

III. *On the Organization of the Fossil Plants of the Coal-measures.*—Part V. *Asterophyllites.* By W. C. WILLIAMSON, F.R.S., Professor of Natural History in the Owens College, Manchester.

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IN 1871 I published, in the 5th volume of the third series of the ‘Memoirs of the Literary and Philosophical Society of Manchester,’ a description of a new Cryptogamic fruit, to which I gave the provisional name of *Volkmannia Dawsoni*. One of the most remarkable features of this curious organism was seen in a transverse section of its central vascular axis, which appeared to be a triangular structure with truncated angles. When the above memoir was read (February 7, 1871) I had seen no stem having a similar structure; but after a careful study of the fruit, I said, “The verticillate arrangement of its bractigerous disks and bracts suggests the probability that we must seek for the parent plant amongst such as have their foliage arranged in corresponding verticils; and if this law of association be a sound one, we are apparently shut up to the three genera, *Asterophyllites*, *Annularia*, and *Sphenophyllum*”*. After reviewing the various features of these plants, I arrived at the conclusion that “it is the fruit either of *Asterophyllites* or of *Sphenophyllum*; and, judging from the general aspect of its bractigerous disks, I am more disposed to identify it with the former than with the latter”†. I was not at that time aware that Professor RENAULT, of Cluny, had found a stem at Autun having a similar triangular axis, and which he also had referred to *Sphenophyllum* (‘Comptes Rendus,’ 1870). My attention was at once directed to the discovery of true stems having a similar structure, and I soon found a few examples in the cabinets of Messrs. BUTTERWORTH and WHITTAKER of Oldham. But these gave me no such evidence as I required respecting the nature of the foliage with which these stems had been clothed, neither did any of them afford proof even that the plant had been a jointed one. I then turned to the coal-seam from which the fossil strobilus was obtained, and was at length rewarded by the discovery of a cluster of stems, each one of which was clothed with its peculiar bark, having the enlarged lenticular nodes exquisitely preserved, and the verticils of *Asterophyllite*-leaves radiating from the thin margin of each nodal disk in precisely the same way as the bracts had done from the corresponding portions of the fruit already described. What had previously been an inferred probability thus became an established fact; hence I have now no hesitation whatever in referring both the above fruit and the stems which I am about to describe to the genus *Asterophyllites*. Amongst the other specimens sent to me from Burntis-

* *Loc. cit.* p. 34.

† *Ibidem*, p. 37.

land by G. GRIEVE, Esq., were some stems having a similar structure, but of larger size than any I had met with in Lancashire; but, though exquisitely preserved, the fragments were internodal ones, and not sufficiently long to exhibit the structure of the nodes.

I shall adopt in this memoir the plan which I followed in the third of this series of monographs, in which I treated of the Burntisland *Lepidodendroid* plants; I shall commence with the youngest twig of the Lancashire type which I have met with, and then trace the gradual development of the organism through the addition of successive exogenous growths by which the twig was thickened and finally converted into branch and stem.

The young Twig.—Plate I. fig. 1* represents a transverse section of a condition of which I have obtained several examples, and which evidently exhibits a twig or branch in its very young state; *c* is a central vascular bundle which has a maximum diameter of $\cdot 016\dagger$ between the most distant tips of the slender divergent angles of its triangular section, the entire section, including the bark, being about $\cdot 06$ in diameter. The bundle consists of a group of vessels, not arranged in any regular order; the maximum diameter of the largest of them is not more than $\cdot 0029$, whilst that of the smallest is not more than $\cdot 0007$. The triangle, as seen in this section, is very slender, its arms being long in proportion to their breadth. The larger vessels occupy its central portion, the smallest being found at the extremities of each of the arms.

A double inner bark (*g*) has disappeared from this specimen, though traces of it are seen in some similar but otherwise less perfect ones. It appears to be of the same nature as that which will be described in the more matured stems. This double inner layer has been surrounded by an outer bark (*k*), with a maximum thickness of about $\cdot 016$. It is composed of compactly aggregated cells, with very thick walls, and which are of about the same diameters as the central vessels. A few of these cells have a diameter of $\cdot 0029$; many others are yet smaller, whilst the great majority range between $\cdot 0015$ and $\cdot 0007$. A remarkable feature of this outer bark is its indentation, on each of its three sides, by a deep constriction (*k'*). These constrictions correspond with deep grooves which channel the surface of each of the internodes, but which disappear as they approach the nodes‡. The position of each groove is opposite each concave lateral surface of the central vascular bundle, when the latter has not been displaced from its normal

* I may observe that, to facilitate the comparison of these specimens, all the following figures have been drawn to the same scale, being enlarged 30 diameters, 1, 2, 3, 4, 5, 9, 10, 11, 12, 14, 15, 16, 18, 19, 20, 21, 27, 34, 45, 50, 51.

† These and all subsequent measurements are given in decimal parts of an inch.

‡ I find precisely similar grooves in a small plant of *Sphenophyllum Schlotheimi* (Plate V. fig. 26) in the museum of the Owens College. In this instance the grooves (Plate V. fig. 26, *k'*) are never vertical to any of the leaves of a verticil, but appear always to be intermediate between two of them. It also appears, from the same specimen, that the positions of these grooves do not change in alternate nodes, but that they form continuous lines down the stem, interrupted only at the nodes. Plate V. fig. 26, *k'*, is an enlarged view of part of the internode and lower node of *k*.

position. One of the grooves (k'') is, in this example, a double one, being divided by a central longitudinal ridge. This is a feature which often reappears in older branches.

Plate I. fig. 2 represents another section from the same coal-seam, which may possibly belong to a different species from the last one; at all events it differs somewhat both in size and form. The central vascular triangle (c) is much more robust, having a maximum diameter of $\cdot 05$, the extreme diameter of the entire section, including the bark, being $\cdot 1$. The largest vessels near the centre of the vascular triangle are about $\cdot 009$ in diameter, those of the angles being smaller, whilst each of the extreme tips of the latter terminates in a cluster of very minute vessels, which do not exceed $\cdot 0006$. External to the vessels of the central bundle, which, as in the last specimen, are not arranged in any linear order, is a single investing row of vessels (d) applied to each of the concave sides of the triangle, and arranged in a linear series; of these, the largest vessels occupy the centre of each concave line, the rest becoming smaller as they approach the apex of each angle. This is the first of a remarkable series of exogenous layers which successively invest the central bundle, and convert the triangular outline of this vascular axis into a circular one. The double inner bark (g) is again wanting. The outer one exhibits the same aspect as in the previous example, only the three lateral furrows (k') are larger and more concave than in Plate I. fig. 1, or indeed than in any other specimen that I have seen.

In Plate I. fig. 3 we have a transverse section of the vascular axis of another specimen, in which the exogenous zone (d) has received a second layer of vessels; and it will now be observed that whilst each of these concentric growths, composed of one lineal series of vessels, maintains its distinct individuality, nearly every vessel of the outer circle is placed in a direct line with one belonging to the circle on the inner side of it, the two combining as parts of a radiating series. This double concentric and radial arrangement is yet better seen in Plate I. fig. 4, where a third circumferential growth has been added. The central triangular axis is now larger than in the primary twig (Plate I. fig. 1). The enlargement is partly due to an expansion of each of its component vessels, and partly to an addition to their number. The extreme diameter of the axis between point and point is $\cdot 06$, and that of its largest and more central vessels about $\cdot 005$. Between these larger vessels and the exogenous layers we now find a thin series of very small vessels, forming the peripheral portion of the triangular axis, to which structure they certainly belong. These appear to me to have been developed (I know not how) subsequently to the appearance of the first exogenous layer. Of this latter portion we have three growths, of which the central one is, in this instance, the smallest. The maximum thickness of this united triple series is now $\cdot 0125$; and, though at one point there is a slight irregularity in the arrangement of the vessels of the two outer rows, they maintain in general the radiating order already spoken of. Owing to the constant large size of the more central vessels of each row, the original triangle with concave sides is now being converted into a convex one, the greater portion of each of its lateral boundaries having become somewhat oblate. In this specimen we have the middle

bark (*h*) preserved. It consists of a very delicate parenchyma, the cells of which have a diameter of about $\cdot 0015$. These are somewhat cubical, and are arranged in linear series, which radiate from the exogenous layers of the wood to the outer bark. This middle cortex does not appear to merge gradually with the outer one, but is separated from it by a somewhat sharply defined line. The outer bark (*k*) exhibits the same features that were seen in the previous specimens. The thick-walled cells are not arranged in linear series, as in the middle bark, but as in ordinary irregular parenchyma. In this example the three external internodal grooves (*k'*) are *all* double ones, the only instance in which I have found this to be the case.

Before proceeding to trace the further development of these stems, it will be convenient to examine the aspect which longitudinal sections of them present at this stage of their growth. This is shown in Plate I. fig. 5, which represents a section made through the centre of the triangular axis, and crossing one node and parts of two internodes. The vessels of the central triangle (*c*) are undistinguishable in this section, save by their central position, from those of the exogenous layers, *d d*. They are all of the reticulated type, seen more highly magnified in Plate I. fig. 6. I have satisfied myself that these reticulations are more distinct on the two sides of each vessel parallel with the direction of the medullary rays than on the sides at right angles to the latter. They are due to modifications of spiral deposits of lignine, and must not be confounded, as they have often been by WITHAM and some of his successors, with the disks of so-called glandular or discigerous fibres of the Conifera.

Though the delicate middle bark (*h*) is rarely well preserved, I have in my cabinet sufficient examples of it to show that it appears, in longitudinal sections, in the form of long narrow prismatic cells (Plate I. fig. 7), with nearly, if not absolutely, square ends. They vary considerably both in length and in diameter. They are usually from $\cdot 012$ to $\cdot 006$ long, the former much more frequently than the latter, the shorter and broader ones occurring near the nodes. One of my sections shows traces of the thin layer of parenchyma (*g*) within this prismatic layer. The outer bark (fig. 5, *k*) is now seen to consist of long, narrow, thick-walled prosenchyma. I have found it difficult to ascertain the greatest length of the component cells, but I have traced them as far as from $\cdot 03$ to $\cdot 035$: as is the case with the cells of the middle bark, they become shorter in the neighbourhood of each node (*k'*). At this latter point the bark swells out rapidly into a broad lenticular disk, from the thin margins of which verticils of long narrow leaflets (*l*) extend in very regular order. At these points the cells of the outer bark assume a very peculiar arrangement. Those which ascend from the internode below the nodal disk (Plate I. fig. 5, *k''*) proceed outwards in a very definite series, forming the lower portion of the disk, whilst those which descend in slightly curving lines (*k'*) from the internode above terminate rather abruptly against the curving lines of those of the lower series. These cellular tissues are prolonged uninterruptedly into the leaves, which I shall describe more fully by-and-by. In several of my specimens I have noticed that, a little below each node, a portion of the cells of the middle bark curve

upwards and outwards, as if to accompany some vascular bundle on its way to the leaves. This is seen in Plate I. fig. 5, *h'*. But in no one instance have I found the slightest trace of an actual vessel accompanying them. Though my sections, made in various directions, are nearly a hundred in number, I cannot trace a solitary example of a divergent vessel. I will not venture to affirm that the leaves of this plant, like those of the living *Psilotum*, were non-vascular; but it is certain that I cannot detect a trace of a vessel, either in the cellular leaves and disks or diverging from the vascular axis in the direction of those organs. In all the transverse sections the vessels retain the undisturbed arrangement shown in the figures, whether such sections are made at the nodes or at the internodes*. It is obvious that these stems have not been jointed or articulated in the same way as the *Calamites*. In the latter plants, the existence of each node alters the entire arrangement of all the tissues, vascular and cellular, to the very centre of the stem. On the other hand, the appearance of articulations seen in the common examples of *Asterophyllites* found in the shales, is an altogether different thing. It is wholly due to modifications of the cortical tissues, which are expanded into disks by a centrifugal development, which does not visibly affect the true vascular axis of the stem. This is an important physiological distinction, to be borne in mind when endeavouring to determine the systematic relations of these plants. The appearance of the cells of the outer bark, as seen in longitudinal sections of the internodes, is represented in Plate II. fig. 8. Each internode is rather more than half an inch in length.

Returning to the circumferential growth of the stem, I find that layers were successively added to the preexisting ones in precisely the same regular manner as seen in the examples already figured. Plate II. fig. 9 represents one of the finest sections I have met with, and which Mr. DRINKWATER, late of Salford, kindly permitted me to make from a specimen which he had obtained from the Oldham deposits. In this example the central triangle has now increased to a maximum diameter of $\cdot 08$, the result apparently of a general increase in the dimensions of the smaller vessels, because the largest ones still retain the maximum diameter of $\cdot 005$ already observed in Plate I. fig. 4. The exogenous zones are now seven in number on two sides of the stem, and eight on the third. With the exception of this intercalation of a zone, the vessels of these exogenous layers maintain the same remarkable regularity of arrangement, both radially and circumferentially, that I have already described. The bark (*h*) remaining in this specimen is but a portion of the middle layer. Plate II. fig. 10 represents a slightly crushed example, in which we find eight exogenous layers on one side, nine or ten on the second, and eleven on the third, indicating that, as the stems increased in diameter,

* Since the above description was written, Professor RENAULT's important memoir, entitled "*Recherches sur l'Organisation des Sphenophyllum et des Annularia*," presented to the Académie des Sciences of Paris in May 1870 and 1873, has reached me. It proves very clearly that vascular bundles are given off from the three angles of the central triangular axis, and that these pass outwards, through the exogeneous zones and bark, to the leaves. Hence there is little doubt that the arrangement represented in my fig. 5, *h'*, indicates the condition suggested in the text.—February 5, 1874.

the irregularity of these growths, owing to some of the layers being crescentic ones, instead of forming perfect circles, became greater. The bark (*h*) in this example also consists of the middle portion. Both the last figures show very clearly the radiating arrangement which the long prismatic cells of this tissue exhibit when divided transversely.

In Plate II. fig. 11 we not only advance yet further, but we now discover that a change has been introduced into the method of growth. The specimen, for which I am indebted to Mr. WHITTAKER, of Oldham, has been somewhat crushed, but this in no way interferes with the easy interpretation of it. Its central portion has developed in the manner described in the case of the preceding examples, the triple arrangement of large vessels alternating with corresponding radiating groups of smaller ones. But when, by successive growths, the vascular axis attained the condition of a perfect circle, an altogether new mode of procedure has manifested itself. The preexisting axis has become the starting-point for a new series of layers, in which all the vessels are abruptly reduced to a very small and nearly equal diameter. Hence the older and the newer growths are separated from one another by a very distinct circular line of demarcation. From the new starting-point the vessels have been disposed as before, but they have increased slowly in size as each succeeding layer invested its predecessors. The entire stem in this instance has only the same diameter as that of Plate II. fig. 9; but I have no reason for supposing, on this ground, that these two belong to distinct plants. I have elsewhere obtained clear evidence that stems having the same diameter may nevertheless have attained to very different stages of growth. Plate II. fig. 12 is a second section seen in the same slide as the last, and is evidently part of another stem or branch of the same plant. The remarkable difference in the sizes of the larger vessels of the central growths seen in the three radiating clusters of them, as compared with the very small vessels composing the later and more external series, is here very striking. At first sight it is difficult to avoid the conviction that the difference is due to some increase in the size of the former, as compared with the corresponding ones of the previous examples; but such is not the case. The largest of those in Plate II. fig. 12 is not more than .005, which we have already found to be a usual size. The difference occasioning the striking contrast has resulted from the very small dimensions of those composing what may be designated the secondary growths. These last two examples exhibit the highest degree of development which I have met with in any stem found in the Lancashire district*.

I succeeded in obtaining a very accurate tangential section of the exogenous portion of Plate II. fig. 9, with the object of ascertaining the exact distribution of the medullary rays separating the several radiating laminae of vascular tissue. Plate II. fig. 13 represents a portion of this section. The medullary rays are numerous, but of

* Since the above two figures were drawn, I have met with a very perfect example of the same stage of growth, in which the tissues are wholly undisturbed by external pressure. It fully confirms my conclusion that the conditions just described are not due to any such disturbance, excepting so far as the accidental displacement of some of the tissues is concerned, but are characteristic of this stage of the growth of the stem.

the simplest possible type. They rarely consist of more than two, and often of but one, linear series of cells; when the former, the two or more cells are rarely exactly vertical to each other; but, as shown in the drawing, the two are somewhat inclined, often in opposite directions, to the vertical line. I have not been able to detect any of these cells in the central triangle; they appear to be confined to the exogenous layers. Of course I am aware of the old argument likely to be renewed against my nomenclature, and to hear the objection that there can be no medullary rays where there is no medulla; but the obvious reply is that a medulla is not necessary. The rays in the thick, ligneous, pithless roots of an exogenous forest tree are the homologues of the similar structures in its stem, notwithstanding the entire absence of a pith from the former organ, just as they continue to be rays in the stem itself when some aged oak has become hollowed into a huge cylinder.

The Leaves.—Having had the good fortune to discover a number of stems invested by a perfect outer bark, with well-preserved nodes at intervals of about half an inch, I at once commenced a vigilant search for leaves, and I was soon rewarded beyond my most sanguine expectations. Having made a vertical section through one stem which exhibited a perfect node, from each side of the thin lenticular margin of which there projected a slender leaf-like organ, as seen in Plate I. fig. 5 and Plate III. fig. 15, I proceeded cautiously to grind away the matrix external to the bark of the same specimen, in hope of discovering evidences of a verticillate arrangement. I soon came upon sections of four leaf-like organs, arranged in regular verticillate order. These sections were of the same type as those represented in Plate III. figs. 14 & 17. But proof was needed that these objects actually belonged to the node seen on the opposite side of the thin slab of stone. To obtain this, I continued to grind until I reached the margin of the disk, which presented itself in the form represented by Plate III. fig. 14, *l l*. The actual relation of the leaf-like organs to the disk was now thoroughly established.

The sections of the individual leaves, as they appeared in the regularly disposed verticil before I ground away that portion of the section, were similar to those still seen at Plate III. fig. 14, *m* & *m'*, but in an inverted position. These were gradually traced backwards to the corresponding portions (*l l l*) of the same figure, in which we have a section of part of the margin of the foliar disk from which the leaves sprang, and the under surface of which has already become grooved at two points, defining the bases of the three leaves *l l l*. At *m''* we have a longitudinal section of one leaf from the side of the disk, whilst at *m' m'* we have the inverted tips of two of the leaf bases *l l*, which had been bent inwards by the pressure of the earthy matrix, and consequently were divided a second time by the same section. At *m'''* is a section of another leaf, which, having been intersected obliquely, is longer than would be the case with an exactly transverse section. Plate III. fig. 15 is a longitudinal and slightly tangential section of the outer bark (*k*) of a stem passing through a node. Here we have a considerable portion of a leaf (*m*) intersected longitudinally. Its upper portion has been bent back upon the stem by external pressure, in the manner already referred to in my description of Plate III.

fig. 14. The somewhat clavate appearance of the free extremity of the leaf (*l*) is due to a slight accidental obliquity in the section at that point due to another flexure of the leaf carrying it out of the plane of the section. The thickness of this leaf ranges between .0043 and .0086.

Besides the evidence afforded by the examples just described, I have obtained several transverse sections made more or less in the plane of the foliar disk, and which display the verticillate arrangement of the divergent leaves in the most definite manner. One of these is represented in Plate III. fig. 16; it will be observed that, in the expanded portion of the disk (*k''*), the cells of the tissue evince somewhat more of a tendency to assume a radial linear arrangement than is usual in the outer bark. The bases of six linear leaves (*m m*) are seen radiating from the lower and left-hand sides of the section with considerable regularity. The breadth of each leaf is about .021. I discover no trace of vascular tissues, either in the leaves themselves or amongst the cellular tissues of the foliar disk from which they arise; and it is a further curious fact that no vacant spaces exist, either in the outer (*k*) or middle (*h*) bark, such as are common amongst the *Lepidodendra*, where they were originally occupied by vessels that have disappeared. The transverse section of the central vascular axis, at this important point of the stem, exhibits its usual appearance; and it is obvious that, if any of the very large vessels composing it had ever been deflected into the leaves, their large size must have made them conspicuous objects, whilst their divergence must have left some considerable gap in the regularly concentric and radial lines of vessels; but no traces of such conditions have been discovered. The leaves appear as if they consisted wholly of cells, which, as we have already seen from Plate I. fig. 5, are mainly, if not entirely, derived from the outer bark*. Unfortunately these foliar tissues are much disorganized and rendered indistinct through carbonization, consequently the exact arrangement of their component elements has yet to be made out; at the same time I have clear evidence that the central part of the leaf, at least, was chiefly composed of long, narrow, parallel-sided cells, and that the remainder was occupied by a somewhat coarse parenchyma.

I have stated that the diameter of the bases of the leaves in Plate III. fig. 16 is .05. This is exactly the breadth of the bases of the leaves in a very distinct verticil of *Asterophyllites* which I possess in an ironstone nodule from the Lower Coal-measures of the Oldham district, and which I think belongs to the same species as the sections described. The leaves in the specimen referred to are more than three quarters of an inch in length, and with twenty-seven or twenty-eight in the verticil. In the example represented in Plate III. fig. 16, I calculate, from their angle of divergence, that there

* Since the above description was written, Professor RENAULT has informed me that he can demonstrate, in one of his stems of *Sphenophyllum*, eighteen vascular bundles given off from the central triangular axis, and passing outwards at a node to be distributed to six leaves, each of the latter receiving three primary bundles which pass outwards to three corresponding teeth at the extremity of the leaf. Of course this observation renders it exceedingly probable that the apparent absence of small vascular bundles from my specimens is due to mineralization and is not a primary feature of the plant. See the note on p. 45.

have been about twenty-four in each verticil. This close correspondence between the leaves in my sections and the size, number, and arrangement of those of ordinary examples of *Asterophyllites* is further maintained if we examine individual sections belonging to the former series. Plate III. fig. 17 represents a group of such sections, brought together from various specimens in my cabinet. It will at once be seen that these are generally identical with similar ones (*m*, *m'*) associated with Plate III. fig. 14. The diameters of these sections vary from $\cdot 05$ to $\cdot 025$, variations which would, of course, exist according to whether the sections were made obliquely near the broader part of the leaf or near its narrow and almost linear tip. In every instance the leaf consists of a single, very thick midrib, with two somewhat succulent and slightly incurved lateral margins. This is exactly the structure of the leaves preserved in ironstone nodules now in my cabinet, the *Asterophyllitean* character of which no one would venture to dispute.

Amongst the numerous interesting specimens from Burntisland in Fifeshire for which I have been indebted to G. GRIEVE, Esq., was one which contained two stems, similar in many respects to those which I have just described. Careful search in other portions of the Burntisland rock revealed other specimens, showing that this plant had passed through stages of growth similar to those of our Lancashire type. But the distinctness of the two is demonstrated by the circumstance that, in the Oldham specimens, the vessels of the central axis are always *reticulated*, whilst those of the Burntisland species are as invariably *barred*.

Plate III. fig. 18 is a transverse section of a young twig, obviously corresponding to Plate I. fig. 1. Its greatest diameter is about $\cdot 017$, and that of the largest of its vessels about $\cdot 0029$, dimensions which closely correspond with those of the Oldham plant. The bark (*k*) exists in this specimen, and I can readily make out its cellular structure; but its outline is not so clearly defined as I could have wished, owing to the density of the vegetable mass in which it is imbedded. I see traces of the lateral grooves, especially at *k*, but these are not very definite. Some other specimens, however, in the same stage of growth as fig. 18, exhibit these grooves very definitely, almost as much so as Plate I. fig. 1. Plate III. fig. 19 represents one of these, in which the triangle is somewhat more robust than in the previous example. The grooves (*k*) are here clearly shown on two sides of the specimen, the third having been accidentally broken off in making the section. The maximum diameter of this twig, including the bark, is $\cdot 054$, or rather more than Plate I. fig. 1. It will be noticed that, in this specimen, the angles of the central triangle are distinctly truncate, reminding us of the same condition in *Volkmannia Dawsoni*. The next stage of growth in which I find this plant is represented in Plate III. fig. 20. The central triangle has now enlarged to $\cdot 054$, and the diameter of its largest vessels to $\cdot 005$. The exogenous layers are three or four in number. In their general arrangement these layers correspond with those of the Lancashire type, but with the apparently specific distinction that the vessels of the former are much more uniform in size and less regular in their arrangement than those of the latter.

These peculiarities, which recur in every one of the Burntisland specimens, result in an absence of that regular parallelism of the successive concentric layers which renders the young states of the Oldham plant so remarkable for their symmetric beauty. The bark now distinctly exhibits its separation into an inner (*g*), a middle (*h*), and an outer layer (*k*). The tissues of the two former are almost entirely destroyed, but the latter obviously consists of the thick-walled prosenchyma characterizing the Lancashire examples. A series of intermediate conditions conducts us to the magnificent stem of which a section is represented in Plate IV. fig. 21. This stem, inclusive of the bark, has a maximum diameter of $\cdot 34$, that of the ligneous zone is $\cdot 25$, that of the primary, or inner, circular zone is $\cdot 091$, and that of the primary triangular axis is $\cdot 063$. All the large central vessels of the triangle have a maximum diameter of $\cdot 0053$, or nearly double the size of those constituting the corresponding portion of the young twig, Plate III. fig. 18. The most conspicuous features to be noticed in this noble section are the extreme distinctness of the change in the growth of the exogenous layers, to which I have already directed attention when describing the Oldham example, Plate II. fig. 11, and a distinct lacuna near the extremity of each arm of the central triangle, indicative of a longitudinal canal at each of those points. We here see that the primary exogenous additions were made in the way already illustrated by Plate III. fig. 20. But when the ligneous axis of this stem attained an almost perfectly cylindrical form and a diameter of $\cdot 091$, it experienced, through some unknown agency, an interruption to the regular continuity of its exogenous growths. Whatever the cause of this check to vegetative action was, it passed away, and circumferential growth was resumed, but under some altered conditions. The new laminae continued to be developed along radiating curves, which followed the same directions as before; those which were continuous with the three sets of small vessels that diverged from the corresponding angles of the central triangle were little, if at all, altered; but the case is otherwise with the three intervening portions. Here the *large* vessels of the primary exogenous layers terminated suddenly, giving place to very small ones; so that the innermost portions of the newer growths consisted of concentric vascular zones composed of vessels of nearly equal size throughout the greater part of each ring. As further successive additions were made, these new wedges became slowly broader, until, at their peripheral portions, the vessels of such as radiated from the *concavities* of the central triangle opposite to *d d d* became almost as conspicuously larger than those proceeding from the *angles* of the triangle opposite to *d' d' d'*, as was the case in the more central primary portions of the woody axis.

