- I. On the Structure and Affinities of Fossil Plants from the Palæozoic Rocks.— On Cheirostrobus, a new type of Fossil Cone from the Lower Carboniferous Strata (Calciferous Sandstone Series).
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[Plates 1-6.]

Introduction.

The higher Cryptogamic Flora of the Palæozoic period was exceedingly rich compared with that of our own day. Confining our attention to those Cryptogams in which the fructification has the form of a definite cone or strobilus, we find that at least eight* distinct types of such strobili are already known from the primary rocks, leaving out of account all minor differences of a merely specific value, and ignoring imperfectly-known forms. From the recent Flora we could not obtain more than three equally distinct classes of Cryptogamic cones.

The fossil strobili at present discovered group themselves under three categories,—the Lycopodiaceous, the Equisetaceous or Calamarian, and the Sphenophyllaceous The two former coincide with well-known recent orders, while the last belong to a purely fossil group, at present only known from the Palæozoic formations, and so far of undetermined affinities.

The form about to be described is widely different from the fructification of any Vascular Cryptogam, recent or fossil, at present recorded, but it appears to approach the third group, that of the Sphenophylleæ, more nearly than either of the others.†

The bed which has yielded this specimen is one of great antiquity, belonging to the Calciferous Sandstone Series, at the very base of the Carboniferous formation, and therefore occurring at an horizon enormously more ancient than that of the Coal Measures, from which the majority of our specimens of Palæozoic plants have been derived. The deposit is at Pettycur, near Burntisland, on the Firth of Forth, and is already well known from the interesting vegetable remains, with structure

- * Calamostachys, Palæostachya, Bornia, Cingularia, Sphenophyllum Dawsoni, Bowmanites Römeri, Lepidostrobus, Sigillariostrobus.
- † See preliminary paper "On Cheirostrobus, a new type of Fossil Cone from the Calciferous Sandstones," 'Proceedings Royal Society,' vol. 60, p. 417; 1897.

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preserved, previously obtained from it, among which may be mentioned Sphenophyllum insigne, Heterangium Grievii, Rachiopteris duplex, Lepidodendron brevifolium, and a Lepidostrobus, possibly of the same plant.* The great geological age of this deposit evidently gives a special interest to the fossil remains which it contains, among which it would not be surprising to find traces of synthetic types, combining the characters of orders of plants otherwise distinct. In the discovery of Cheirostrobus there is reason to believe that this possibility has been to some extent realised.

The only specimen of the cone at present known was found by Mr. James Bennie, of Edinburgh, in 1883. Sections of the specimen were in the possession of Mr. R. Kidston, F.G.S., to whom I am deeply indebted, as he not only called my attention to this fossil, but lent me his own sections for investigation, and obtained for me from the owner the remainder of the original block, which has yielded a number of new sections of great value.

As explained in the preliminary paper,† I had previously examined a fragment in the Williamson Collection, which has turned out to be, in all probability, the peduncle of another specimen of the same fructification. The peculiarities of this fragment were sufficient to show that it must have belonged to an undescribed plant, probably with some affinity to Sphenophyllum,‡ When, through Mr. Kidston's kindness, I had the opportunity of investigating the actual cone, this conclusion became confirmed in a degree hardly to have been anticipated.

Although the examination of the peduncle came first in point of time, it will be more convenient, in the present memoir, to go on at once to the fructification itself, which is the object of chief interest, postponing the necessary details as to the peduncle to a later page.

The specimen is calcified, the block in which it occurs being of exceptionally uniform texture, and thus well suited for obtaining good sections. The structure is fortunately preserved with great perfection, so that from the solitary specimen a fairly complete knowledge of the strobilus can be obtained. I am imformed that the original length of the fragment was about two inches. It includes the base of the cone, with part of its peduncle, but the apex is absent, and as dimensions and structure remain uniform so far as the specimen extends, we have no means of saying what the full length may have been. In its present state the cone is somewhat flattened, measuring about 5 centims. in greatest, by 2 to 2 3 centims. in least diameter. In parts the sporophylls have been a good deal displaced, but the flattening is due, not so much to crushing, as to the partial destruction of the appendages on two opposite sides (see Plate 1, photograph 1). From measurements

^{*} See Williamson, "Organisation of the Fossil Plants of the Coal Measures," 'Phil. Trans.,' 1871-93, passim.

[†] Loc. cit., p. 417.

^{‡ &#}x27;British Association Report,' 1896, p. 1024.

of the most perfect portion, it appears that the diameter of the strobilus in its natural condition was at least 3.5 centims.

GENERAL MORPHOLOGY.*

The axis of the cone maintains, throughout the specimen, a diameter of about 7 millims. Its appendages are borne in somewhat crowded verticils; fourteen of such verticils occupied a portion of the axis about an inch (2.5 centims.) in length. The members of successive whorls are not alternate, but superposed, lying exactly above each other in vertical lines. This important point is shown most decisively in tangential sections of the cone, such as that represented in Plate 1, photograph 6, with which Plate 2, photograph 8, may be compared. The number of members in each whorl was twelve. The whole number is not shown in any one transverse section, but follows from the number and arrangement of the leaf-traces, and their relation to the appendages, as shown for example in Photograph 2. The axis is traversed by a vascular cylinder, the wood of which is polyarch, with twelve prominent angles, each of which corresponds to one of the vertical series of appendages (see Plate 1, photographs 1-3). The exact relation of the anatomy to the external organisation will be fully considered below.

The appendages may be called sporophylls, as they are foliar structures, which ultimately bear the sporangia. Their organisation, however, is remarkably complex, more so than in any strobiloid Cryptogam at present known.

The length of each sporophyll, from its insertion on the axis to its distal extremity, was about 1.4 centim., as determined from the best-preserved parts of the specimen. Its general direction, when not displaced, was horizontal; at the base of the cone, however, where the appendages are shorter, they have a downward inclination (see Plate 3, photograph 15). These basal sporophylls will be dealt with afterwards; at present only those of the ordinary form, such as occupy the greater part of the strobilus, will be considered.

The sporophyll remains undivided for only a very short distance from its insertion. The leaf-base, or phyllopodium,† which has a slight upward slope, is about 1 millim. long—its transverse section (shown in tangential sections of the cone) is roughly oblong, with a width of about 2 millims., and a height of nearly 1 millim. (see Plate 1, photographs 4, 5, and 6; Plate 2, photograph 7). The leaf-bases of the same verticil are distinctly connate, so as to form a continuous ring round the axis (see Photographs 2 and 6).

The sporophyll, at a distance of about a millimetre from the axis, divides into an upper and a lower lobe or limb, the one placed directly above the other (see Photo-

^{*} See, in addition to the photographs and figures, the diagram of the cone on p. 7.

[†] Bower, "Comp. Morph. of the Leaf in Vasc. Cryptogams and Gymnosperms," 'Phil. Trans.,' 1884, Part II., p. 569.

graphs 4, 5, 6, and 7). Each lobe immediately undergoes subdivision in a palmate manner, into three segments, so that a normal sporophyll consists of six segments in all, three of which belong to the upper and three to the lower lobe. These subdivisions are best observed in tangential sections of the cone, passing through the region of the sporophyll bases (see Photographs 6 and 7). Occasionally the number may be less than six, especially at the bottom of the cone, but the six segments, three inferior and three superior, are the rule.

The segments, or leaflets, have a very peculiar form: each consists of a long, straight, slender petiole, or more correctly, petiolule,* the average diameter of which is only about 35 millim. (Plates 1-3, photographs 4, 5, 8, 9, and 14). This extends horizontally for a distance of a centimetre or more, and then terminates in a relatively large laminar expansion. The segments are of two kinds, the one fertile, bearing the sporangia, the other sterile. So far as the petiolules are concerned, the fertile and sterile segments are almost exactly alike, but their laminæ are very different (Plates 2 and 3, photographs 9-13).

The fertile segment, or sporangiophore, as it may conveniently be termed, has a bulky lamina, the general form of which is peltate, but with a somewhat complex contour (see photographs above cited) and considerable thickness. On its inner or adaxial side the lamina bears (in most cases at least) four diagonally placed outgrowths, on each of which a sporangium is borne. The number of sporangia on each sporangiophore has been determined chiefly from the comparison of radial and transverse sections, in both of which views the attachments of two sporangia are usually shown (see Photographs 9 and 12), and also from the grouping of the sporangia around the petiolules, as shown in tangential sections (Photograph 14). In some cases three sporangia are shown in the radial section of a sporangiophore (Photograph 9, f.4); this may be merely due to displacement, or may indicate that five in all may occasionally have been present.

The sporangia are long and narrow, extending back along the petiolules, so as nearly or quite to reach the axis (see Photographs 1 and 4). As the axis is approached the space available obviously diminishes, and to accommodate themselves to these conditions, about half the sporangia stop short of the axis, while the remainder extend quite to its surface, fitting into the spaces between the sporophyll-bases and their segments (Photographs 2, 5, and 7). The sporangia thus have a curiously elongated form, for, roughly speaking, they are about a centimetre long, by about a millimetre in mean diameter (Photograph 4). At the outer end a sporangium may

^{*} In the preliminary paper the word *pedicel* was used for these organs, from analogy with the sporangiferous pedicels of *Sphenophyllum*. It seems preferable, however, to adopt a term more in harmony with the foliolar nature of the segments.

⁺ Shown by the diminished number of sporangia, as compared with that of the petiolules, in tangential sections approaching the axis.

measure about 1.5 millim. in its horizontal diameter, but it tapers towards the axis to a more or less pointed extremity.

The fertile laminæ fit pretty closely together both as seen in radial and transverse section (see Photographs 9 and 12). The sterile segments, however, are longer than the sporangiophores, and their laminæ overlap those of the latter. The arrangement of sterile and fertile segments is such that they alternate regularly with each other in the same vertical series, as shown in a radial section such as that represented in Photograph 10. As the fertile laminæ are of sufficient dimensions to occupy by themselves the whole of the available space, it is evident that they must be grooved on their upper and lower surfaces so as to allow the sterile segments above and below them to reach the exterior. That this is so is shown by radial sections, where the sterile lamina is often seen encroaching on its fertile neighbour (Photographs 9, st.4, and 11 st.), and by transverse sections, such as that shown in Photograph 13, where the two lateral wings of a fertile lamina are seen with the sterile segment passing between them. Indications of the arrangement can also be seen in tangential sections, but, unfortunately, such sections through the region of the laminæ are rarely satisfactory. The transverse section shown in Photograph 12 cuts the fertile laminæ in a more median plane, so as nearly to miss the groove.

Before further considering the relative positions of the fertile and sterile segments we will complete the description of the latter.

The sterile segment begins to widen out as it passes through the groove of the fertile lamina and spreads out beyond it, as seen in transverse sections of the cone (Photograph 13) into a kite-shaped blade with lateral lobes. The comparison of radial with transverse sections, however, shows that the sterile lamina is really of a very complex form. On its under surface it has a pair of blunt downward projections, placed side by side, which cover the external surface of the fertile lamina next below (see Photographs 10, st.3, and 11, st.). In the opposite direction the apex of the lamina divides into two more slender prolongations, which turn upwards, overlapping the sterile lamina next above, and extending up for a distance equal to several internodes. In this particular the account given in the preliminary paper requires modification, for both the "upturned foliaceous scale" and the "shorter and stouter downward prolongation" there spoken of * are really double. This is seen very clearly in transverse sections, as in that shown in Photograph 12, st. 1, and st. Outside the fertile lamina f^1 , we see two pairs of appendages cut transversely. inner pair, which are the larger, and consist of somewhat large-celled tissue, represent the downward prolongations of the sterile lamina next above; while the outer pair, which are rather smaller, and of denser structure, represent the upward prolongations of the sterile lamina next below. The comparison with the radial section (Photographs 10 and 11) shows clearly that this is the right interpretation (see the

DESCRIPTION OF DIAGRAM.

- The upper part of the diagram shows half the cone in transverse section; the lower part is shown in radial section; the position of the various organs corresponds in the two sections.
- 1. Transverse section. Six complete sporophylls are shown, each with three segments. The three sporophylls to the left are represented as in median section through the fertile segments (f.); the three to the right as in median section through the sterile segments (st.). On each side one sporophyll is shown in detail. s.m., sporangia.
 - Sp. b. One sporophyll, showing the three peltate fertile segments, or sporangiophores, united at the base. Two sporangia are shown inserted on each lamina, and extending almost to the axis. To the outside of each fertile lamina are seen the two downward outgrowths (st.₁) of the sterile segment next above and the apices (st.₂) of that next below (cf. Photograph 12).
 - Sp. a. One sporophyll, showing the three foliaceous sterile segments. Each of these passes through the groove of a fertile lamina, the two lobes of which (f., f.) (bearing sporangia) are seen to the right and left of each sterile lamina where it begins to expand. To the outside are seen the double apices of the sterile segments next below $(st._2)$ (cf. Photograph 13).
 - In the axis the stele, and two verticils of leaf-traces are shown, the inner undivided $(v.b._1)$, the outer after division into four bundles each $(v.b._2)$ (cf. Photograph 2).
- 2. Radial section. The sporophylls are separated from one another by a space which does not exist in nature, in order to show their form more clearly. Each sporophyll (as at Sp.) is drawn on the assumption (probably correct) that the upper segments (f.) are fertile, and the lower (st.) sterile.
 - ph. Base, or phyllopodium, of a sporophyll; f., one of its peltate fertile segments, on which two sporangia are visible; st., a foliaceous sterile segment (cf. Photographs 9-11). Ax, axis; cy., stele. Note the antero-posterior division of the leaf-trace bundles (v.b.) (cf. Photographs 4 and 5). s.m., sporangia.
- The representation, while strictly diagrammatic, is in all essentials true to nature, and is drawn approximately to scale, about four times natural size.

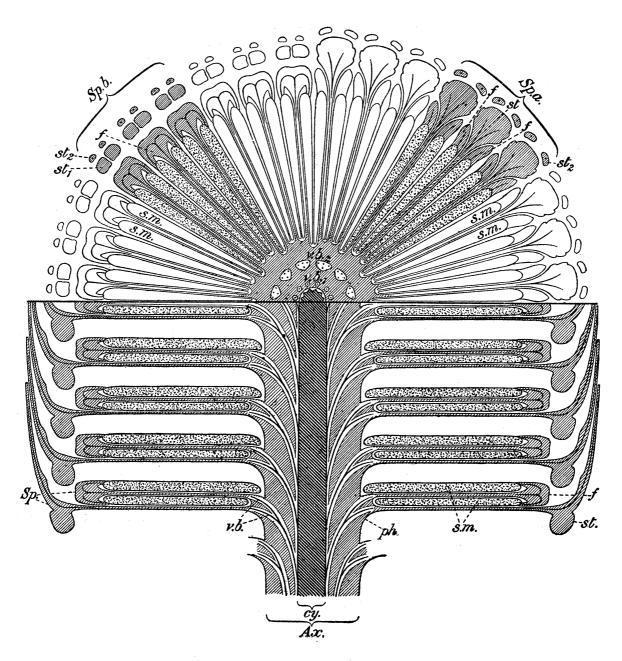


DIAGRAM OF CHEIROSTROBUS PETTYCURENSIS.

diagram, p. 7). With this elaborate system of fertile and sterile laminæ, it is evident that the exterior of the cone was very efficiently protected.

The sterile and fertile segments, as we have seen, are placed alternately one above the other, so that in every vertical series there is an equal number of each kind. In the transverse plane there is no alternation. At the same level all the segments cut medianly are sterile or all fertile (Photographs 12 and 13). It follows from these facts that of the six segments of each sporophyll, either the three upper must be fertile and the three lower sterile, or vice versa. The question whether the upper or lower segments are fertile may seem a simple one to determine, but as a matter of fact it has presented great difficulties, and for a long time it was not possible to obtain direct and conclusive evidence from the material available. The segments are long and slender and in only one instance could the same segment be traced through its whole length from axis to periphery. This was in the case of one of the inferior segments of a sporophyll, shown in the approximately radial section of the basal part of the cone (see Plate 3, photograph 15, and Plate 5, fig. 15A). In this region the sporophylls are comparatively short, and the whole of the segment in question is shown, with only one or two fractures of no importance. Unfortunately, so near the base of the strobilus the form of the segments is not characteristic, so we cannot at once decide the important question, whether this inferior segment was fertile or sterile. There is, however, no indication that any sporangium was attached to it, so the presumption is that it was sterile, though, if this were all, it might be possible to suppose that the sporangial attachments had simply been missed by the plane of section. Happily, we are not left to depend on negative evidence; the important point is, that the sporangium immediately below the segment in question, is distinctly inserted, at its distal end, on a portion of a fertile lamina, which must thus have belonged to the superior segment of the next lower sporophyll (see Plate 5, fig. 15A, a). This evidence is of the greatest value, for in all other cases observed the continuity of the segments is interrupted, and the displacements are too great for any one of them to be traced in a convincing manner. The indirect evidence bearing on the question is comparatively unim-There is no constant difference between the petiolules of the sterile and fertile segments, such as might enable them to be identified at different parts of their course. Where any difference can be recognised the superior petiolules are found to be rather the larger (as seen at the proximal end), and the fertile petiolules rather the larger (as seen at the distal end). This supports the identification of the upper with the fertile segments, but no great stress can be laid on such trifling distinctions.

