

On the Organisation of the Fossil Plants of the Coal-Measures. Part XVIII

William Crawford Williamson

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255

V. On the Organisation of the Fossil Plants of the Coal-Measures.—Part XVIII.

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[Plates 25-28.]

In my last Memoir, Part XVII.,* I called attention to a spore-bearing strobilus, first described by me, under the name of Volkmannia Dawsoni, in 1871, in the 'Memoirs of the Literary and Philosophical Society of Manchester.' This latter description was based upon sections made from a small fragment for which I was indebted to my old auxiliary Mr. John Butterworth, of Shaw, near Oldham, in the autumn of 1870. Beyond two insignificant fragments, seventeen years elapsed before any additional example of this very rare strobilus was discovered. Hence, during that interval, I had no means of confirming, or otherwise, the conclusions arrived at in that early Nevertheless, in my Part V. of this series ('Phil. Trans.,' 1874) having to deal with some allied forms of Asterophyllitean stems, I again referred to this plant. I pointed out the resemblance between the forms of transverse sections of its central vascular axis (loc. cit., Plate 5, figs. 28, c, and 29) and those of the centres of the Asterophyllitean stems figured on Plates I., II., and III. of the same Memoir. The references to this fructification in Part XVII., mentioned above, were connected with my discovery of the vegetative stem of this plant, the structure of which further sustains my conclusions in my Memoir V., not that any specific identity exists, such as I fear some of my expressions in that Memoir might seem to imply, but that in any botanical classification, their positions, though they are generically distinct, must be very near to one another, especially so far as their vegetative organs are concerned. More recently, as stated in a footnote to p. 99 of Part XVII., Mr. Lomax, of Radeliffe, has brought to me a series of specimens which he has discovered and which are of considerable importance, since they make clear a number of features which have hitherto been obscure. On the other hand, several structures of importance, well shown in the specimens figured in my Memoir of 1871, are not preserved in my new examples. Hence, in order that all of what we know of this remarkable plant may be consolidated in the present

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3.7,91.

PROFESSOR W. C. WILLIAMSON ON THE ORGANISATION

examination of it, I have reproduced some figures of the more characteristic structures described in 1871.

As shewn in Memoir V., fig. 28, transverse sections of the axial vascular bundle of this strobilus have a triangular form, the three projecting angles being broad and abruptly truncated. These features are illustrated by fig. 1, which represents this bundle as seen in the section in my cabinet numbered 1049. The mean diameter of this bundle, measuring from the truncated end of one angle to the more projecting angles of the other two, is about '05 of an inch. The breadth of each angle at its truncated extremity varies from '02 to '03. These measurements approximate closely to what I find in all my specimens, excepting one, of which I have two transverse sections (C. N. 1898, I and L), in which the maximum diameter of the bundle is about '0144, and that of the truncate extremity of the angle '0032, measurements the proportions of which approximate much more nearly to those of the young twig of Asterophyllites, fig. 1, Memoir V., than is usual in the homologous bundle of Bowmanites. The maximum diameter of the tracheids of this axial bundle, fig. 1, is about 004. None of the other tissues which must once have filled the circular area a'' in the centre of which this bundle is placed, are preserved in any of my specimens, with the exception of the narrow line a' of fig. 1, which shows no definite structure; neither have I been able to discover any indications of vascular threads passing outwards from the bundle to the surrounding tissues of the axis; yet it is scarcely to be doubted that some such extensions must have existed. Fig. 1, b, represents a small portion of the innermost surface of what remains of the axial cortex. This organ is seen more perfectly in fig. 2, b (C. N. 1040 B), and a portion of the same is further enlarged in fig. 3. Throughout the greater part of its thickness, this cortex chiefly consists of a rather open parenchyma (fig. 3, b), but, at its outer border b'', the tissues are more dense and opaque. Longitudinal sections of this stem (fig. 4, b, C. N. 1050) show that these cortical cells are more or less elongated vertically; the outermost of them passing into the prosenchymatous condition shown in fig. 5.

Round the inner margin of this zone (fig. 2, b,) we find a number of small isolated clusters of tracheids. Three of these clusters are seen at c in the further enlarged These tracheids must have been derived from the bundle, fig. 1, α , but as already stated, no traces of such an origin have yet been observed. Fig. 6 represents the most absolutely transverse section I have yet obtained of this strobilus; all the others in my cabinet being more or less oblique. This specimen was collected by Mr. LOMAX.