The bark in this stem displays very clearly its separation into an indistinctly double inner layer (*g* and *h*) and an outer one (*k*). We also see very distinctly, especially in the former portion, the individual cells of which it is composed; but these have been flattened and more or less detached from each other by pressure or mineralization, so that their primary arrangement is indistinctly indicated. As in the younger branches, the inner and middle barks have suffered more from these causes than the outer one.

Tangential sections of the exogenous layers (Plate IV. fig. 22) show the intersected extremities of the medullary rays (*f*). These are arranged in precisely the same way as in the Oldham plant (Plate II. fig. 13), the longer axes of the individual cells being frequently inclined (*f'*) to the vertical line separating the two vessels enclosing the ray. The vertical length of the cells in this section varies from $\cdot 0017$ to $\cdot 00087$. Each ray frequently consists of a single cell, rarely of more than two or three: such cells are more densely crowded together at fig. 22, *f*, than is usual. Their more general aspect is that presented by those on the left of the same series, and by the second lower series in the figure. On endeavouring to trace these medullary rays in sections made parallel to their course (Plate IV. fig. 23), if we employ low magnifying-powers, we have no difficulty in seeing that such sections are crowded with them; but, owing partly to the small number of the cells disposed vertically in each ray, and partly to the exceeding delicacy of their cell-walls compared with the coarser tissues of the vessels, it is a more difficult thing to decipher their details where high powers are used. Plate IV. fig. 23, *f*, exhibits their appearance under such powers. In many instances we see that the cells in these latter sections appear to be almost cubical; but, owing to their limited number in each ray, and the consequent absence of mutual pressure, their sides are more turgid and their general aspect less mural than in other examples of Coal-measure plants. This difficulty in tracing the details of their form is further increased by the fact that their vertical divisions frequently coincide with those of the vessels, owing to the dimensions of the two being correspondent in the radial direction. Nevertheless there is no real difficulty in demonstrating that these organs exhibit substantially the ordinary structure and arrangement of exogenous medullary rays.

I have already stated that the vascular elements of these stems differ from those of the Oldham plant, in consisting wholly of barred vessels instead of reticulated ones. Their general aspect is seen in the highly magnified portion of one of them represented in Plate IV. fig. 24. But small portions of vessels frequently exhibit the aspect shown in Plate IV. fig. 25; and it is easy to see that the reticulations of Plate I. fig. 6 are but modifications similar to those of Plate IV. fig. 25, only carried to a much greater extent and occurring in every vessel. They are both modifications of fibro-vascular tissue, and have no relationship to the discigerous fibres of the Conifera.

Though my sections of the Burntisland plant are numerous, all the fragments have been short ones, and I have not been fortunate enough to meet with one exhibiting clearly a nodal foliiferous disk with associated leaves. One small and crushed twig, however, appears in one of my slides, which I do not doubt is of this character; but it is too distorted by pressure for me to make much use of it. It appears to me that this species has been characterized by very long internodes.

Attention has been directed to the fact that, amongst the Oldham specimens, I have in no one instance discovered any trace of a lateral deflection of the vessels of the vascular axis either into leaves or into branches. Amongst my Burntisland examples I

have obtained one such section, represented in Plate V. fig. 27. In it we find a branch (*x*) projecting through the bark from the exogenous vascular laminae which radiate from one arm of the central triangle. It appears as if most of the small vessels of one of the three segments radiating from these several angles were more or less deflected into this divergent appendage*. I am not quite sure that any of the central vessels of the triangle take any part in the new structure; but I have little doubt that the smaller ones constituting the extremity of the angle do so, since I find them to be distinctly deflected in the direction of the new growth. It is obvious that the vascular axis of this branch consists of a mass of vessels, some of which may be derived from the extremity of one angle of the central triangle; but the greater number of which certainly consist of the small vessels of the exogenous layer, which here radiate in converging lines from that angle. We thus obtain our first glimpse of the special use of the three alternating groups of small vessels seen in transverse sections of these stems, viz. to afford the vascular supplies required by some of the lateral appendages†. If this is a correct interpretation, there arises for further inquiry the interesting question whether or not the verticillate lateral branches are grouped with angles of divergence of 120° ; or, in other words, are they arranged in ternate verticils, as appears to be most probable? I have found no example like the one just described amongst my Oldham specimens. But this is doubtless accounted for by the fact that nearly every one of the latter, in connexion with which I have found the nodes, have been young terminal twigs, as indicated by the regularity with which the leaf-bases remain *in situ*: consequently all their lateral buds were as yet undeveloped.

The bark of Plate V. fig. 27 obviously exhibits the innermost layer (*g*) in a contracted or compressed condition, whilst the outer one (*k*) is of fully double the thickness of that seen in the large stem, Plate IV. fig. 21. This enlargement corresponds with what we have already seen in the transverse section of the nodal disk in Plate III. fig. 16, and leaves no doubt on my mind but that the former is also a nodal section. There is no doubt, therefore, that the Burntisland plants exhibited the same nodal expansion of the bark that we find in the Lancashire type. It will further be observed from Plate V. fig. 27, *g'*, that the inner and middle barks accompany the branch in its outward course, as might have been anticipated, supposing my interpretation of this structure to be correct.

After combining the facts which I have enumerated, I have no doubt that these

* It is interesting to find that M. RENAULT has discovered solitary branches in some of his Autun specimens occupying exactly this position. He says respecting them, "Les rameaux que j'ai eu occasion de rencontrer encore adhérents à la tige étaient *solitaires* sur leur articulation." "Ceux que j'ai observés étaient toujours orientés de façon à être contenus dans le plan de l'un des angles saillants de l'axe central de la tige" (*loc. cit* p. 8, plate i. fig. 3).—February 9, 1874.

† M. RENAULT's discovery of the position and origin of the true foliar bundles already referred to (pp. 45 & 48) leaves no room for doubting that these deflected laminae have been connected with a lateral *branch*, and not merely with *leaves*, since we have seen that the exogenous laminae do not contribute to the formation of the merely foliar bundles.—February 9, 1874.

Burntisland stems are examples either of the genus *Asterophyllites* or of *Sphenophyllum*. The absence of leaves in these Scotch specimens renders it impossible at present to determine with which of these two genera they ought to be associated. Before attempting to ascertain the bearing of these facts upon the question of the systematic position of the plants, we must examine some other organs which, I am now satisfied, belonged to similar plants.

The first inquiry which suggests itself is, What are the relations subsisting between the stems described in these pages and the numerous fruits that have been described and figured by various observers on previous occasions? In 1853 Dr. HOOKER published, in the 'Quarterly Journal of the Geological Society of London,' vol. x. p. 199, a description and figure of a terminal strobilus from Carluke, to which he gave the name of *Volkmania Morriasi*. EICHWALD, in his 'Lethæa Rossica,' tab. xv. fig. 1, figures, under the name of *Annularia densifolia*, a stem with eight verticils of circular nodal scars, and with cones given off from each verticil, similar cones having obviously been detached from the scars referred to. GEINITZ figures, in his 'Die Steinkohlen-Formation in Sachsen,' under STERNBERG's name of *Asterophyllites rigidus*, a fruiting spike; and in tab. xx. figs. 7 & 7 a, a second cone-bearing plant under the name of *Sphenophyllum emarginatum*. GERMAR, in his 'Steinkohlen-Gebirges von Wettin und Löbejün,' tab. vi., figures, under the name of *Sphenophyllites Schlotheimi*, some narrow strobili, about two and a half inches long, and attached by short peduncles to the axils of leaves. At tab. viii. fig. 6, he figures another fruit-bearing axis, with both lateral and terminal cones, under the name of *Sphenophyllites angustifolius*. In 1867 Mr. CARRUTHERS published, in the 'Journal of Botany' for December 1867, a paper "On the Structure of the Fruit of *Calamites*," describing and figuring under this name some fruits discovered by Mr. BINNEY, to which he gave the name of *Volkmania Binneyi*. These same fruits were further illustrated by Mr. BINNEY himself, in his 'Observations on the Structure of Fossil Plants found in the Carboniferous Strata,' plates iv. and v.; whilst on plate vi. of the same publication he figured some other fruits of an allied character. Still later (1870) the same observer published, in the 'Transactions of the Literary and Philosophical Society of Manchester,' vol. iv., third series, a "Note on the Organs of Fructification and foliage of *Calamodendron commune* (?)." In 1870 I published, in the same volume of 'Transactions,' a description of "A new Form of Calamitean Strobilus from the Lancashire Coal-measures;" and the fifth volume of the same series (1871) contained another of my memoirs, "On the Organization of *Volkmania Dawsoni*." In his 'Traité de Paléontologie Végétale,' SCHIMPER has republished several of the figures to which I have referred. To the *Volkmania Binneyi* of CARRUTHERS he has given the name of *Calamostachys Binneyana*. Such, so far as I am aware, are the chief fruits hitherto described that claim to belong to the genus *Asterophyllites* or its allies.

In the great majority of the instances referred to, there is no doubt whatever that the fruits belong to the several genera (*Asterophyllites* and *Sphenophyllum*) to which they are ascribed by their describers, because the leaves of these respective plants are found

attached to the stems supporting the strobili. But, unfortunately, in no one of these cases is any thing known of the internal organization of the strobili. The only recorded examples in which such organization is preserved are Mr. BINNEY'S *Calamostachys Binneyana*, my Calamitean strobilus, and the *Volkmannia Dawsoni*, also described by myself. In my memoir on Calamites, published in vol. clxi. of the 'Philosophical Transactions,' and forming the first part of the present series, I discussed briefly the probable affinities of these three fruits (p. 501); and in the subsequent memoir on *Volkmannia Dawsoni*, I again examined their respective claims. Since that memoir appeared, I have investigated a very considerable number of specimens, all of which have tended to confirm the conclusions at which I previously arrived, viz. *that the only British strobilus, of which the internal organization has hitherto been described, that has any claims to be regarded as the fruit of Calamites, is that which I figured in the fourth volume of the 'Transactions of the Manchester Literary and Philosophical Society.'* Such being my conviction, I may exclude this plant from further detailed consideration at the present time, and inquire what light my more recent investigations have thrown upon the two remaining ones.

With this aim I have given, in Plate V. fig. 28, a transverse section of the *Volkmannia Dawsoni* just referred to, but from a section not figured in my previous memoir. In order to comprehend this figure, it is necessary to understand that this fruit is a strobilus, giving off lenticular bractigerous disks from each node, whilst the intervening spaces, corresponding with the internodes, are occupied by successive layers of sporangia, each layer consisting of four concentric verticils and occupying a single internode. Since the bracts fringing the margin of each nodal disk curve upwards and outwards, the transverse section, which has crossed the fruit somewhat obliquely, has cut through the sporangia belonging to two such internodes: those marked *u* belong to two verticils of the inner and upper series, and those indicated by *u'* form a small portion of the peripheral part of the next inferior internodal series, ascending to the level of the central portions of the one above it, as it extended upwards and outwards; *c* indicates the central vascular axis, surrounded by a vacant space originally occupied by cellular tissue, of which the only traces now found are some of their innermost portions (*g*), which evidently constitute a thin inner series of cells closely investing the vascular bundle, but which have shrunk away from it through desiccation, and now adhere only to its angles. The part of the inner circle marked *k* is a transverse section of the outer bark at one of the internodes. On the upper side of the same circle this cylinder of bark appears to be much thickened, because the slightly oblique section has here passed through one of the nodal disks. Being so near the central axis, we here see no trace of the division of that disk into its peripheral verticil of bracts; but this is clearly seen at *t*, *t'*, which letters indicate the margin of the next inferior nodal disk which ascends as it is extended centrifugally. At *t'* we can trace the first division of this disk into separate bracts, the base of each of which here exhibits an almost square section, but with a slight central projection on the outside,

marking the position of a midrib. Following this circle round to $t\ t$, we now see that the bracts have become independent of each other, proving that the section has intersected the specimen at a higher point to the left of the figure than to the right hand. At t'' we discover a third range of bracts, ascending from a yet lower node, but intersected at a point where this range is still separated from those of the intermediate node by the outermost circle of the sporangia (u'), which occupy the intermediate internodal space; at the upper part of the figure ($t\ t$) these two series of bracts (t , t' & t'') come into contact, because at this point they both project beyond the outermost verticils of sporangia. Such are the general features of this fruit; but, for the purpose of exact comparison with the stems of *Asterophyllites*, each point must be examined somewhat more in detail. The central bundle of vessels which appears to represent the central triangle in the axis of *Asterophyllites* consist wholly of vessels. Their state of conservation does not show clearly whether they were barred or reticulate, but several indications suggest that the latter was the case. The greatest diameter of this vascular axis is $\cdot 065$, that of the largest of its component vessels being about $\cdot 0037$. In my original memoir I stated that "its transverse section may be described as a triangle with concave sides and concavely truncated angles" (*loc. cit.* p. 30), which description, it must be remembered, was published before I had seen any stems of *Asterophyllites* suggesting the triangular idea. Plate V. fig. 29 is a still more enlarged representation of the transverse section of this axis. We see from it that the arrangement of the vessels in the bundle corresponds exactly with that of the central triangles of the stems. They are grouped without any definite order, except that the extremities of the three primary angles are occupied by much smaller ones than the more central portions. It is very obvious that the two angles, $c'\ c'$, are merely enlarged and subdivided representatives of the undivided angle c . I wish to call attention to this tendency towards an hexagonal division, from its bearing upon the affinities of *Calamostachys Binneyana*. I discover no evidence whatever of any vessels being given off from this vascular axis to supply the bractigerous disks; but the state of carbonization of the specimen gives this negative appearance but a limited value. That the circle immediately surrounding this vascular axis was composed of delicate cortical parenchyma, may be inferred from the almost entire disappearance of the tissue. The layers, g , alone remain to represent its innermost portion. The outer bark (k), on the other hand, is exquisitely preserved, and, like that of *Asterophyllites*, consists of thick-walled parenchyma, corresponding in every respect with the structures seen in the outer bark of the stems. At each node this outer bark is extended centrifugally into a thick lenticular disk, breaking up at its margin into a peripheral series of bracts, t' . These nodal disks were arranged in successive verticils about $\cdot 9$ apart. I find it difficult to ascertain the exact number of the bracts in each verticil; but, judging from the size of the primary subdivisions of the disk t , compared with the arc of the circle, there appear to have been about thirty-two in each verticil. Each bract was thick at its base, becoming thinner and more foliaceous towards its extremity. It curved upwards and outwards in a some-

what rigid manner, projecting considerably beyond the verticils of sporangia. The sporangia, as seen in a fractured fragment not yet cut up into sections, are obtusely angular, especially at their inner sides, the result of the mutual compression of concentric circles of rounded spheres. They were attached to the bractigerous disks by numerous long, slender, cylindrical sporangiophores, *v.* Since writing my original memoir, I have ascertained that these sprang from each margin of the base of each bract so as to constitute two parallel series. This relation of the sporangiophores to the bracts from which they spring is well seen at *t'*, where the bases of the pairs of sporangiophores appear to project inwards (though they are really proceeding upwards and outwards) from each subdivision of the nodal disk. I have already pointed out that each bract obviously had one thick midrib especially conspicuous near its base. In my memoir, speaking of the spores, I stated that "at the first glance we should be tempted to infer that their exteriors had been spinous; but I have not been able to satisfy myself that such has been the case" (*loc. cit.* p. 34). But since the above sentence was penned I have obtained yet finer examples of these spores, some of which are represented in Plate V. fig. 30, affording proof that long spines projected from their outer surfaces, the bases of these spines being connected by a coarse network of thickened ridges, reminding us of the aspect of the macrospores of *Selaginella inæquifolia* and other Lycopodiaceous fruits. The size of my newly discovered spores, including the length of the spines, is about $\cdot 0044$. In my memoir I stated that it was $\cdot 0037$; but the small discrepancy is accounted for by the fact that in the latter the spines were imperfectly preserved, hence their remarkable length was not known, and consequently not included in the measurement*.

I think that the preceding description must satisfy the most incredulous that this fruit belongs to the same plants as the stems described in the earlier part of the present memoir†. The two agree exactly in the form and composition of the central, non-exogenous, vascular axis, in possessing a bark of which the inner portion was composed of delicate cells whilst the outer one consisted of coarse parenchyma, and in the expansion of the latter *at each node* into a prosenchymatous leaf-bearing disk. The identity of the triangular axis forming the centre around which the exogenous growths were developed in the stems of *Asterophyllites* with the entire axis in the fruit is precisely what we should expect. I have pointed out, in my previous memoir on the Burntisland *Lepidodendra*, that the structure of the vascular bundle or bundles of a strobilus, which is usually a deciduous *annual* growth, is, as might have been anticipated, almost identical with that of the corresponding twigs developed upon the branches within the same limited period.

* These spores appear to me to bear a resemblance to the objects from the Coal-measures described by Mr. CARRUTHERS as radiolarian rhizopods, and to which he has given the generic name of *Traquairia*. See the Report of the British Association for the Advancement of Science for 1872 (Trans. of Sect. p. 126).—February 9, 1874.

† I conclude that the fruit belongs to *Asterophyllites* rather than to *Sphenophyllum*, from the circumstance that its nodal disks subdivide into numerous narrow bracts instead of into a small number of broader ones.

Such a fruit is but one of these twigs whose development has been arrested. Now we have seen from figs. 1, 2, and 18 that, in such twigs of *Asterophyllites*, the vascular bundle has essentially the same triangular form as in the fruit. Then, in addition to these important positive evidences, we have equally important negative ones. A vascular bundle of a triangular form, and having truncated angles, is a rare phenomenon, whether in a strobilus or in a true branch—a phenomenon of which no trace exists in the Oldham beds, save in *Asterophyllites* and, as Professor RENAULT appears to have discovered, in the allied genus *Sphenophyllum*. When, therefore, we find, in a stratum scarcely exceeding a foot in thickness, a fruit possessing such an axis associated with a verticillate arrangement of foliar appendages, and we also find, in the same bed, numerous stems of *Asterophyllites* having a similar primary axis, also associated with a verticillate foliage, we have every possible reason for concluding that the two objects are parts of the same plant; and when, after prolonged and careful search, we fail to find, either in this or in any other part of the Coal-measures, any other plant possessing such a triangular axis, we have as near an approximation to certainty as we can ever hope to attain in these fossils, short of finding the two growing upon the same stem. This has not yet been done in the case of specimens of which the minute organization is preserved; but we do find specimens so associated which exhibit every outward appearance of identity with that of which I have described the internal structure.

In two of his memoirs already referred to, Mr. BINNEY published figures of fruits of *Asterophyllites* from Brooksbottom in Lancashire, where a rich deposit of these curious organisms was discovered in a thin bed of shale by my friend Captain JOHN AITKEN, of Bacup. Captain AITKEN has kindly favoured me with an abundant supply of these interesting specimens, thus enabling me to subject these fruits to a very careful investigation. In my memoir on *Volkmannia Dawsoni*, as also in that on the organization of *Calamites*, I expressed my belief that Mr. BINNEY'S figures of these specimens represented Calamitean fruits; but, after studying the specimens themselves, I am satisfied that such is not the case. I believe them to be of the same type as *Volkmannia Dawsoni*. In the Calamitean strobilus which I described the free ends of the bracts are closely pressed against the sporangia, whilst in the *Volkmannia Dawsoni*, on the other hand, they project considerably beyond the sporangia. A similar projection appears in Captain AITKEN'S specimens, as shown in Plate V. fig. 31, which represents one of the finest of these fruits enlarged to twice its natural size. They are found attached to stems and branches which are undoubtedly Asterophyllitean; and, as Mr. BINNEY has correctly pointed out, some of them were terminal, whilst others were arranged in successive verticils springing laterally from the axils of leaves, where they appear to have been sessile. There is no doubt that in this fruit every node sustained its layer of sporangia, instead of their being developed on alternate nodes, as in the *Calamostachys Binneyana*.

Plate V. fig. 32 represents a fine specimen of the fruit of another species of *Asterophyllites*. I know that the specimen was obtained from one of the shales of the Coal-measures near Manchester, though I am not certain as to the exact locality. The

drawing represents the specimen of the size of nature, but I am convinced that it was originally much longer than now. My cabinet contains two other fragments, which I believe belonged to it; but whether they did or not, the specimen is obviously broken off abruptly at each end. As it is, we have seven verticils of pedunculated strobili, two or three of which strobili only appear on the surface of the shale at each node. That this fructification has belonged to a different species of *Asterophyllites* to Plate V. fig. 31, appears from the fact that in the former all the strobili were pedunculate, whilst in the latter most of the lateral ones are sessile. In this respect the latter plant seems to resemble the *Annularia densifolia* figured by EICHWALD*, which also agrees with the Brooksbottom type in the presence of verticils of very distinct scars, marking the points from whence strobili have been detached. Fig. 32 appears to be very similar to the pedunculated fruit originally figured by STERNBERG under the name of *Volkmannia polystachia*. The *Sphenophyllites Schlotheimi* of GERMAR† is also of the same type. In my specimen each slender peduncle is about .37 in length. It is slightly thickened where it springs from a node of the central axis, and still more so as it enters the strobilus. It obviously consists of a single joint or internode. The principal axis (*k*) consists of a series of long internodes, most of which range between 1.1 and 1.2 in length, and which are delicately but distinctly striated longitudinally; at each node this axis enlarges somewhat into a small lenticular disk, and attached to several of these we observe isolated leaves of *Asterophyllites*, constituting in each case the leaf from the axil of which the adjacent strobilus has sprung. Each strobilus consists of a linear series of verticils of bractigerous disks, disposed at intervals of about .125. Each disk on leaving the axis first curves somewhat downwards, and then upwards and outwards. The marginal fringe of bracts continues in the latter course, so that their tips stand out free, as in *A. Dawsoni*, instead of coming into close contact with the next superior verticil. Each of these bractigerous disks sustains a stratum of sporangia upon its upper surface. The exact arrangement of the latter cannot be ascertained with accuracy; but I am quite satisfied that they are disposed, as in *A. Dawsoni*, in more than one concentric ring. Neither have I been able to determine with absolute certainty the exact number of bracts in each verticil; but it is obviously about fifteen or sixteen, which is a rather smaller number than in *A. Dawsoni*.

The preceding facts suffice to show that whilst various authors have figured different modifications of a common type of Asterophyllitean fruits, none of them obtained any clue to the internal organization of that type. *A. Dawsoni* has given us that clue. Secondary modifications have doubtless existed amongst the various species; but that the external forms and the inward organization of these fruits of *Asterophyllites* and *Sphenophyllum* are now substantially correlated is a fact about which I entertain no doubt.

An important question still seeks an answer, viz. What is *Calamostachys Binneyana*? Mr. BINNEY and Mr. CARRUTHERS both reply, it is the fruit of a Calamite. But my

* Lethæa Rossica, tab. xv. fig. 8.

† Steinkohlen-Gebirges von Wettin und Löbejün, tab. vi.

doubts expressed long ago on this point remain not only unremoved, but strengthened by further researches. My cabinet contains nearly fifty sections of these fruits, and I have examined others in the cabinets of my friends. That the sporangia of these strobili adhere to the sporangiophores in a manner closely resembling those of the modern *Equisetaceæ*, as pointed out by Mr. CARRUTHERS, is undoubtedly true; and, assuming the *Calamites* to be *Equisetaceæ*, the above fact might be deemed a strong confirmation of the conclusion arrived at by the above observers. Mr. CARRUTHERS, in addition, thinks that he sees elaters attached to the spores, which conclusion, if true, would be an important additional fact pointing in the same direction. But, for reasons to be given immediately, I am unable to accept this interpretation of the structures in question. Notwithstanding what has been done by the two eminent observers referred to, sufficient remains to be discovered in this fruit to justify my re-examination of it. Its general plan of construction is, as Mr. CARRUTHERS has shown, very different from that of *Asterophyllites Dawsoni*. It has a jointed axis with enlarged nodes, each of which gives off appendages which are alternately bractigerous disks, somewhat resembling those of *Asterophyllites Dawsoni* deprived of their sporangia, and verticils of sporangiophores, which are almost identical in their organization, as well as in their mode of sustaining their sporangia, with those of the living *Equisetums*. Mr. CARRUTHERS has figured all these structures in his memoir referred to, but on a small scale; Mr. BINNEY has figured them on a much larger scale, but without including some features which appear to me important, especially in connexion with the transverse sections. The only sections of this latter class which that gentleman has given in his monograph on *Calamites* and *Calamodendron* are two on plate iv., both of which have been made in the plane of the verticillate sporangiophores, so that those of the bractigerous disks and of the internodes are not represented by him. I have not deemed it necessary to reproduce any longitudinal sections, because Mr. BINNEY's excellent figures on his plate v., combined with the smaller ones of Mr. CARRUTHERS, leave little to be desired in this direction.

