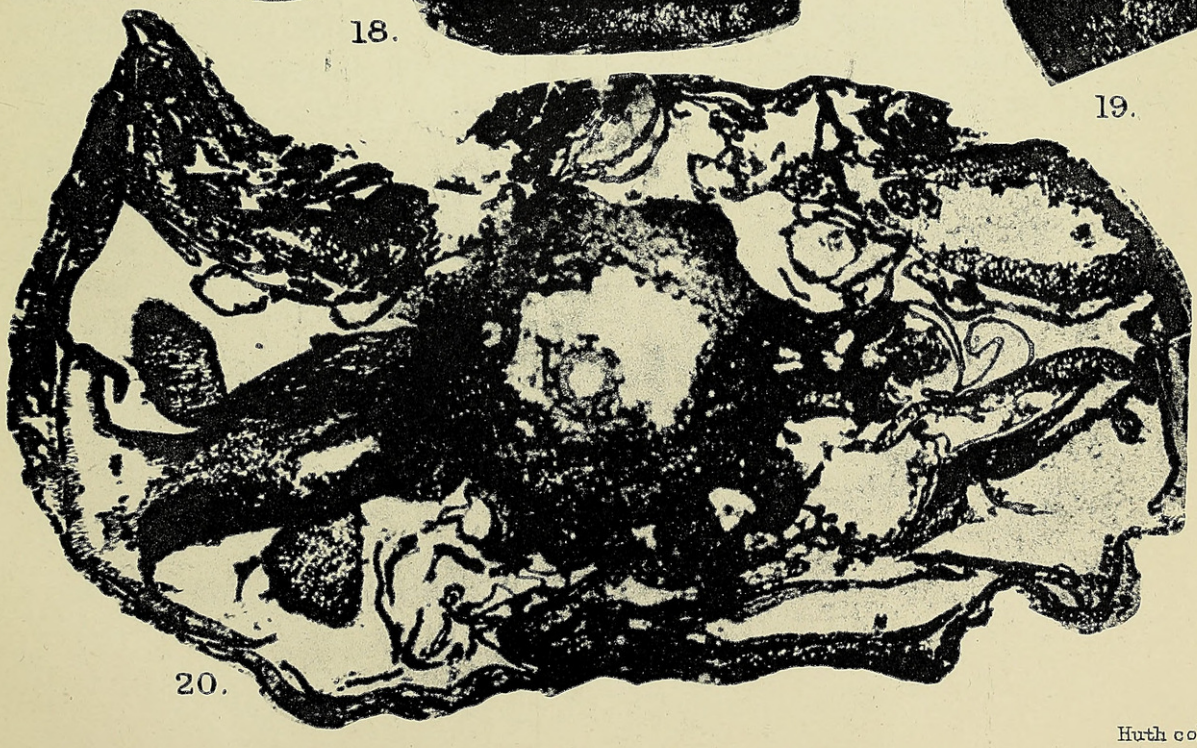

20.

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