Figs. 4, 6, 7, and 8 demonstrate that at each node of the axis of the strobilus the cortex expands into a conspicuous disk. The diameter of this disk in the specimen fig. 7 has been about 156. At its free margin this disk subdivides into a verticil of numerous narrow ascending lobes, which for the present I propose to designate This disk chiefly consists of an aggregation of radially elongated parenchymatous cells (see fig. 5, d). A vertical section through it (fig. 4, d) shows that it is

bears some important organs on its upper surface.

thickest where it originates in a centrifugal extension of the cortical tissues, becoming gradually thinner as it ascends to its marginal fringe of disk-rays. In the obliquely transverse section, fig. 2, one side of this disk has been intersected at d, and in fig. 7, d, a wedge-shaped segment of a similar one extends outwards from the central axial cavity a''. The disk is crossed obliquely in the section of which fig. 1 is the central axis, as shown at d in fig. 9. (C. N. 1049 A.) The section has passed through the saucer-shaped disk at a lower part of the node at d' where its tissues are blended with those of the cortex b, b, but the two structures separate at d'', d'', because, on the side opposite to d', the section has crossed the disk and cortex at a level nearer to the centre of the internode above. We shall see directly that each of these nodal disks

In figs. 4 and 8 we find the peripheral margin of each disk prolonged upwards and outwards at e into a circle of leaf-like extensions. These latter I propose, for the present, to designate disk-rays, for the purpose of avoiding any term indicative of the possible homology of these organs. Fig. 10 represents a tangential section of a strobilus made through three verticils of these rays, e', e', e', in a plane a little outside the margins of the three corresponding disks. We here find that these disk-rays are arranged in symmetrical verticils, and are of fairly uniform shapes and dimensions. lateral diameter at this point is about '03, and their vertical thickness about '02. The same organs are seen at fig. 2, e, e. Fig. 11 is an enlarged transverse section of one of these rays from the section C. N. 1898 B. It has a very distinct quasi-epidermal layer of cells, a, enclosing the area a' which seems to be wholly occupied by parenchymatous cells, amongst which I can detect no traces of a tracheidal bundle. remains of four or five of these rays, each having a diameter of about '02. Returning to fig. 2 we find that at the two opposite points, e' and e', the periphery of the strobilus is preserved in the section, which is not the case with the two intermediate spaces. At each of the regions e', e', we have a mass of transverse sections of the more apical portions of the disk-rays, two of which are further enlarged in fig. 12. In each of these we still have the quasi-epidermal layer, a, of fig. 11, and at the centre of each ray, a', we have also the parenchyma already seen in the same figure; but at each of the two margins of each ray this parenchyma has disappeared in almost every one of the numerous examples which my cabinet contains of sections of the apical portions of these rays. I have obtained no clue to the cause of this disappearance. Here again, as in fig. 11, I can discover no traces of a vascular bundle in the internal parenchyma which remains. Each of these rays seems to consist wholly of cellular tissue.

The number of these disk-rays seen at the portions e', e', of fig. 2, makes it manifest that at each of these peripheral portions of the strobilus we have more of the disk-rays than could be supplied by one or even two nodal verticils. The thin extremities of the rays of each verticil must have been sufficiently prolonged to overlap, and assist to protect the three or four verticils of sporangia superior to the nodal disk of which each ray was an extension.

MDCCCXCI.-B.

Appendages to the thickened nodal disks.—Returning to the transverse section, fig. 9, made through the most central part of a nodal disk, d, we find the circular line of small translucent points, f, the centre of each of which is occupied by a few barred tracheids. Fig. 13 represents one of these points, further enlarged, in which f' represents the intersected tracheidal bundle, and f'' some of the surrounding cells of which the disk is composed. It is obvious that these tracheidal bundles are not identical with those cortical ones seen at c of fig. 3, because we find the representatives of these latter bundles at several points, as at fig. 9, c, along the inner border of the cortical zone b. But I expect that the two verticils are homologous ones. I believe that as these latter cortical bundles ascended to a higher node of the axis they would there bend outwards into, or at least send branches to, a disk circle similar to those at fig. 9, f, now under consideration. Each of these latter points represents the base of a sporangiophore, of which very many spring from the entire upper surface of the nodal disk. The exact plan of distribution of these sporangiophores is not clearly made out. At fig. 5 we have one, f, ascending from the innermost border of the disk, d, where the latter forms an axillary angle with internodal cortex, b. On the other hand in fig. 7, where the outermost border of the disk is subdividing into the disk-rays, e, e, it is still giving off similar sporangiophores at f. In fig. 8, in which the upper surface of the disk is intersected at least midway between the inner and outer border of that seen at d in fig. 6, we still find the bases of a number of sporangiophores springing from it. In fig. 2, d'', we see the same section of a disk as that represented at d in fig. 9; only in the former case, owing to the obliquity of the section, we can trace the outward and upward extension of the disk. Along its upper surface, represented in the section by its inner margin, we count at least thirteen of these sporangiophores, the bases of which are still united with the disk. One of these is further magnified in fig. 14, and shows its tracheidal bundle at f. In the section represented by fig. 28 of Memoir V., we have a section (C. N. 1047) of a disk corresponding to fig. 2, d'', only crossing the organ at a line still nearer its peripheral margin, where it is even beginning to break up into its component disk-rays; yet even here we find a number of the sporangia organically connected with it. In fig. 10 we have a tangential section of a strobilus, cut vertically in a plane a little external to the margins of the disks, and consequently passing through three verticils of disk rays, e', e', where they are free from their respective disks. Immediately above each of these verticils, we have at f, f, very distinct rows of sporangiophores, now wholly free from the disk-rays upon which they simply rest. All these combined facts demonstrate that we have in this strobilus a condition to which I have seen no parallel elsewhere.