Plate VI. fig. 33 is a transcript of a specimen in my cabinet, with about nine foliar disks; whilst at *v* and *v'*, owing to the removal of the surface of the specimen and the consequent disappearance of the central series of leaves, tangential sections of some of the sporangiophores are brought into view. We here see, as Mr. CARRUTHERS has already pointed out, that the foliar disks (*k''*) reach nearly to the surface of the fruit, where they break up into verticils of leaves, the latter being abruptly bent upwards, almost at right angles to the plane of the disk. This illustration enables us to understand Plate VI. fig. 34, which represents a transverse section made in the plane of the foliar disk (fig. 33, *k''*). At *c* we have part of the central vascular axis; *k* is the cellular lenticular disk; at *t* we have the bases of the upturned bracts intersected transversely, whilst at *t'* we have sections of the ends of those of the next inferior verticil, which, as Mr. CARRUTHERS has described, always alternate with those of the two neighbouring foliar verticils. In Plate VI. fig. 35 we have part of the periphery of a

similar section to the last, but with portions of the leaves of three foliar disks. Thus at t we have the bases of those belonging to the principal disk; at t' we have the alternating series of the disk below; whilst at t'' we again have the tips of the leaves of the inferior disk but one opposite to t , showing that the leaves fringing the disks are arranged in an order equivalent to that of the decussate plan, in which each third verticil returns to the disposition exhibited by the first. In both the above figures the disks are seen to consist of two kinds of coarse, thick-walled, cellular tissue; broad lines leading from the central axis to the base of each leaf (t) consist of prosenchymatous cells elongated in the direction of the plane of the disk, the intermediate triangular spaces being occupied by a coarse parenchyma. In Plate VI. fig. 34 especially we observe that the sections of the leaves (t') exhibit transverse sections of the same elongated prosenchyma. It is of some importance to note that neither in these nor in any other similar sections of these disks have I succeeded in detecting either a barred vessel or a vacant space which such a vessel may originally have occupied; yet two longitudinal sections in my cabinet afford clear proof that Mr. CARRUTHERS is correct when he affirms that a very slender bundle of such vessels runs up the centre of each leaf, and, to do so, it must have traversed the disk. I have only succeeded in detecting their presence in two out of some fifty sections of the fruit under examination, yet they once existed in every fruit. At uu in Plate VI. fig. 34, the section has passed out of the plane of the disk and intersected two sporangia. There have been fourteen leaves in each verticil of this specimen. Plate VI. fig. 36 is a transverse section made in the plane of a verticil of sporangiophores: of these there are usually six in each verticil; but in this verticil there are seven, being half the number of the bracts of the adjacent foliar disk (Plate VI. fig. 34); this numerical relation corresponds with one already observed by Mr. CARRUTHERS, though in the specimens examined by him the respective numbers appear to have been six and twelve. Mr. BINNEY'S figures also represent his transverse section as possessing six sporangiophores; but as the foliar appendages are not present in the latter sections, we have no evidence as to their number. On turning to the vascular axis (fig. 36, c), we discover a distinct triangular structure with concavely truncated angles, thus producing the hexagonal form which is ordinarily characteristic of the axis of these fruits. In the present specimen the axis has accommodated itself to the accidental modification which has produced *seven* sporangiophores instead of six, by the angle c' terminating in two arcs instead of one. At the first glance this axis would appear to be almost a repetition of that of *Asterophyllites Dawsoni* (Plate V. fig. 29); but, as will be seen shortly, this is not exactly the case. We find the vascular bundle under consideration separated into a central and a peripheral portion. This bundle is surrounded by the vacant space (g) representing the missing inner bark, external to which we have the outer prosenchymatous bark (k) arranged in a series of crescentic curves, portions of two of which unite to form the two sides of each of the sporangiophores (v). In the latter structures the prosenchymatous cells of the bark become long, narrow, and parallel-sided, being drawn out at great length

in the radial direction. At its outer extremity the two sides of each sporangiophore diverge in very regular curves, the peripheral intervening space (v') being occupied by a mass of parenchyma which, especially at v' , v'' , and v''' , is seen to constitute disks of considerable thickness. The same appearances recur in whatever direction the section is made; hence my specimens confirm Mr. CARRUTHERS'S statement, that these sporangiophores correspond very closely with those of the living *Equiseta*, and do not sustain Mr. BINNEY'S opinion, that the sporangia are enclosed in "six heart-shaped bags." These sporangiophores undoubtedly contain barred vessels, since, like Mr. CARRUTHERS, I have found them in the pedunculated portion of the organ; and they are still more copiously developed where its two surface-layers diverge in regular curves to embrace the peripheral extremities of the sporangia attached to its opposite sides. That the sporangia adhere by those outer extremities to the proximate concavities formed by the inner surface of the terminal disks of the sporangiophores is certain. Hence, when a section is accurately made in the central plane of a sporangium, detached from the sporangiophore, as at fig. 36, u' , the outer end of the sporangium is always the part ruptured. The transverse sections of the leaves of the next inferior foliar disk are represented in the above figure at t t , and the tips of those of the next but one at t' .

Plate VI. fig. 37 represents another transverse section of the fruit, made across the internode between a foliar disk and a verticil of sporangiophores, from the same specimen as Plate VI. fig. 36. We here find the vascular axis surrounded by a small double cortical ring, k . The sporangia are now reduced to twelve, showing that the verticil of sporangiophores to which they were attached were but six in number. Hence it appears that variations from six to seven sporangiophores may coexist in contiguous verticils of the same strobilus. The sporangia (u) are here arranged with great regularity; and seven of the twelve exhibit that rupture of their outer ends to which I have just referred. The thin margins of the sporangiophores are seen at v , and a circle of the sections of the leaf-tips at t .

The central vascular axis of this specimen exhibits an important feature, which has not been recorded in any of the specimens described either by Mr. BINNEY or by Mr. CARRUTHERS; and as the section fig. 37 shows the peculiar structure very clearly, I have further enlarged it in Plate VI. fig. 38. The centre of this section is composed of a cluster of barred vessels grouped in the usual way; its periphery consists of a ring (d) of similar vessels, but arranged in radiating laminæ, and which evidently represent an exogenous growth superadded to the central bundle. I have never met with this condition in any other specimen, but the presence of this circumferential growth is important. It will be noticed that many of the radiating laminæ follow a curvilinear direction, and that the inner extremities of those laminæ manifest a decided tendency to bend inwards towards the respective central points opposite to d d . What their condition may have been at d' I cannot tell, because some accidental pressure has disturbed their natural arrangement here. I shall call attention to this peculiar disposition after examining the root-structures of *Asterophyllites*.

Mr. CARRUTHERS has described the wall of the sporangium as "composed of irregularly elongated cells, with projections of a secondary deposit extending at right angles into the interior of the cells." This is strictly correct; but there is something beyond this to be noted. The longer axes of these cells are radial in relation to that of the fruit-axis, and parallel with the longer sides of the sporangium. When we see only the outer surface of the sporangium-wall, we observe that the latter appears as represented in Plate VI. fig. 39, and by Mr. CARRUTHERS in his fig. 5; but its inner surface frequently exhibits the aspect seen in Plate VII. fig. 42. When a transverse section, like Plate VII. fig. 40 (again represented by Mr. CARRUTHERS in his fig. 45), is made across the shorter diameters of these cells, we see that each cell has very thick walls on its inner and two lateral surfaces; whilst the outer wall, forming part of the outer surface of the entire sporangium, is very thin. But if the section is made through the long axes of these cells, so that their lateral walls are brought into view, we then obtain the appearance indicated by Plate VII. fig. 41, where the parallel bars are much more numerous and more perfectly parallel in their arrangement than in Plate VII. fig. 42. The bars in fig. 40 are obviously different from those of fig. 41. The former represent the cell-walls of a corresponding number of distinct cells; the latter represent the transverse bars thickening the walls of one individual cell. It is obvious that we have here a modification either of the spiral or of the annular cell; but instead of the lignine, forming the thickened bars of Plate VII. figs. 41 & 42, being continued entirely round the transverse circumference of the elongated cell, some unknown influence has prevented their deposition on the outer surface of every cell—a curious example of the effect of unknown forces in regulating the distribution of these secondary deposits in fibro-vascular structures.

Mr. CARRUTHERS has represented in his fig. 1 a cluster of spherical spores, from the outer wall of each of which there project delicate thread-like appendages. He describes these as follows:—"The spores are simple globular bodies, frequently exhibiting an outer and an inner wall. Sometimes, however, they appear to be composed of a single wall, and then the outer wall is represented by lines more or less separated from the spores. These I believe to be elaters, similar in structure to those of *Equisetum*." As to the first of these statements respecting the outer and inner walls, my observations agree with those of my indefatigable friend, but from his elater hypothesis I am compelled to dissent. The following appears to me to be the probable explanation of these appearances.

Plate VII. fig. 43 represents a number of these spores selected from two strobili in different stages of development. The larger ones exhibit a series of examples in which we have an inner cell enclosed within an outer one. Of these, Plate VII. fig. 43, *w* are the forms which approach nearest to the condition in which Mr. CARRUTHERS recognizes elaters. In these specimens the point of contact between the inner and outer cells represents, according to his view, that at which the elaters of an Equisetiform spore are united to the actual spore; but the other examples figured show that this contact is accidental and not essential. In most of them the spore lies free in the centre of the

outer cell. That the latter breaks up when matured, is undoubtedly true. In a ripe strobilus the difficulty is to find a spore of which this layer is not broken up. But in none of the fragments do we discover the four club-shaped organs known as elaters. I have in my cabinet thousands of these spores, but in no solitary instance have I found a true clavate elater. On the other hand, I think I have abundant evidence that what Mr. CARRUTHERS regards as such are but the shreds of the mother-cells which were derived primarily from the interior of the sporangium-wall. An examination of true Equisetiform spores during their development, and a perusal of the records of the same process as it is described by HOFFMEISTER and SACHS, tend to confirm my view; not that any exact parallism can be traced between the fossil spores and those of the living *Equisetum*! far from it; but we do find in the one the broad outlines of what may have taken place in the other, as in many varied cryptogamic growths. Be this as it may, I affirm unhesitatingly that had the outer wall of the fossil spore ever resolved itself into true elaters, we should see their spiral lines, as they are accurately represented by SACHS*, crossing the circular disks of the spores in innumerable instances. The tissues of which these spiral bands consist are precisely such as would be likely to be preserved, and be conspicuous, in the fossil state; whereas, I repeat, no one has ever pretended to have seen them in this condition in any solitary instance.

The correctness of my explanation receives further support from the spores of a strobilus in my cabinet which has not attained to its full maturity. Four of these spores represented to the right of the group (Plate VII. fig. 43, *w'*, *w''*) will be recognized by their smaller size and darker tint. Their inner spheres especially are little more than half the size of those constituting the rest of the group, and their outer cell-walls are as yet unruptured. We have here the precise stage of growth in which the transverse spiral bands should be conspicuously present; and from this stage up to the final disruption of the cell they ought to become increasingly obvious, but nothing of the kind is to be seen. In every instance we have a simple cell-wall of uniform density, instead of that alternation of thick and thin bands, the formation of which precedes the liberation of the former as true elaters. In addition to this negative evidence, some of these specimens exhibit testimony of a positive kind. It must be remembered that elaters are formed out of the outer investing layer of each individual spore; but at *w'* I have represented two examples in which each outer cell-wall encloses *two* distinct spores—a condition that would have been genetically impossible had these cells represented the outer layers of individual spores, as is necessary on the elater hypothesis; but on the supposition that they are mother-cells almost every difficulty disappears. SACHS correctly describes the mother-cells of *Equisetum* as “ceasing to be a continuous tissue, and not only isolating themselves, but floating freely in a liquid, filling the sac of the sporangium” (*loc. cit.* p. 355). The disputed structures appear to me to have originated in some similar manner; and what Mr. CARRUTHERS has described as elaters I believe to be merely fragments of their irregularly torn cell-walls, which naturally broke up when the contained spores became

* Lehrbuch, fig. 280, C.

matured and required liberation. Why a larger number of the mother-cells did not contain more than one spore is but one of the many anomalies seen in this very perplexing fruit. The further question now arises—To what plant does this strobilus belong?

Mr. BINNEY answers this question by affirming that it is the fruit of *Calamodendron*; and Mr. CARRUTHERS, regarding it in the same light, says that it is the fruit of a *Calamite*. The latter observer arrives at this conclusion under the conviction that *Calamites* and *Asterophyllites* are identical plants. The spores throw little light upon this problem, because they exhibit too generalized a form to indicate any special relations. Mr. CARRUTHERS has referred to the semispiral deposits in the cells of the sporangia as representing the true spiral fibres in the sporangial cells of *Equisetum*. But such deposits are not confined to *Equiseta*. We have them in the corresponding sporangial cells of *Marchantia conica*, in a condition much more closely resembling those of our fossil fruit than do the Equisetaceous ones. The sporangia of our fossil very closely resemble those of *Equisetum* both in their form, in the mode of their attachment to the sporangiophores, and in the general aspects of the latter organs; but they differ in the fact that only alternate verticils of the nodal expansions bear sporangia in the fossil, whereas they are attached to every verticil in the recent type. It appears to me that in the former the sporangia are ruptured by detachment from the sporangiophore, instead of by longitudinal ventral dehiscence as in the latter. When we come to the central axis, the difference between the two types becomes increasingly manifest; though even here we are not without some curious features of resemblance. If we make a transverse section through the node of a recent Equisetaceous strobilus, *in the plane of a verticil of sporangiophores*, we see that the bark from which these sporangiophores spring expands into a small lenticular disk, the structure of which is almost identical with that of the *sterile* disks of *Calamostachys*, as seen in Plate VI. fig. 34, and proportionately different from the corresponding section of the *fertile* sporangiophores represented by Plate VI. fig. 36. Thus we have agreement between the recent and fossil types in the structure of parts whose general aspects are so different, and differences of structure where the outward forms agree. The double layer of the bark of *Calamostachys* corresponds exactly with what we have in *Asterophyllites*, whilst this tissue consists of a single uniform layer in *Calamites**. This is a distinction of the greatest importance. It would be contrary to all experience to expect to find so great a change in a continuous *aërial* bark investing the stem and the fruit-axis of a Cryptogam as would be involved in the sudden separation of a single parenchymatous bark into two strongly marked layers of parenchyma and prosenchyma. Yet we have to admit the possibility of such an anomalous condition as is here suggested, if we are to recognize in *Calamostachys* the fruit of *Calamites*.

The vascular part of the axis differs from the corresponding portion of *Calamites* even yet more than the bark does, approximating in the same ratio to that of *Asterophyllites*.

* See my memoir on *Calamites*. Phil. Trans. 1871, Plate xxiii. fig. 9.

In even the smallest known branches of the former plants we find exactly the same type of organization as we do in the largest and most matured stems. We invariably have a central cellular medulla, which becomes fistular at a very early period, and which is surrounded by a ring of distinctly separated vascular bundles or wedges, each one of which has a well-marked longitudinal canal at its inner angle. The same conditions recur with the greatest exactness in the cone which I have described in the Transactions of the Literary and Philosophical Society of Manchester as being that of a Calamite; but in *Calamostachys* all these conditions are reversed. Here we have neither a cellular medulla nor a fistular cavity. In their place we invariably have a solid, central axis of barred vessels, such as we find only in the very young twigs of Lepidodendroid plants and in *Asterophyllites*. The only indication of the structure of the exogenous zone of the parent stem of *Calamostachys* which we have found is that represented in Plate VI. fig. 38. Here, at all events, we might have expected to discover some trace of Calamitean arrangements, had these been Calamitean strobili; but nothing of the kind appears. It is as unlike the exogenous zone of a Calamite as it is like the corresponding tissue found in the roots of *Asterophyllites*. The central axis does not display the very definitely triangular form seen in that of *Asterophyllites*, but there is a decided approach towards it; and we detect a further indication of a trifid arrangement in Plate VI. fig. 38, at the two points indicated by the letters *d d*. Each of these constitutes a centre, on either side of which the radiating laminae of the exogenous zone converge towards the letter *d* as they proceed outwards. I presume that a similar point may have existed to the left of the lower part of the figure indicated by *d'*; but here, as already mentioned, the tissues have been accidentally displaced by some disturbing force masking their primary condition.

We shall find a similar tendency to that just described recurring in the roots of *Asterophyllites*.

It appears to me that the number and symmetrical grouping of the nodal appendages round the central axis of *Calamostachys* is not without significance. In its normal and almost invariable condition each verticil, whether of leaves or of sporangia, exhibits some multiple of 3. Thus we have six sporangiophores and twelve foliar divisions of the barren verticils. Whatever these facts indicate they are in harmony with the prevalence of the trimerous type of structure so characteristic of the stem of *Asterophyllites*.

After balancing these various facts and arguments, I am led to the conclusion that *Calamostachys Binneyana* has much closer affinities with *Asterophyllites* than with *Calamites*. With the latter it has no one structural feature in common. There is no solitary point in which the two plants resemble each other. The resemblance of the fertile sporangia of *Calamostachys* to those of *Equisetum* has been combined with the foregone conclusion that the *Calamites* were Equisetaceous plants, in leading to the belief that the two were parts of the same plant; but I cannot conceive of any conditions in which the stem of a *Calamites* could be prolonged into that of the *Calamostachys*.

mostachys. I have carefully investigated the relations which the fertile stems of the *Equiseta* bear to axes of their terminal fruit-spikes, and I find that their respective structures are typically identical. The transition from the stem to the fruit-axis produces no structural changes save such as are of the most trivial kind; the general type remains unaltered and continuous. But to plant *Calamostachys Binneyana* upon the top of a Calamite would be as abnormal as to surmount the stem of an *Equisetum* with the strobilus of a Lycopod.

Whilst expressing my conviction that *Calamostachys* is allied to the Asterophyllitean plants, I cannot as yet correlate it with any particular stem. I have no evidence indicating that it belonged to any of those described in the preceding pages, and suspect that the plant of which it is the fruit has yet to be discovered. Diligent search must continue to be made in the narrow vertical zone of beds within which the specimens occur, until some absolutely demonstrative facts are obtained removing the obscurity which still invests this very remarkable and interesting fruit.

I have already referred briefly to one or two examples of fruiting axes of *Asterophyllites* and *Sphenophyllum* in which circular scars, arranged in verticils at the nodes, marked the points from whence strobili had been detached. Plate VII. fig. 44 represents a similar stem, which I found amongst Captain AITKEN'S Brooksbottom specimens. The scars (*r*) appear as if they were located below the node; but this appearance has, I think, merely arisen from the circumstance that the strobili were detached before the plant was enclosed in the shale, thus allowing the bases of the bracts to be compressed against the stem; the carbonaceous matter having subsequently become detached revealed the cicatrices in question*. Each cicatrix is nearly oval, but slightly narrower at its lower than at its upper extremity, and with a distinct central depression marking the position of a vascular bundle. There appears to me to be a close resemblance between this specimen and the plant figured by LINDLEY and HUTTON under the name of *Calamites verticillatus*, but respecting which I have already expressed my conviction that it had no affinity whatever with the genus *Calamites*†. The stem last mentioned appears to be the same as that figured by GEINITZ‡ under the name of *Equisetites infundibuliformis*. It becomes an interesting question whether this plant will not prove to be an arborescent stem of an *Asterophyllites* or *Sphenophyllum*; if so, are the characteristic scars large because they bore large strobili, or have they become larger through the expansion of the bark subsequently to the shedding of the strobili, and consequent upon the exogenous enlargement of the vascular portion of the stem? Each of the large oval cicatrices of this plant has a central impression more or less regularly defined, indicating the former passage of a central vascular axis at this point, such as is seen in each of the scars of Plate VII. fig. 44. In some instances they probably indicate the position of branches.

Plate VII. fig. 45 represents a fine example of *Calamites verticillatus* in the Museum

* It is possible that the young buds may have burst through the slightly confluent bases of the leaves, as the rootlets and branches of *Equiseta* do through their nodal sheaths.

† Phil. Trans. 1871, p. 507.

‡ Die Steinkohlen-Formation in Sachsen, tab. x. figs. 4, 5.

of the Owens College, and found in one of the upper coal-shales of Lancashire. The figure is reduced to two thirds the size of the original. It is not without significance that the only vegetable remains seen in the same large slab are an abundance of leaf-bearing stems and twigs of *Asterophyllites* of various sizes, which appear to be in all respects *facsimiles* of those described in the preceding pages. This example of the stem consists of a number of well-marked internodes of various sizes. These are marked by numerous faintly defined parallel longitudinal grooves, with others of a much more sharply defined character at irregular intervals. The latter have obviously been cracks in the original bark, into which the matrix has entered, causing the latter to stand out in projecting ridges. In this specimen the large cicatrices are planted in a verticillate manner upon each third node; in another and otherwise similar specimen in the Owens College collection they are only planted upon every eighth node, thus exhibiting variations in this plant which may possibly have been specific ones. The latter specimen further indicates what is but obscurely shown in the example figured, viz. that the cicatrices appear as if planted *upon* the node, and not *above* or *below* it.

The general resemblance of these large stems to Plate VII. fig. 44 is very striking. The facts now stated, combined with the difficulty of collocating these examples with any other known plant, strongly incline me to the belief that they are the arborescent stems of the *Asterophyllites* with which they are associated in the specimen figured.

In August 1869 I published in the 'Monthly Microscopic Journal' the brief memoir referred to in No. IV.* of the present series, in which I separated two very distinct groups of plants which had hitherto been regarded as allied to each other, viz. those belonging to ENDLICHER'S genus *Dadoxylon*, whose wood-cells were truly discigerous, and those in which this character was only apparent, not real, it being due to a mere modification of fibro-vascular tissue. In that memoir I said:—"It appears necessary, therefore, to establish a new genus for all the plants whose woody tissues consist of reticulated fibres, and the name of *Dictyoxylon* appears an appropriate one for it. I should propose, for the present, to include in this genus *all* the reticulated types. At some future time their further separation into two or more genera may be requisite"†. When giving a sketch of this new genus at the Edinburgh Meeting of the British Association, I included in it, in accordance with the above determination, a new plant from the Coal-measures, to which I assigned the name of *Dictyoxylon radicans*. But in working out the details of the genus for the fourth memoir of the present series, I found that the necessity for further generic subdivision which I had anticipated was already urgent. In a letter to Dr. SHARPEY‡, I observed, respecting the *D. radicans*:—"I think it not improbable that this has been the subterranean axis of some other plant, since I have succeeded in tracing its ultimate subdivisions into rootlets. I propose for the present to recognize it by the generic name of *Amyelon*. My specimens of this plant are very

* Philosophical Transactions, 1873, p. 378.

† *Loc. cit.* p. 68.

‡ Proceedings of the Royal Society, vol. xx. p. 436.

numerous." "They may prove to be rhizomes and roots of the *Asterophyllite* described in my last letter to you."

I think I have now accumulated most satisfactory evidence that the above hypothesis is correct, and am able to prove that *Amyelon* is the root and rootlets of the stems described in the preceding pages. I would observe at the outset that the first examination of the former plant would scarcely lead a naturalist to the above conclusion, since it exhibits no appearance of joints or special nodes, much less of verticillate arrangements of any kind, such as are seen in the rhizomes of *Calamites*. On the other hand, it is branched like the roots of an ordinary exogenous tree. Its bark also differs from that of *Asterophyllites*; but I think that I shall have no difficulty in tracing the homologous relations of the two conditions. In describing these specimens I will commence with the most characteristic example that I have seen, one of a series of valuable sections which I obtained from a nodule for which I am indebted to Mr. NIELD of Oldham. Plate VII. fig. 46 is a transverse section of a young root surrounded by a cluster of branching rootlets, which have been chiefly, if not wholly, given off from two points in the section. The central axis (*d*) consists of a series of reticulated vessels of small size, the largest of them not exceeding .0018. These are arranged, in the usual exogenous manner, in very regular radiating laminæ or wedges. The centre, whence these laminæ spring, exhibits no trace of a medulla, nor, *in the present section*, of any other special tissue. In other sections to be described important differences present themselves in this respect. The vascular axis in fig. 46 consists of a large central mass of vessels, partly enclosed in a second crescentic layer representing a secondary exogenous growth. The latter portion, it will be observed, does not entirely enclose the central one—a condition to which I have referred in previous memoirs as not being uncommon amongst the Cryptogamic plants of the Coal-measures.

This vascular axis is surrounded by a bark consisting of two very distinct layers. The peculiar aspects of this tissue are better seen in Plate VIII. fig. 47, which is enlarged eighty diameters. Its inner layer (*g*) is an ordinary parenchyma, consisting of cells of very unequal sizes. Many of these are very small, but others are .0038, these larger ones being especially predominant towards the exterior of the layer. Many of these external cells (*g'*) are subdivided tangentially to the circumference of the stem by a number of secondary cell-divisions. This parenchyma passes rapidly, but not abruptly, into the outer layer (*h*), in which cells, compressed tangentially, are arranged in irregular columns perpendicular to the surface of the structure. The boundary lines between contiguous columns are strongly marked, usually more so than the transverse septa of their component cells. The individual columns sometimes extend from the inner bark to the periphery; at others they terminate at various points midway, where they become intercalated between other similar ones.

Plate VIII. fig. 48 represents a radial longitudinal section of part of the root, a portion of a similar one being still further enlarged in Plate VIII. fig. 49. In the former figure the vessels of the axis (*d*) are seen to be crossed by numerous small medullary rays (*f'*),

whilst the vessels themselves exhibit, in this aspect, very distinctly marked reticulations on the inner surfaces of their walls. In Plate VIII. fig. 49 we find the bark of this section exhibiting very similar appearances to those of fig. 47. We have the same inner layer of parenchyma (*g*), some of the cells of which (*g'*) are again subdivided by secondary septa, whilst those of the outer bark (*h*) are arranged in centrifugal columns, similar to those of the transverse section. We thus learn that the outer bark consists of numerous horizontally disposed lines of compressed cells, whose parallel sides are lines more or less parallel with the periphery of the bark. The origin of this peculiar structure is sufficiently obvious; but were it otherwise, Plate IX. fig. 54 would make it plain, as I shall shortly demonstrate.