We shall see below that the evidence from the course of the vascular bundles indicates that the inferior segments probably represent the vegetative part of the sporophyll, just as is the case in *Sphenophyllum Dawsoni*.* Analogies, however,

^{*} WILLIAMSON and Scott, "Further Observations on the Organization of the Fossil Plants of the Coal Measures," Part I., 'Phil. Trans.,' B, 1894, p. 937.

might be cited in support of either view; if we compare our cone with the plant just mentioned, we must expect to find the sporangiophores in the superior position; but in *Cingularia* we find a good example of the opposite arrangement. On the whole, I think, the evidence, though depending chiefly on a single instance, strongly in favour of the conclusion that in each sporophyll the upper segments are fertile and the lower ones sterile. The mode of overlapping of the laminæ also harmonizes best with this interpretation.

ANATOMICAL STRUCTURE.

The Axis.

The axis of the strobilus is traversed by a central cylinder about 2.4 millims, in diameter, of which the wood only is preserved. The structure is dodecarch, the smallest elements occurring at the twelve prominent angles, which are separated from each other by deep furrows (Photographs 2 and 3). Towards the interior the tracheæ increase in size, and become more laxly arranged, having no doubt been intermixed with conjunctive parenchyma, of which little trace has remained. The interior of the xylem is not perfect, but enough remains to show that it extended to the centre, so that no pith existed (Photograph 3). Longitudinal sections, where they pass through one of the projecting angles of the xylem, show the narrow spiral tracheæ at the periphery, proving the centripetal development of the wood (Plate 4, fig. 1).* Advancing inwards from the protoxylem we find the tracheæ reticulately marked (Fig. 1), and further towards the interior they all show several rows of round or elliptical pits, on which, in favourable cases, the border can be detected (Plate 3, photograph 17; Plate 4, fig. 2). Many of the more internal tracheæ are short, with horizontal transverse walls, on which a reticulate thickening is evident in transverse section (see Figs. 3 and 3A), recalling the well-known structure of Lepidodendron selaginoides. The lateral walls of these short tracheides often differ somewhat from those of the long ones, having a reticulate rather than a pitted structure. There are no appreciable remains of phloëm, nor is there, in the axis of the cone itself, any trace of secondary tissues, though, as we shall see, such tissues were formed in the peduncle.

The cortex surrounding the stele has an undulating inner limit, the bays of which correspond to the prominent protoxylem-angles (see Photographs 2 and 3). We will next follow the course of the leaf-trace bundles, postponing the detailed anatomy of the cortical tissues.

* In this case the most disorganized tracheæ lie a short distance within the extreme edge—an appearance which recurs at several points, and which can hardly be explained altogether by deviation of the section from the radial plane. It is probable that after the differentiation of the very first protoxylem-elements one or two tracheæ may have been added to the outside, possibly in connection with the insertion of the leaf-trace bundles. In any case the centripetal development of the primary wood, as a whole, is not affected.

From each of the twelve prominent angles of the stele a single vascular bundle passes outwards, having at first only a slight upward inclination, and bending more sharply upwards as it enters the cortex (see Plate 1, photographs 3 (l. t.) and 5; Plate 4, fig. 4). The insertions of the leaf-traces on the stele form vertical series, the xylem angles running without interruption through the nodes (as in Sphenophyllum), and not forming a reticulum as in Lepidodendron* (see Photographs 4 and 8). The wood thus has the form of a fluted column. This characteristic arrangement is obviously correlated with the superposition of the foliar whorls.† The course of the outgoing leaf-trace extends through two internodes, or rather more, so that the traces of two successive whorls, sometimes with part of a third, appear in the same transverse plane. The existing transverse sections of the cone are really somewhat oblique, the difference in level of two opposite sides nearly equalling the length of an internode. This is a fortunate circumstance, as it enables us to follow the changes which the bundles undergo at every part of their outward course (see Photograph 2). The tangential sections likewise are somewhat inclined to the axis, so that in this view also the whole course of the traces is revealed by comparing the successive members of the same vertical series (see Photograph 8).

The single bundle, which is destined to constitute the vascular supply of one sporophyll, begins to subdivide when about one-third of the way through the cortex (see Plate 1, photograph 2, and Plate 4, fig. 6). The division is into three bundles, lying at first in the same tangential plane. Sometimes one of the two lateral bundles is given off a little before the other. The median bundle is much the largest of the three, for it has to undergo further sub-division. The three bundles gradually diverge from one another, and when about half-way through the cortex the median one divides again, but in a plane at right angles to that of the first division, so that one branch is posterior and the other anterior (see Photographs 2, 5, and 8, Plates 1 and 2; figs. 7, 8, and 9, Plate 4).

The posterior or upper branch is here the larger, for it is this which still has further divisions before it. Almost at the level where the three anterior bundles begin to leave the stem and enter the sporophyll-base, the posterior bundle itself subdivides into three, just in the same way as in the first branching (Photograph 2). There are thus six bundles in all—three lower or anterior, and three upper or posterior. All six enter the base of the sporophyll, as is shown with the greatest clearness in such tangential sections as that represented in Photographs 6 and 7. The three anterior bundles pass out into the three inferior segments, and in like manner the three superior segments (probably the sporangiophores) are supplied by the three posterior bundles.

^{*} Bertrand, 'Remarques sur le Lepidodendron Harcourtii,' 1891. Hovelacque, 'Recherches sur le Lepidodendron selaginoides,' 1892. Renault, 'Tiges de la Flore Carbonifère,' 1879, p. 258.

[†] Cf. Solms-Laubach, 'Fossil Botany,' Engl. Ed., p. 348; "Bowmanites Römeri, eine neue Sphenophylleen-Fructification," 'Jahrbuch der K. K. Geolog. Reichsanstalt, 1895, p. 241.

Irregularities are seldom observed; in one case (slide K, 84°*) only two bundles are present after the first division, where there should normally be three. In the trace immediately outside this only two posterior bundles are visible instead of three, so it seems that at least two successive leaves had this peculiarity, which, however, does not appear in other sections. At the base of the cone, however (Photograph 15, Plate 3), there seems to have been only two bundles (and no doubt the same number of segments) to each lobe.

Elsewhere the sub-divisions of the leaf-trace take place with diagrammatic regularity.

As regards the details of structure of the leaf-trace bundles there is not much to be said. Near the stele the undivided bundles certainly seem to be collateral, for the xylem adheres closely to the inner side of the gap, which has presumably been left by the decay of the phloëm. A little further out, but before the first subdivision, the xylem takes up a more central position, surrounded by thin-walled tissue. Probably this tissue was only in part of the nature of phloëm, the outer zone being parenchymatous (peridesm of Van Tieghem). The distinction can be detected in Plate 4, fig. 6, but it is more marked in the base of the sporophyll (Plate 5, figs. 10 and 11). The presumption, however, is that the leaf-trace bundles, except where still quite close to the central cylinder, had a concentric structure.

The position of the first-formed tracheæ of the bundle is by no means evident, but was most probably central (Figs. 9 and 10). Usually, all the tracheæ are spirally thickened, but in the clearer cases the more central are the smaller, and in the longitudinal section just referred to a lax spiral is seen in the middle of the xylem strand.

I find no difference in orientation or structure between the bundles of the upper and lower lobes, a point to which special attention has been directed. It will be noticed that it is only after all the three bundles for the inferior segments have separated that those for the superior segments are given off. It is this fact which appears to indicate that the lower segments represent the main part of the leaf, just as is the case in the strobilus of *Sphenophyllum Dawsoni*.

The structure of the cortex of the axis is fairly uniform throughout, consisting of slightly elongated, rather thick-walled cells, becoming smaller towards the outside. As seen in transverse section, the cortex appears marked out into areas, each enclosing a bundle, or a group of bundles, belonging to the same leaf-trace (see Photograph 2). The cells forming the boundaries of these areas are slightly compressed.

The most characteristic point in the structure of the cortex is the presence of large elements, with dense brown or black contents (see Fig. 4, ss.). In longitudinal sections we see that they are long sacs, with pointed ends, and are sharply

^{* [}The numbers referring to slides in Mr. Kidston's collection are preceded by the letter K; those referring to my own collection, by the letter S.—Sept. 24, 1897.]

distinguished from the ordinary parenchyma. We may provisionally regard these elements as of the nature of secretory sacs (Fig. 5, ss.). They are most conspicuous in the inner cortical layers. On the exterior the cortex is bounded by a well-defined small-celled epidermis (Fig. 7, ep.).

The Sporophylls.

The bases of the sporophylls consist of tissue quite like that of the cortex of the axis (Photographs 5 and 7). The six vascular bundles in each base are well shown, especially those running to the upper segments (see Plate 2, photograph 7; Plate 5, fig. 10). In each bundle the xylem, which has its smallest elements towards the centre, is surrounded by a very delicate small-celled tissue, which was no doubt the phloëm.* This again is enclosed in a large mass of thin-walled parenchymatous cells. Here, as in the axis, the bundle appears to be concentric, but lies towards the upper surface of the parenchymatous envelope.

The bundles belonging to the lower segments are similar, but in the few cases where their structure can be made out at all clearly, the xylem-group seems to be rather smaller, and the phloëm less well-defined (see Fig. 11). No great stress can be laid on such differences, but so far as they go they support the conclusion that the upper segments most probably supplied the sporangia, which would make a much greater demand on their conducting tissues than would the barren laminæ of the other segments. The tissue of the sporophyll-base is abundantly supplied with "secretory sacs," especially around the vascular bundles.

Nothing need be said as to the anatomy of the petiolules of the segments. Owing to the growth of the sporangia packed between them, they are all more or less compressed, and little structure can be made out. Here and there the vascular bundle running through each petiolule can be traced.

The laminæ, however, are well preserved, and present some characteristic features. We will take the fertile laminæ first.

When the petiolule begins to widen out into the lamina, its vascular bundle at once bifurcates into two diverging branches, lying in the same radial plane (see Plate 5, fig. 12, vb.). Each branch of the bundle again divides, and the four ultimate vascular strands curve sharply back, each running to the base of a sporangium (see Fig. 12, vb'.). The whole arrangement is closely similar to that in a *Calamostachys*† or a *Palæostachya*.

In *Cheirostrobus* each sporangium is seated on a short but definite stalk, which ensheaths its base. Hence, when the stalk is cut tangentially, it appears longer than

- * The structure of the vascular bundles is not unlike that of the foliar bundles in some species of Selaginella. See Harvey Gibson, "Anatomy of the Genus Selaginella," Part 3, 'Annals of Botany,' vol. 11, 1897, Plate 9.
- † WILLIAMSON and Scott, "Further Observations," Part I., plate 81, figs. 29 and 32; also WILLIAMSON, "Organization," Part XI., pl. 54, fig. 23, and Part XV., plate 2, fig. 8.

when the section passes through its median plane (see Plate 2, photographs 9 and 10; Plate 5, fig. 12). It is not easy to fix the limit between the sporangium and its stalk, for the characteristic sporangial wall runs up for a little way over the tissue of the stalk, especially on the side towards the petiolule of the sporangiophore (Fig. 12). There is a considerable resemblance to the mode of attachment of the sporangium in Sphenophyllum Dawsoni and in Bowmanites Römeri.*

The parenchyma of the sporangial stalk is very delicate; that of the peltate lamina itself is formed of large cells, with thicker walls, interspersed with secretory sacs (Photographs 9–12, fig. 12). Some of the elements have the look of stone-cells, but this appearance is probably due to a peculiar alteration in the cell-contents of some of the sacs.

The resemblances between the fertile lamina in *Cheirostrobus* and the peltate scale of a *Calamostachys* are too great to be ignored. In the former the lamina is rather thicker, and the peltate shape less neat; possibly we have here a somewhat more primitive form of the peltate sporangiophore.

The vascular bundle of the sterile, like that of the fertile segment, bifurcates at the base of the lamina, but here the two branches lie in the same transverse plane (Photograph 13). They pass out into the two upturned prolongations, in which they can be recognised both in radial and transverse sections. On the other hand, the blunt, downwardly-directed outgrowths appear to contain no vascular tissue; they consist of rather large-celled parenchyma, with secretory sacs (Photograph 11). The tissue of the main part of the sterile lamina is similar to that of the fertile segment. The upward prolongations contain fibrous sclerenchyma outside the bundle, and towards the apex the fibrous tissue constitutes almost the whole of the organ.

The Sporangia and Spores.

The structure of the sporangia, in spite of their great size, is exceedingly simple. The wall, as preserved, consists of a single layer of cells, except at the point of insertion, where as already pointed out, the stalk passes gradually over into the sporangium. The absolute thickness of the wall is about '025 millim, and is fairly constant in all parts. The constituent cells of the wall are much elongated in the direction of the long axis of the sporangium. Their cell walls are excessively delicate, but are stiffened by buttresses which stand out from the radial walls at right angles, and extend throughout the whole height of the cell, becoming broader towards its inner surface. The buttresses on either side of the same radial wall are usually opposite each other, but sometimes alternate (see Fig. 13). It will be seen that this characteristic structure is precisely the same as that of the sporangial wall of a

^{*} Williamson, "Organization," Part XVIII., plate 27, fig. 16; Williamson and Scott, "Further Observations," Part I., plate 86, fig. 58; Solms-Laubach, "Bowmanites Römeri," plate X., fig. 5.

Calamostachys. The agreement is especially close with C. Ludwigi, CARR, where the cells of the wall have the same elongated form as in Cheirostrobus.*

There is also a close resemblance to the sporangial wall of *Sphenophyllum Dawsoni*. Taken in connection with the whole organization of the sporangiophores, these detailed resemblances to Calamarieæ and Sphenophylleæ seem to me to have an important bearing on the affinities of our fossil. The massive base on which each sporangium is borne, appears to indicate that its development must have been of the "eusporangiate" type, *i.e.*, that a number of initial cells took part in its formation.

The weak mechanical construction of such large sporangia (far larger than any known to us among recent Cryptogams) may seem surprising, but was no doubt compensated for by the way in which the sporangia are densely packed, so as to support each other, the whole mass being held together by the investiture of the peripheral laminæ.

If we confine our attention to the sporangiophores and sporangia, it may be said with confidence that there is no essential difference, so far as these organs are concerned, between *Cheirostrobus* and a Calamarian fructification of the *Calamostachys* type. Taking the position of the sporangiophores into account there is a still more striking analogy with *Palaostachya*.

The spores are of uniform size and structure in all parts of the specimen, including the sporangia at the base of the cone (compare Fig. 14 with Fig. 15B). This specimen therefore affords no evidence of heterospory. The average diameter of the spores, determined by a large number of measurements, is '065 millim. The variations on either side of the mean are inconsiderable, and were no doubt even less in life than they appear in the necessarily somewhat distorted spores of the fossil.

The spores are approximately spherical in form; the membrane generally is thin, but marked by conspicuous thickened ridges, dividing up its surface into four areas. The ridges in all probability correspond to the lines of junction of the four spores of a tetrad; three of the areas would thus have been occupied by the three sister-cells, the fourth being free. The arrangement of the spores would thus appear to have been tetrahedral, but they have not been found actually united in tetrads (see Plate 3, photograph 16; Plate 5, figs. 14 and 15B). No remains of any cellular body within the spore, nor indeed of any cell-contents, could be detected.

In the less well-preserved parts of the specimen the thin membrane of the spores has to a great extent perished, leaving little more than the thickened ridges, which are often partly straightened out, and grouped so as to form an irregular mesh work; the appearance presented in these cases is very different from that of the uninjured spores (see Fig. 12).

As regards the dimensions of the spores, they are much larger than the microspores

* C. E. Weiss, "Steinkohlen-Calamarien," II., in 'Abhandlungen z. Geologischen Specialkarte v. Preussen,' vol. 5, Heft II., 1884, Plate 23, fig. 2, and plate 24, figs. 3, 4, and 5; Williamson and Scott, "Further Observations," part I., 1895, p. 909, plate 81, fig. 31.

of most Lepidostrobi, though not much exceeding those of L. Brownii, and are nearly as large as those of Calamostachys Casheana. They are somewhat smaller than the spores of the homosporous C. Binneyana and than those of Sphenophyllum Dawsoni.

The Peduncle.

The peduncle on which the cone was supported remains to be described. The description will be based in the first instance on the specimen in the Williamson collection and the evidence for the identification of this specimen with *Cheirostrobus* will then be stated. A good description of the general structure of this fragment was given by Williamson in 1872, but he was under the mistaken impression that it might belong to the Burntisland *Lepidostrobus*.*

The diameter of the specimen is about 7 millims, which agrees with that of the axis of the cone. It is traversed by a polyarch stell about 2 millims, in diameter (Plate 3, photograph 18; Plate 6, figs. 18 and 20). The number of prominent xylem-angles varies from twelve to nine in the different transverse sections. When the number is less than twelve we find that one or more of the angles are blunt, and sometimes evidently double, representing a fusion of two prominences (Fig. 20). The interior of the stell is solid, and occupied by intermixed thick-walled and thin-walled elements; the longitudinal sections show that the former are tracheæ, the latter conjunctive parenchyma (Figs. 22 and 23). There is thus no medulla, the wood extending to the centre.

A well-marked zone of secondary tissue is present, the thickness of which varies, both in the different sections and in different parts of the same section (see Photograph 18; figs. 20 and 21). In the section with twelve xylem-angles (Cabinet Number 539) the maximum thickness of the secondary wood is six elements; while in the sections with nine or ten angles it has attained in places to a thickness of ten tracheæ. It is probable that the number of angles increased, and the thickness of the secondary wood diminished, from below upwards; for we know that in the axis of the cone itself (judging from our solitary specimen) the stele was dodecarch, and without any secondary formations.