There are many cases in which a single verticil of sporangiophores springs, like the solitary one, f, shown in fig. 5, from each axil formed by the junction of the nodal disk with the internodal cortex. It is so in the strobili of *Calamites* described in my Memoir XIV., but in this case each sporangiophore carries all the four sporangia which occupy that radial segment of the internodal circle of which they form a part. The

sporangiophores of several species of *Palæostachia* described by Weiss arise from similar axillary positions. But in *Bowmanites* alone do we find a nodal disk occupying a comparatively enlarged area, from the entire surface of which numerous sporangiophores arise, each one of which, as will immediately be demonstrated, supplies a single sporangium. This is a peculiar condition which must not be overlooked when we endeavour to determine the homological relations of the various organs of fructification of the *Calamariæ*, including those of the recent *Equisetums*.

At the lower part of their course each of these sporangiophores of *Bowmanites* has a diameter of about 001. Good transverse sections of these, like that represented in fig. 15, are numerous in my cabinet specimen numbered 1898 H, where an epidermal layer begins to be more clearly differentiated from the cells which it invests. In no case does a sporangiophore spring from a disk-ray. They are wholly confined to the disk itself. A further study of these organs must follow an examination of the sporangia of the strobilus. A glance at the various sections referred to in the foregoing pages will show that the interval between each pair of verticils of disks and disk-rays corresponds to an internode of the axis of the strobilus. that each of these internodal areas is occupied by a single layer of conspicuous Since these sporangia vary somewhat in size and shape they are not packed with exact symmetrical horizontality. The vertical sections, figs. 4 and 8, indicate that there were from two to three concentric circles of sporangia in each of these areas, and since the size of these sporangia varies but in a limited degree, it follows that the outermost circle has contained more than the middle one, as it in turn had more than the innermost. We see also, from fig. 10, that the outermost ring, g, g', extended beyond the periphery of the disk and was lodged between the two verticils of disk-rays, e, e'. In most of my sections these sporangia exhibit a rounded contour, but a broken fragment in my cabinet (C. N. 1055 A) shows that mutual compression has given to some of them an angular, pyramidal form, as is also seen at g' of fig. 10. Their mean diameter approximates to about '06.

The sporangial wall consists of a single layer of simple cubical cells, with a thickness of about '003. These cell-walls exhibit no special structures such as are seen in the homologous ones of the living Equisetums and the Carboniferous Calamostachys, but we find some marked peculiarities where each sporangiophore is united to its sporangium. We have already seen, from fig. 10, that the sporangiophores, f, pass outwards from their origins on the disk to their several destinations in individual sporangia in a layer lodged between the upper surface of the former and the under surfaces of the latter. This seems to be true even of each individual sporangiophore and the sporangium to which it belongs.

From what is observable amongst the sporangia of the upper end of fig. 2, it appears that each sporangiophore becomes united to its sporangium not at its proximal but at its distal side. It first passes completely under the sporangium and then bends backward upon itself to join the peripheral side of that organ. This is distinctly

shown by the two sporangia f', f'. Ordinarily the entire interior of the sporangium is occupied by the spores, but in each of the two examples g, g, of fig. 2, we find the peripheral end prolonged beyond the spores, and the small space thus produced is occupied by an extremely delicate form of parenchyma. From the two sporangia f', f', we further learn that this parenchyma is but an extension into the sporangium of the delicate cellular tissue occupying the interior of the sporangium. The uppermost of the above two is further magnified in fig. 16. The first fact to be noted here is that the recurved sporangiophore, f, has enlarged as it approached the sporangium, g, from a diameter of '001, its size at its proximal end, to '0133. At the same time the cells of its outermost or epidermal layer have become much more conspicuously differentiated from the delicate parenchyma, f', which they enclose. We further see that the wall of the sporangium is not only continuous with that of the sporangiophore, but that the one is merely an extension of the other. At f'' the tracheidal bundle of the sporangiophore is in virtually the same condition as in the proximal part of the organ; but at f''', as is so commonly the case amongst these vascular Cryptogams, where the sporangiophore joins its sporangium the tracheids have increased both in number and in size. We further see that where the delicate parenchyma, f', comes in contact with the spores, it terminates in a sharply defined boundary-line, which may possibly be prolonged inwards so as to constitute a thin membrane lining the entire inner surface of the sporangium wall.