Plate VIII. fig. 50 is a tangential section of part of the vascular axis, magnified seventy-five diameters. The vessels do not exhibit their characteristic reticulations on the surfaces which are parallel to this section. In every one of the sections which I have made in this plane I have obtained the same result. The reticulated structure is conspicuous in the vascular walls parallel with the medullary rays; but instead of being continued round the entire tube, the reticulations appear to terminate abruptly, and with defined though irregular margins, as represented at *d'*, on reaching the tangential surfaces, which latter merely exhibit a thin, uniform, and apparently structureless layer of carbonaceous matter. These facts must be correlated with what I have previously mentioned, viz. that in the stems of *Asterophyllites* (see *antea*, p. 44) the reticulations of the vessels were more definite on such of their walls as are parallel with the medullary rays than are those tangential to them. The rays themselves (*f*) are numerous, and, like those of the stem (Plate II. fig. 13), consist of from one to four cells (rarely five) arranged in a single vertical line. Plate VIII. fig. 51 represents the lateral aspect of one of these medullary rays, where the cells (*f*) are seen to have a regular mural arrangement. They have a vertical diameter of about $\cdot 0015$.

Returning to Plate VII. fig. 46, we find that at two points, one to the left and the other at the upper margin of the bark, the outer layer of that tissue divides and allows of the centrifugal extension of the inner parenchyma. The former rapidly thins out as it accompanies the latter for a very short distance, when it soon disappears. The inner parenchyma soon spreads out into a cluster of diverging rootlets (*o*), which stream in every direction. Some of these are seen in longitudinal (*o''*), others in oblique (*o'*), and others again in transverse (*o*) sections. In the longitudinal section (Plate VIII. fig. 48) we again see one of these root-clusters, commencing as a large globular mass (*o'*), dividing into separate rootlets. Extending directly inwards from this root-cluster we see a column of the cells of the inner bark (*g'*) prolonged through the outer one. In the particular portion of the section here represented much of this inner layer has been accidentally destroyed, but in the remainder of the specimen the tissue appears in its normal state. At *n* we see a bundle of vessels passing horizontally outwards through the vascular zone to reach the root-cluster. On turning to Plate VIII. fig. 52, we have one of these root-bundles divided transversely (*n*), and pushing aside the vascular laminae as it

emerges to reach the bark. These bundles appear in all tangential sections of the roots. I have endeavoured to discover some regularity in their taxis, but have failed to do so. The clusters of rootlets were evidently given off alike from all parts of the circumference of the primary axis and its branches, but not in quincuncial or any other regular order. Sometimes two or three of the vascular bundles appear in close approximation in one tangential section; in others they are fewer in number and much further apart. It thus appears obvious that the clusters of rootlets are arranged irregularly on the periphery of the bark. On making a tangential section of the outer bark-layer, *h* (Plate IX. fig. 55), this latter tissue appears as a thick-walled parenchyma, composed of very uniform cells having a tolerably mean diameter of $\cdot 0019$. Where the vascular root-bundles pass outwards through this tissue, they do so enclosed in a sharply defined, round cylinder composed of the cells of the inner bark, and which ultimately expands to form the principal parenchyma of the individual rootlets. This cylinder has usually a diameter of about $\cdot 038$ to $\cdot 04$, and is obviously the same structure as that seen in Plate VIII. fig. 48, *g*. Though the individual rootlets correspond in their general aspects with those of *Stigmara*, they differ in several points of detail, but especially in their smaller size, and in the circumstance that all their component tissues are almost invariably preserved, whilst the middle parenchyma is rarely seen in those of *Stigmara*. Plate IX. fig. 53 represents a longitudinal section of part of a rootlet. The root-bundle (*n*) consists of a few slender vessels, which are sometimes barred and at others reticulated. This bundle is surrounded by a sheath (*o''*), which is often very clearly defined, especially in the transverse sections (Plate VII. fig. 46, *o*). It consists of long, narrow, thin-walled, and parallel-sided cells. This is invested by the principal parenchyma (*o'*), the cells of which are somewhat lengthened in the longitudinal direction; and the whole is enclosed in a well-marked and often very sharply defined parenchymatous cortical investment (*o*), which only differs from that upon which it rests in the cells being yet more elongated and compressed. These rootlets further differ from those of *Stigmara* in being of a darker colour, and more suggestive of a robust and less delicate texture.

I have called attention to the peculiar aspect of the outer bark as seen in all vertical and transverse sections of it, and also to the fact that the largest and outermost cells of its inner parenchyma are frequently intersected by secondary cell-walls, which are parallel to each other as well as to the periphery of the axis. It appears obvious to me that we have here a meristem structure analogous to some peculiar bark-tissues described in two of my previous memoirs*. It also appears clear that the outer parenchymatous cells of the inner bark were the source from whence additions were constantly being made to the inner surface of the outer bark, by the elongation of those cells in a radial direction, and the contemporaneous development within each cell of the numerous parallel tangential cell-walls already referred to. It obviously follows that each long column of parallel cells, seen in Plate VIII. figs. 47, *k*, & 49, *k*, with their common, strongly marked, radially arranged boundary lines, represent what had originally

* Phil. Trans. 1872, Part I. Plate xxxi. figs. 54 & 57. Ibidem, Part II. p. 313.

been one single cell. It is only by some such explanation as this that I can reconcile the appearances of the two sections just referred to with those of a tangential section made through the same structures. The latter section, as I have already stated, merely exhibits a very ordinary thick-walled parenchyma (Plate IX. fig. 55), affording no indication of the peculiarities seen in the sections represented in Plate VIII. figs. 47 & 49. The robust strength of the cell-walls of fig. 55 is altogether different from the more delicate transverse divisions of fig. 47, *h*, making it probable that the genesis of the two had been different. It was difficult to believe that these radial and tangential sections belonged to the same structures. By making an obliquely radial section through the tissue, I obtained the result seen in Plate IX. fig. 54, which I think demonstrates the accuracy of my interpretation. In this section I obtained, practically, a foreshortened view of the oblong cellular columns of Plate VIII. figs. 47 & 49, which reduced each column to the condition which one of the cells of Plate IX. fig. 55 would exhibit if elongated somewhat radially. The two radial and tangential sections now appear to harmonize without difficulty, and, unless I am seriously mistaken, they combine to sustain the genetic hypothesis which I have ventured to advance. This hypothesis is not without interest when viewed in connexion with various similar phenomena described in my previous memoirs; all these examples exhibit the innermost cellular bark approximating to the conditions which it ultimately attained in the cambium of exogenous stems.

In the examples of the root which I have hitherto described, the maximum diameter of the vascular axis is not more than .075. But I possess others of larger dimensions, especially one for which I am indebted to Mr. NIELD, of Oldham, in which the ligneous axis, deprived of its bark, measures fully an inch in diameter. All these specimens more or less resemble Plate IX. fig. 56, which represents a transverse section of a vascular axis, enlarged nine diameters. They exhibit numerous very strongly defined lines of circumferential growth, which are always irregularly concentric, each layer of vascular tissue being of unequal thickness on opposite sides of the stem, even when it forms a complete circle; but they very frequently only form crescentic segments of circles. We have already seen that the second exogenous layer of Plate VII. fig. 45 is of this character; and several of the thin outermost ones at the lower part of Plate IX. fig. 56 exhibit the same aspect. Had the deficiency in these growths always been on the same side of the axis, we might have supposed that it was due to some peculiarity in the position of the growing plant relatively to light or moisture; but this is not the case. The strongly marked boundaries of these concentric layers render this one of the most remarkable examples of exogenous growth in a Cryptogamic plant that has hitherto come under my notice.

I have as yet brought forward no evidence to prove the correlation of these roots with the stems of *Asterophyllites*; but such evidence is not lacking. At an early stage of my inquiries I observed in several of my sections of these roots indications that some peculiarity existed in what ought to have been their medullary centres. In some of these there was only a triangular cleft; in others I observed some clusters of vessels, of larger

size than those constituting the exogenous layers, occupying the same central position, and suggesting the idea of a primary vascular axis whose arrangements had been disturbed during the subsequent growth of the root. All these appearances received their explanation on my obtaining some additional sections, one of which is represented in Plate IX. fig. 57; I am indebted for this fine example to Mr. J. WHITTAKER, of Oldham. Both its general structure and its peculiar bark at once identify this as being identical with Plate VII. fig. 46.

Plate IX. fig. 58 is an enlarged view of the central portion of fig. 57, in which we find the triangular axis of *Asterophyllites* in its most definite form. The identity of this structure in the two conditions of stem and root, both in its contour and in the arrangement of its vessels, is most obvious. Its diameter, too, corresponds closely with that of the axes of the larger aërial stems; the only difference that I can detect appears in the larger size of its vessels, compared, for instance, with those of Plate II. fig. 9. It will be observed also that the laminae of the young exogenous growth curve away from each of the angles of the central bundle in exactly the same fan-shaped manner as is seen in *Asterophyllites*—an arrangement to which I have already alluded when I said that the axis of *Calamostachys Binneyana* (Plate VI. fig. 38) exhibited some Asterophyllitean features in its exogenous layer. The vessels of the exogenous layers of the root-structures are much smaller than in the aërial stems described. This difference may be merely characteristic of a distinction between the roots and stems, or it may be due to the circumstance that the roots belong to a different species from those of which I have described the stems. The latter view is sustained by the fact that I possess several examples of undoubted amyeloid* roots having the structure seen in Plate IX. fig. 59. Some similar ones discovered since this figure was drawn are not only much larger and more perfect, but are invested by the characteristic bark of these amyeloid roots, removing all doubt as to the generic identity of the entire series of specimens. Plate IX. fig. 59 is drawn to the same scale as the corresponding sections of the aërial stems. We thus see that the vessels of the former correspond closely, both in size and arrangement, with what we see in Plate II. fig. 10, allowance being made for the non-existence in Plate IX. fig. 59 of the central triangle. The closeness of these general as well as detailed resemblances renders it probable that, whatever may be the case with Plate VII. fig. 46, Plate IX. fig. 59 belongs to the same species as Plate II. fig. 10 and the allied sections. We see in Plate IX. fig. 59 the same tendency to the formation of crescentic exogenous growths as appeared in Plate VII. fig. 46 & Plate IX. fig. 56.

There are a few physiological features in the roots now described meriting attention.

* As my investigations progressed, I have found it necessary to assign provisional generic names to certain well-marked types of structure on the same principle that the Lepidodendroid and Sigillarian roots were designated Stigmariæ before their real nature was known. Nor is this process wholly without a permanent use; even after the true correlation of the objects with well-known and previously named plants is discovered, such names serve as convenient descriptive adjectives. Thus we now speak of sternbergian piths and diploxyloid stems. So the term amyeloid conveniently designates these pithless roots of the Coal-measures.

I have already referred to the fact that the ligneous reticulations are deposited on the inner surfaces of the walls of the vessels of *Asterophyllites*, and that these deposits are more distinct on those sides that are in contact with the medullary rays than on those which are tangential to the circumference of the stem. In the axis of the root this difference becomes yet greater, since on the tangential surfaces the reticulations disappear altogether. When we remember that precisely similar conditions exist in the distribution of the circular disks on the corresponding portions of the fibres of Coniferous stems, we may suspect that some similar influence regulates that distribution in both cases. Not that I mean to infer the existence of any systematic relationship between *Asterophyllites* and the Conifera, but of some influence common to both which has produced differences between the deposits and secondary growths of the radial and tangential surfaces of their fibro-vascular elementary tissues. That some relations subsist between the intervacular disks of Coniferous fibres and the ligneous deposits within the same fibres is well known*.

The most determined opponent of exogenous development must admit that we have here circumferential growth, as unmistakable as that of an oak-tree both in the stems and in the roots. Not only have we the lines of growth, so distinctly seen in Plate IX. fig. 56, but the newer laminae not unfrequently split off from the older ones, as in Plate IX. fig. 59. In both stems and roots these new vascular layers can only have originated in the inner portions of the inner bark, *g*. This unity of function leads us to the conclusion that the parenchymatous cells of the inner bark of the stem (Plate II. fig. 10, *g*) are homologous with the non-radiating parenchyma of the roots (Plate VIII. figs. 47 & 49, *g*), and that in both cases this layer has been the chief seat of genetic activity. I have already shown that in the case of the roots the *outer* layer of the bark has clearly been derived from the outer surface of the *inner* parenchyma by the development of new and parallel tangential divisions within the interior of its constituent cells; so that, in this organ at least, the parenchyma has been subject to a double waste of its cell-supply—an inner one to furnish new vessels, and an outer one thickening the outer bark-layer. This exhaustion, whether it was continuous or periodic, must necessarily have been antagonized by a corresponding activity of cell-reproduction. It thus appears that this inner parenchyma was a meristem layer in a more or less constant state of intense genetic activity. I have not been able to satisfy myself in the same conclusive manner respecting the origin of the prosenchymatous outer bark of the aërial stems. How far the latter is the altered homologue of the exterior of the outer bark of the roots is also an open question. It is not improbable that both these tissues may be genetically identical, but modified in their form to suit the aërial and subterranean conditions under which they had to fulfil their respective functions.

The most difficult question of all yet remains to be considered—What is *Asterophyllites*? In the first place, it has the closest possible affinity with *Sphenophyllum*. I

* See on this point my memoir “On the Structure and Affinities of some Exogenous Stems from the Coal-measures,” Monthly Microscopical Journal, August 1, 1869.

assume this, being convinced that the observations of Professor RENAULT at Autun are accurate; that able observer is much too cautious to speak so decisively as he has done respecting the stems of *Sphenophyllum* for his evidence to be doubted. He has kindly sent me examples of his stems, and they agree closely with my own; so that the near affinity of *Asterophyllites* and *Sphenophyllum* must now be accepted, not as a probable hypothesis, but as a determined fact*. It is equally clear that these stems have no relationship to *Calamites*. M. GRAND'EURY some time ago arrived at this conclusion at St. Etienne (see 'Comptes Rendus,' tome lxxviii., "Observations sur les *Calamites* et les *Astérophylrites*") from the study of their external forms; Dr. DAWSON has insisted upon the same distinction in the case of his Canadian specimens. Professor RENAULT writes to me respecting the stems of *Sphenophyllum*:—"Il serait difficile de vous donner la description des détails de structure de ces tiges curieuses, qui n'ont jamais rien eu de commun avec les *Calamites*." I am convinced that the same conclusion is true in the case of *Asterophyllites*. To continue to affirm that these plants were the branches and foliage of *Calamites* in the face of this combined testimony of independent observers, whose positions have given them opportunities for forming a judgment on the question, will surely be to stultify all scientific testimony.

But, unfortunately, determining what these plants are not does not tell us what they are. Whether or not the so-called *Calamites verticillatus* was the arborescent stem of *Asterophyllites*, as I have deemed probable, my large specimens of amyeloid roots prove that these stems must have attained to a comparatively arborescent form. This conclusion has also been arrived at by M. GRAND'EURY.

In the disposition of the vessels of their primary triangular vascular bundle they seem to me to approach the *Lycopodiaceæ*. In Professor RENAULT's specimens the vessels forming the extreme apex of each arm of the triangle appear to be more barred than reticulated; and both in his specimens and mine their small size, compared with that of the more central vessels, as well as the entire exclusion of all cellular elements from the interior of the bundle, are strongly indicative of a genesis like that of the similar bundles of the Lycopods. The nearest approach to this structure that I am acquainted with amongst the living *Lycopodiaceæ* is seen in the five- or six-angled bundle of *Psilotum triquetrum*; but in this example the central procambium is not converted into vessels, but into a compact rod of thick-walled, permanent prosenchyma. Some of the vessels of *Psilotum* exhibit a remarkable tendency to abandon the scalariform, and assume an irregularly reticulate type of structure. The bark of this recent plant affords an instructive instance of the differences between the several parts of a continuous tissue destined to live under different conditions and to perform different functions. In the aërial stem its outer layer consists of long narrow prosenchymatous cells with parallel sides. The same tissue in the subterranean axis, now generally regarded as an underground stem rather than as a root, is composed of very large, coarse, thick-walled, irregular

* I have already (page 42, note) called attention to the fact that some species of *Sphenophyllum*, at least, exhibit the three superficial grooves of the bark so characteristic of young twigs of *Asterophyllites*.

parenchyma. The difference between these two tissues is quite as great as that which I have shown to exist between the corresponding ones of *Asterophyllites*. In both cases the narrow prosenchyma of the aërial bark is converted into the modified parenchyma of the subterranean one.

These resemblances to *Lycopodiaceæ* are further sustained by the nature of the fructification. A German critic of my memoir on *Volkmania Dawsoni* objected to my determination that it was a fruit of *Asterophyllites* on the ground that it appeared to be Lycopodiaceous in its aspect, and I have already pointed out the resemblance of its spores to the macrospores of *Selaginella inæquifolia*. At the first glance a verticillate jointed Lycopod appears an anomaly, but the jointed character of *Asterophyllites* is *more apparent than real*. In this respect the plant differs altogether from *Calamites* and *Equisetum*. In *Asterophyllites* the node is a mere centrifugal expansion of the bark, since the central vascular axis pursues its course through the node altogether unaffected by its presence. In the two latter genera, on the other hand, the node affects the entire structure of the stem from its circumference to its innermost centre, altering equally the arrangements of the tissues in the bark, in the ligneous zone, and in the medulla. Such being the case, the merely verticillate arrangement of the leaves does not constitute a difficulty of much importance. In reference to this latter point, Professor SACHS writes to me:—"With regard to the question concerning the possibility of verticillate leaves in Lycopods, I believe that *Lycopodium complanatum* with its apparently decussate pairs, and *Lycopodium selago* with from three to five-membered apparent verticils, present analogies which are not to be entirely rejected." And, after giving me further evidence in the same direction, he adds:—"I should accordingly find in the existence of verticillate leaves no reason for excluding a plant from the *Lycopodiaceæ*." Cordially agreeing with these statements, I am at present of opinion that *Asterophyllites* and *Sphenophyllum* are plants allied in the closest possible manner, if they do not belong to one genus, and that they are to be regarded as somewhat aberrant members of the Lycopodiaceous family. In 1865 Dr. DAWSON wrote concerning *Sphenophyllum*:—"A beautiful specimen of *Sphenophyllum emarginatum* from New Brunswick, in the collection of Sir W. E. LOGAN, has enabled me to ascertain that its stem had a simple axis of one bundle of reticulato-scalariform vessels, like those of *Tmesipteris* as figured by BRONGNIART. These curious plants were no doubt cryptogamous, having a habit of growth like that of *Equisetaceæ*, leaves like those of ferns or *Marsiliaceæ*, and fructification and structure like those of *Lycopodiaceæ*. They were closely allied to *Asterophyllites* and *Annularia*"*. I need scarcely point out how this significant paragraph foreshadows part of what has since been worked out with more elaborate detail by Professor RENAULT and myself.

I have received from Professor RENAULT a copy of the "Rapport" of MM. DAUBRÉE and BRONGNIART upon his two memoirs, extracted from the 'Comptes Rendus,' t. lxxvi., which contains several important conclusions agreeing with those embodied in my

* Quarterly Journal of the Geological Society, vol. xxii. p. 135.

memoir. Thus, speaking of *Sphenophyllum*, the "Commissaires" say:—"La structure interne de ces parties indique les rapports de ces végétaux avec les Lycopodiacees et les Marsiliacees." The report then proceeds to examine certain spikes of fructification, including those described by M. LUDWIG and Mr. BINNEY. Speaking of the fruit associated by the latter author with *Calamodendron commune*, the report remarks:—"Il reste cependant encore bien des doutes à éclaircir; si les épis de fructification d'Autun appartient, sans aucun doute aux *Annularia*, ceux décrits par MM. LUDWIG et BINNEY sont-ils réellement des fructifications, soit de *Calamites*, soit de *Calamodendron*? Ne se rapporteraient-ils pas plutôt à des *Sphenophyllum*, dont ils se rapprochent par le nombre moindre des organes verticillés, et d'après les figures de M. BINNEY, par leur axe plus grêle et vasculaire dans son centre?" In making the above and other comparisons contained in the "Rapport," M. BRONGNIART has overlooked my still more significant *Volkmannia Dawsoni*. I can only conclude that the disturbances occasioned by the war have prevented him from receiving the copy of the memoir which I sent to him.

I have again to acknowledge my obligations to Messrs. BUTTERWORTH, WHITTAKER, and NIELD for their valuable assistance in procuring specimens for my investigation from the Oldham district, and to G. GRIEVE, Esq., for aiding me in like manner with examples from those Burntisland beds which the right of discovery has made so peculiarly his own. I may further observe, in reference to the Plates illustrating this memoir, that having made every drawing myself with the most scrupulous care, upon lithographic paper, so that they reappear in the Plates exactly as they left my hands, they may be relied upon as faithful transcripts of the objects represented.

[As this memoir is passing through the press I have received from M. RENAULT a copy of his valuable memoir entitled "Recherches sur l'organisation des *Sphenophyllum* et des *Annularia*," the publication of which has been delayed through the disturbances occasioned by the war. It demonstrates most clearly the very close general resemblances existing between his specimens of *Sphenophyllum* and mine of *Asterophyllites*. But there is one singular difference. In the French specimens, the zone corresponding with my exogenous zone, and of which the *transverse* sections correspond in the most minute manner with my figures 3, 4, & 9, chiefly consists not of long vessels, but of cubical cells arranged in vertical piles. Like my vessels, the walls of these cells are beautifully reticulated. It appears as if these cells were arranged in vertical lines preparatory to their coalescence and conversion into vessels, but that this double process had never taken place. This substitution of remarkably distinct reticulated cells for equally distinct reticulated vessels is a curious physiological fact. It is also perfectly clear that the vessels given off to supply the leaves in the French examples spring from the central triangular axis, and not from the exogenous layers, as I have already pointed out in the note on page 45, the former having been the primary vascular bundle of the young shoot. On the other hand, the vascular bundles given off to the *rootlets* evidently spring, not from the triangular axes of the roots, but from the exogenous layer. These arrange-

ments are exactly identical with those found respectively in *Lepidodendroid* stems and in their *Stigmarian* roots, as I pointed out in my third memoir*. The close relationship between *Asterophyllites* and *Sphenophyllum* being thus established upon the sound basis of closely identical organizations, the inquiry which suggests itself is, What are the real distinctions in their foliage? It appears to me that typically there are none. The leaf of *Asterophyllites* has a single midrib; that of *Sphenophyllum* has three or more. May not each cuneiform leaf of *Sphenophyllum* be regarded as composed of three or more of the divergent leaves of *Asterophyllites*, which have coalesced throughout the greater part of their length, but whose typically separate origin is indicated by the number of the teeth usually seen at their broad extremities? This explanation further accounts for the small number of the leaves usually composing each foliar verticil of *Sphenophyllum* compared with those of *Asterophyllites*.

M. RENAULT's specimens demonstrate very clearly the existence of a layer of ordinary delicate parenchyma within the radiating lines of parenchyma seen in my figures 4, 9, 10, & 15. As mentioned in the preceding memoir, I have only caught a glimpse of this layer in one or two of my specimens, it having almost invariably disappeared from them, leaving a vacant space as in fig. 16, *g*. This demonstration materially simplifies the identification of the layers of the bark in the stems and roots. Thus the layer *g* in figures 47, 49, & 57 is identical with the innermost parenchyma of Professor RENAULT; it corresponds with the layer *g* in figures 9, 10, 11, & 21. In the same way the layer *h* in these latter figures is identical with *h* in figures 47, 48, 49, & 57. If these conclusions are correct, the roots of *Asterophyllites* have a bark like that of the stems, but almost or altogether deprived of the superficial prosenchyma seen in the latter organs; this layer, however, may be regarded as reappearing in the outermost parenchyma (fig. 53, *o*) of the rootlets.

I may add that a second copy of my memoir on *Volkmannia Dawsoni*, which I sent to M. BRONGNIART, has reached him. In a note to M. RENAULT's paper, M. BRONGNIART, acknowledging this memoir, recognizes the important points in which the organization of that fruit agrees with that of the structures described by M. RENAULT, as well as those on which it differs, "au moins spécifiquement."—Manchester, February 20, 1874.]

DESCRIPTION OF THE PLATES.

The letters of reference in the accompanying memoir have been used to indicate as nearly as possible the same structures as in the previous memoirs of the series. The letters are not alphabetically continuous, because some of the structures existing in other plants are wanting in *Asterophyllites*; and I have thought it preferable to omit the letters referring to these absent structures, rather than to introduce confusion by employing the same letter to represent organs and tissues that were not homologous. The only exceptions to this rule will be found in a few of the final letters of the alphabet, which have been used for special purposes.

* Philosophical Transactions, 1872, Part II. p. 307.

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|---------------------------------------|-----------------------------------|
| <i>c.</i> Medullary vessels. | <i>o.</i> Rootlets. |
| <i>d.</i> Ligneous zone. | <i>r.</i> Cicatrices of strobili. |
| <i>f.</i> Medullary rays. | <i>s.</i> Strobilus-axis. |
| <i>g.</i> Inner bark. | <i>t.</i> Bracts of strobilus. |
| <i>h.</i> Middle parenchymatous bark. | <i>u.</i> Sporangia. |
| <i>k.</i> Prosenchymatous outer bark. | <i>v.</i> Sporangiohores. |
| <i>l.</i> Leaves. | <i>w.</i> Spores. |
| <i>n.</i> Root-bundles of vessels. | <i>x.</i> Lateral branch. |

PLATE I.