In all the sections the secondary zone is more or less incomplete, extending round the greater part, but not quite the whole, of the periphery of the stele. It is not limited to the furrows, but extends also round the angles of the primary wood (Fig. 20), though sometimes with a diminished thickness at these points.

In the primary xylem the smallest elements are placed at the prominent angles. Sometimes where an angle is very obtuse, two distinct groups of small tracheæ are present, showing that the angle in this case is really a double one. Radial sections show that the small peripheral elements are spiral tracheæ (Fig. 22), and thus

^{*} WILLIAMSON, "Organization," Part III., p. 297. See Preliminary Paper on Cheirostrobus, Proc. Roy. Soc, vol. 60, p. 418.

represent the protoxylem. Here, as in the axis of the cone, there is some reason to doubt whether differentiation of the xylem began absolutely at the exterior, for sometimes the smallest elements are bounded externally by one or two slightly larger ones, which seem still to belong to the primary wood. In any case the differentiation must have been almost wholly centripetal.

The tracheæ of the interior of the stele are not scalariform, but bear several rows of rounded or polygonal pits, which, as shown in the clearer cases, are distinctly bordered (Figs. 22 and 23). At some places the tapering ends of the tracheides are seen. Some of the more central tracheides are square-ended, but not so commonly as in the axis of the cone. The parenchymatous cells intermixed with the tracheæ are sometimes well preserved. Some of these elements are filled with dark brown contents, and may have been of a secretory nature.

The secondary wood is at once distinguished from the primary by the regular radial seriation of its elements; between the series of tracheæ distinct medullary rays are present (Fig. 21). The true secondary wood is not shown really well in any longitudinal section; so far as can be made out the pits on the radial walls of its elements are transversely elongated, so that there is here an approach to scalariform structure (Fig. 22, x.²).

At some places remains of the cambium can be detected at the exterior of the secondary wood (Fig. 21, cb.). Beyond this we find in the furrows of the stele, groups of large thin-walled elements, recalling those in the phloëm of Sphenophyllum insigne* (Fig. 21, ph.). Longitudinal sections show that these elements were elongated, but no further details can be made out. There is, however, no reason to doubt that they represent a portion of the phloëm of the stele. There is a wide gap between stele and cortex, from which the remainder of the phloëm and anything there may have been of the nature of pericycle has perished. The width of the gap, however, appears to be partly due to shrinkage of the stele, the tissues of which show some signs of shrivelling.

The inner limit of the cortex is undulating, the bays corresponding to the angles of the stele, as in the axis of the cone.

The structure of the cortex is fairly uniform throughout its thickness, without any differentiation into distinct zones. It consists of short-celled parenchyma, in which large elongated elements, containing masses of dark carbonaceous substance, are scattered. In these respects there is a complete agreement with the structure of the axis of the cone.

We now come to an important point,—the course of the leaf-trace bundles.†

In the peduncle the leaf-trace bundles are not so well preserved as in the cone Sometimes we at first only recognise them by gaps in the tissues, but careful observa-

^{*} WILLIAMSON and Scott, "Further Observations," Part 1, Plate 84, figs. 51 and 52.

[†] Cf. WILLIAMSON, "Organization," Part 3, Plate 44, fig. 30, with photographs 4 and 5.

tion, as a rule, reveals the presence of tracheæ within or adjacent to these cavities (see Plate 3, photograph 18; Plate 6, figs. 26 and 27).

In some of the transverse sections (especially C.N. 540) we see the vascular bundles just leaving the stele, and here it is evident that a single strand starts from each angle, except when the angle is really a double one, in which case there are two outgoing strands. Very soon after entering the cortex, however, the outgoing leaf-trace divides; the division, where clearly shown, is triple, the three resulting bundles lying in the same tangential plane. The evidence, however, is not sufficient to prove that this triple division was constant. Probably it was fairly so, for at one place three triple bundles of the same whorl are seen side by side (C.N. 539).

From the comparison of the radial sections it is evident that an antero-posterior division of the trace also took place* (C.N. 543). The transverse sections rarely show this division, but in one place (Plate 5, fig. 17) it is quite clear. The group of bundles corresponds almost exactly to that shown from the axis of the cone in Plate 4, fig. 7. We see the three strands resulting from the first division, and the middle one of the three has just divided again to form an anterior and a posterior branch. So far, then, the course of the bundles in the Williamson specimen appears to agree exactly with that found in the axis of *Cheirostrobus*.

The bases of leaves or bracts are present, and the radial sections show that each of these appendages is bilobed, one lobe being superior or ventral, and the other inferior or dorsal (see Plate 6, figs. 24 and 25; also Williamson's fig. 30 above cited). The lobes were, no doubt, each sub-divided into segments in the horizontal plane (see Photograph 18, figs. 26 and 27; also Williamson's fig. 29), but only the stumps of these segments remain. The lower lobe appears to have been the broader, for at several places in the radial sections it is shown in its full extent, where the upper lobe is either missed altogether, or only partially shown (Figs. 24 and 25). The lower lobe was often, perhaps always, trifid, receiving the three anterior branches of the leaf-trace; the upper lobe appears to have been more frequently bifid, receiving two bundles only (see Photograph 18, and fig. 9), but sometimes this also received three bundles, as shown in Fig. 27. That this is really an upper lobe is shown by the fact that its bundles do not separate until quite near the periphery.

Owing to the paucity of the sections of the peduncle[†] and their frequent obscurity, it has not been possible to work out the course of the bundles with the same minuteness and certainty as in the axis of the cone. Enough, however, is shown to prove that their course and subdivisions follow the same general rules as in the axis, with

^{*} Indicated in Williamson's figure, "Organization," Part 3, Plate 44, fig. 30.

There are seven sections altogether, all in the Williamson collection. Four of these (C.N. 539-542) are transverse; two (C.N. 543 and 544) are approximately radial; and one (C.N. 545) tangential. The last mentioned is too obscure to throw much light on the course of the bundles; where it passes obliquely through the bases of the leaves, however, it shows that at least two bundles entered each lobe, perhaps three (see fig. 19).

the exception that one of the lobes (probably the upper) usually received two bundles instead of three.

The phyllotaxis of the specimen is not perfectly clear, but the arrangement of the leaf-bases, and more especially of the outgoing leaf-trace-bundles, as shown in the tangential section (Fig. 19), is strongly suggestive of superposed verticils. As we know that the number of orthostichies changed between one end of the fragment and the other, we cannot expect great regularity. The transverse sections are slightly oblique; allowing for this, the arrangement of the bundles and leaf-bases which they show is just what would result from a whorled phyllotaxis, and cannot be reconciled with any spiral system (see Fig. 19). That the whorls were superposed is further indicated by the fact that, in transverse sections, a protoxylem-angle, a leaf-trace, and a leaf all lie in the same radial line, where the arrangement is clearly shown.

We will now sum up the points of agreement between the peduncle and the axis of the cone. The chief points are as follows:—

- 1. The polyarch stele with prominent angles, at which the protoxylem is situated. In one section of the peduncle the actual number of angles (12) is identical with that in the cone.
- 2. The internal structure of the stele; the conjunctive tissue intermixed with tracheides; the multiseriate bordered pits on the tracheal walls.
- 3. The structure of the cortex, consisting of a uniform parenchyma, containing secretory (?) sacs.
- 4. The course of the leaf-trace bundles; the first division into three; the anteroposterior division of the middle bundle; the subdivision of its posterior branch.
- 5. The division of the leaf-base into a superior or ventral, and an inferior or dorsal lobe, the former receiving the posterior and the latter the anterior set of bundles resulting from the division of the trace.
 - 6. The subdivision of each lobe into segments.
 - 7. The arrangement of the appendages in superposed whorls.

The agreement is thus so close, and extends to so many points, as to leave no doubt that the Williamson fragment and the actual cone belonged to the same species, especially if we take into consideration their identical dimensions, and the fact that they occur in the same deposit.

In all probability the fragment is the peduncle of a cone. This is suggested by the exactness of the agreement in many points of structure and in dimensions, and especially by the fact that the leaf-bases of the fragment are so closely similar to the sporophyll-bases of the cone. Most probably they were bracts, or sterile sporophylls, rather than vegetative leaves.

An important fact remains which disposes of the only considerable difference in structure between the two specimens, and also raises the probability that the WILLIAMSON fragment is a peduncle almost to a certainty.

The section through the base of the cone (Plate 3, photograph 15) shows the upper

part of the peduncle in connection with it. The wood of this part is shown in tangential section, and is evidently secondary wood, the plane of section missing the primary part. The tracheides agree in size and structure with those of the secondary wood in the Williamson specimen, while the more central primary tracheides are much larger both in peduncle and axis. The medullary rays are exceedingly evident, and can at once be distinguished from the primary conjunctive parenchyma shown in other sections (see Plate 5, fig. 16). Where the fertile sporophylls begin the secondary wood dies out, but the exact level at which it disappears cannot be determined, as the plane of section here passes outside the wood (Plate 3, photograph 18). In some cases the secondary tracheides show a delicate pitting on their tangential walls (Fig. 16, B). We thus see that the peduncle of the actual cone agrees in every respect, including secondary growth, with the Williamson fragment.

So far as can be judged, the secondary zone of the peduncle in connection with the cone is decidedly thicker than in the Williamson peduncle, so they cannot both have belonged to the same specimen. There is therefore a possibility that the strobilus belonging to the separate peduncle may still be found in the Pettycur material.

In the same preparation which shows the base of the cone there is contained an approximately radial section of what appears to be a branching stem. The secondary wood is well shown, and its histological structure agrees closely with that of the peduncle of *Cheirostrobus*, though in the doubtful fragment its development is much greater. The parenchymatous tissues are partly preserved, and contain structures much like the "secretory sacs" of our fossil. I think it not improbable that we have here a fragment of the vegetative organs of the plant to which the new cone belonged, but the specimen is in many respects obscure, and unless it should be possible to obtain additional preparations, no conclusion of value can be drawn from it.

Summary.

- 1. Cheirostrobus Pettycurensis was a pedunculate cone of large size, consisting of an axis bearing numerous crowded verticils of compound sporophylls.
- 2. The sporophylls of successive verticils are superposed; the number in each verticil is twelve.
- 3. Each sporophyll is divided nearly to its base, into an upper (ventral or posterior) and a lower (dorsal or anterior) lobe; each lobe is deeply sub-divided in a palmate manner into segments, of which, as a rule, there are three to each lobe. In the sporophylls at the base of the cone, and in the bracts of the peduncle the number of segments is sometimes reduced.
- 4. Each segment consists of a long and slender horizontal stalk or petiolule bearing a lamina at its distal end.
- 5. Of the segments of each sporophyll half are fertile and half sterile. Most

- probably it is the three upper segments in each case which are fertile, and the three lower which are sterile.
- 6. The lamina of a fertile segment or sporangiophore is thick and peltate, and bears the sporangia on its adaxial surface, as in *Calamostachys* or *Equisetum*.
- 7. The sporangia are of great length, extending back nearly or quite to the axis. Each sporangiophore bears as a rule four sporangia, and consequently there are usually twelve sporangia in all to each sporophyll.
- 8. The structure of the sporangial wall is identical with that of a Calamostachys or of Sphenophyllum Dawsoni.
- 9. The spores are uniform in size and structure in all parts of the specimen, including the sporangia at the base of the cone. Their average diameter is '065 millim.
- 10. The laminæ of the sterile segments overlap those of the sporangiophores. The sterile lamina is of complex form, having two long upturned apices, and two shorter downward prolongations.
- 11. The petiolules and sporangia are closely packed together, and the surface of the cone completely invested by the fertile and sterile laminæ.
- 12. Axis and peduncle are traversed by a polyarch stele, with solid, centripetal primary wood. In the axis the number of xylem-angles is twelve, gradually sinking to nine in the peduncle.
- 13. A single leaf-trace bundle leaves each angle of the stele for each sporophyll.

 The leaf-trace subdivides in both planes on its way through the cortex, to supply the ventral and dorsal segments of the sporophyll.
- 14. In the peduncle, as distinguished from the axis, secondary tissues were formed by a normal cambium.

It may be well to repeat here the provisional generic and specific characters as given in the preliminary paper.

Cheirostrobus, gen. nov.

Cone consisting of a cylindrical axis, bearing numerous compound sporophylls, arranged in crowded many-membered verticils.

Sporophylls of successive verticils superposed.

Each sporophyll divided, nearly to its base, into an inferior and a superior lobe; lobes palmately sub-divided into long segments, of which some (probably the inferior) are sterile, and others (probably the superior) fertile, each segment consisting of an elongated stalk bearing a terminal lamina.

Laminæ of sterile segments foliaceous; those of fertile segments (or sporangiophores) peltate.

Sporangia, large, attached by their ends remote from the axis to the peltate laminæ of the sporangiophores.

Sporangia on each sporangiophore, usually four.

Spores very numerous in each sporangium.

Wood of axis polyarch.

C. Pettycurensis, sp. nov.

Cone, 3-4 centims in diameter, seated on a distinct peduncle. Sporophylls, twelve in each verticil.

Each sporophyll usually sexpartite, three segments belonging to the inferior, and three to the superior lobe.

Sporangia densely crowded.

Spores about '065 millim. in diameter.

Horizon: Calciferous Sandstone Series.

Locality: Pettycur, near Burntisland, Scotland. Found by Mr. James Bennie, of Edinburgh.

Affinities of Cheirostrobus.

The cone which has been described is an isolated specimen; apart from the peduncle, and the doubtful fragment of stem referred to on p. 19, we have not the slightest clue, as yet, to the nature of the vegetative organs of the plant which bore it. The one part which we possess, however—the fructification—is happily the most important from a taxonomic point of view; so, considering the perfection of its preservation, we may profitably enter on a discussion of the probable affinities of the fossil.

The first question which presents itself is this: was Cheirostrobus a Cryptogam or a Phanerogam? The latter alternative is not one to be rejected off-hand; the fructification might quite conceivably have been the male cone of a Gymnosperm. The remarkable morphology of the sporophylls, in fact, at once suggests a comparison with certain Coniferous strobili. The superior and inferior lobes of the sporophyll, especially if, as is almost certainly the case, the upper segments be the sporangiophores, may well be compared to the ovuliferous and carpellary scales of the Abietineæ. It is true that this would be to compare a male with a female strobilus; but it might be theoretically possible to suppose that an organization now limited to flowers of one sex might in early geological times have extended to those of the other also.

It is not, however, probable that this comparison amounts to anything more than a remote analogy. We can hardly compare an early Palæozoic fossil directly with a group, which, so far as we know, only makes its appearance well on in the Secondary period. The Gymnosperms known to us from the older rocks offer no definite points of analogy with *Cheirostrobus*.*

^{*} Renault's figure of the male cone of *Cordaianthus Penjoni*, shown in longitudinal section ('Tiges de la Flore Carbonifère,' 1879, pl. 16, fig. 13), suggests at first sight a certain analogy with *Cheirostrobus*, but the resemblance is probably merely a superficial one.

The anatomical structure appears to negative the idea of Gymnospermous affinities. The polyarch centripetal wood is essentially a Lycopodiaceous character, and we have at present no evidence for the occurrence of this type of structure in any Gymnosperm, whether recent or fossil. It seems, therefore, that the alternative of Phanerogamic affinities must be eliminated, from want of evidence, and that the allies of *Cheirostrobus* must be sought among Vascular Cryptogams.

Cheirostrobus is a highly organized strobilus, more complex, perhaps, than that of any other Pteridophyte known to us, whether recent or fossil. We should therefore naturally look for its affinities among the strobiloid groups of Cryptogams, a limitation which would appear to exclude the Filicineæ from our consideration. It is not certain, however, that the possibility of Fern-relationship can be thus summarily dismissed. If we are justified in the belief that Filicineæ gave rise to Gymnosperms of the Cycadean type,* we must assume that at some stage or other, certain families of the Fern phylum acquired a cone-like fructification. In the female flower of Cycas we have still, perhaps, a reminiscence of such a transition. In the Pettycur deposit we have found in Heterangium Grievii, a plant which, according to its vegetative structure, shows a divergence from a Fern-type in a Cycadean direction. The idea crossed my mind whether there might not be something in common between Cheirostrobus and Heterangium. Certain points in the structure of the wood and cortex even seemed to suggest such a comparison, and the very complex form of the sporophylls in our cone was rather favourable to the idea of Fern-affinities. hypothesis, however, had to be rejected almost as soon as formed; in particular, the superposed verticils of *Cheirostrobus* appeared fatal to it, and generally the sum of characters pointed too decidedly in other directions.

Cheirostrobus combines in a striking manner the characters of three of the main divisions of Pteridophytes: the Equisetineæ, the Lycopodineæ, and the Sphenophylleæ. With the Equisetineæ (taking the group in the wide sense, as co-extensive with the Calamarieæ of Weiss) there is the closest agreement in the organization of the sporangiophores and sporangia. The resemblance of the fertile segments of Cheirostrobus to the peltate scales of a Calamostachys or Palæostachya is most striking, extending even to such details as the distribution of the vascular bundles in the lamina.