The spores, so densely packed in the interiors of the sporangia differ from all others hitherto obtained from Carboniferous fructifications. Their rather thin exosporium is thickened along coarse reticulated lines, from each of the junctions of which reticulations there projects an elongated radiating spine. The spherical body of the spore is usually about '004 to '0048 in diameter, whilst from tip to tip of the projecting spines it is about from '0048 to '0063.

Independent of the verticillate arrangement of its organs suggestive of a general relationship to the Calamarian family, this strobilus is very distinct from all the numerous known Calamarian fructifications. In its nodal disks with their disk-rays, it approximates to Calamostachys and to Cingularia; but it differs widely from both in the origins of its sporangia and their attachments to their sporangiophores. In the triangular section of its protoxyloid central axis, seen alike in the fruit and in the vegetative stem, it approaches very near to Sphenophyllum and to my Asterophyllites, the affinities of which were discussed in my last Memoir when recording the discovery of the stem.* But here again all resemblances end. My specimens throw no direct light upon the foliage of this plant; but this deficiency is abundantly supplied by Mr. Bowman's original specimen figured by Mr. Binney.† Externally its stem and leaves are exactly those of an Asterophyllites. The former was jointed, with very

^{*} Memoir XVII., p. 100.

[†] On the Structure of Fossil Plants found in Carboniferous Rocks.' Part II., Plate XII., figs. 1, 1a, 1b, 1c, Paleontographical Society's volume for 1870,

OF THE FOSSIL PLANTS OF THE COAL-MEASURES.

prominent nodes, and the latter were linear, uninerved, and arranged in nodal verticils. The Calamarian affinities suggested by these facts are further supported by the Sphenophylloid structure of its vegetative axis described in my last Memoir. We thus obtain from *Bowmanites* a fresh illustration of the fact that the old genus *Asterophyllites* is a purely provisional one, comprehending several very different plants.

The plant has been obtained from the Calcareous nodules of Coals which have furnished us with so rich a harvest of new forms. I have received it from the Footmine near Oldham, from the hard-bed at Cinder Hills near Halifax, and from Dulesgate. For my specimens of it I have been indebted to Mr. J. Butterworth, of Shaw, near Oldham, to Mr. Spencer, of Halifax, and to Mr. Lomax, of Radcliffe.

Rachiopteris ramosa.

With the object of restricting, as far as possible, the multiplication of ill-defined genera, I have, in my preceding Memoirs, described a number of Fern-like objects under the provisional name of *Rachiopteris*. I have occasionally, for some time past, obtained portions of what appeared to be a distinct plant belonging to the above type, but which were not sufficient to satisfy me respecting the essential details of its organisation. Now, however, my cabinet contains a sufficient number of sections to make those details intelligible; a transverse section of the main axis of the plant is represented in fig. 19.

The central vascular bundle, fig. 19, α , consists of a dense aggregation of barred tracheids, the inner ones of which are rather smaller than those at its periphery. Most of the former have a diameter of '0008, whilst many of the latter reach '0016. The majority of the smaller ones are simply barred; but most others, especially those of larger size, are of the reticulated type so often met with amongst the Carboniferous plants, and of which two are enlarged in fig. 25. This bundle was invested by a zone of small, thin-walled, parenchymatous cells; but which are not preserved in the section figured. It is seen in another section in my cabinet (C. N. 1918 A). The uniform composition of this latter zone gives it more the aspect of an inner cortex than of a concentric phloëm. In this respect it corresponds with many similar ones in Rachiopterides that I have previously described, and of which the homologous relations are open to question. In the figure 19 this zone is only represented by the vacant space surrounding the central bundle α .

The thick and conspicuous outer cortex, b, b, consists of numerous strongly defined, vertically elongated, parenchymatous cells, intermingled with others, especially in its more external portions, of a more prosenchymatous type.