- Fig. 1. Transverse section of a very young twig from Oldham, showing the primitive vascular bundle, the equivalent of the medullary vessels of the *Lycopodiaceæ*, magnified 30 diameters.
- Fig. 2. Similar section of a twig, with one exogenous layer of the ligneous or vascular zone surrounding the primitive bundle, enlarged 30 diameters.
- Fig. 3. Similar section of a young branch with two exogenous layers, magnified 30 diameters.
- Fig. 4. Similar section of a young branch, with double bark-furrows and three exogenous layers, magnified 30 diameters.
- Fig. 5. Longitudinal section of a young branch, with three exogenous layers, magnified 30 diameters.
- Fig. 6. One of the vessels of the ligneous zone of fig. 5, seen on the side parallel with the medullary rays, magnified 420 diameters.
- Fig. 7. Cells of the inner bark, from a longitudinal section like fig. 5, magnified 200 diameters.

PLATE II.

- Fig. 8. Longitudinal section of some of the prosenchymatous cells of the outer bark, magnified 130 diameters.
- Fig. 9. Transverse section of the vascular axis and inner bark of a more matured stem, magnified 30 diameters.
- Fig. 10. Similar section to the last, but of a more fully developed stem and with a thicker inner bark, magnified 30 diameters.
- Fig. 11. Transverse section of a yet further developed stem, exhibiting a secondary series of concentric exogenous growths, magnified 30 diameters.
- Fig. 12. Similar section to fig. 11, with very large vessels in the inner exogenous laminae, magnified 30 diameters.
- Fig. 13. Tangential section of two vessels of the exogenous layers of the same specimen as fig. 9, showing the medullary rays, magnified 125 diameters.

PLATE III.

- Fig. 14. Tangential section of the peripheral margin of a nodal cortical disk with sections of leaves, magnified 30 diameters.
- Fig. 15. Longitudinal but slightly tangential section of part of the outer prosenchymatous bark, exhibiting a longitudinal section of a leaf prolonged from the margin of the nodal disk, magnified 30 diameters.
- Fig. 16. Slightly oblique transverse section of a branch passing through a nodal foliar disk, so as to intersect the verticil of leaves on the left of the section, magnified 30 diameters.
- Fig. 17. Series of transverse sections of leaves, magnified 30 diameters.
- Fig. 18. Transverse section of a young twig of *Asterophyllites* or *Sphenophyllum* from Burntisland, corresponding to fig. 1, magnified 30 diameters.
- Fig. 19. Similar section to fig. 18, but slightly oblique, and exhibiting two of the three superficial cortical grooves, magnified 30 diameters.
- Fig. 20. Transverse section of a branch from Burntisland, with three or four exogenous layers, magnified 30 diameters.

PLATE IV.

- Fig. 21. Transverse section of a more matured stem from Burntisland, magnified 30 diameters.
- Fig. 22. Tangential section of part of the exogenous zone of fig. 21, showing the intersected extremities of the medullary rays, magnified 130 diameters.
- Fig. 23. Radial longitudinal section of part of the same zone as fig. 22, made in the plane of the medullary rays, magnified 130 diameters.
- Figs. 24 & 25. Portions of the barred vessels of fig. 23, magnified 420 diameters.

PLATE V.

- Fig. 26. Fragment of *Sphenophyllum Schlotheimi*. 'k', lower portion of the internode k, with its lateral groove and the bases of a verticil of leaves.
- Fig. 27. Transverse section of part of a stem from Burntisland, giving off a branch, magnified 30 diameters.
- Fig. 28. Transverse section of *Volkmannia Dawsoni*, a fruit of *Asterophyllites* or *Sphenophyllum*, magnified $7\frac{1}{2}$ diameters.
- Fig. 29. Central vascular axis of fig. 28, magnified 22 diameters.
- Fig. 30. Three spores like those of fig. 28, magnified 140 diameters.
- Fig. 31. Single strobilus of *Asterophyllites* from a bed of shale at Brooksbottom, magnified 2 diameters.
- Fig. 32. Fruiting stem of an *Asterophyllites* from the Lancashire Coal-measures. Natural size.

PLATE VI.

- Fig. 33. External aspect of the upper part of a small strobilus of *Calamostachys Binneyana* from Oldham, enlarged 6 diameters.
- Fig. 34. Transverse section of part of a sterile foliar disk of *Calamostachys Binneyana*, magnified 24 diameters.
- Fig. 35. Part of the periphery of a similar section to fig. 34.
- Fig. 36. Transverse section of *Calamostachys Binneyana* made in the plane of a verticil of sporangiophores, magnified 27 diameters.
- Fig. 37. Transverse section of the same specimen as fig. 36, but made in the plane of an internode, intermediate between a fertile and a barren verticil, magnified 12 diameters.
- Fig. 38. Central vascular axis of fig. 37, enlarged 80 diameters.
- Fig. 39. Part of the outer surface of a sporangium, magnified 98 diameters.

PLATE VII.

- Fig. 40. Section of the wall of a sporangium of *Calamostachys Binneyana* made transversely to the longer axes of its cells, magnified 98 diameters.
- Fig. 41. Section of a cell of the wall of a sporangium of the same, made parallel with its longer axis, and showing one of its barred lateral walls, magnified 98 diameters.
- Fig. 42. Inner surface of part of a sporangium-wall of the same, magnified 98 diameters.
- Fig. 43. Cluster of spores of *C. Binneyana*, showing the spores enclosed in mother-cells, magnified 140 diameters.
- Fig. 44. Fertile stem of an *Asterophyllites*, from Brooksbottom, from which strobili have been detached, enlarged 2 diameters.
- Fig. 45. "*Calamites*" *verticillatus*, reduced to two thirds of the natural size.
- Fig. 46. Transverse section of a young root with two clusters of rootlets of *Asterophyllites*, from near Oldham, magnified 12 diameters.

PLATE VIII.

- Fig. 47. Part of the bark of fig. 46, enlarged 80 diameters.
- Fig. 48. Vertical section of part of the same root with one cluster of rootlets, enlarged 18 diameters.
- Fig. 49. Portion of a similar section to fig. 48, showing the two layers of bark, enlarged 80 diameters.
- Fig. 50. Tangential section of the vascular axis of fig. 46, enlarged 75 diameters.
- Fig. 51. Part of a radial longitudinal section of the same vascular axis, made in the plane of a medullary ray, enlarged 100 diameters.
- Fig. 52. Tangential section like fig. 50, but passing transversely through a vascular bundle going to one of the clusters of rootlets, enlarged 75 diameters.

PLATE IX.

- Fig. 53. A longitudinal section of part of a rootlet of *Asterophyllites*, enlarged 30 diameters.
- Fig. 54. Obliquely tangential section of the outer bark of fig. 46, enlarged 90 diameters.
- Fig. 55. Tangential section of part of the outer bark of fig. 46, enlarged 90 diameters.
- Fig. 56. Transverse section of the vascular axis of a large root, exhibiting the successive lines of concentric growth, enlarged 9 diameters.
- Fig. 57. Transverse section of a similar root to fig. 46, but exhibiting the central prismatic axis seen in the aërial stems of *Asterophyllites* and *Sphenophyllum*, enlarged 12 diameters.
- Fig. 58. Central part of fig. 57, showing the central triangular axis, enlarged 30 diameters.
- Fig. 59. Transverse section of the vascular axis of another species of amyeloid root with very large vessels, corresponding closely with the stems figs. 1 to 16, enlarged 30 diameters.

Fig. 1

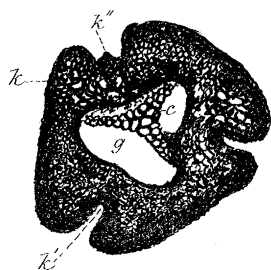
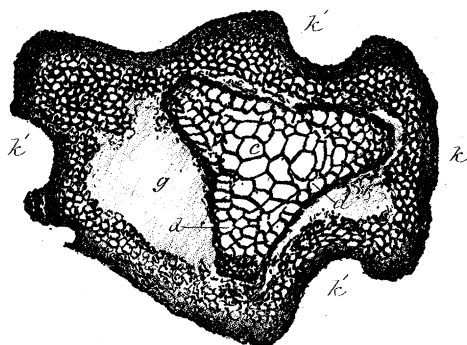


Fig. 2.



Fig

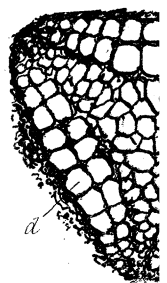
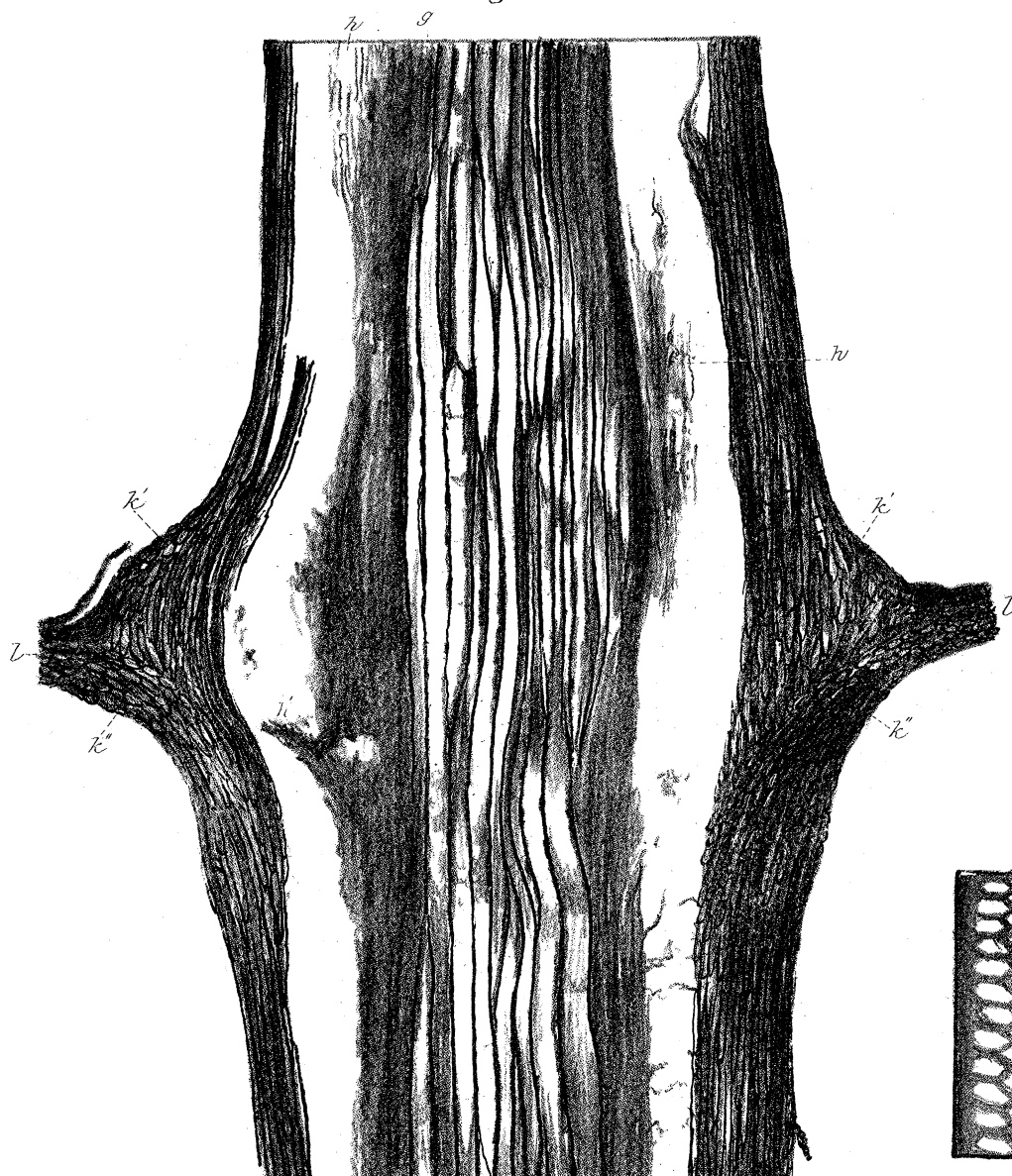


Fig. 5.



Fig

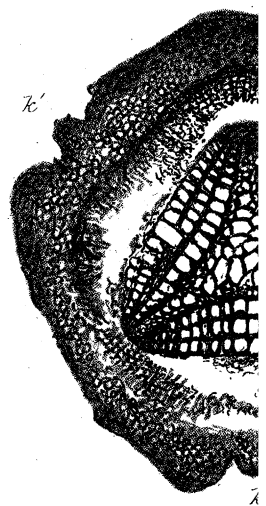


Fig. 6.

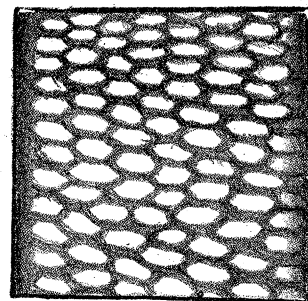


Fig. 3.

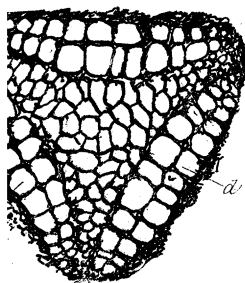


Fig. 4.

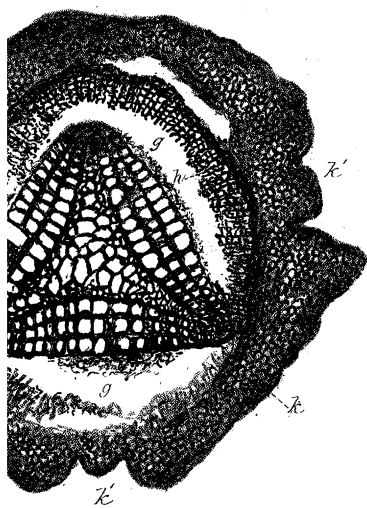
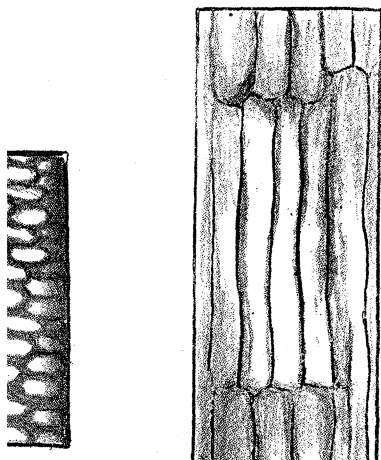


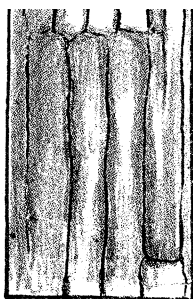
Fig. 7.





k h g d c d g h k





Machure & Macdonald, Lith. London

Fig. 8.

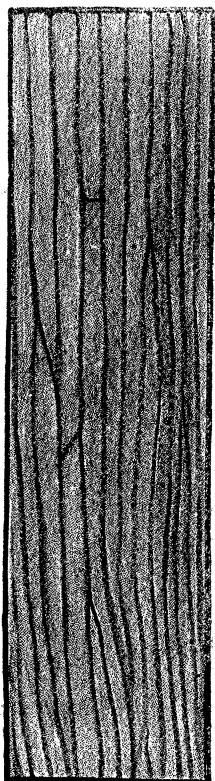


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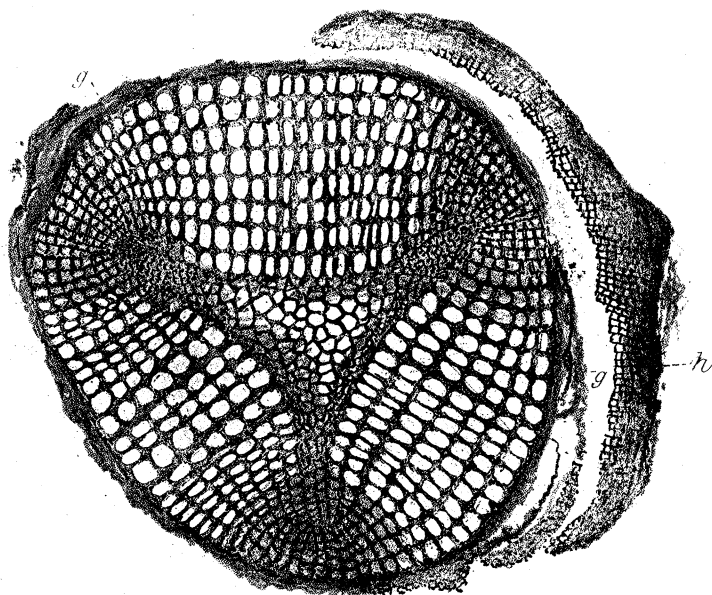


Fig.

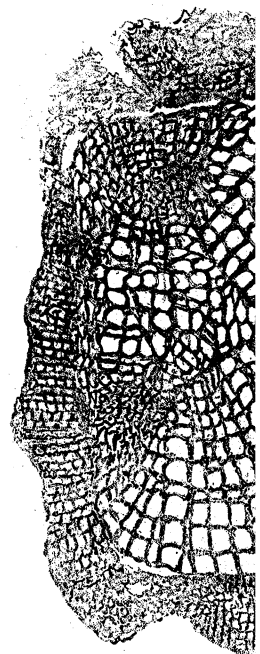


Fig. 12.

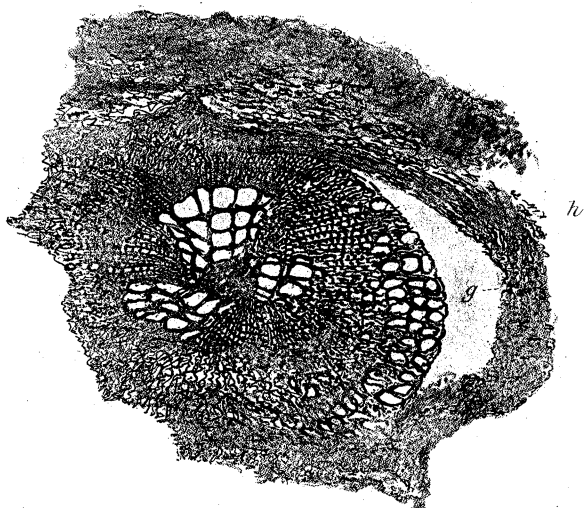


Fig.

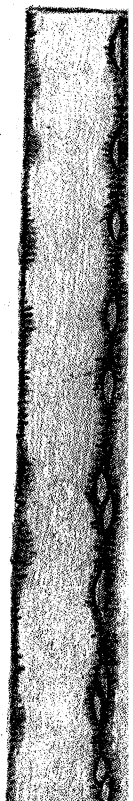


Fig. 11.



Fig. 10.

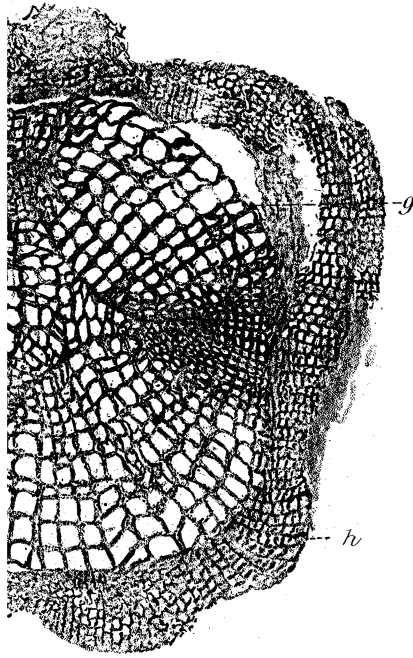
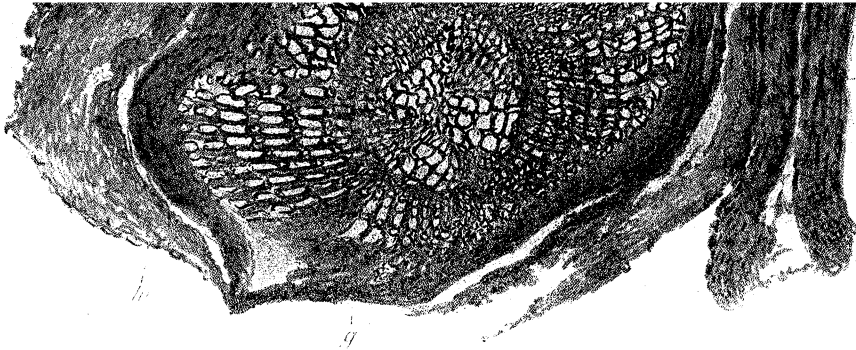
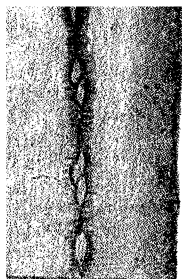


Fig. 13.





W. C. Williamson Auto-lith.



Machine & Macfarland, Lith. London

Fig. 14.

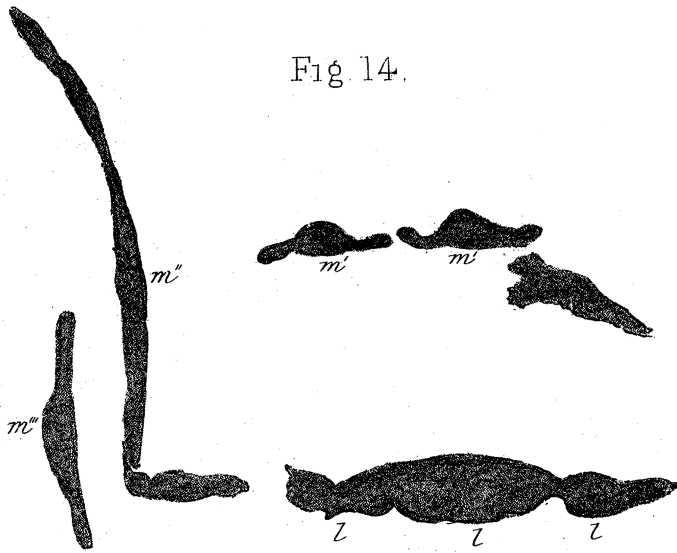


Fig. 15.

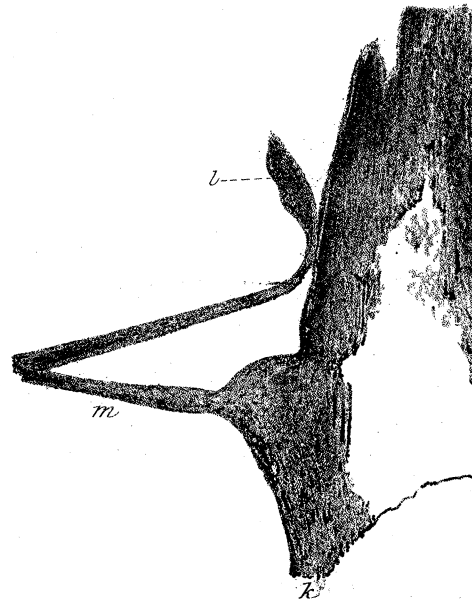


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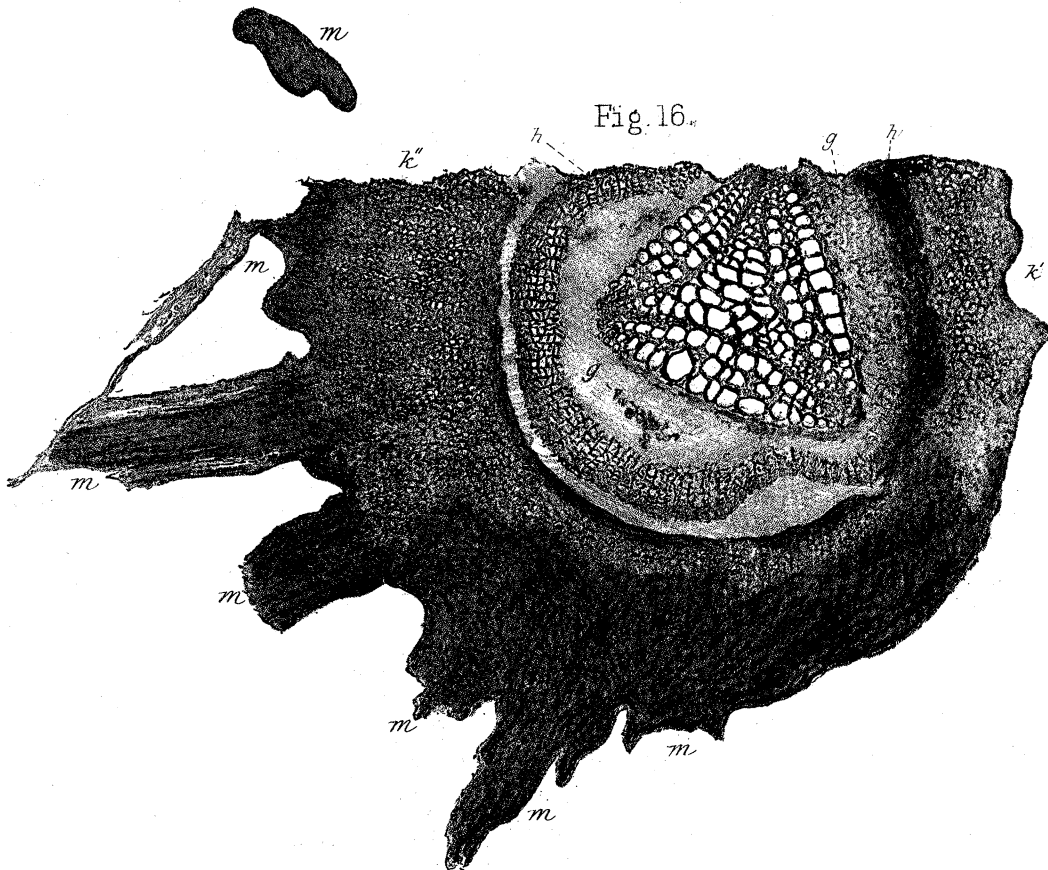


Fig. 17.