So, too, with the sporangia; in number, mode of attachment, and histological structure, they are absolutely identical with those of *Calamostachys*, and even their greatly elongated form can be paralleled from plants of that group.‡

- * See Williamson and Scott, 'Further Observations,' Part III., p. 769. D. H. Scott, 'Address to Botanical Section of Brit. Association,' 1896, p. 16; also Warming, 'Systematic Botany,' Engl. Ed., p. 252; Solms-Laubach, 'Bot. Zeitung,' 1893, p. 207. [The discovery by Ikeno and Hirase, of the multiciliate spermatozoids of *Cycas* and *Ginkgo* strikingly confirms this conclusion. June 25, 1897.]
- † Compare especially Williamson, 'Organisation,' Part XV., pl. 2, fig. 8; Renault, 'Ann. des Sci. Nat.,' ser. 6, vol. 3, pl. 2, fig. 5, with our photographs 9-12, and fig. 12.
- ‡ As in Calamodendrostachys Zeilleri, Renault, 'Flore fossile d'Autun et d'Epinac,' Part II., Plate 60, figs. 3-8.

These points of agreement are far too numerous and exact to be passed over, and cannot readily be explained otherwise than by real affinity.

The resemblances to Lycopodineæ are limited to the anatomy, but, so far as they go, are striking enough. The general structure of the polyarch stele with centripetal wood is suggestive of a Lepidodendron, though the agreement does not extend to details. The principal differences consist in the straight vertical course of the protoxylem-angles, which do not form a network as in Lepidodendron, and in the pitted, as distinguished from scalariform tracheæ.* The anatomy of the central cylinder is, at any rate, sufficient to prove that we have not to do simply with a Calamarian cone.

It is with the Sphenophylleæ that the points of agreement are most numerous. They were briefly enumerated in the preliminary paper,† but it is necessary to recapitulate them somewhat more fully:—

- 1. The arrangement of the appendages in superposed verticils is a striking point of resemblance to Sphenophyllum, in which genus the fact of superposition is well established for the vegetative region, and indeed appears to be necessarily correlated with the anatomical structure.‡ Whether the superposition extended to the bracts of the strobilus in Sphenophyllum is somewhat doubtful. Count Solms-Laubach finds that this was the case in his Bowmanites Römeri, and thinks it may also have been so in the other fructifications of the family.§ The fact that the number of members in a whorl is a multiple of three (12 in the cone, diminishing to 9 in the peduncle) also recalls Sphenophyllum, though in Cheirostrobus these numbers do not bear the same relation to the anatomical structure as in that genus.
- 2. The palmatifid segmentation of the foliar appendages is a point in common with many species of *Sphenophyllum*, where every degree of such segmentation is found in many species, e.g., S. tenerrimum, S. cuneifolium.
- 3. The sub-division of the sporophyll into inferior and superior lobes, which are respectively sterile and fertile. As shown above, all the indications point to the superior segments being the fertile ones, though this could only be proved directly in a single case. Assuming that this is so, we have a remarkable agreement between Cheirostrobus and Sphenophyllum Dawsoni, or cuneifolium, in which the sporangio-phores have the position of superior or ventral lobes of the bracts—a view of their nature which was taken by M. Zeiller; the comparison may, of course, be extended

^{*} The very prominent angles of the primary wood, giving it a stellate transverse section, are not usually so marked in the *Lepidodendrew*, but can be paralleled in the axis of *Lepidostrobus Brownii*. See Bower, 'Annals of Botany,' vol. 7, 1893, Plate 16, fig 3a.

[†] Loc. cit., p. 423.

[‡] Solms-Laubach, 'Fossil Botany,' Eng. Edit., p. 348; Zeiller, 'Etude sur la constitution de l'appareil fructificateur des Sphénophyllum,' Mém. de la Soc. Géol. de France; 'Paléontologie,' Mém. 11; Renault, 'Cours de Bot. Fossile,' vol. 4 p. 29, 1885.

^{§ &#}x27;Bowmanites Römeri, eine neue Sphenophylleen-Fructification,' p. 242.

^{||} Loc. cit., p. 37.

to Bowmanites Römeri of Count Solms-Laubach. In Cheirostrobus the sterile and fertile segments are on so equal a footing that there can scarcely be a doubt as to the foliolar nature of the sporangiophores, and this, if our view of their position be correct, tends strongly to confirm M. Zeiller's interpretation in the case of Sphenophyllum. If, on the other hand, the evidence had pointed to the lower segments of the sporophyll in Cheirostrobus being the sporangiophores, we should then have had an analogy with Cingularia, a comparison which occurred to several botanists to whom I communicated my first observations. In Cinqularia, according to the researches of Weiss, each whorl of sporangiophores is placed immediately below a whorl of sterile bracts, and in close contact with them. Cingularia agrees with our cone in having the members of the verticils superposed; in other respects, however, it is very different, notably in the form of the sporangiophores, which are not peltate, but strap-shaped, bearing the sporangia on their lower surface. I do not think it necessary to pursue the comparison further, until there is some better evidence for the relationship of this fossil to our cone. The affinities of Cingularia itself are likely to remain dubious, unless specimens with structure preserved should be found.*

- 4. The sporangiophores themselves, with the sporangia attached to a laminar enlargement at the distal end, are quite comparable to those of *Bowmanites Römeri*, Solms, in which each sporangiophore bears two sporangia.† The latter species, so far as this character is concerned, holds an intermediate position between *Sphenophyllum Dawsoni* and *Cheirostrobus*, which, in its turn, connects *B. Römeri* with *Palæostachya* and *Calamostachys*.
- 5. In the structure of the sporangia the agreement with Sphenophylleæ, and especially with *Sphenophyllum Dawsoni*, is as marked as with the Calamarian fructification.‡
- 6. The course of the leaf-trace bundles, their insertion on the prominent angles of the primary wood, and their repeated subdivision within the cortex, to supply the lobes and segments of the foliar organs, are strongly suggestive of Sphenophyllum. It was this character more than any other which led to the hypothesis of an affinity with Sphenophyllum, at a time when the peduncle only of Cheirostrobus was known to me. As regards the branching of the leaf-trace in one plane, S. quadrifidum and S. Stephanense, investigated by M. Renault, may be cited for comparison, while for the antero-posterior division we have a good analogy in the bundles supplying the bracts and sporangiophores of S. Dawsoni.

^{*} Weiss, 'Steinkohlen-Calamarien,' Heft 1, 1876, pp. 88-102, Plates 6-9; Solms-Laubach, 'Fossil Botany,' p. 334.

[†] Cf. Solms, Bowmanites Römeri, Plate 10, figs. 4 and 5.

[‡] Cf. Solms, loc. cit., p. 237.

^{§ &#}x27;Brit. Assoc. Report,' 1896, p. 1024.

^{| &#}x27;Ann. des Sci. Nat., Bot., 'series 6, vol. 4, Plate 7; 'Cours de Bot. Fossile,' vol. 2, Plates 14 and 15.

WILLIAMSON and Scott, 'Further Observations,' Part 1, p. 937, Plate 85, figs. 55 and 56.

7. The details of the structure of the vascular cylinder offer various points of resemblance to Sphenophyllum. The polyarch character is a difference, but not an insurmountable one. In some species of Sphenophyllum, e.g., S. plurifoliatum and S. insigne, the stele is simply triarch; in others, as S. Dawsoni and the French forms, it appears to be hexarch. In Cheirostrobus we have the numbers 9 and 12. The vertical course of the xylem-angles agrees with Sphenophyllum rather than with Lepidodendreæ; of the distribution of the secondary tissues in the peduncle the same may be said; the pitted tracheæ are quite similar to those of most species of Sphenophyllum of which the anatomy is known, though they differ from those of the contemporary S. insigne. In a word, the anatomy of the axis and peduncle is essentially that of a polyarch Sphenophyllum.

Taking all the characters collectively, it seems clear that *Cheirostrobus* has more in common with *Sphenophyllum* than with any other known group, recent or fossil, and that *Sphenophyllum* is thus no longer left perfectly isolated in the Vegetable Kingdom. At the same time, I do not consider the affinity between the two genera a very close one. If we regard the known Vascular Cryptogams as representing four main stocks or phyla—Filicineæ, Lycopodineæ, Equisetineæ, and Sphenophyllineæ, then we may fairly place *Cheirostrobus* in the last of the four series. Within the series Sphenophyllineæ, however, we must, I think, regard *Cheirostrobus* as the type of a new *family*, as distinct perhaps from that of *Sphenophyllum* as the Psiloteæ are from the Lycopodieæ.

As regards the question of heterospory, no profitable comparison can be drawn between *Cheirostrobus* and *Sphenophyllum*, for in neither case is the evidence by any means decisive. Our solitary specimen of the former shows only one kind of spore, and though it includes the base of the cone, where macrospores might, from analogy, be expected to occur, it is manifest that no conclusion can be drawn one way or the other from such slender evidence.

As regards Sphenophyllum, there is a fairly strong presumption that S. Dawsoni, the best-known fructification, was homosporous, for here a considerable number of specimens have been examined* without finding more than one kind of spore. In text-books, it is customary to assert positively that Sphenophyllum was heterosporous.† This assertion rests on M. Renault's interpretation of a single specimen, an interpretation which was always doubtful, and which he has now himself withdrawn.‡ It is true that M. Renault still inclines on other grounds to regard Sphenophyllum as heterosporous, but the remaining evidence is of an altogether indecisive character.

Having dealt with the relation of Cheirostrobus to Sphenophyllum, something

^{*} WILLIAMSON and Scott, 'Further Observations,' Part 1, p. 939.

[†] See, for example, Van Tieghem, 'Traité de Botanique,' 2nd ed., p. 1444; Warming, 'Systematic Botany,' Engl. Ed., p. 233; Schimper u. Schenk, 'Palæophytologie,' p. 178; Goebel, 'Grundzüge der Systematik,' p. 216.

^{‡ &#}x27;Flore Fossile d'Autun et d'Epinac,' Part 2, 1896, p. 158.

remains to be said on the broader question of the relation of the Sphenophylleæ to other Vascular Cryptogams. That Sphenophyllum itself combines in certain respects Equisetaceous with Lycopodiaceous characters has long been recognized.* Schenk and Van Tieghem have dwelt more particularly on the points which it has in common with the latter—Stur, and more recently Potonié, on those which it shares with the former. Sphenophyllum approaches the Equisetineæ in its whorled leaves and bracts, resembling Bornia, Sterne, in particular, in the superposition of the verticils, and in the sometimes forked leaves; the fructifications also have something in common with those of Calamarieæ, the resemblance, so far as the sporangiophores are concerned, being most marked in the Bowmanites Römeri of Solms-Laubach.

The points in common between *Sphenophyllum* and Lycopodineæ are mainly anatomical—the centripetal primary wood being the chief resemblance. The agreement in vascular structure is most striking with the family Psiloteæ.

Curiously enough the resemblances in both directions are accentuated in Cheirostrobus. The marked Calamarian features have been sufficiently dwelt on above (p. 22). They are far too strong to be ignored. On the other hand, the structure of the stele is distinctly Lepidodendroid, in spite of the differences in detail already pointed out.

We may attempt to estimate the significance of these twofold resemblances as follows:—

Cheirostrobus is a more ancient form than the Sphenophylleæ with which we are best acquainted, for we know nothing as yet of the fructification of its contemporary, S. insigne. Yet it is highly complex, perhaps more so than any Calamarian, and certainly more so than any known Lycopod. As we have seen, it combines the characters of the two groups in a striking way. We may hazard the inference that Cheirostrobus as well as Sphenophyllum sprang from a very old stock, which existed prior to the divergence of the Lycopods and Calamarians. This common stock survived for a certain period side by side with these two divergent branches—between them, as it were. Sphenophyllum is a group which had advanced very far along this third line of descent, so that its common characters with the other lines have become comparatively obscure. Cheirostrobus has retained more of the common character, though reaching a high degree of complexity on its own lines.

This interpretation is of course highly hypothetical, but the fact stands firm that this early type of cone, while having much in common with *Sphenophyllum*, is at once more Calamarian and more Lycopodiaceous in character than that genus.

It must be remembered that in discussing the fructification of Sphenophyllum we are in some danger of generalizing from too few examples. The type of S. Dawsoni

^{*} See Zeiller, "Bassin Houiller de Valenciennes-Flore Fossile," 1888, 'Texte,' p. 406.

[†] See Potonié, "Die Beziehung der Sphenophyllaceen zu den Calamariaceen," 'Neues Jahrbuch für Mineralogie, &c.,' vol. 2, 1896, p. 141. The author lays special stress on the comparison with *Bornia*, for which *Asterocalamites*, Schimper, and *Archaeocalamites*, Stur, are synonyms.

and that of Bowmanites Römeri are fairly well known, but there can be no doubt that other forms of strobilus existed within the group. Thus, Mr. Kidston showed me a fructification of S. majus in his collection, in which the sporangia are distinctly grouped in fours. In S. trichomatosum, on the other hand, they appear to be single and axillary, though the possibility of a short pedicel having been present is not excluded. Evidently the range of variation within this so-called genus was very considerable. It is by no means certain that the simpler forms of fructification in Sphenophyllum were the more primitive. The analogy of Cheirostrobus rather points the other way, for here the sporangiophores are complex organs, bearing several sporangia, while at the same time they still show a marked similarity to the sterile segments of the sporophyll. Possibly we may regard the unisporangiate pedicels of Sphenophyllum Dawsoni as due to reduction, accompanied perhaps by chorisis, as there are two pedicels to each bract.

It is evident that the comparison with *Cheirostrobus* is likely to have a considerable influence on our views of the morphology of the Equisetineous strobilus; the apparent resemblance to *Palæostachya* has already been pointed out. This is a subject, however, which it would be premature to pursue further on the present occasion.

The fructifications of the typical Lycopodineæ, represented by Lepidostrobus, Lycopodium, and Selaginella, have little in common with those of the Sphenophyllineæ. On the other hand, the Psiloteæ deserve consideration from this point of view. It is not impossible that the synangium of Psilotum or Tmesipteris may represent a ventral sporangiophore with its sporangia, comparable to a fertile segment of the sporophyll in Sphenophyllum or Cheirostrobus. Such a conception appears to be quite consistent with the relative position of the parts, and with the course of the vascular bundles, and would tend to reconcile some at least of the divergent views which have been held as to the morphology of the Psilotaceous synangium.*

The Psiloteæ are undoubtedly highly modified plants, very remote from the ancient Sphenophyllineæ, but anatomically they have much in common with them, while they diverge very widely from the typical Lycopods.

The sub-division of the sporophyll in *Cheirostrobus* into fertile and sterile segments, of which, in all probability, the fertile are the superior in position, offers an obvious analogy with the Ophioglosseæ. A frond of *Ophioglossum palmatum* or some forms of *O. pendulum*,† for example, might be compared with a sporophyll of *Cheirostrobus*. I do not myself recognize anything more than an analogy here, but those authors who lay stress on the comparison of Ophioglosseæ with the Lycopods in general,‡ or with the Psiloteæ

^{*} Cf. F. O. Bower, "Studies in the Morphology of Spore-producing Members—Equisetinese and Lycopodinese," 'Phil. Trans.,' B, vol. 185 (1894), p. 539.

[†] F. O. Bower, 'Spore-producing Members,' Part II., 'Ophioglossaceæ,' 1896, Plates 8 and 9.

[‡] F. O. Bower, 'Ophioglossaceæ.'

in particular,* may not improbably regard *Cheirostrobus* as affording support to their views. M. Zeiller has already suggested on similar grounds the possibility of an affinity between *Sphenophyllum* and the Ophioglosseæ.†

To discuss these possibilities at length would carry us too far: the conclusion which I draw from the investigation of *Cheirostrobus*, is that this ancient form is most naturally placed in the same main division of Pteridophyta with *Sphenophyllum*, hitherto an isolated group. The characters of the new genus throw great light on those of its ally, and lead us to regard the Sphenophyllineæ as representing a generalized type, combining many of the features of Equisetineæ and Lycopodineæ, and indicating the common origin of these two series.

I cannot bring this memoir to a conclusion without again expressing my warm gratitude to my friend Mr. R. Kidston, to whom I owe my knowledge of the existence of his unique specimen, and the opportunity of investigating it.

The additional sections which I had prepared from the original block were cut for me by Mr. F. Chapman.

The illustrations to this paper are partly photographic, the micro-photographs having been taken for me direct from the sections by Dr. E. C. Bousfield. The other figures are from camera-lucida drawings by my assistant, Mr. W. C. WORSDELL.

The diagram on p. 7 was prepared for me by Mr. J. Allen, from a rough sketch by Mrs. D. H. Scott.

EXPLANATION OF PLATES 1-6.

Plates 1-3.—Photographs from the actual sections, taken by Dr. E. C. Bous-FIELD. Many require to be examined with a lens.

PLATE 1.

Photograph 1. Transverse section of the whole cone. In the middle is seen the axis, surrounded by the flattened mass of sporangia and sporophylls. st., a sterile lamina, marking limit of specimen on the left; on the right the displaced sporangia, sp., extend to the broken edge; l., limit of specimen towards top of figure; Lep., foreign body (Lepidodendroid cortex) limiting the specimen below. $\times 1\frac{1}{2}$ diam. Slide K, 84A (see p. 2).

^{*} See Solms-Laubach, "Aufbau des Stockes von Psilotum triquetrum"; 'Ann. du Jard. Bot. de Buitenzorg,' vol. 4, p. 185, 1884.