The Branches.—These are given off in great numbers. It is not uncommon to see five or six primary ones, d, d, given off, even from a very thin transverse section like fig. 19. Since these branches radiate equally in every direction, it is evident that figs. 19 and 20 were ascending aerial stems and not rhizomes. In fig. 20, which

represents a vertical section of the plant under consideration, these primary branches, d, are given off at a considerable angle; but more frequently, as in fig. 19, they appear to pass outwards through the cortex of the main axis more horizontally. This direction produces the abrupt change seen in transverse sections like fig. 19, c', represented, still further enlarged, in fig. 28. The tracheids of the axial bundle, a, are intersected transversely, whilst those at b, going to the branch, are intersected more longitudinally.

Sections of the main stem, in whatever direction they are made, are always surrounded by a swarm of similar sections of the large and small branches, though of varying shapes and sizes. These are seen to some extent at e, e, in figs. 19 and 20; but they occur in far greater numbers in other sections in my cabinet (e.g., C. N. 1018, 1018 A, and 1018 B). Fig. 20 is a longitudinal section of a specimen corresponding in all respects to fig. 19. In it we have the central tracheidal bundle at α , enclosed within its cortical cylinder, b, b. Large primary branches, each with more or less of its branch bundle, are seen at d, d. I have in the cabinet a tangential section (C. N. 1918 C) made from the same specimen as fig. 20, but passing through the external cortex. We learn from it that the secondary branches are given off irregularly and not in any defined order either of size or of position. Fig. 21 represents part of one of the larger of these branches. Other smaller ones are seen in figs. 22–23 and 24. Amongst the smaller ones like figs. 23 and 24, the bundle α is frequently pushed to one side of the cavity in which it is lodged, as if the remainder of the cavity had been occupied by a collateral phloëm; but I am satisfied that fig. 22 represents the normal position of the bundle. In a few of these sections I see evidence that in these branches the bundle was surrounded by a cellular zone like that already described as investing the bundle of the central stem in the Cabinet specimen 1918 A. Sections still smaller than fig. 24 are common enough, in which the bundles consist only of one or two minute tracheids. Such sections as those smaller ones just described are wholly undistinguishable from those of other and different Rachiopterides. Indeed the variations in the size, form, and other features of these smaller branches afford a fresh illustration of their insufficiency as foundations whereon to establish distinct genera. Some of my sections, especially the Cabinet specimens 1918 C and 1918 D, afford clear evidence that the exterior of the cortex was more or less clothed with multi-cellular hairs. Fig. 27 represents two of these hairs from the former of the above sections, and fig. 26 is part of the cortex of the latter one with the hairs in situ. Both the sections belong to the same stem as fig. 20, in which also the bases of some of these hairs are seen at g, g. It is quite possible that this plant may prove to be merely a more fully developed and less hirsute form of the Rachiopteris hirsuta described in Memoir Part XV., in which case it may stand as R. hirsuta, var. ramosa. Beyond this its real affinities are, as yet, uncertain. Many of its features suggest a relationship with the Ferns, but since no traces of its foliage have yet been discovered, this affinity cannot at present be determined. It is a curious fact that we

OF THE FOSSIL PLANTS OF THE COAL-MEASURES.

have as yet only discovered the leaves of one of the many supposed Fernstems which I have described—and that is precisely the one (Lygynodendron Oldhamium) the general features of which, at the first glance, were the least suggestive of any affinities with the Filicina. Most of our recent ferns have their vascular bundles composed of a xylem element associated with a concentric phloëm, but this was certainly not the case with all the Carboniferous Ferns. In the Myelopteris described in my Memoir VII., I found vacant spaces associated with the vascular bundles; I erroneously confounded these spaces with the gum-canals which are so abundant in the same stems. Since that Memoir was published I have obtained fine specimens of the same plant, in which these vascular bundles are more perfectly preserved, and which show that the supposed canals in close union with the xylem of each bundle were really spaces from which a true phloëm had disappeared. The specimens in question vary so much that it is difficult to say exactly what is the true relation of the phloëm to the xylem in these plants, but the preponderant indication is that the bundle is a collateral rather than a concentric cone. In dealing with the primæval Ferns we must not expect to find in them the exact histological conditions that are characteristic of living ones. Hence for the present, notwithstanding its anomalous features, I am inclined to class Rachiopteris ramosa with the Filicina. Some of my specimens of this plant were obtained by Mr. BINNS from the Hard Bed at Halifax. For others from the same district I am indebted to Mr. Spencer, and my later ones have been collected by Mr. Lomax, of Radcliffe.

INDEX TO THE PLATES.

Bowmanites Dawsoni, Williamson.