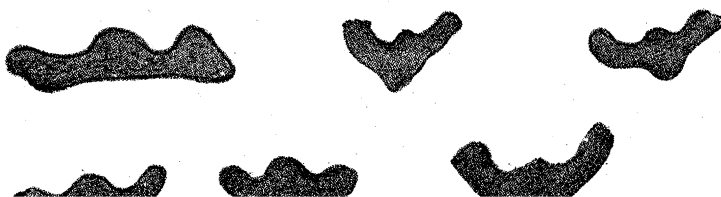


Fig. 20.





Fig. 18.

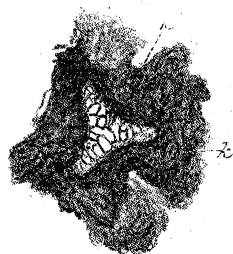
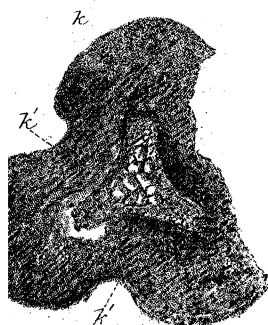
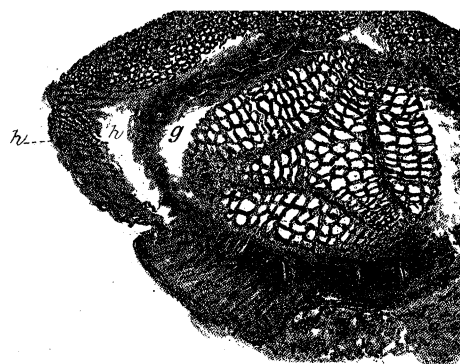
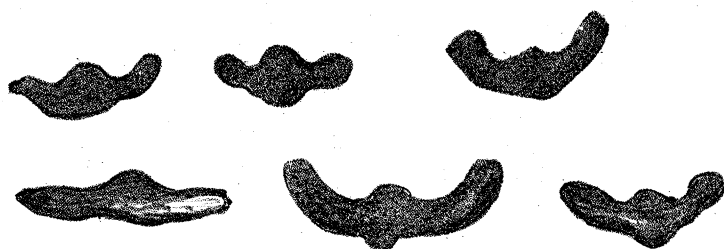


Fig. 19.





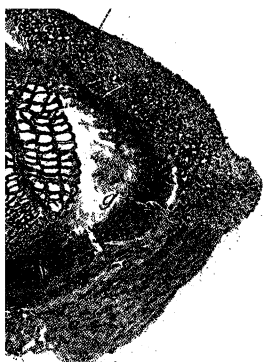


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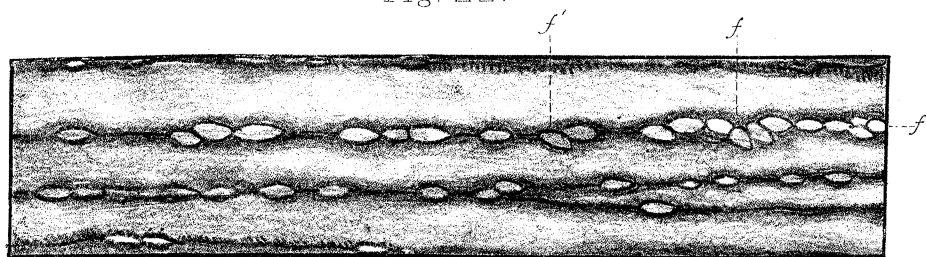


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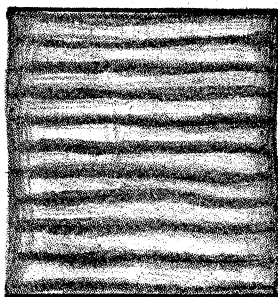


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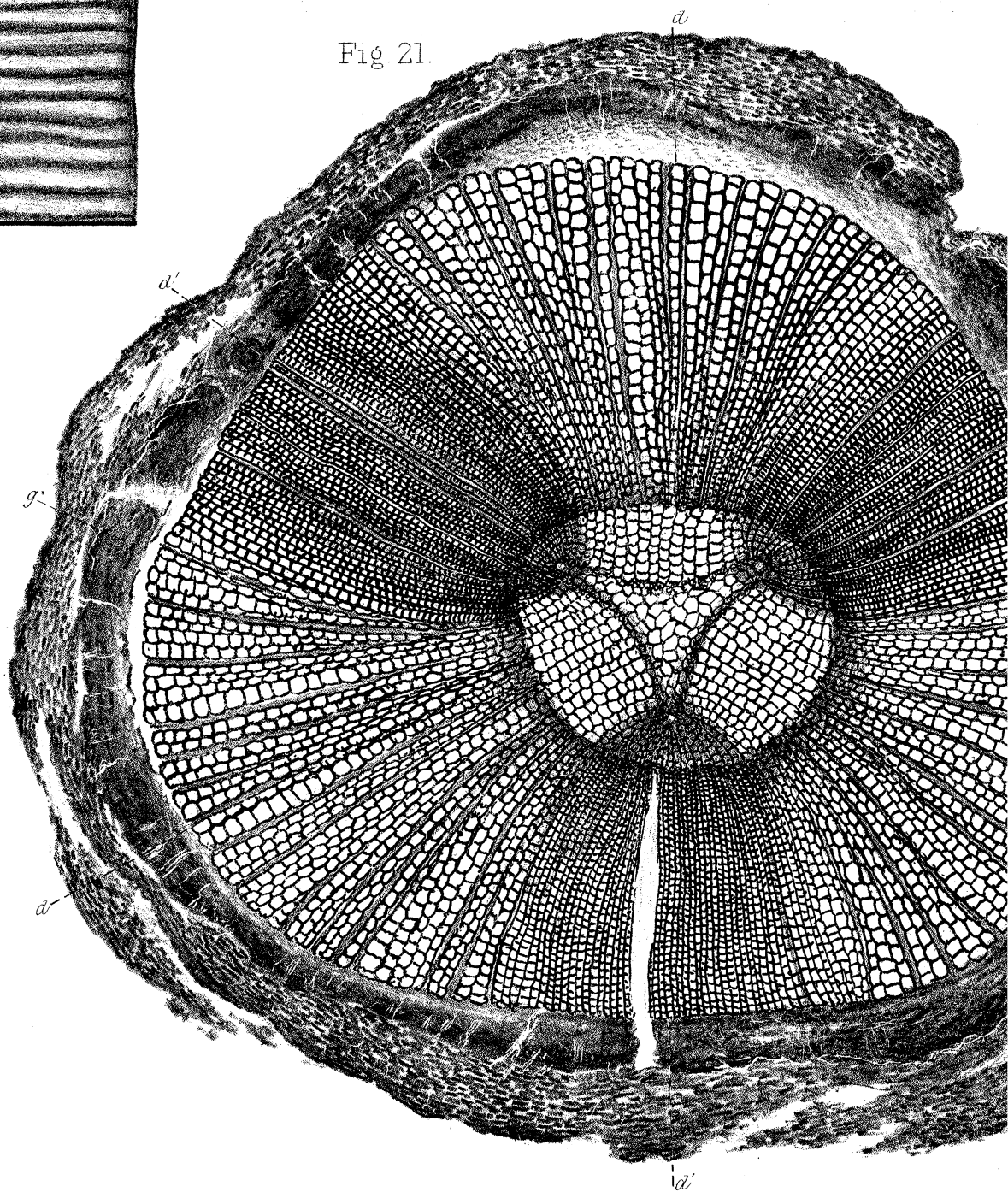
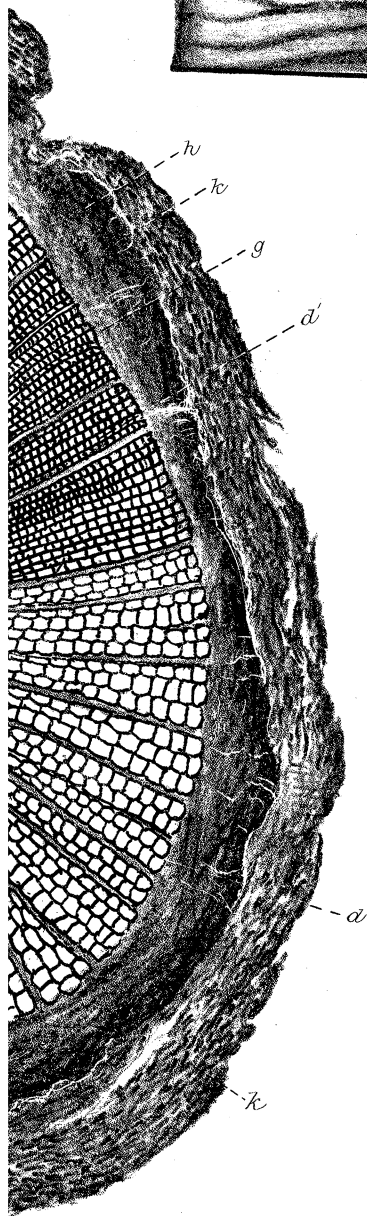
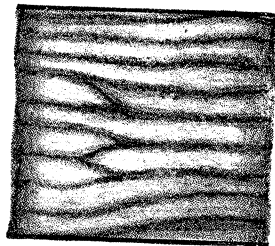


Fig. 23.





Fig. 25.



^u
Fig. 23.

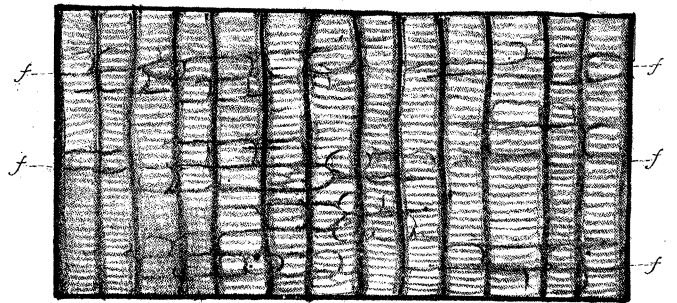


Fig 31.

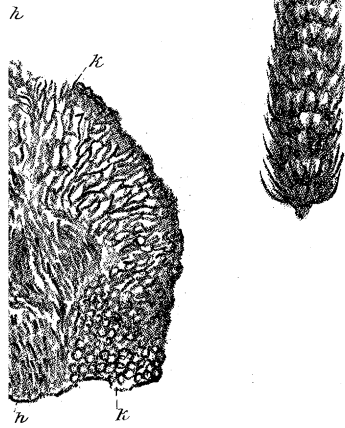
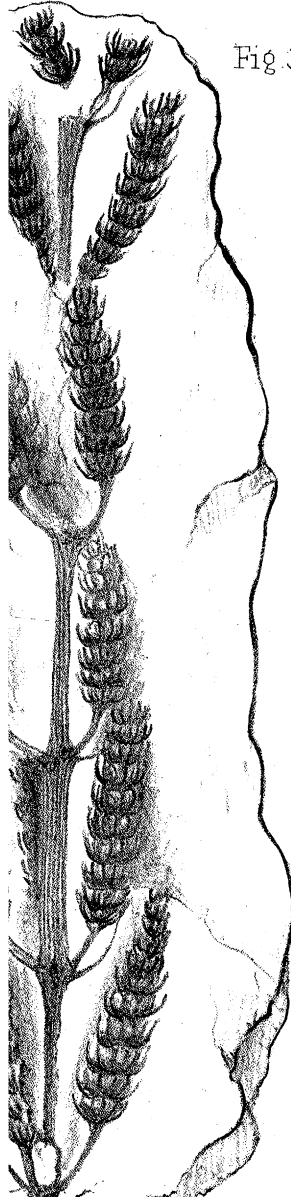
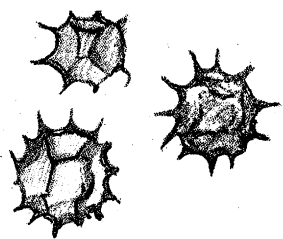
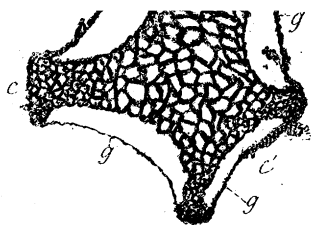


Fig 32.





W. C. Williamson, Auto Lith.

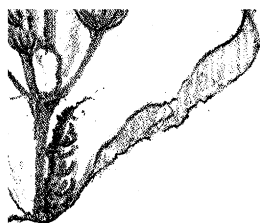


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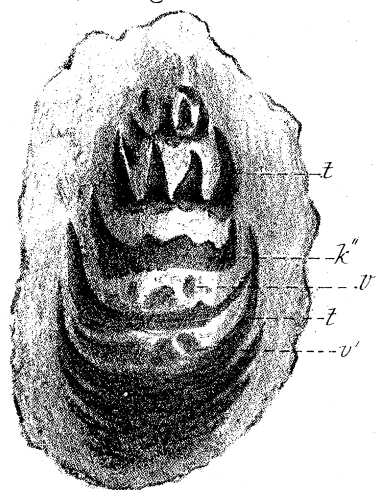


Fig. 34.

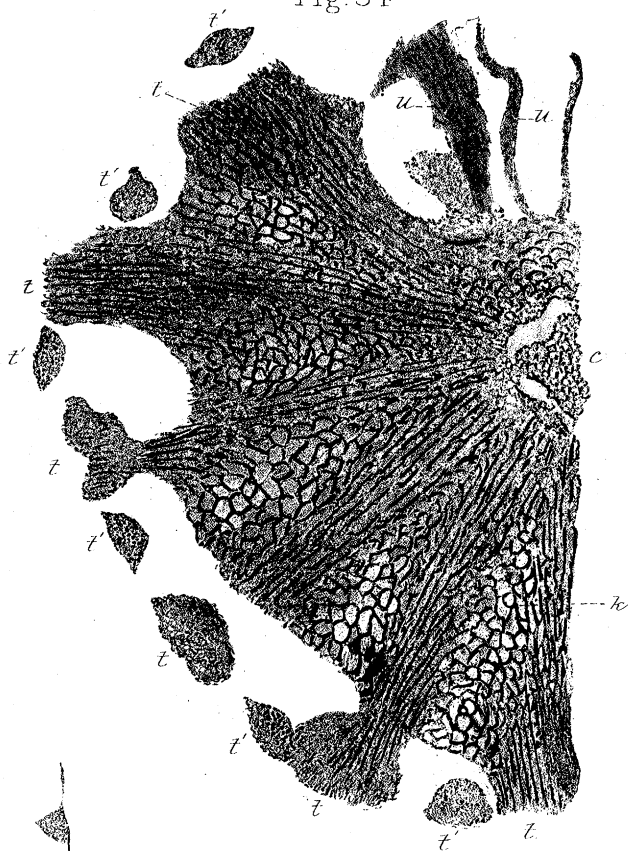


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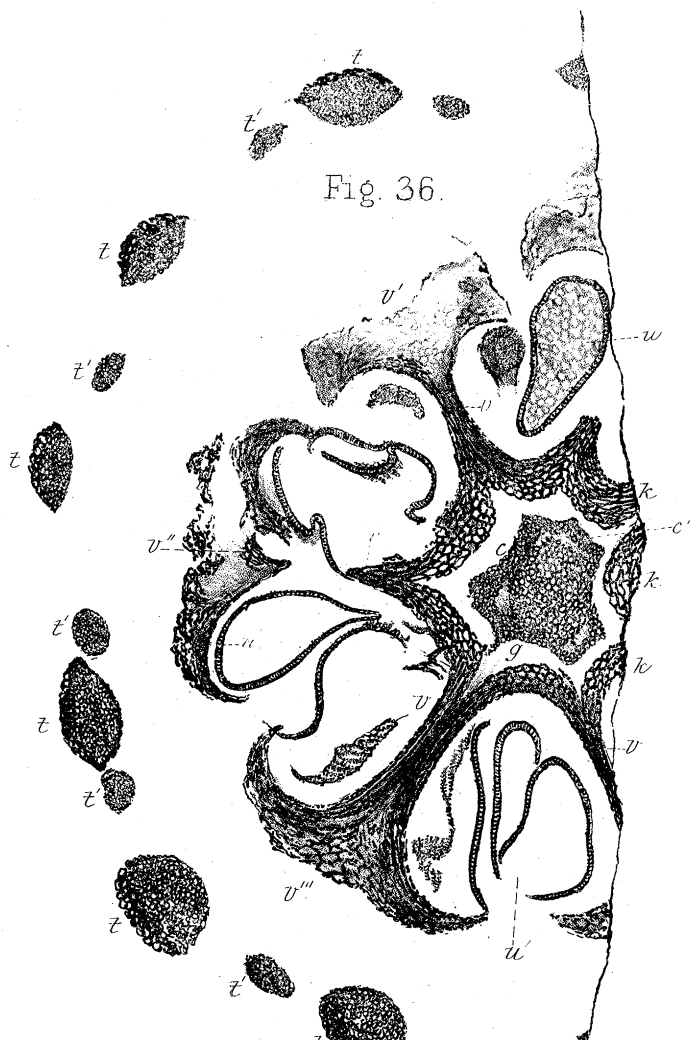


Fig.

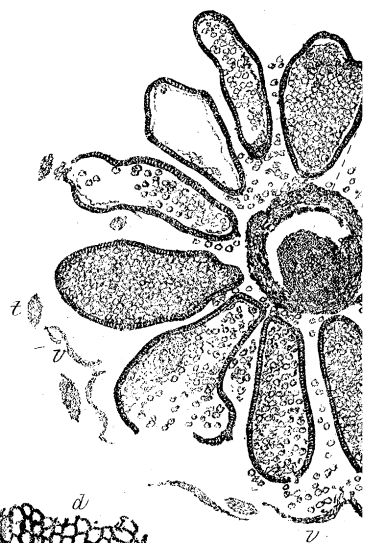
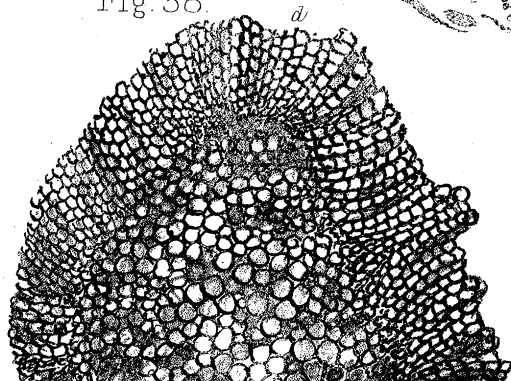
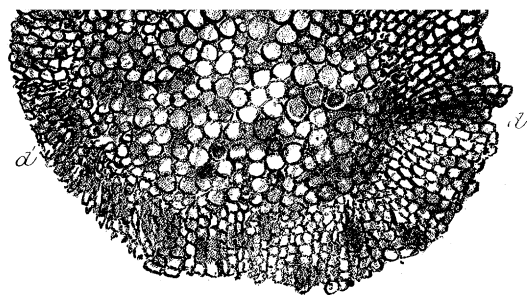


Fig. 38.





W. C. Williamson, Auto-Lith.

Macu



Maclure & Macdonald, Lith. London.

Fig. 45.



Fig. 46.



Fig. 41.



Fig. 40.

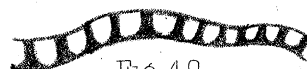


Fig. 43.



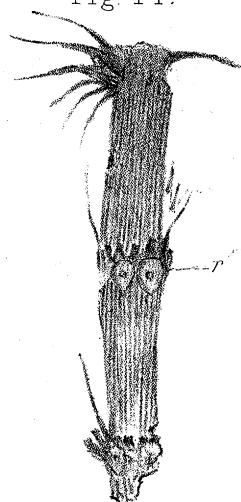
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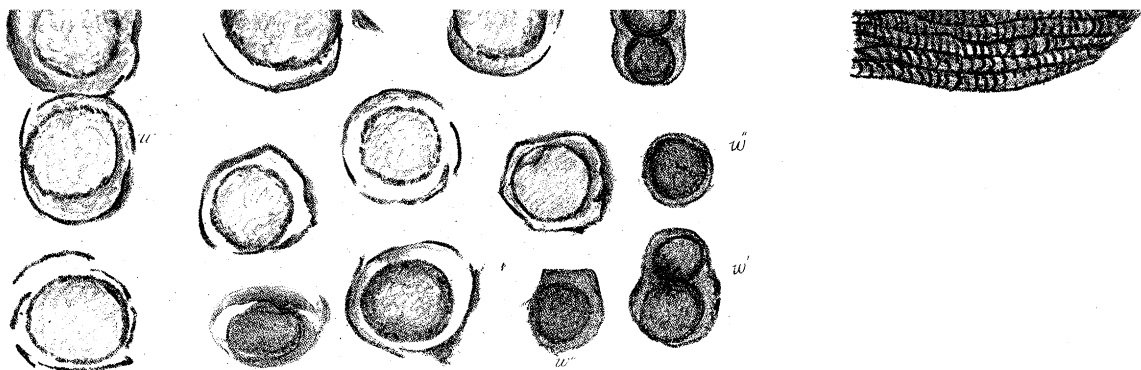


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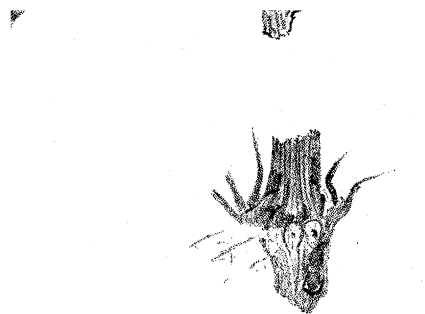


Fig. 44.





W. C. Williamson, Ant. 1871.



Machure & Macdonald, Lith. London.

Fig 47.

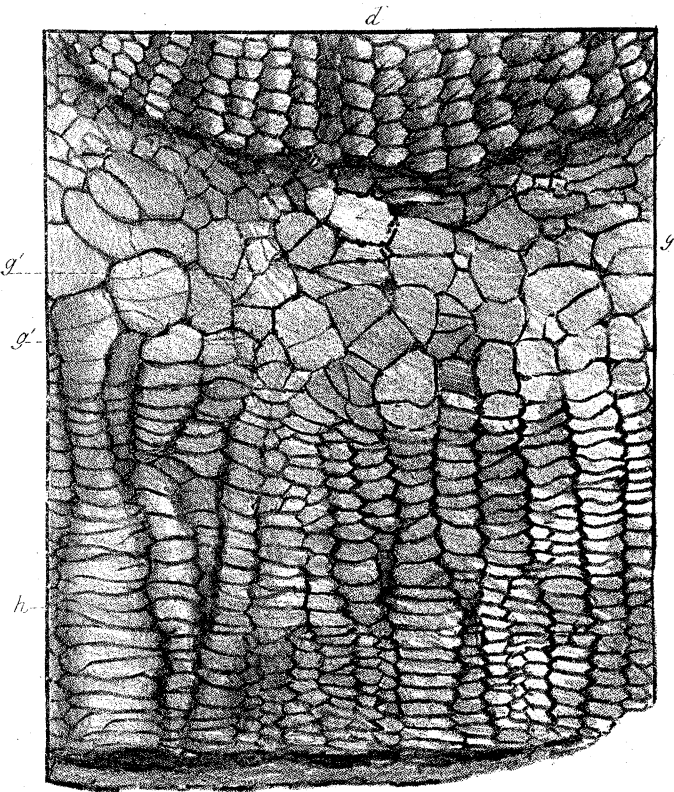


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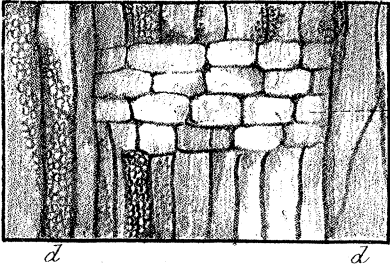


Fig. 52.

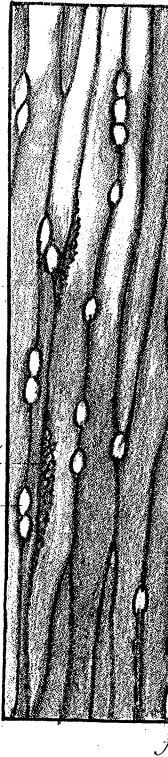
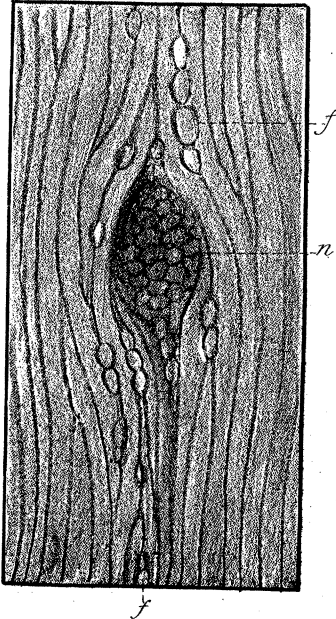


Fig. 48.