[†] Loc. cit., p. 37,

- Photograph 2. Axis, enlarged, from same preparation. In the middle is the dodecarch stele. One complete whorl of twelve leaf-traces is shown, with parts of others. The successive divisions of the leaf-trace bundles can be followed. l.t.¹, trace just divided into three; l.t.², trace showing antero-posterior division of median bundle; l.t.³ (in outer whorl), same division more advanced; s.b., sporophyll-bases; s.b.¹, shows the three posterior bundles entering the sporophyll. The spaces between the segments are packed with sporangia. × about 8 diam. Slide K, 84A (see pp. 3 and 10).
- Photograph 3. Central part of axis, from another transverse section. px, one of the twelve protoxylem-angles of the stele; l.t., a leaf-trace bundle passing out from one of the angles; l.t., another leaf-trace, which has already divided into three. Note that the tracheæ extend to the centre of the stele. \times 24 diam. Slide S, 519 (see p. 9).
- Photograph 4. Radial section of cone, showing axis, bearing sporophylls, with sporangia. pet., one of the petiolules; s.l., laminæ of the sporophyll-segments; sp., the radially elongated sporangia. $\times 2\frac{1}{2}$ diam. Slide K, 85 (see p. 4).
- Photograph 5. Part of the same section, enlarged. stele, central cylinder of the axis. To the right several bases of sporophylls are shown, each dividing into an upper (sup.) and a lower (inf.) lobe. The antero-posterior division of the bundle supplying the lobes is also seen. pet., one of the petiolules belonging to the superior lobe of a sporophyll; sp., sporangia, packed between the sporophyll-bases and their segments. × about 8 diam. Slide K, 85 (see p. 4).
- Photograph 6. Tangential section of cone, passing through the sporophyll-bases, s.b. Fourteen verticils are shown. Towards the bottom the sporophylls are seen breaking up into segments. s.l., laminæ of sporophyll-segments, at periphery of cone. Between the laminæ and the leaf-bases the section passes through the petiolules and sporangia. × about 2 diam. Slide S, 528 (see pp. 3, 4 and 12).

PLATE 2.

Photograph 7. From the same tangential section as Photograph 6, enlarged, showing sporophyll-bases of six successive verticils. s.b.¹, sporophyll-base, showing the six bundles, three above and three below; it is coherent below with the adjacent sporophyll on the left; the two left-hand segments of the latter are seen separating, as the plane of section passes outwards. s.b.², sporophyll cut through at the level where the lower segments begin to separate; s.b.³, separation of segments more advanced; s.b.⁴, still more so. On either side petiolules intermixed with sporangia are seen. × about 8. Slide S, 528. (See pp. 4 and 12).

- Photograph 8. Tangential section, passing through the cortex of axis, showing the leaf-trace bundles at various points of their outward course. The vertical series, l.t., is in accurately tangential section, but the plane of section passes slightly outwards, from below upwards. Hence the bundles at the bottom of the figure are still undivided, while those further up are seen undergoing their successive divisions. The uppermost trace is in the same stage of division as that shown in Plate 4, fig. 8. Other leaf-traces and the bases of sporophylls are seen in oblique section. Outside the axis, the section passes through petiolules (pet.) and sporangia. × nearly 4 diam. Slide S, 520. (See p. 10).
- Photograph 9. Radial section through the outer part of cone, showing the attachment of the sporangia to the peltate laminæ of the fertile segments or sporangiophores. $st.^1$, sterile segment (partly shown); pet., its petiolule; $st.^2-st.^4$, other sterile segments, alternating with the fertile segments, f^2-f^5 ; sp., sp., the two sporangia attached to the laminæ of the fertile segment f^3 ; f^4 shows the attachments of three sporangia. To the left are seen the apices of lower sterile laminæ. \times about 10. Slide S, 521. (See pp. 4 and 12).
- Photograph 10. Similar section to last, showing better the alternation of sterile $(st.^1-st.^3)$ and fertile (f^1-f^4) laminæ. At $st.^3$, the form of the sterile lamina is well shown. The insertion of the sporangia on the fertile laminæ is also shown. \times about 10. Slide K, 87. (See pp. 5 and 12).
- Photograph 11. Another radial section, showing the form of a sterile lamina (st., st.) specially well. Note the stout downward protrusion, overlapping the fertile lamina f, and the thinner upturned apex, both of which are double, as shown in Photograph 12. a., attachment of one of the sporangia to a fertile lamina. \times about 12. Slide K, 87. (See p. 5).
- Photograph 12. Transverse section from the periphery of the cone, passing medianly through two fertile laminæ, f. and f. showing their sporangia. st. the two downward protrusions belonging to the sterile lamina next above f.; st., the two apical outgrowths belonging to the sterile laminæ next below f. (cf. Photographs 10 and 11). \times about 16. Slide K, 84B (see pp. 4 and 5).

PLATE 3.

Photograph 13. Similar transverse section to Photograph 12, but passing medianly through the *sterile* laminæ, st. The apices of others are shown in transverse section. f., f., the two lateral lobes of a fertile lamina; through the groove between them the sterile segment passes out. The insertion of the sporangia is clear (cf. Photograph 11). × about 16. Slide S, 519 (see pp. 4 and 5).

Photograph 14. Tangential section across the petiolules (pet.), the vertical series of

- which are evident. l., l., laminæ at the periphery, cut obliquely. Note the closely-packed sporangia, twice as numerous as the petiolules, and therefore four times as numerous as those of the fertile segments. $\times 3\frac{1}{2}$. Slide S, 525 (see p. 4).
- Photograph 15. Approximately radial section from the base of the cone. The section becomes decidedly tangential towards the top and right-hand side. *l.*, laminæ at periphery. *s. inf.*, inferior segment of a sporophyll, the only one which can be traced through its whole length (*cf.* Plate 5, fig. 15A). x. *2, secondary wood of peduncle (*cf.* Plate 5, fig. 16). \times about 3. Slide K, 88A (see p. 8).
- Photograph 16. Spores from middle part of cone. × about 110 (see p. 14).
- Photograph 17. Tracheides from interior of primary wood, to show bordered pits, b.p. × about 200. Slide K, 85 (see p. 9).
- Photograph 18. Transverse section of peduncle (Williamson specimen). stele, central cylinder, with nine xylem-angles. l.t., leaf-trace before dividing; l.t.¹, l.t.¹, forking bundles, derived from division of leaf-trace. Het., foreign body (Heterangium cortex). × about 8 (see p. 15). C.N. 541.
 - Plates 4-6.—Figures from camera-lucida drawings by Mr. W. C. Worsdell.

PLATE 4.

- Fig. 1. Part of an approximately radial section, passing through an angle of the wood. px, disorganized spiral or annular tracheides of the protoxylem; x., more densely spiral tracheides at the extreme angle; x., tracheides of the more internal wood. \times 390. Slide S, 521 (see p. 9).
- Fig. 2. Pitted tracheide from the interior of the wood, shown in a radial section.

 The outline of an adjacent thin-walled element is shown. × 200. Slide

 K, 85 (see p. 9).
- Fig. 3. Short reticulate tracheide from the interior of the wood, seated on another, trumpet-shaped, tracheide. × 200. Slide K, 85 (see p. 9).
- Fig. 3A. Three tracheides from the interior of the wood, seen in transverse section, showing the reticulate transverse walls. × 200. Slide S, 519 (see p. 9).
- Fig. 4. Part of a transverse section, showing one of the angles of the wood and a portion of the inner cortex. px, protoxylem-group; l.t., leaf-trace bundle passing out from the angle of the stele; ss., ss., "secretory sacs" in the inner cortical tissue (cf. Photograph 3). \times 85. Slide K, 84A (see pp. 10 and 11).
- Fig. 5. Part of the inner cortex, in radial section. ss., ss., "secretory sacs," imbedded in the cortical parenchyma. × 85. Slide K, 85 (see p. 11).
- Fig. 6. Group of three bundles, resulting from the first division of a leaf-trace, seen in transverse section, from the middle part of the cortex. The lower side of the figure is towards the exterior of the axis. med., median bundle;

- x., its xylem; ph., its phloëm; chiefly preserved on the outer side; lat., lat., the two lateral bundles of the trace (cf. Photograph 2, l.t.). \times 130. Slide S, 519 (see p. 10).
- Fig. 7. Group of four bundles, resulting from the first and second divisions of a leaf-trace, seen in transverse section, from the outer part of the cortex. ant., anterior median bundle; post., posterior do. do.; the posterior bundle is beginning to divide further. lat., lat., the two lateral bundles of the trace; ep., epidermis of axis (cf. Photograph 2, l.t.³). × 35. Slide S, 519 (see p. 10).
- Fig. 8. Group of four bundles, resulting from the first and second divisions of a leaf-trace, seen in tangential section of the cortex. *ant.*, anterior median bundle; *post.*, posterior do., do.; *lat.*, *lat.*, the two lateral bundles of the trace. × 57. Slide K, 86 (*cf.* Photograph 8), (see p. 10).
- Fig. 9. Antero-posterior division of the median bundle of a leaf-trace, seen in radial section of the cortex. ant., anterior bundle; post., posterior bundle. They unite below. × 85. Slide K, 85 (cf. Photograph 5), (see p. 10).

PLATE 5.

- Fig. 10. One of the upper or posterior bundles in the base of a sporophyll, seen in transverse section, *i.e.*, in tangential section of the whole cone. *x.*, xylem of bundle, with the smallest elements towards the centre; *ph.*, phloëm, surrounding the xylem; *pc.*, pericyclic or peridesmic tissue. × 390. Slide S, 528 (*cf.* Photograph 7), (see p. 12).
- Fig. 11. Similar section of one of the lower, or anterior bundles. Lettering as before. × 390. Slide S, 522 (see p. 12).
- Fig. 12. Peltate laminæ of sporangiophores, showing the attachment of the sporangia, seen in approximately radial section. The whole of one lamina is shown, with insertions of two sporangia, and half the next with the insertion of one of its sporangia; v.b., v.b., two vascular bundles of the lamina, diverging from the main bundle in the pedicel ped.; v.b.¹, ultimate branch of the bundle in the other lamina, passing to the base of a sporangium. × 30. Slide S, 522 (cf. Photographs 9-11), (see pp. 4 and 12).
- Fig. 13. Structure of sporangial wall. A, in surface view, showing the "buttresses" jutting out from the radial cell-walls. B, in radial section, showing the edges of the "buttresses." C, in tangential section, showing the "buttresses" in their full width. The upper surface is towards the sporangial cavity. × 130. A and B, slide K, 85; C, slide S, 528 (see p. 13).
- Fig. 14. Three spores, from the middle part of the cone, showing the ridges on their membrane (cf. fig. 15B). × 130. Slide S, 521 (see p. 14).
- Fig. 15. A. Part of an approximately radial section of the base of the cone, showing

basal sporophylls, and sporangia. sup., one of the superior segments of a sporophyll; inf., inferior segment of the same sporophyll, seen in its full extent. It is to all appearance sterile; a, attachment of a sporangium to a fertile segment of the next sporophyll below; ax-ax, cortex of axis; v.b., v.b., vascular bundles on their way to the sporophyll. $\times 12\frac{1}{2}$ (cf. photograph). Note that the fractures in the sporophyll shown in the photograph are here filled up; in all other respects the figure is exact. (see p. 8). B. Spores from one of the basal sporangia. \times 130. Slide K, 88A (cf. fig. 14) (see p. 14).

- Fig. 16. A. Part of the secondary wood from the base of the axis of the cone, seen in tangential section. tr., tracheides; r., medullary rays. × 85. B. Part of a tracheide enlarged, to show the delicate tangential pits. × 200. Slide K, 88A (cf. photograph 15) (see p. 19).
- Fig. 17. Part of a transverse section through the cortex of the peduncle (Williamson specimen), to show a group of bundles resulting from the division of a leaf-trace. The left-hand side corresponds to the exterior of the cortex. ant., anterior; post., posterior, branch of the median bundle; lat., lat., the two lateral bundles of the trace (cf. fig. 7). The parenchyma is somewhat diagrammatic. × 30. C.N. 540* (see p. 17).

PLATE 6.

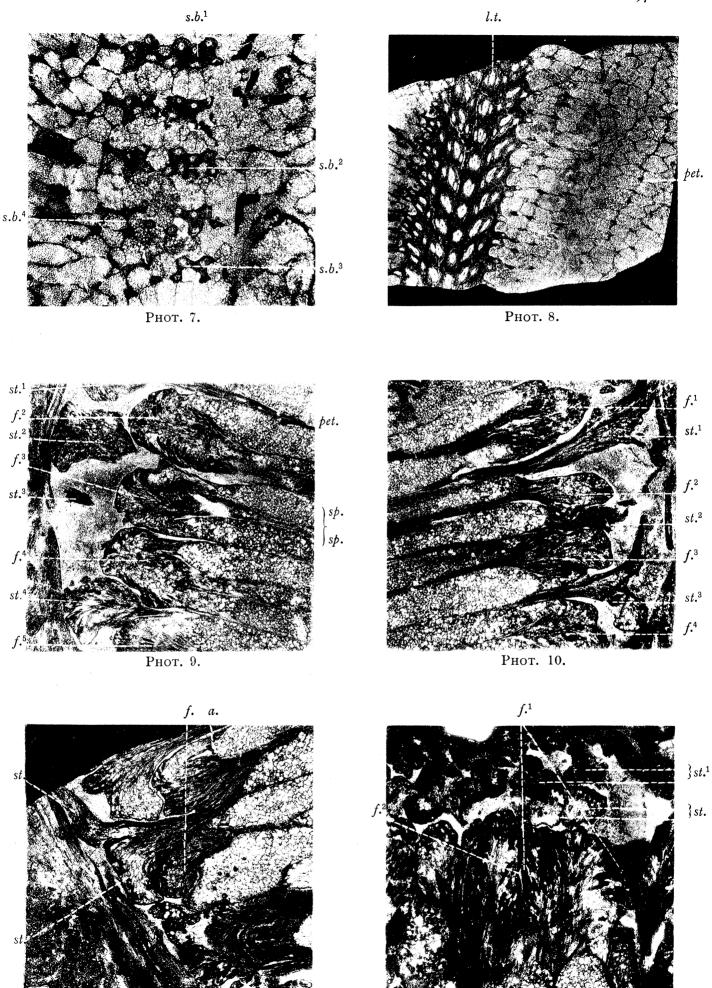
(All these figures are from the Williamson specimen).

- Fig. 18. Transverse section of the peduncle. st., stele; l.t., leaf-trace bundles passing through the cortex; L, L, bases of leaves; that to the right is evidently bilobed, and is entered by two vascular bundles converging towards the interior. × 4. C.N. 540 (see p. 15).
- Fig. 19. Tangential section through the cortex of the peduncle. *l.t.*, leaf-trace bundles, some of which occur in pairs; L, L, bases of leaves; one to the right shows four vascular bundles. × 4. C.N. 545 (see p. 17).
- Fig. 20. Transverse section of the stele, which at this level shows nine prominent angles. px, one of the groups of protoxylem; there is one such group in most of the angles, but probably two in that to the right; x^2 , secondary wood, distinguished by its radially-arranged elements; ph, one of the phloëm-groups, which are situated in the bays between the prominences. The whole interior is occupied by tracheæ, intermixed with thin-walled cells. \times 30. C.N. 541 (see p. 15).
- Fig. 21. One of the prominences of the stele, enlarged. px, group of protoxylem at the angle; x, part of the primary wood; x^2 , secondary wood, consisting

^{* &}quot;C.N." indicates Cabinet number in the Williamson Collection.

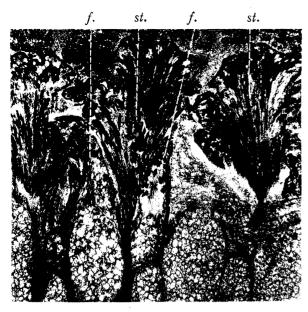
- of radial series of tracheæ, separated by medullary rays (r.); ph., ph., two of the phloëm-groups; cb., remains of cambium. \times 175. C.N. 541 (see p. 16).
- Fig. 22. Part of a radial longitudinal section passing through one of the angles of the stele. The exterior is towards the right. px, protoxylem-group, consisting of spiral tracheæ; x., probably secondary wood; the pitting is obscure; x., large tracheide of the primary wood, with numerous bordered pits \times 200. C.N. 544 (see p. 15).
- Fig. 23. From another part of the same section, showing a portion of the interior of the primary wood. tr., tr., tracheides, one of which shows two rows of very distinct bordered pits; c.p., conjunctive parenchyma. \times 300. C.N. 544 (see p. 16).
- Fig. 24. From a radial section of the peduncle, showing the base of a leaf, which is distinctly bilobed. v.l., upper or ventral lobe; d.l., lower or dorsal lobe; f.b., f.b., vascular bundles passing into the two lobes. × 15. C.N. 543 (see p. 17).
- Fig. 25. Another leaf-base, in radial section. v.l., ventral lobe, here almost disappearing; d.l., dorsal lobe; f.b., vascular bundle. \times 15. C.N. 544 (see p. 17).
- Fig. 26. Part of the same transverse section from which figs. 20 and 21 are taken, to show the cortex. L, L, bases of two leaves; f.b., f.b., the foliar vascular bundles, showing tracheæ. The two bundles which enter each leaf form a V, meeting towards the interior. The dark cells in the cortex may be secretory sacs. Part of the stele is shown. px., px., protoxylem-groups; ph., phloëm. × 30. C.N. 541 (see p. 17).
- Fig. 27. Part of another transverse section, showing the base of a leaf, which here has three lobes. *f.b.*, the three vascular bundles entering the leaf, and all converging towards the interior. The dotted lines to either side indicate the contour of the cortex. × 45. C.N. 539 (see p. 17).

l. s.bsp. $l.t.^3$ Lep.Рнот. 1. Рнот. 2. pet. Рнот. 4. Рнот. 3. sup. inf. s.b.Рнот. 5. Рнот. 6.