- Plate 25, fig. 1. Transverse section through the axial vascular bundle of a strobilus: a, the tracheids; a'', part of the area originally occupied by the innermost cortex, traces of which remain in the narrow bands a', a'; b, a portion of the inner border of the outer cortex. \times 50. C. N.,* 1049.
- Plate 26, fig. 2. Specimen in which an oblique transverse section has intersected three nodal and the same number of internodal verticils of organs: a", centre of the axis from which the bundle like fig. 1 has disappeared; b, cortex of the internodal verticil, immediately below the disk d; d, a portion of the nodal disk, sustaining the uppermost of the three verticils of sporangia; d", section through the nodal disk next inferior to d, and giving off sporangio-phores, f, from its upper border; e, e, transverse section of the disk-rays of the disk next below d"; e' e', numerous sections of the elongated upper portions of the disk-rays of several inferior nodal disks; e", basis of two of the disk-rays of the disk d; f, f, transverse sections of several sporangio-
- * As in previous memoirs, this symbol indicates the number at which the specimen referred to wil be found in the author's cabinet.

PROFESSOR W. C. WILLIAMSON ON THE ORGANISATION

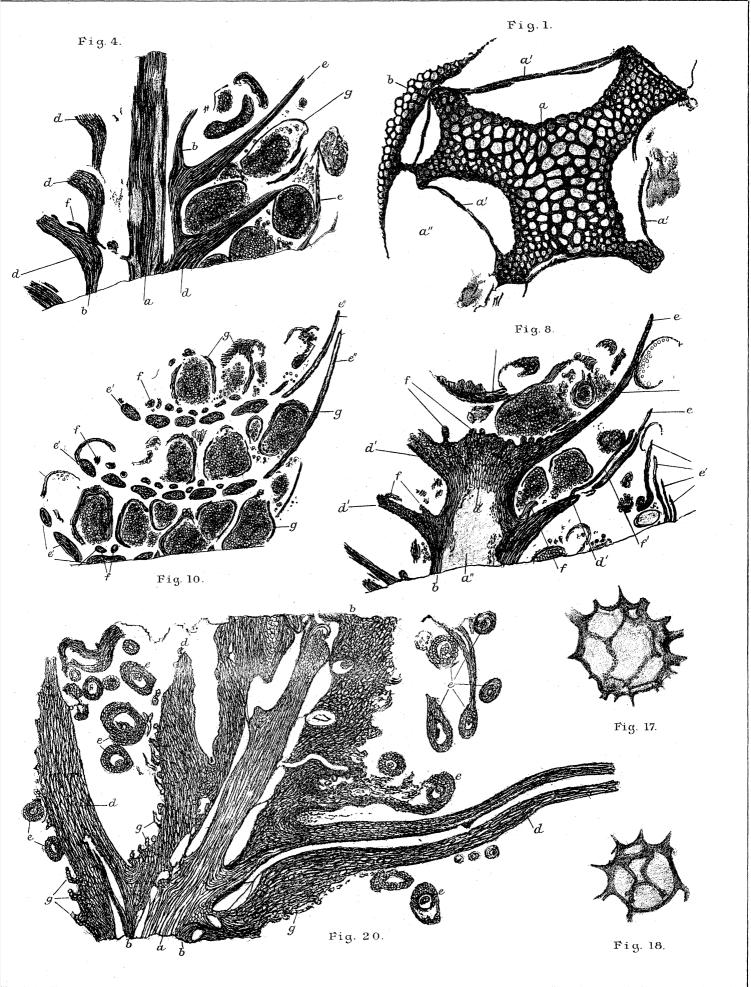
- phores; f' and f'', instances of sporangiophores united to their several sporangia; g, sporangia of the uppermost of the three verticils; g', the second and lower verticil of sporangia; g'' the third and yet lower verticil of sporangia. \times 13. C. N., 1049 B.
- Plate 27, fig. 3. A portion of the cortex, b, of fig. 2, further enlarged: b', the inner parenchyma of the cortex; b'', its outer portion; c, c, cortical bundles of tracheids. \times 150.
- Plate 25, fig. 4. A vertical section through the centre of a strobilus: α, the vascular bundle corresponding to fig. 1; b, b, the cortex; d, d, sections through the nodal disks; e, a disk-ray; f, a sporangiophore; g, sporangia.
- Plate 26, fig. 5. The axil, f, of fig. 8, showing the base of a sporangiophore, and the cellular structure of the neighbouring organs; b, the cortex; d, the nodal disk; f, the sporangiophore.
- Plate 28, fig. 6. Slightly oblique section through a node of a strobilus: a'', centre of the axis from which a vascular bundle, like fig. 1, a, has disappeared. At the upper and left-hand sides of the figure the section has passed through a lower portion of the strobilus than elsewhere; d, the uppermost nodal disk; e, e, part of a verticil of disk-rays belonging to the disk next below d; e', sections of the upper portions of the disk-rays belonging to still lower disks; g, g, verticil of sporangia occupying the internodal area next below the nodal disk, d; g', part of a verticil of sporangia belonging to an internode below that occupied by g, g. × 15. C. N., 1051 C.
- Plate 26, fig. 7. Segment from the centre of a second oblique section, made from the specimen which furnished fig. 2: α'' , central cavity of the axis; d, part of the nodal disk; e, e, portions of three of the disk-rays; f, f, three sporangiophores. \times 15. C. N., 1049 C.
- Plate 25, fig. 8. Tangential section from the same specimen as fig. 4, but made through the cortex outside the axial vascular bundle: a'', central cavity of the axis; b, cortex of an internode; d, section through a nodal disk within its peripheral margin; d', d', two opposite peripheries of a nodal disk; e, e', diskrays; f, bases of sporangiophores springing from the upper surface of the disk, d; f, f', f'', sporangiophores springing from various parts of the surface of the disk, d'. \times 8. C. N., 1058.
- Plate 27, fig. 9. Part of a second obliquely transverse section of the same specimen as fig. 2, made in a plane where the tissues of the disk d, d', blend with those of the cortex b, b; a'', the central axial cavity; b', the inner parenchyma of the cortex; c, small vascular bundles, like those, c, of fig. 3; f', small circular areas underlying the bases of the innermost series of sporangiophores, each area containing a minute vascular bundle in its interior. $\times 110$. C. N., 1049 A.
- Plate 25, fig. 10. Tangential section passing through three nodes and internodes of a strobilus, a little outside the margins of the nodal disks; e', e', free disk-