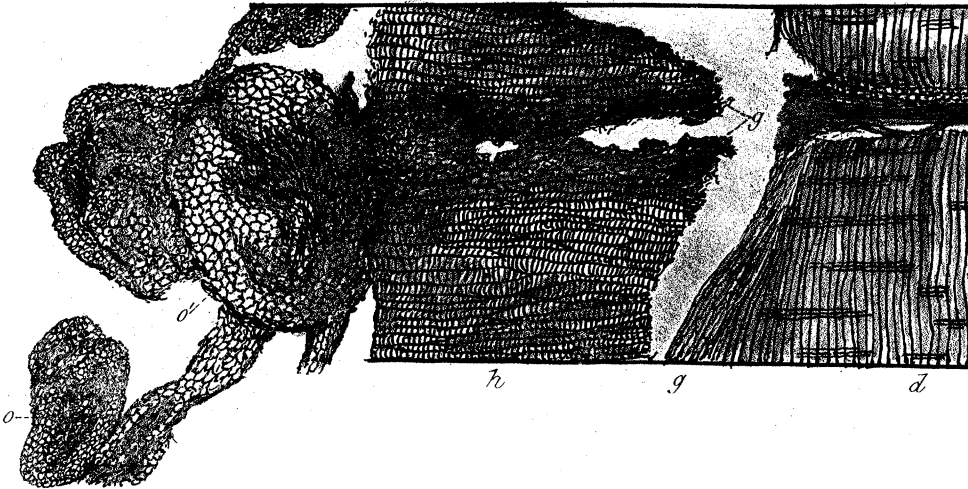


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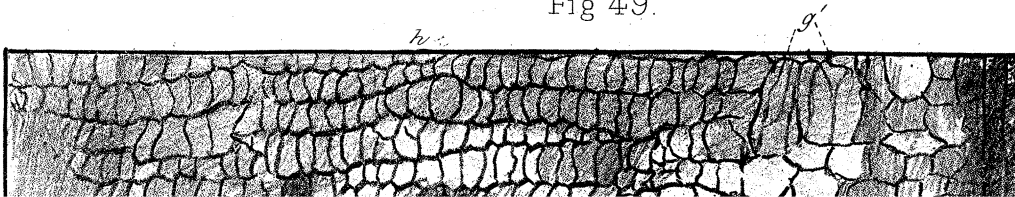
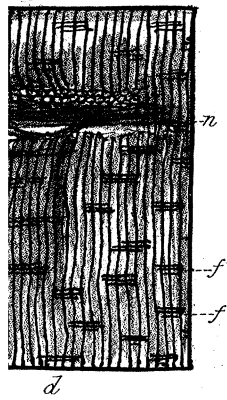
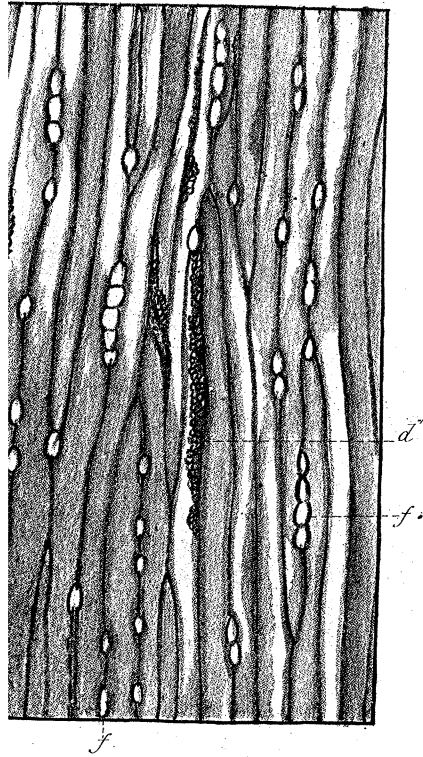
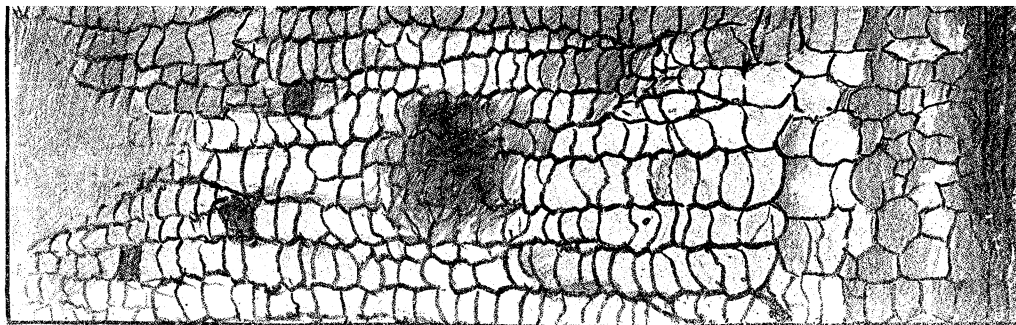


Fig. 50.





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Fig. 53.

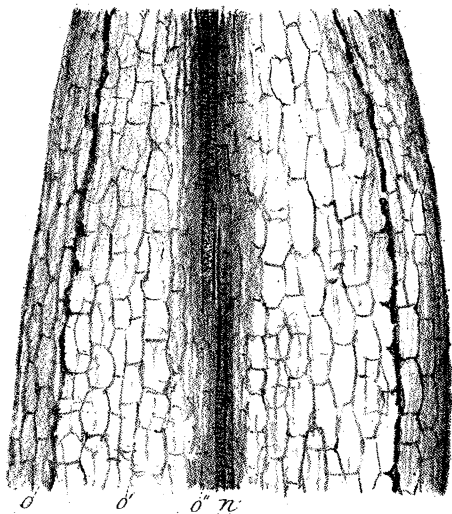


Fig. 54.

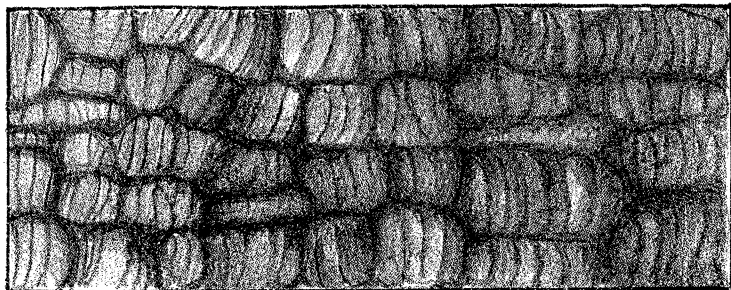


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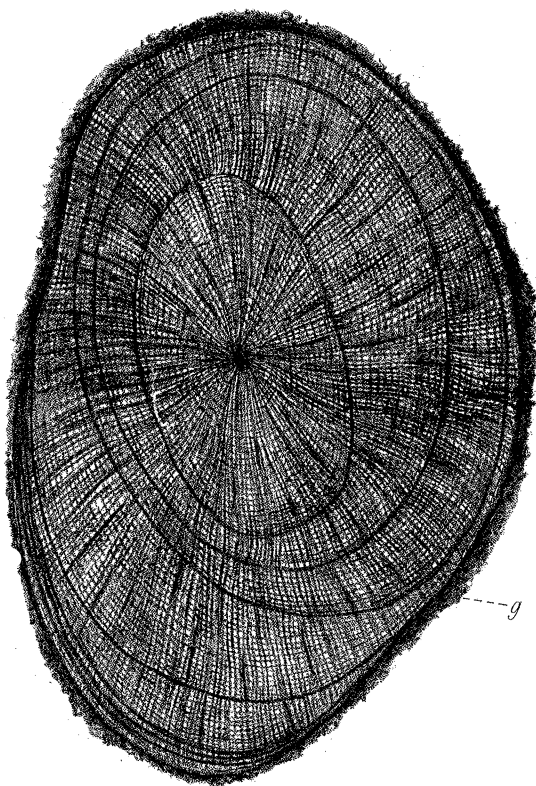


Fig. 55.

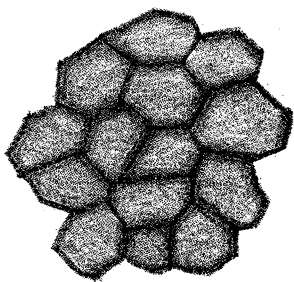


Fig. 59

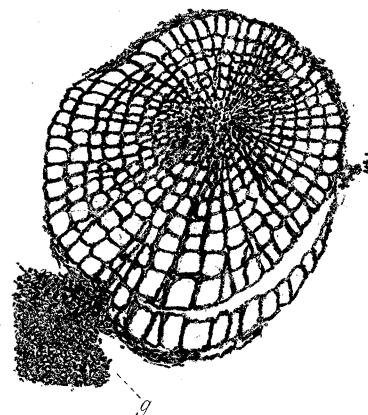


Fig. 57.

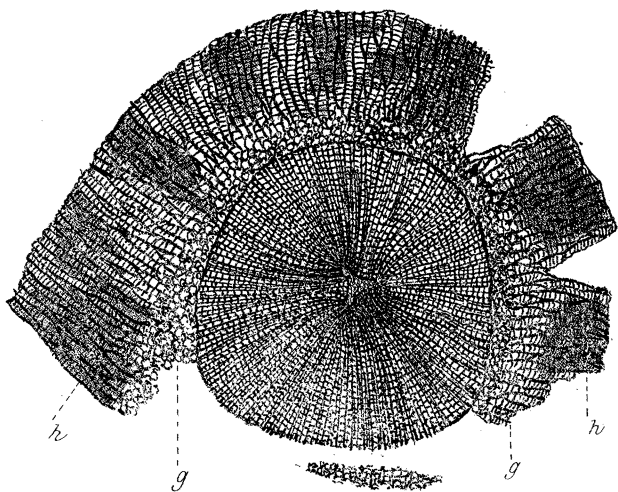


Fig. 58.

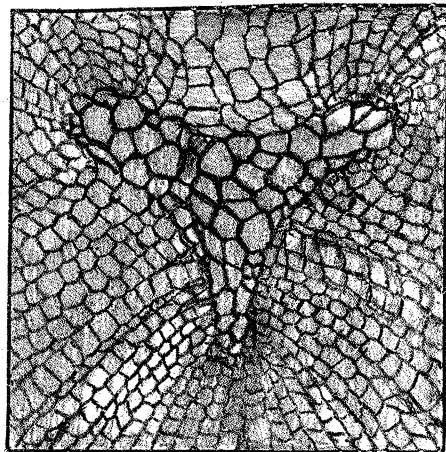


Fig 1



Fig 2.

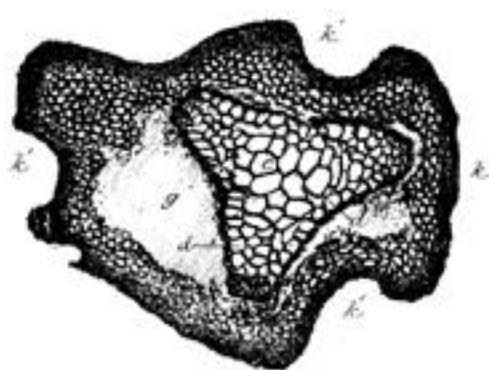


Fig. 3.

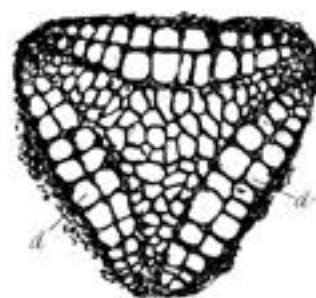


Fig. 5.

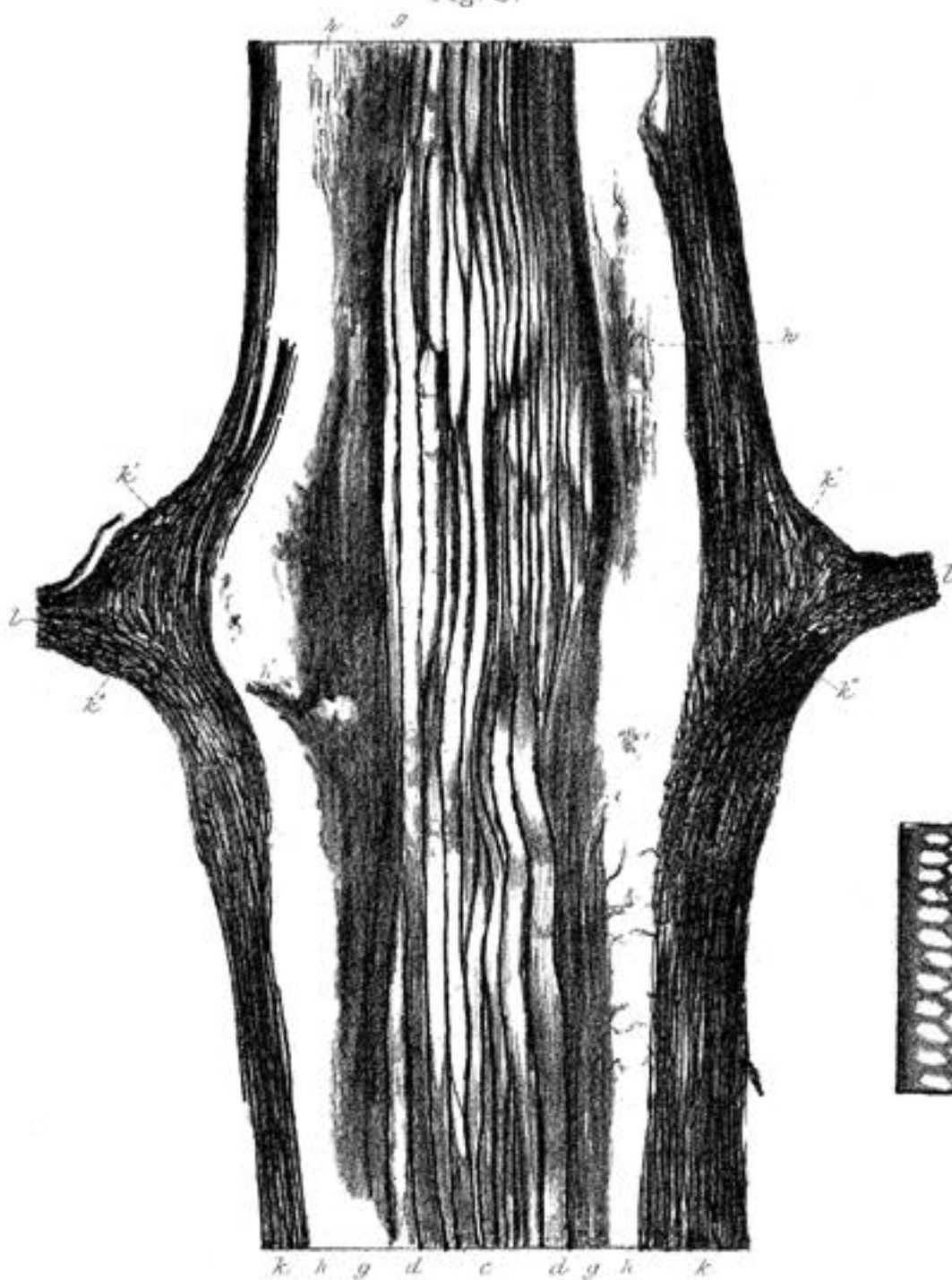


Fig. 4.



Fig. 6.

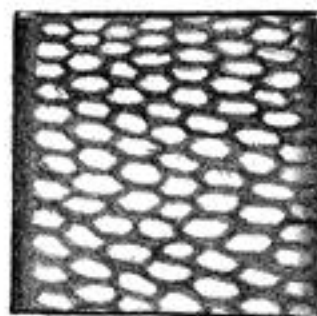


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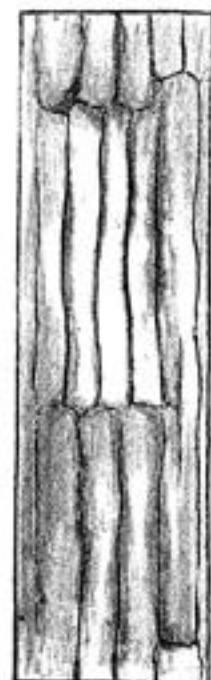


Fig. 8.

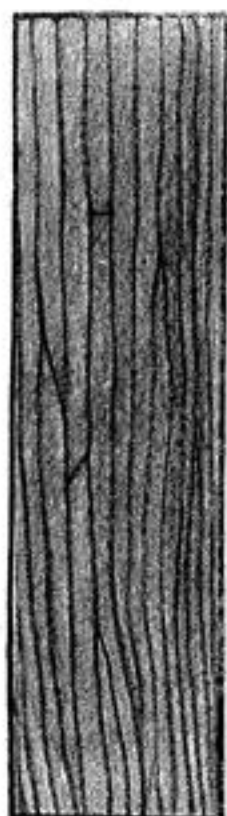


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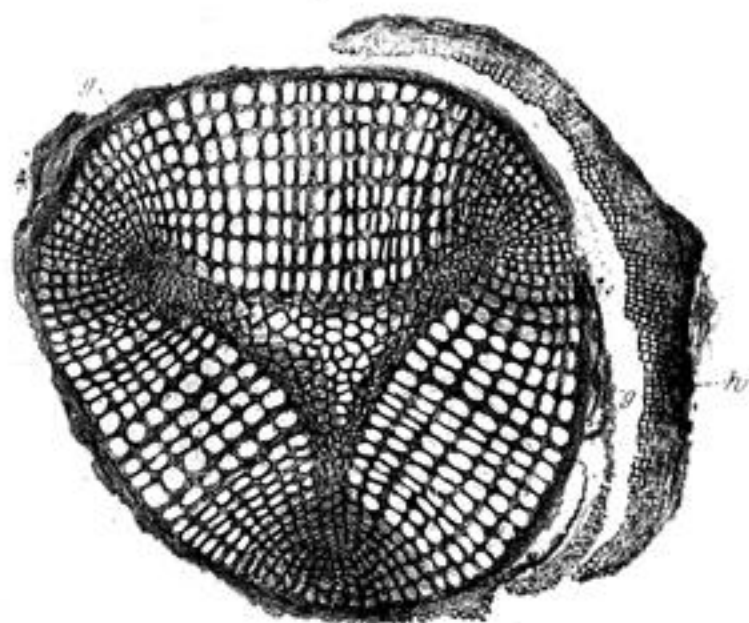


Fig. 10.



Fig. 12.

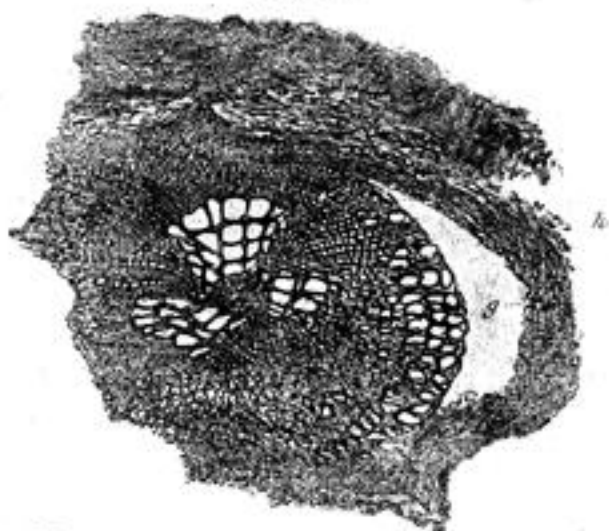


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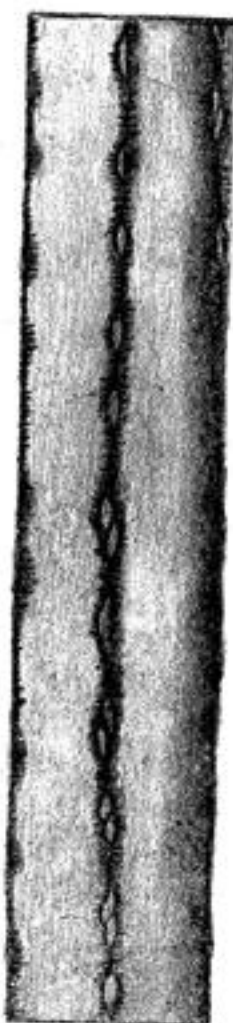


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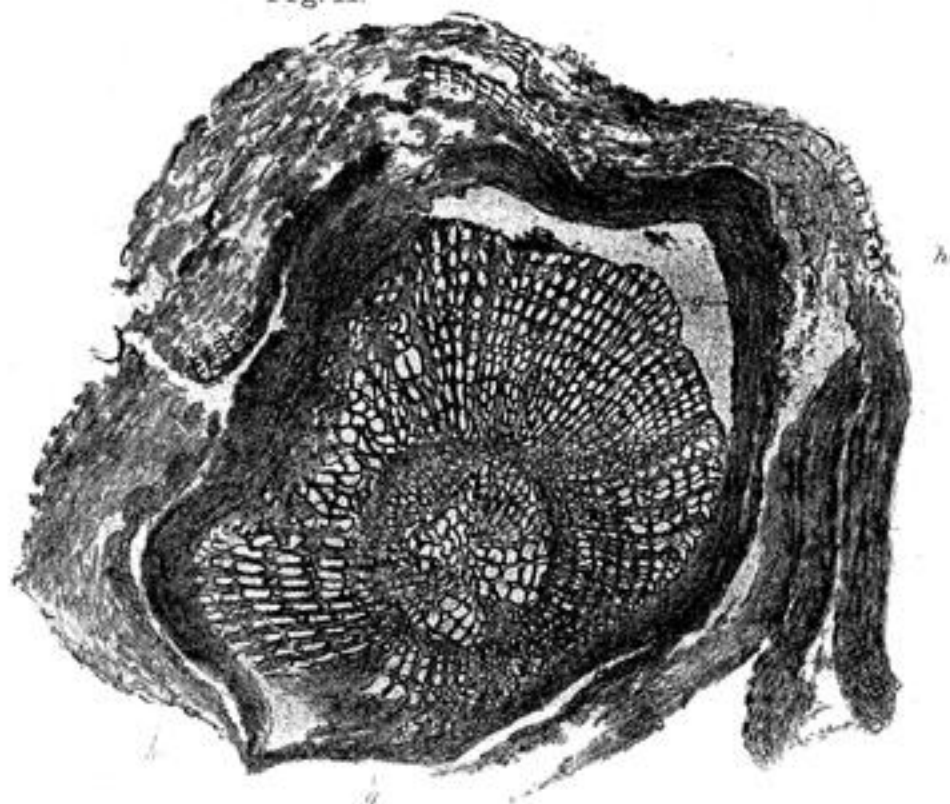


Fig 14.

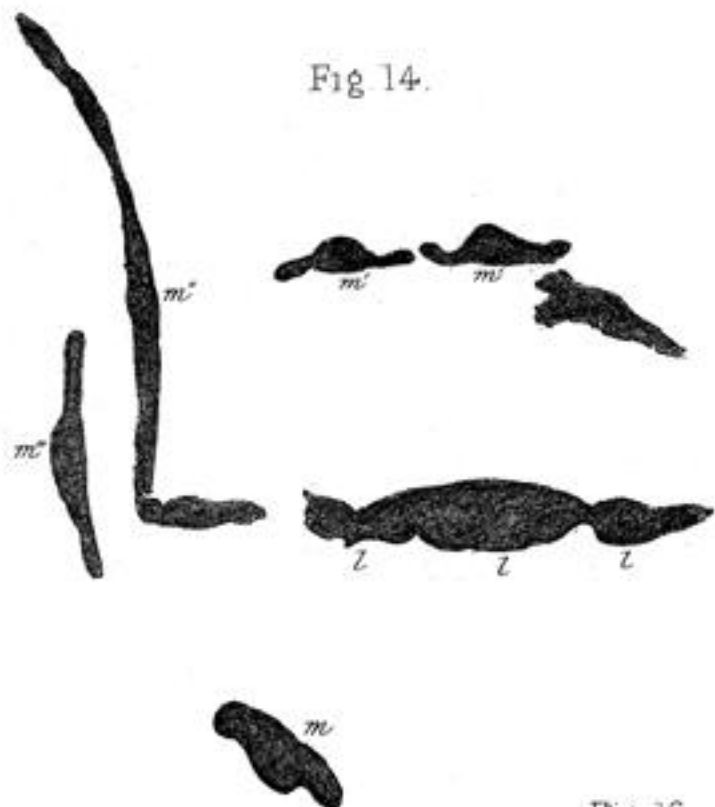


Fig 15.

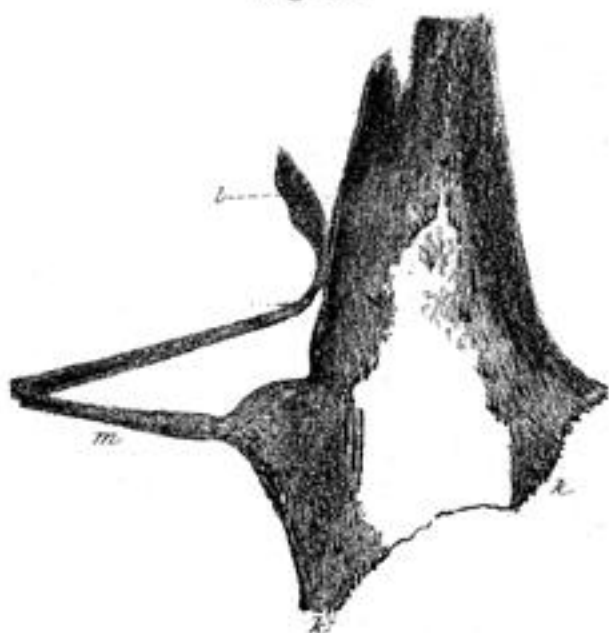


Fig. 16.