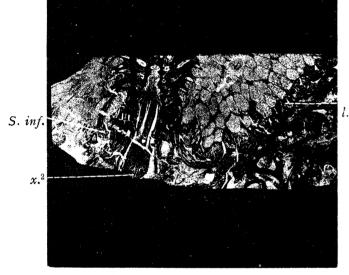
Рнот. 12.

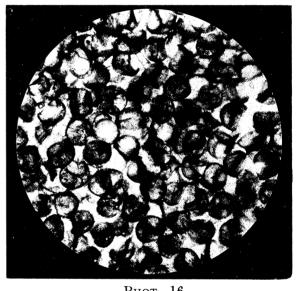
Рнот. 11.



Рнот. 13.

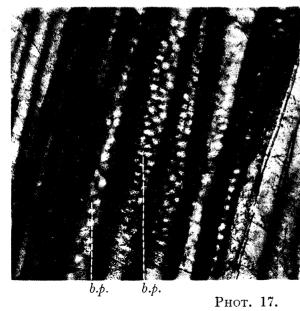
Рнот. 14.

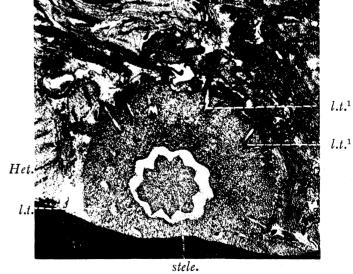




Рнот. 15.

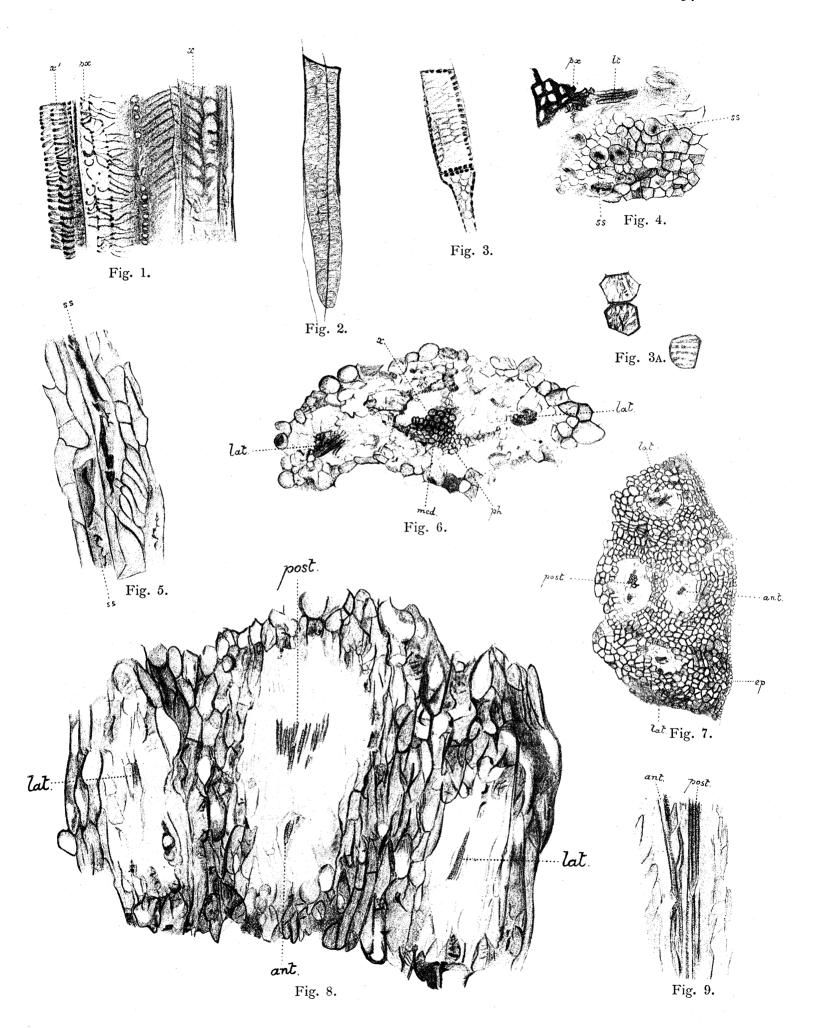
Рнот. 16.



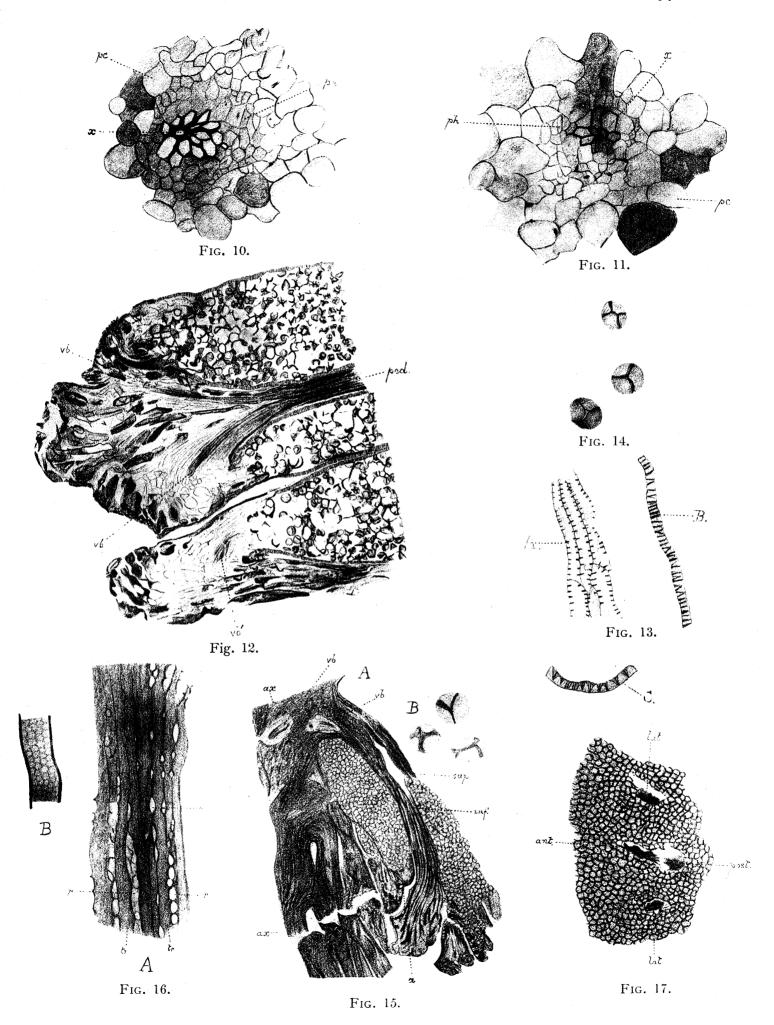


Рнот. 18.

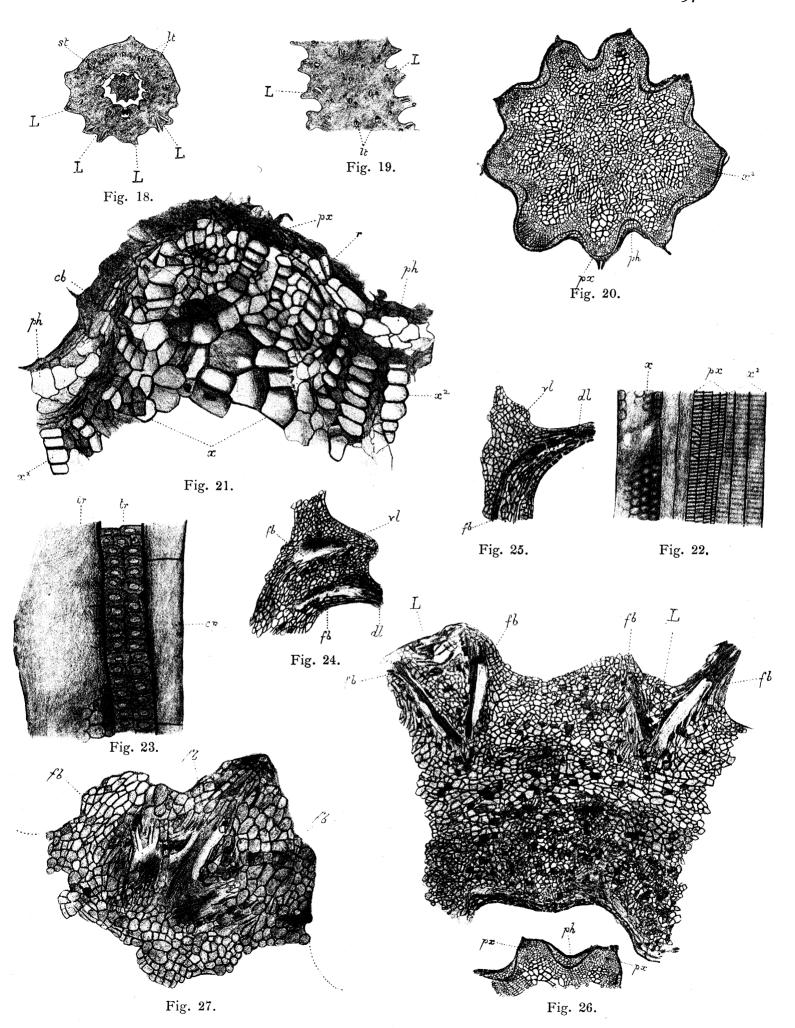
E. C. Bousfield, Photo.



Cheirostrobus Pettycurensis.



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Cheirostrobus Pettycurensis.

Рнот. 6.

stele

Рнот. 5.

Photograph 1. Transverse section of the whole cone. In the middle is seen the axis, surrounded by the flattened mass of sporangia and sporophylls. st., a sterile lamina, marking limit of specimen on the left; on the right the displaced sporangia, sp., extend to the broken edge; l., limit of specimen towards top of figure; Lep., foreign body (Lepidodendroid cortex) limiting the specimen below. $\times 1\frac{1}{2}$ diam. Slide K, 84A (see p. 2).

PLATE 1.

Photograph 2. Axis, enlarged, from same preparation. In the middle is the dodecarch stele. One complete whorl of twelve leaf-traces is shown, with parts of others. The successive divisions of the leaf-trace bundles can be followed. l.t., trace just divided into three; l.t., trace showing antero-posterior division of median bundle; $l.t.^3$ (in outer whorl), same division more advanced; s.b., sporophyll-bases; s.b., shows the three posterior bundles entering the sporophyll. The spaces between the segments are packed with sporangia. × about 8 diam. Slide K, 84A (see pp. 3 and 10).

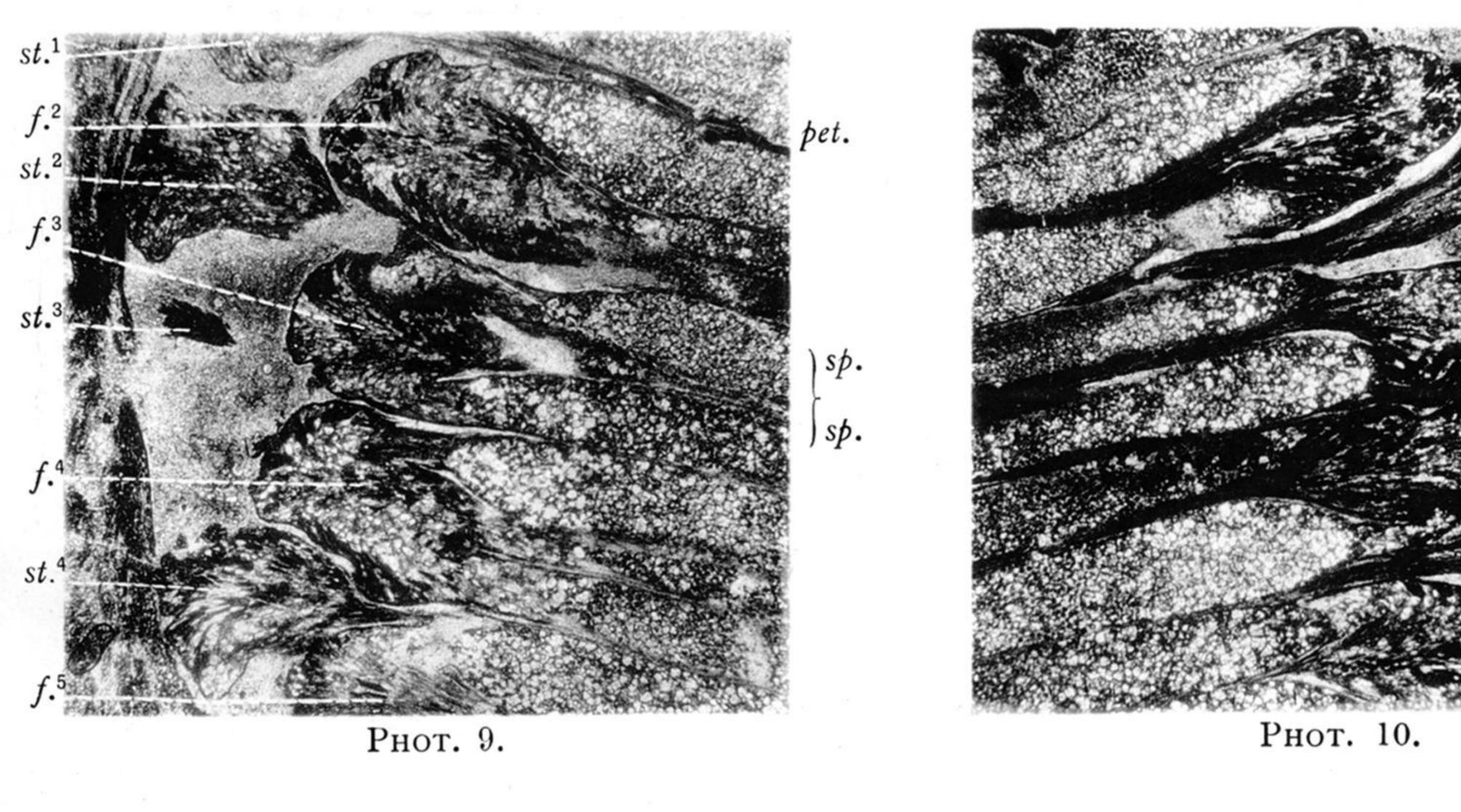
Photograph 3. Central part of axis, from another transverse section. px, one of the twelve protoxylem-angles of the stele; l.t., a leaf-trace bundle passing out from one of the angles; l.t., another leaf-trace, which has already divided into three. Note that the tracheæ extend to the centre of the stele. \times 24 diam. Slide S, 519 (see p. 9).

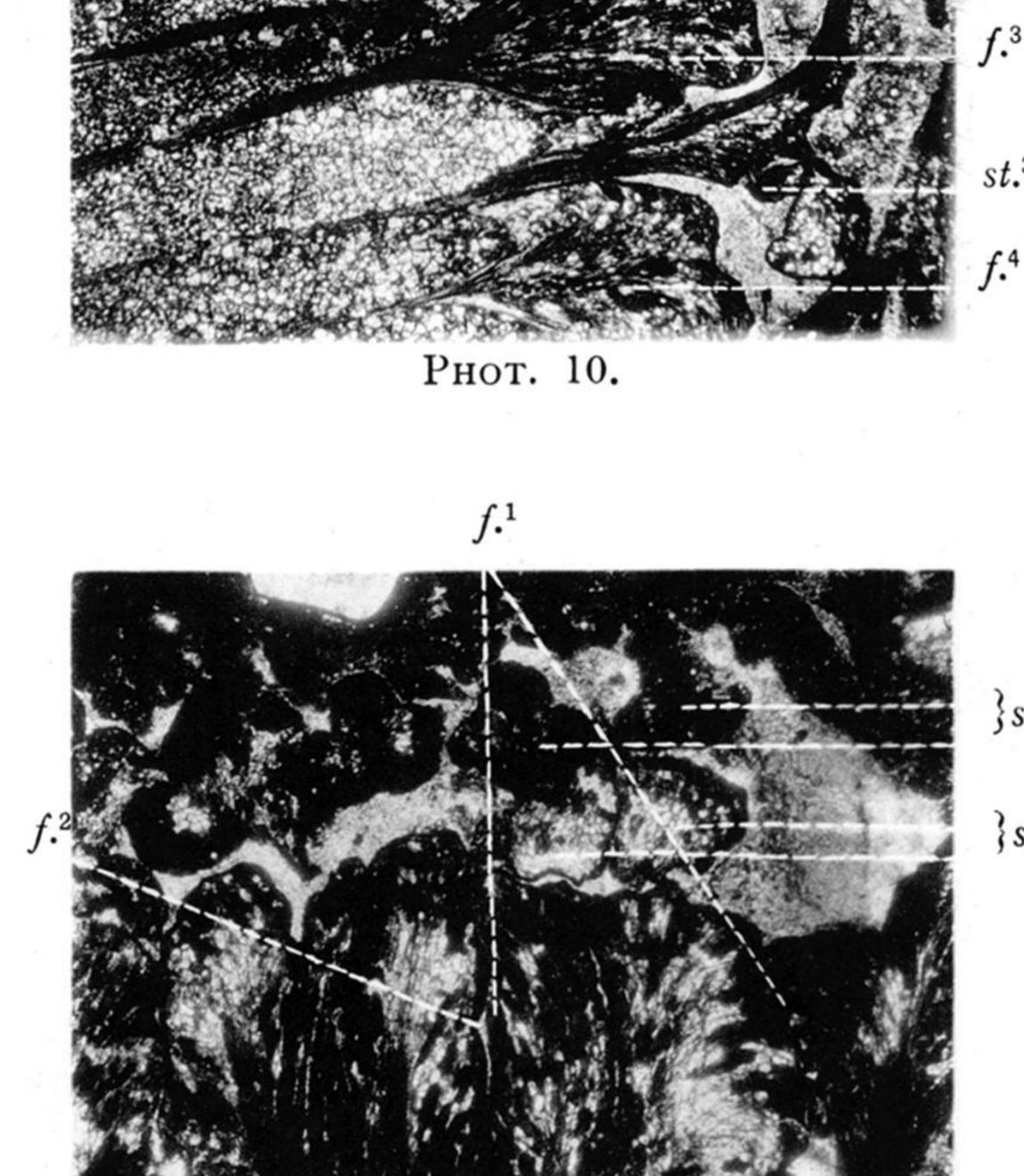
Photograph 4. Radial section of cone, showing axis, bearing sporophylls, with sporangia. pet., one of the petiolules; s.l., laminæ of the sporophyllsegments; sp., the radially elongated sporangia. $\times 2\frac{1}{2}$ diam. Slide K, 85 (see p. 4).