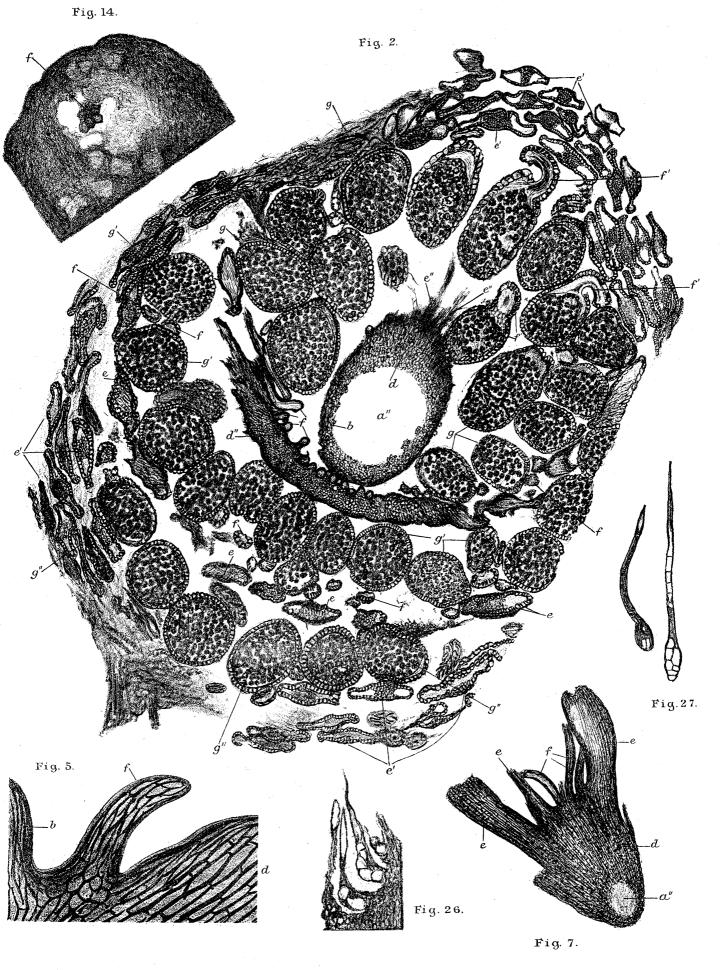
OF THE FOSSIL PLANTS OF THE COAL-MEASURES.