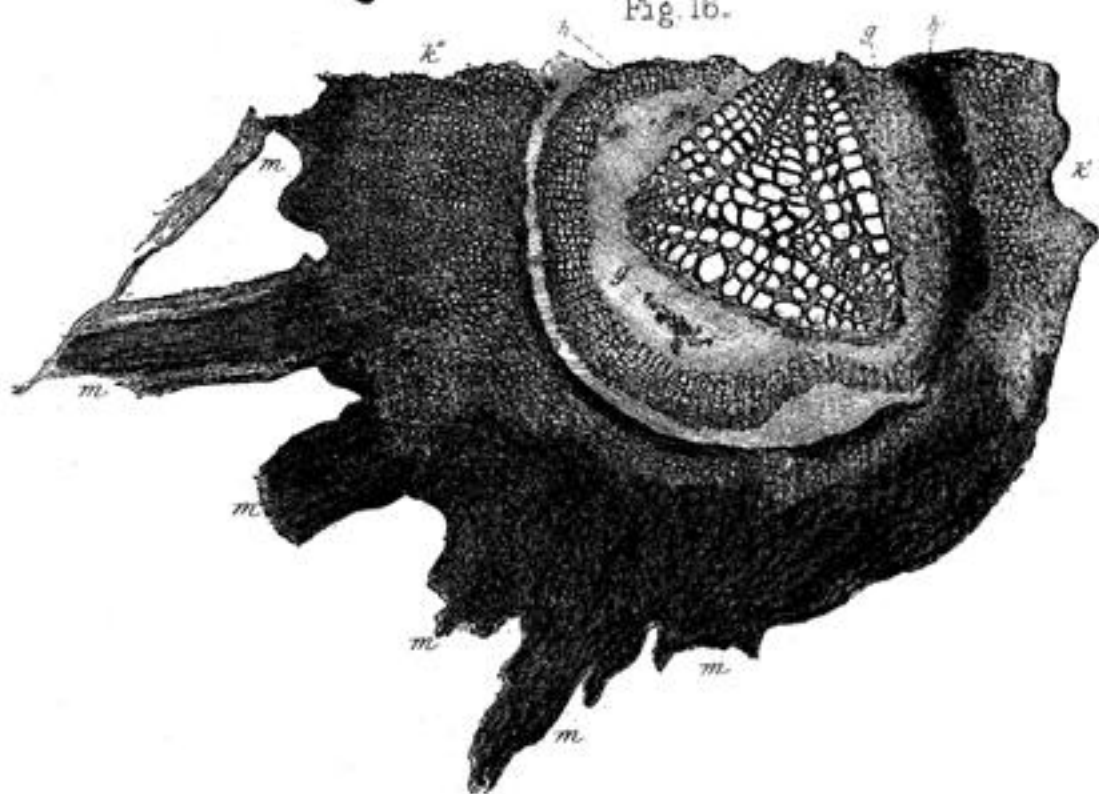


Fig. 18.



Fig. 19.



Fig. 17.



Fig 20.



Fig. 22.

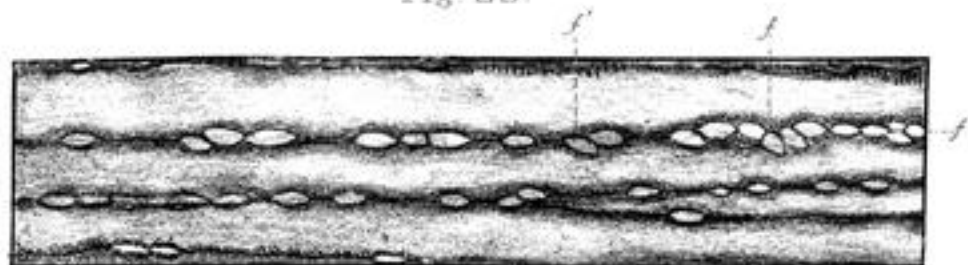


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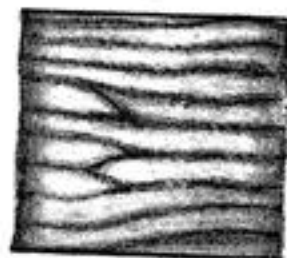


Fig. 24.



Fig. 21.

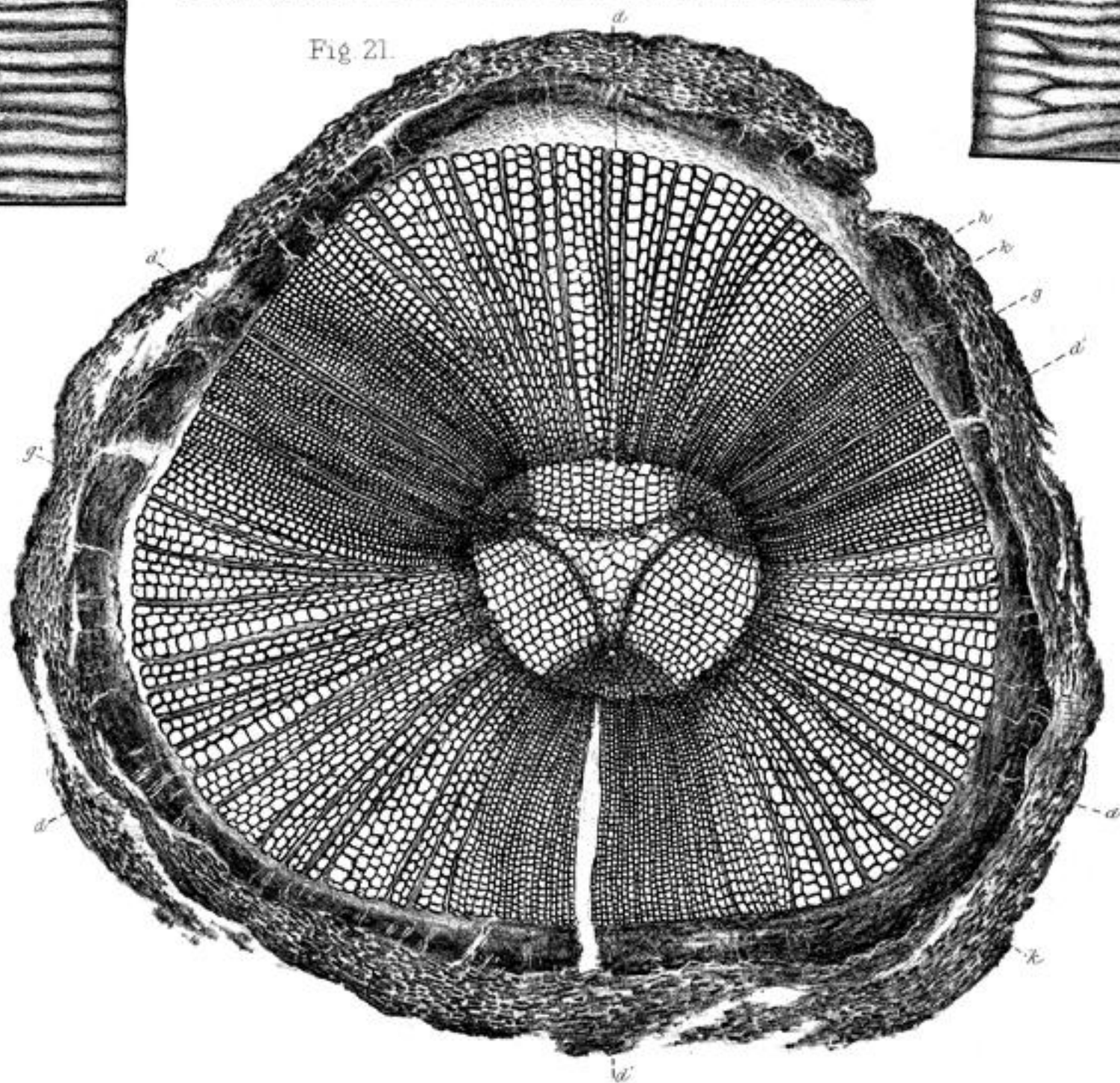


Fig. 23.

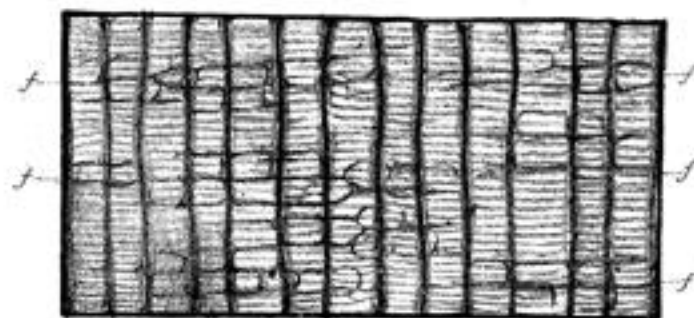


Fig 26.

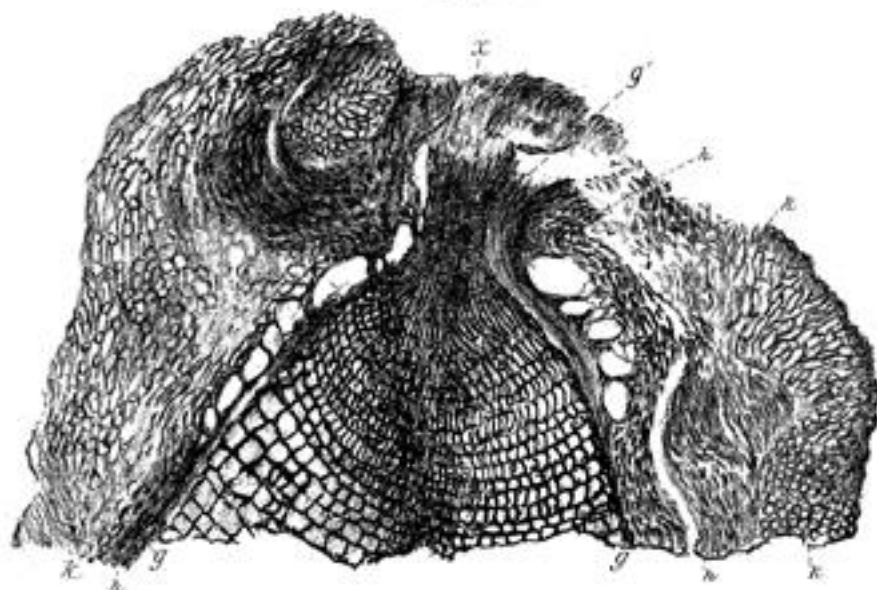
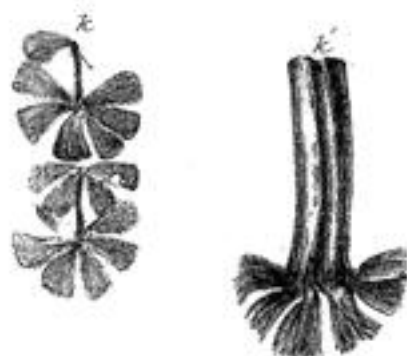


Fig 31.



Fig 28.

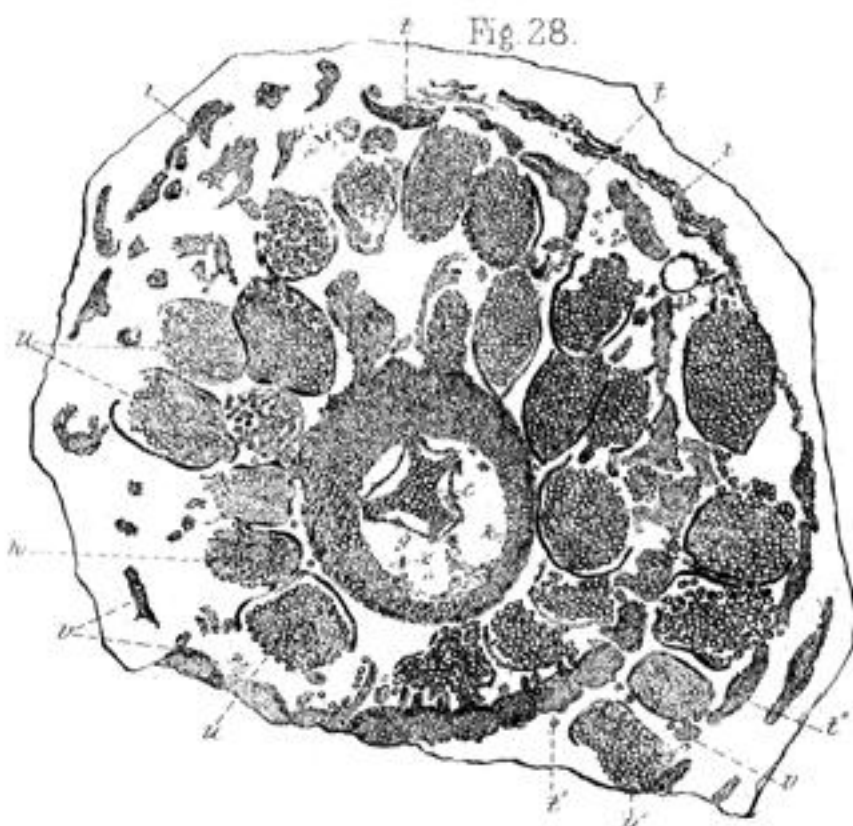


Fig 32.



Fig 29.

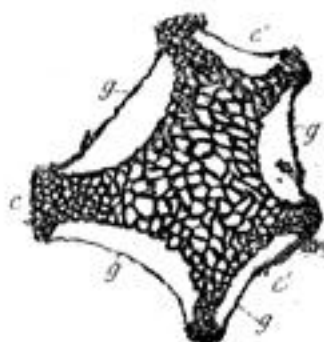


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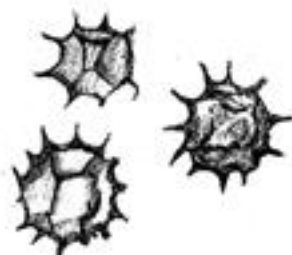


Fig. 33.



Fig. 34.



Fig. 35.



Fig. 36.



Fig. 37.

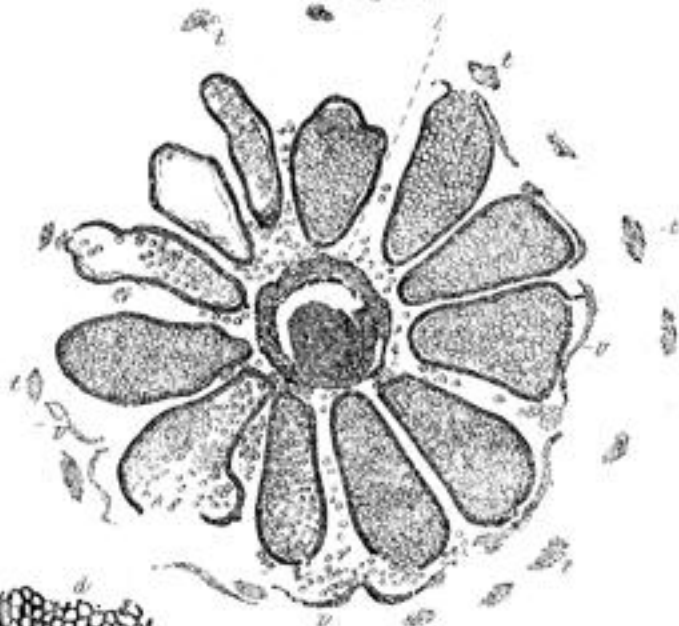


Fig. 38.

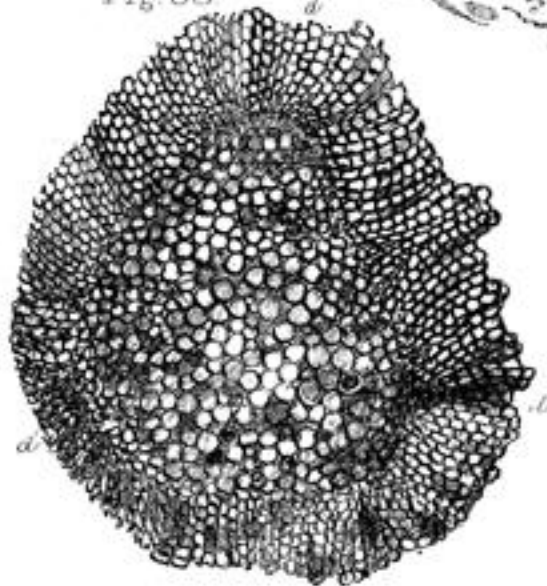


Fig. 39.



Fig. 45.



Fig. 46.

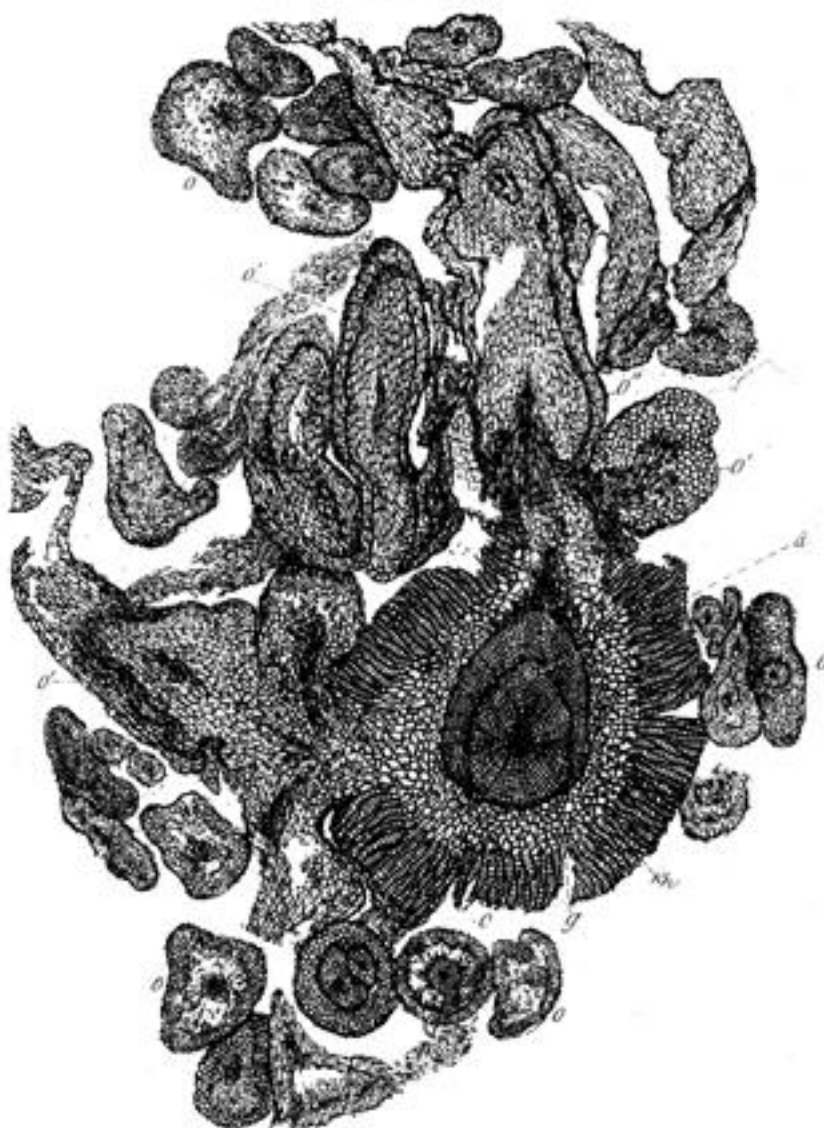


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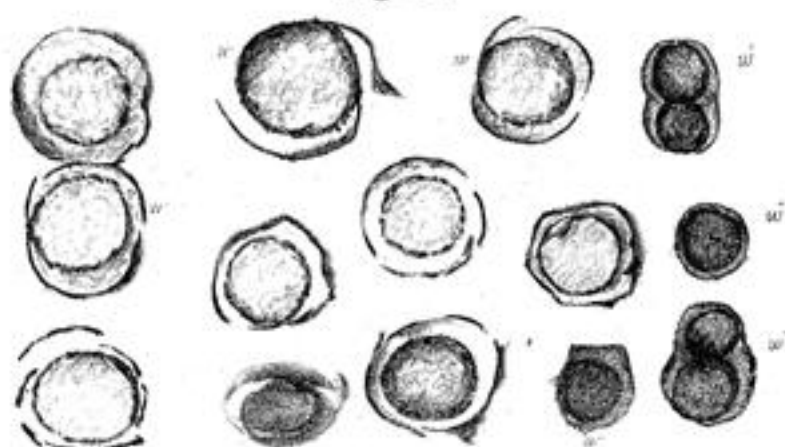


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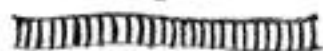


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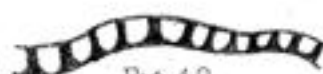


Fig. 42.



Fig. 44.



Fig. 47.

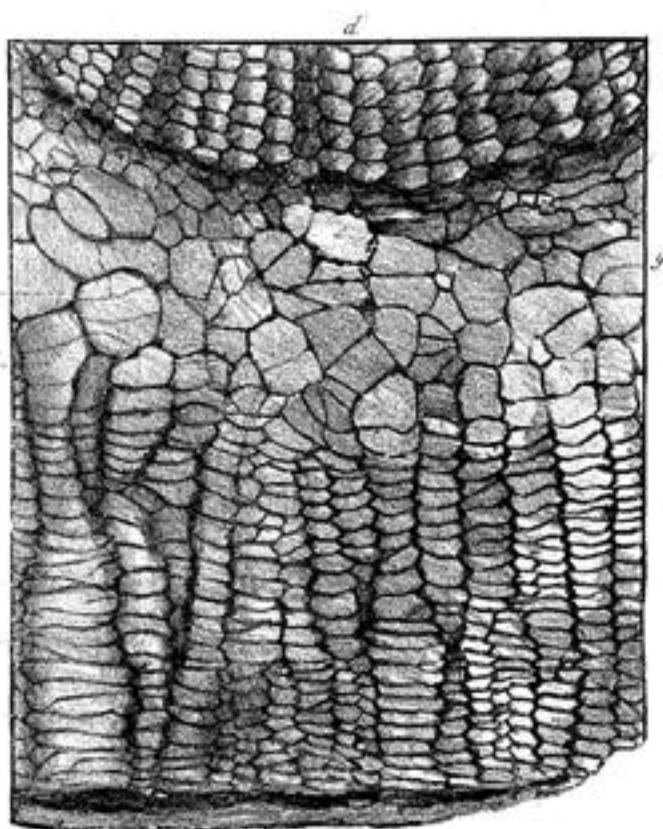


Fig. 51.

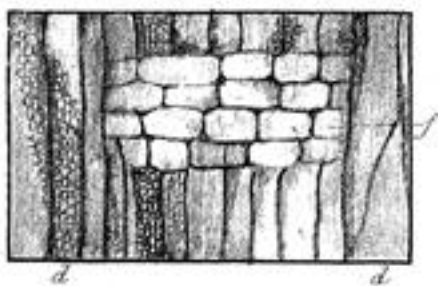


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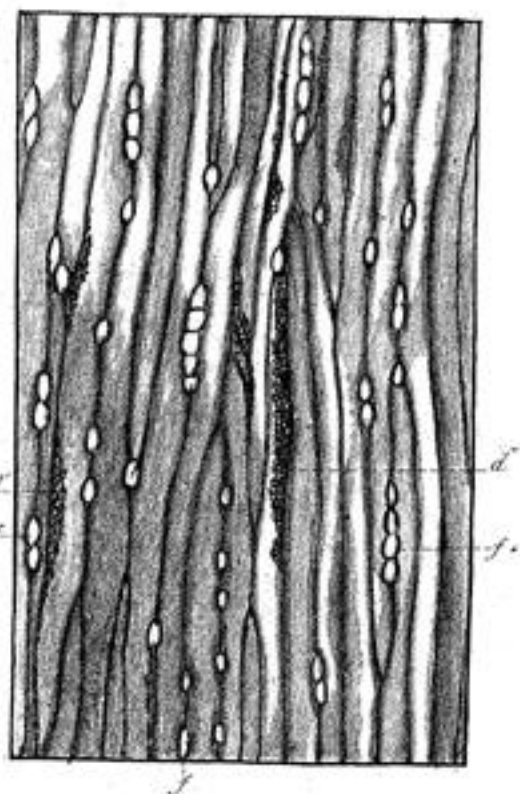


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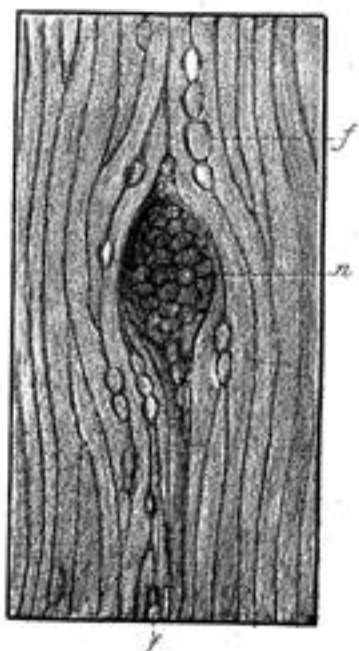


Fig. 48.

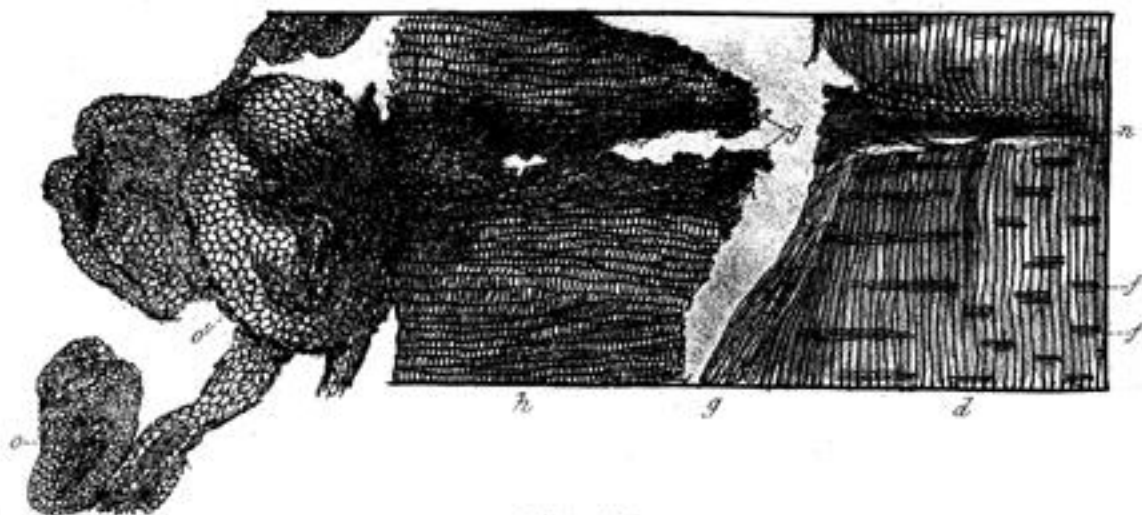


Fig. 49.