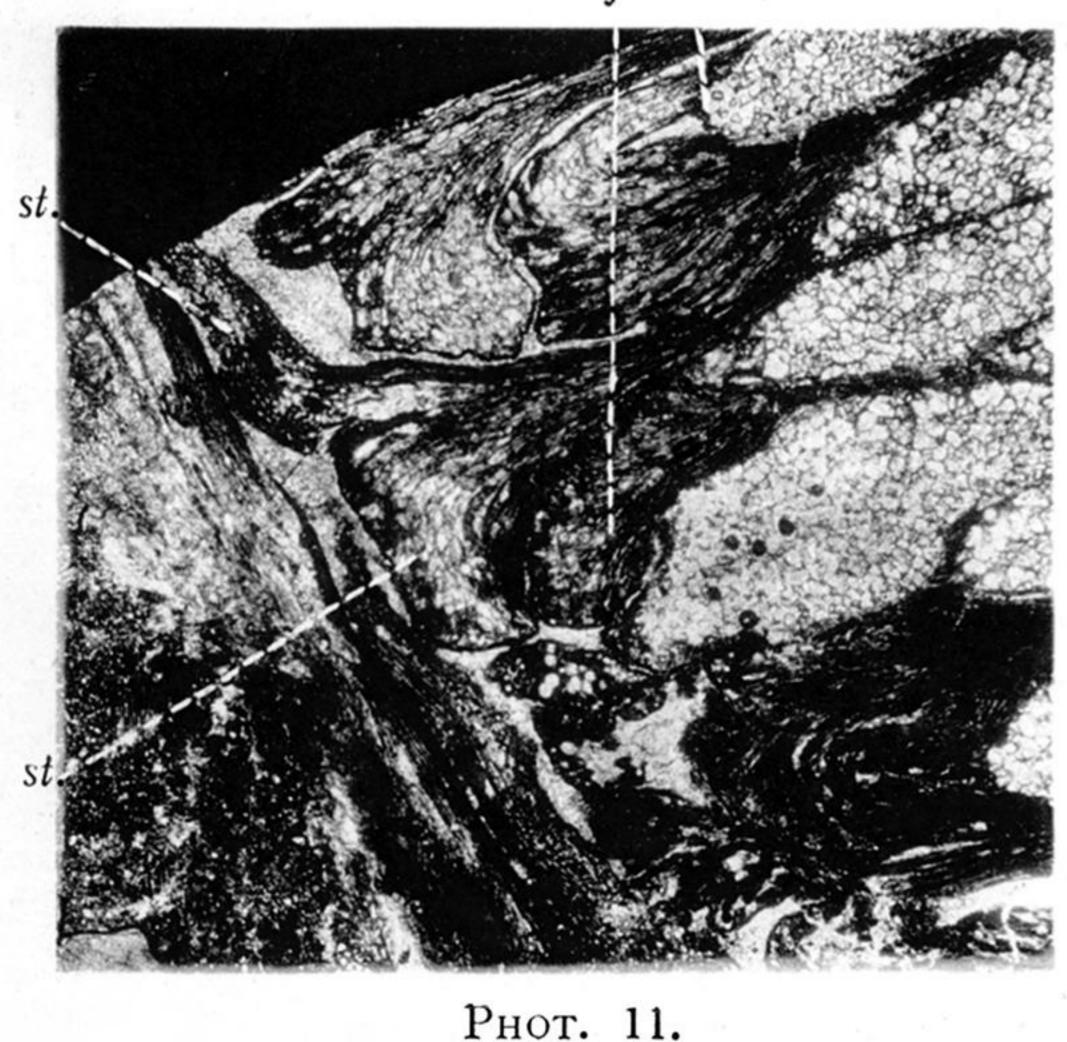
Photograph 5. Part of the same section, enlarged. stele, central cylinder of the axis. To the right several bases of sporophylls are shown, each dividing into an upper (sup.) and a lower (inf.) lobe. The antero-posterior division of the bundle supplying the lobes is also seen. pet., one of the petiolules belonging to the superior lobe of a sporophyll; sp., sporangia, packed between the sporophyll-bases and their segments. × about 8 diam. Slide K, 85 (see p. 4).

Photograph 6. Tangential section of cone, passing through the sporophyll-bases, s.b. Fourteen verticils are shown. Towards the bottom the sporophylls are seen breaking up into segments. s.l., laminæ of sporophyll-segments, at periphery of cone. Between the laminæ and the leaf-bases the section passes through the petiolules and sporangia. × about 2 diam. Slide S, 528

(see pp. 3, 4 and 12).







Рнот. 12.

PLATE 2.

Photograph 7. From the same tangential section as Photograph 6, enlarged, showing sporophyll-bases of six successive verticils. s.b.1, sporophyll-base, showing the six bundles, three above and three below; it is coherent below with the adjacent sporophyll on the left; the two left-hand segments of the latter are seen separating, as the plane of section passes outwards. s.b.2, sporophyll cut through at the level where the lower segments begin to separate; s.b.3, separation of segments more advanced; s.b.4, still more so. On either side petiolules intermixed with sporangia are seen. × about 8. S, 528. (See pp. 4 and 12).

Photograph 8. Tangential section, passing through the cortex of axis, showing the leaf-trace bundles at various points of their outward course. The vertical series, l.t., is in accurately tangential section, but the plane of section passes slightly outwards, from below upwards. Hence the bundles at the bottom of the figure are still undivided, while those further up are seen undergoing their successive divisions. The uppermost trace is in the same stage of division as that shown in Plate 4, fig. 8. Other leaf-traces and the bases of sporophylls are seen in oblique section. Outside the axis, the section passes through petiolules (pet.) and sporangia. \times nearly 4 diam. Slide S, 520. (See p. 10).

Photograph 9. Radial section through the outer part of cone, showing the attachment of the sporangia to the peltate laminæ of the fertile segments or sporangiophores. st.¹, sterile segment (partly shown); pet., its petiolule; st.2-st.4, other sterile segments, alternating with the fertile segments, f^2-f^5 ; sp., sp., the two sporangia attached to the laminæ of the fertile segment f^3 ; f^4 shows the attachments of three sporangia. To the left are seen the apices of lower sterile laminæ. × about 10. Slide S, 521. (See pp. 4 and 12).

Photograph 10. Similar section to last, showing better the alternation of sterile $(st.^1-st.^3)$ and fertile (f^1-f^4) laminæ. At $st.^3$, the form of the sterile lamina is well shown. The insertion of the sporangia on the fertile laminæ is also shown. × about 10. Slide K, 87. (See pp. 5 and 12).

Photograph 11. Another radial section, showing the form of a sterile lamina (st., st.) specially well. Note the stout downward protrusion, overlapping the fertile lamina f, and the thinner upturned apex, both of which are double, as shown in Photograph 12. α ., attachment of one of the sporangia to a fertile lamina. × about 12. Slide K, 87. (See p. 5).

Photograph 12. Transverse section from the periphery of the cone, passing medianly through two fertile laminæ, f^{1} and f^{2} , showing their sporangia. st, the two downward protrusions belonging to the sterile lamina next above f^{1} ; st.1, the two apical outgrowths belonging to the sterile laminæ next below f.1 (cf. Photographs 10 and 11). \times about 16. Slide K, 84B (see pp. 4 and 5).

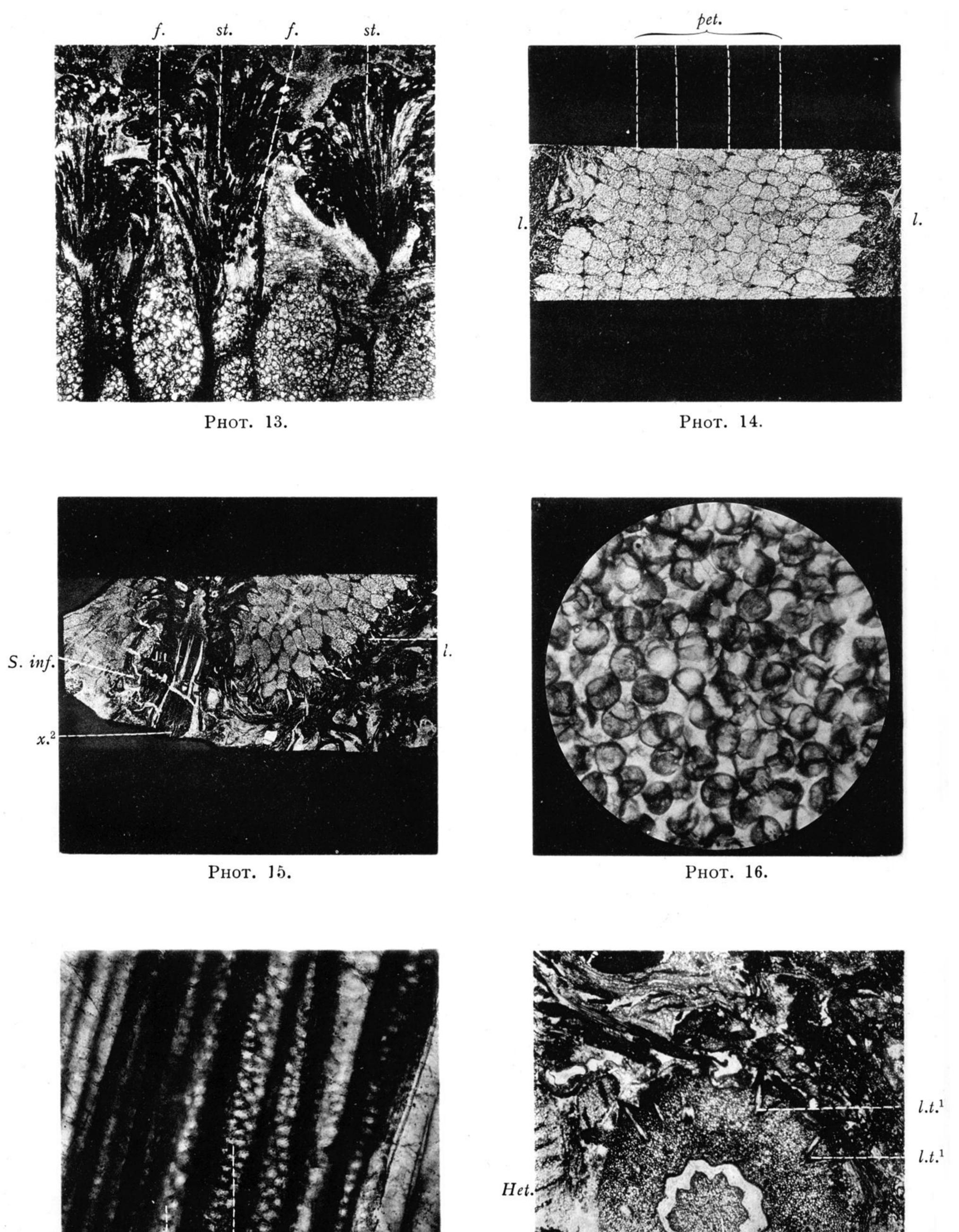


PLATE 3.

Рнот. 17.

b.p.

stele.

Рнот. 18.

Photograph 13. Similar transverse section to Photograph 12, but passing medianly through the *sterile* laminæ, st. The apices of others are shown in transverse section. f., f., the two lateral lobes of a fertile lamina; through the groove between them the sterile segment passes out. The insertion of the sporangia is clear (cf. Photograph 11). × about 16. Slide S, 519 (see pp. 4 and 5).

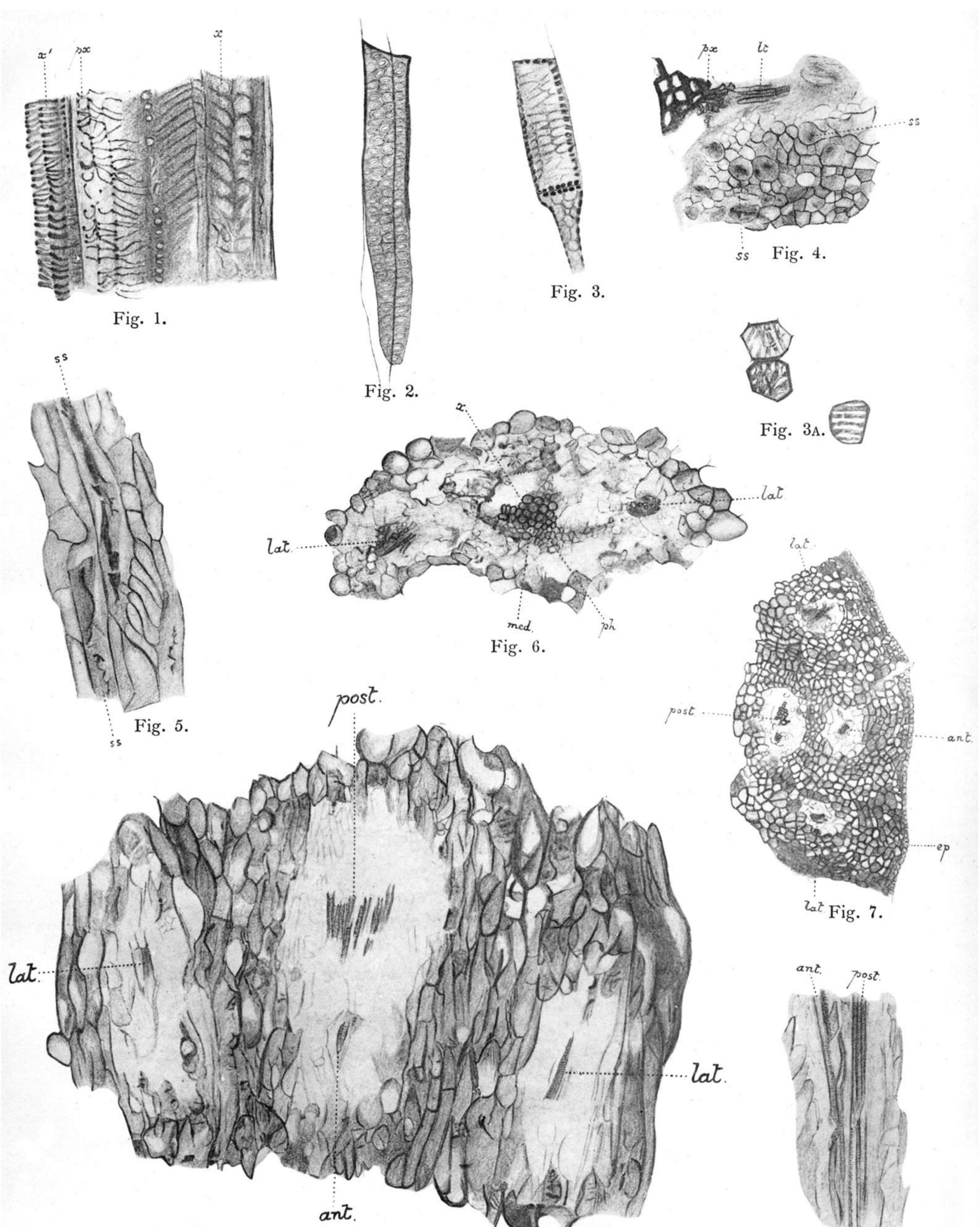
Photograph 14. Tangential section across the petiolules (pet.), the vertical series of which are evident. l., l., laminæ at the periphery, cut obliquely. Note the closely-packed sporangia, twice as numerous as the petiolules, and therefore four times as numerous as those of the fertile segments. $\times 3\frac{1}{2}$. Slide S, 525 (see p. 4).