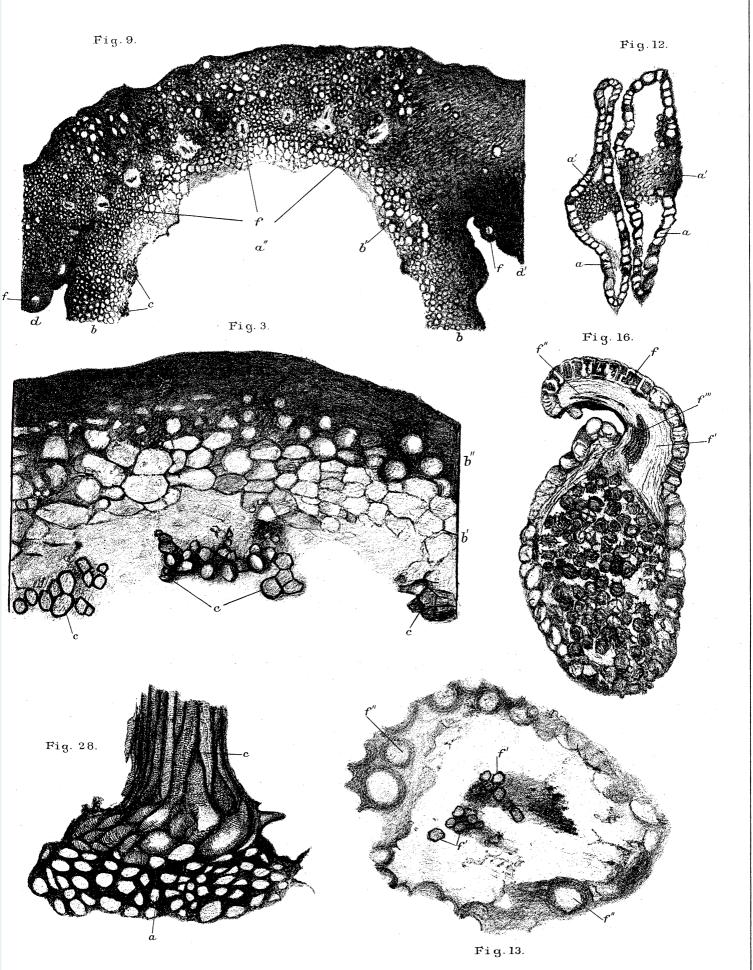
- rays intersected transversely; e'', longitudinal sections of two disk-rays prolonged beyond the outermost verticils of sporangia; f, f, transverse sections of sporangiophores proceeding to the more external sporangia; g, verticils of sporangia. \times 8. C. N., 1045.
- Plate 28, fig. 11. Enlarged transverse section of a disk-ray near its base; α , epidermal layer; α' , internal parenchyma. \times 250. C. N., 1898 B.
- Plate 27, fig. 12. Transverse sections of two disk-rays made nearer to their extremities than fig. 11; α , epidermal layer; α' , central portion of the internal parenchyma. \times 40. C. N., 1049 B.
- Plate 27, fig. 13. One of the small circular areas, f, of fig. 9, further enlarged; f', central bundle of tracheids; f'', parenchymatous cells of the disk. \times 280. C. N., 1049 A.
- Plate 26, fig. 14. Transverse section of one of the small sporangia, f, projecting from the upper surface of the section through the disk, d'', of fig. 2; f, its tracheidal bundle. \times 230. C. N., 1049 B.
- Plate 28, fig. 15. Transverse section of a sporangiophore further removed from its base than fig. 14; f, its tracheidal bundle. \times 140. C. N., 1898 C.
- Plate 27, fig. 16. The uppermost of the two sporangiophores, f', f', which are attached to their sporangia in the section fig. 2; f, epidermal coat of the sporangiophore; f', inner cellular tissue of the sporangiophore; f'', f''', tracheidal bundle of the sporangiophore; g, spores. \times 40. C. N., 1049 B.
- Plate 25, figs. 17 and 18. Two spores. × 186. C. N., 1053.

Rachiopteris ramosa, Williamson.

- Plate 28, fig. 19. Transverse section of a stem; a, the central axial bundle composed wholly of tracheids; b, the outer cortex; c, c', bundles of tracheids going off to primary branches; d, large primary branches. \times 30. C. N., 1851 A.
- Plate 25, fig. 20. Longitudinal section of a stem like fig. 19; a, axial bundle of tracheids; b, cortex; d, d, primary branches; e, sections of secondary branches; g, g, cortical hairs. \times 10. C.N., 1918 B.
- Plate 28, fig. 21. Transverse section of a primary branch; α , the tracheidal bundle; b, the cortical zone. \times 30. C. N., 1851.
- Plate 28, figs. 22 and 23. Transverse sections of secondary branches; a, tracheidal bundle; b, cortex. \times 30. C. N., 1851.
- Plate 28, fig. 24. Transverse section of a yet more distal twig. × 30. C. N., 1851.
- Plate 28, fig. 25. Two of the reticulate tracheids of the axial bundle, a, of fig. 20.
- Plate 26, fig. 26. Portion of the cortex with some of its peculiar hairs in situ. × 35. C. N., 1918 D.
- Plate 26, fig. 27. Two isolated hairs like those of fig. 26. × 35. C. N., 1918 C.
- Plate 27, fig. 28. The base of the vascular bundle supplying one of the primary branches of fig. 25, and illustrating the sudden deflexion of the branch tracheids, c, from those belonging to the central bundle a.







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