Photograph 15. Approximately radial section from the base of the cone. The section becomes decidedly tangential towards the top and right-hand side. l., laminæ at periphery. s. inf., inferior segment of a sporophyll, the only one which can be traced through its whole length (cf. Plate 5, fig. 15A). x., secondary wood of peduncle (cf. Plate 5, fig. 16). \times about 3. Slide K, 88A (see p. 8).

Photograph 16. Spores from middle part of cone. × about 110 (see p. 14).

Photograph 17. Tracheides from interior of primary wood, to show bordered pits, b.p. × about 200. Slide K, 85 (see p. 9).

Photograph 18. Transverse section of peduncle (Williamson specimen). stele, central cylinder, with nine xylem-angles. l.t., leaf-trace before dividing; l.t., l.t., forking bundles, derived from division of leaf-trace. Het., foreign body (Heterangium cortex). × about 8 (see p. 15). C.N. 541.



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Fig. 9.

Fig. 8.

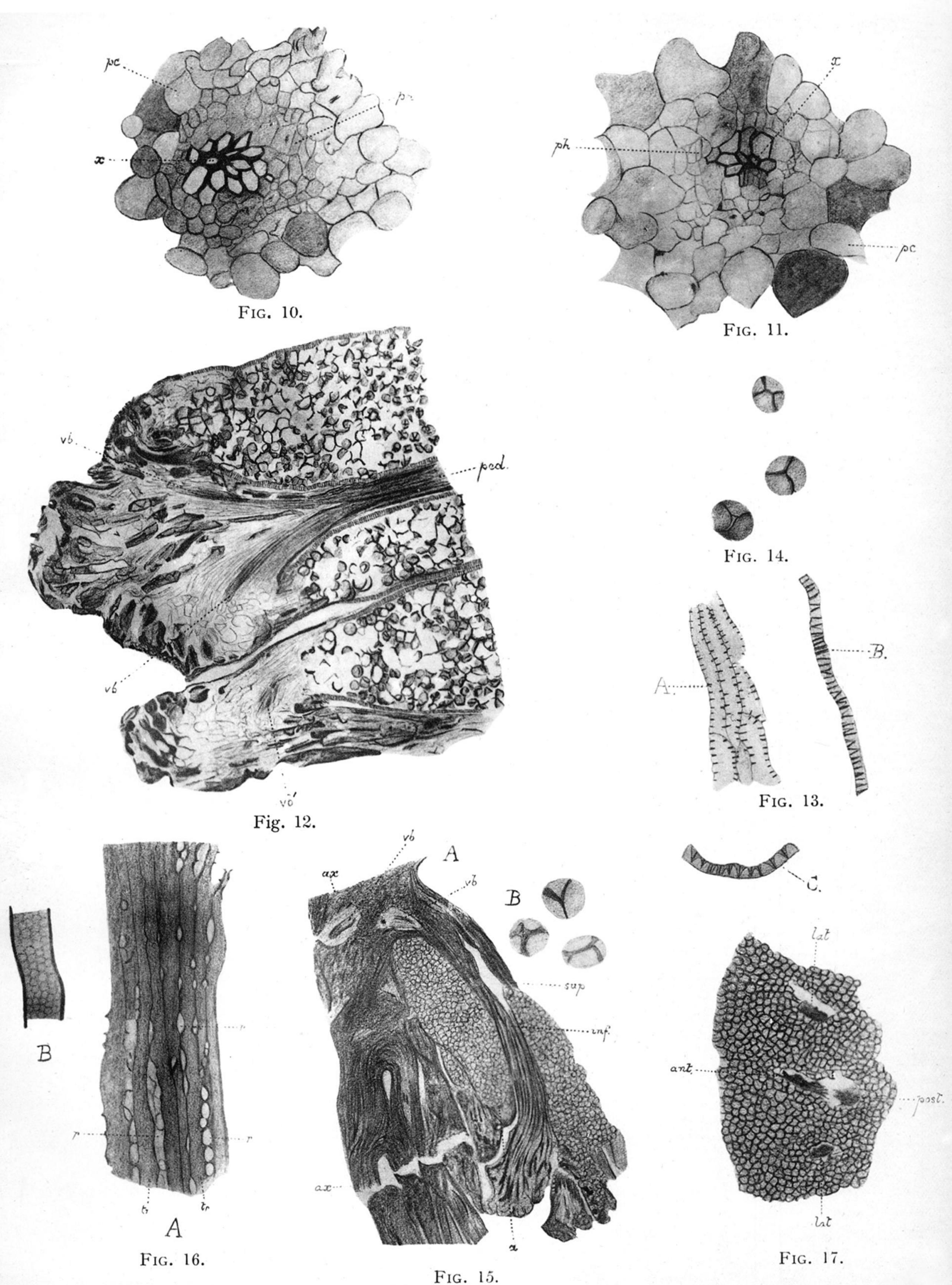
PLATE 4.

- Fig. 1. Part of an approximately radial section, passing through an angle of the wood. px., disorganized spiral or annular tracheides of the protoxylem; x., more densely spiral tracheides at the extreme angle; x., tracheides of the more internal wood. \times 390. Slide S, 521 (see p. 9).
- Fig. 2. Pitted tracheide from the interior of the wood, shown in a radial section. The outline of an adjacent thin-walled element is shown. × 200. Slide K, 85 (see p. 9).
- Fig. 3. Short reticulate tracheide from the interior of the wood, seated on another, trumpet-shaped, tracheide. × 200. Slide K, 85 (see p. 9).
- Fig. 3A. Three tracheides from the interior of the wood, seen in transverse section, showing the reticulate transverse walls. × 200. Slide S, 519 (see p. 9).
- Fig. 4. Part of a transverse section, showing one of the angles of the wood and a portion of the inner cortex. px., protoxylem-group; l.t., leaf-trace bundle passing out from the angle of the stele; ss., ss., "secretory sacs" in the inner cortical tissue (cf. Photograph 3). × 85. Slide K, 84A (see pp. 10 and 11).
- Fig. 5. Part of the inner cortex, in radial section. ss., ss., "secretory sacs," imbedded in the cortical parenchyma. × 85. Slide K, 85 (see p. 11).
- Fig. 6. Group of three bundles, resulting from the first division of a leaf-trace, seen in transverse section, from the middle part of the cortex. The lower side of the figure is towards the exterior of the axis. med., median bundle; x., its xylem; ph., its phloëm; chiefly preserved on the outer side; lat., lat., the two lateral bundles of the trace (cf. Photograph 2, l.t.). × 130. Slide S, 519 (see p. 10).
- Fig. 7. Group of four bundles, resulting from the first and second divisions of a leaf-trace, seen in transverse section, from the outer part of the cortex. ant., anterior median bundle; post., posterior do. do.; the posterior bundle is beginning to divide further. lat., lat., the two lateral bundles of the trace; ep., epidermis of axis (cf. Photograph 2, l.t.³). × 35. Slide S, 519 (see p. 10).
- trace; ep., epidermis of axis (cf. Photograph 2, l.t.3). × 35. Slide S, 519 (see p. 10).

 Fig. 8. Group of four bundles, resulting from the first and second divisions of a leaf-trace, seen in tangential section of the cortex. ant., anterior median bundle; post., posterior do., do.; lat., lat., the two lateral bundles of the
- trace. × 57. Slide K, 86 (cf. Photograph 8), (see p. 10).

 Fig. 9. Antero-posterior division of the median bundle of a leaf-trace, seen in radial section of the cortex. ant., anterior bundle; post., posterior bundle. They

unite below. \times 85. Slide K, 85 (cf. Photograph 5), (see p. 10).



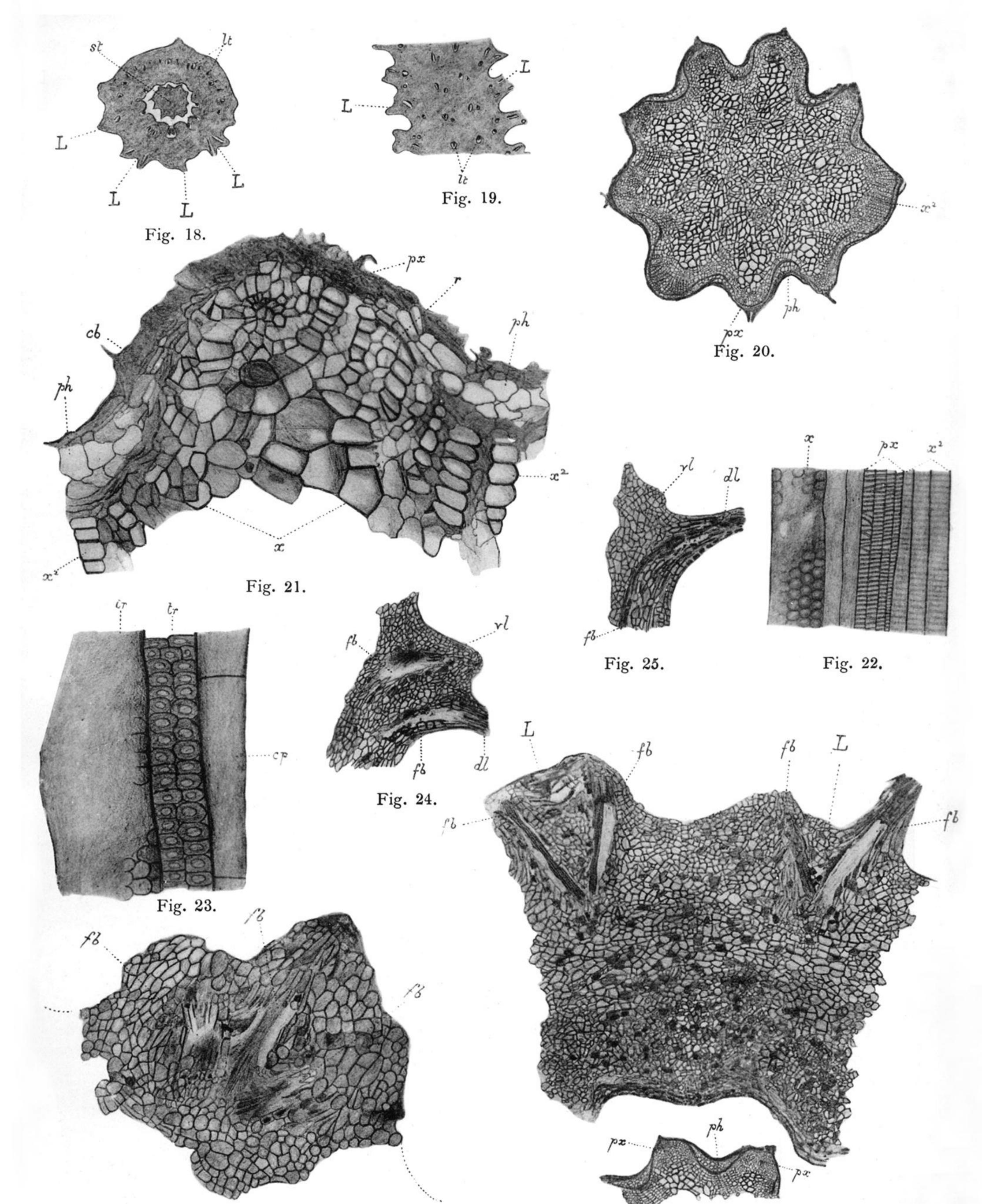
Cheirostrobus Pettycurensis.

PLATE 5.

- Fig. 10. One of the upper or posterior bundles in the base of a sporophyll, seen in transverse section, *i.e.*, in tangential section of the whole cone. x., xylem of bundle, with the smallest elements towards the centre; ph., phloëm, surrounding the xylem; pc., pericyclic or peridesmic tissue. × 390. Slide S, 528 (cf. Photograph 7), (see p. 12).
- Fig. 11. Similar section of one of the lower, or anterior bundles. Lettering as before. × 390. Slide S, 522 (see p. 12).
- Fig. 12. Peltate laminæ of sporangiophores, showing the attachment of the sporangia, seen in approximately radial section. The whole of one lamina is shown, with insertions of two sporangia, and half the next with the insertion of one of its sporangia; v.b., v.b., two vascular bundles of the lamina, diverging from the main bundle in the pedicel ped.; v.b.¹, ultimate branch of the bundle in the other lamina, passing to the base of a sporangium. × 30. Slide S, 522 (cf. Photographs 9-11), (see pp. 4 and 12).
- Fig. 13. Structure of sporangial wall. A, in surface view, showing the "buttresses" jutting out from the radial cell-walls. B, in radial section, showing the edges of the "buttresses." C, in tangential section, showing the "buttresses" in their full width. The upper surface is towards the sporangial cavity. × 130. A and B, slide K, 85; C, slide S, 528 (see p. 13).
- Fig. 14. Three spores, from the middle part of the cone, showing the ridges on their membrane (cf. fig. 15B). × 130. Slide S, 521 (see p. 14).
- Fig. 15. A. Part of an approximately radial section of the base of the cone, showing basal sporophylls, and sporangia. sup., one of the superior segments of a sporophyll; inf., inferior segment of the same sporophyll, seen in its full extent. It is to all appearance sterile; a, attachment of a sporangium to a fertile segment of the next sporophyll below; ax-ax, cortex of axis; v.b., v.b., vascular bundles on their way to the sporophyll. \times $12\frac{1}{2}$ (cf. photograph). Note that the fractures in the sporophyll shown in the photograph are here filled up; in all other respects the figure is exact. (see p. 8). B. Spores from one of the basal sporangia. \times 130. Slide K, 88A (cf. fig. 14) (see p. 14).
- K, 88A (cf. fig. 14) (see p. 14).

 Fig. 16. A. Part of the secondary wood from the base of the axis of the cone, seen in tangential section. tr., tracheides; r., medullary rays. × 85. B. Part of a tracheide enlarged, to show the delicate tangential pits. × 200. Slide K, 88A (cf. photograph 15) (see p. 19).
- Fig. 17. Part of a transverse section through the cortex of the peduncle (Williamson specimen), to show a group of bundles resulting from the division of a leaf-trace. The left-hand side corresponds to the exterior of the cortex. ant., anterior; post., posterior, branch of the median bundle; lat., lat., the two lateral bundles of the trace (cf. fig. 7). The parenchyma is somewhat

diagrammatic. \times 30. C.N. 540* (see p. 17).



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Fig. 26.

PLATE 6.

Fig. 27.

(All these figures are from the Williamson specimen).

- Fig. 18. Transverse section of the peduncle. st., stele; l.t., leaf-trace bundles passing through the cortex; L, L, bases of leaves; that to the right is evidently bilobed, and is entered by two vascular bundles converging towards the interior. × 4. C.N. 540 (see p. 15).
- Fig. 19. Tangential section through the cortex of the peduncle. *l.t.*, leaf-trace bundles, some of which occur in pairs; L, L, bases of leaves; one to the right shows four vascular bundles. × 4. C.N. 545 (see p. 17).
- Fig. 20. Transverse section of the stele, which at this level shows nine prominent angles. px, one of the groups of protoxylem; there is one such group in most of the angles, but probably two in that to the right; x^2 , secondary wood, distinguished by its radially-arranged elements; ph, one of the phloëm-groups, which are situated in the bays between the prominences. The whole interior is occupied by tracheæ, intermixed with thin-walled cells. \times 30. C.N. 541 (see p. 15).
- Fig. 21. One of the prominences of the stele, enlarged. px., group of protoxylem at the angle; x, part of the primary wood; x^2 , secondary wood, consisting of radial series of tracheæ, separated by medullary rays (r.); ph., ph., two of the phloëm-groups; cb., remains of cambium. \times 175. C.N. 541 (see p. 16).
- Fig. 22. Part of a radial longitudinal section passing through one of the angles of the stele. The exterior is towards the right. px, protoxylem-group, consisting of spiral tracheæ; x. x, probably secondary wood; the pitting is obscure; x, large tracheide of the primary wood, with numerous bordered pits \times 200. C.N. 544 (see p. 15).
- Fig. 23. From another part of the same section, showing a portion of the interior of the primary wood. tr., tr., tracheides, one of which shows two rows of very distinct bordered pits; c.p., conjunctive parenchyma. × 300. C.N. 544 (see p. 16).
- Fig. 24. From a radial section of the peduncle, showing the base of a leaf, which is distinctly bilobed. v.l., upper or ventral lobe; d.l., lower or dorsal lobe; f.b., f.b., vascular bundles passing into the two lobes. × 15. C.N. 543 (see p. 17).
- Fig. 25. Another leaf-base, in radial section. v.l., ventral lobe, here almost disappearing; d.l., dorsal lobe; f.b., vascular bundle. \times 15. C.N. 544 (see p. 17).
- Fig. 26. Part of the same transverse section from which figs. 20 and 21 are taken, to show the cortex. L, L, bases of two leaves; f.b., f.b., the foliar vascular bundles, showing tracheæ. The two bundles which enter each leaf form a V, meeting towards the interior. The dark cells in the cortex may be secretory sacs. Part of the stele is shown. px., px., protoxylem-groups; ph., phloëm. × 30. C.N. 541 (see p. 17).
- Fig. 27. Part of another transverse section, showing the base of a leaf, which here has three lobes. f.b., the three vascular bundles entering the leaf, and all converging towards the interior. The dotted lines to either side indicate the contour of the cortex. \times 45. C.N. 539 (see p. 17).