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On the Organisation of the Fossil Plants of the Coal-Measures. Part XIII. Heterangium tiliaeoides (Williamson) and Kaloxylon Hookeri

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XII. *On the Organisation of the Fossil Plants of the Coal-Measures.*—PART XIII. Heterangium Tiliæoides (WILLIAMSON) *and* Kaloxylon Hookeri.

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[PLATES 21—24.]

IN 1872 I described ('Phil. Trans.,' 1873, "On the Organisation of the Fossil Plants of the Coal-Measures—Part IV."), under the name of *Heterangium Grievii*, one of the most interesting of the various plants which I discovered in the Burntisland deposit of Carboniferous limestone at Kinghorn. More recently we have obtained, from the Halifax beds, a very distinct plant, which, though differing in many important features from *H. Grievii*, resembles it so closely in others that I propose to include it in the same genus, under the name of *Heterangium Tiliæoides.* Its central medullary axis, A, differs in no conspicuous manner from that of *H. Grievii* when transverse sections of the two are compared.

Fig. 1 represents such a section enlarged 15 diameters, the medullary portion being seen at A, and a similar section is shown at fig. 2, A; whilst fig. 3 represents a small portion of a section enlarged 103 diameters. From the latter of these sections it will be seen that this medullary axis consists of irregular clusters of vessels or tracheids, *b*, the intervals between which are filled with ordinary parenchyma, *a*. The vessels near the periphery of this axis are smaller than those constituting the more central bundles—a feature best shown in fig. 2, *b′*. The character of these vessels will be referred to immediately.

Closely surrounding the medullary axis is a well-defined exogenous zone, B. This consists of a circle of vascular wedges, *c*; each wedge being composed of a number of laminæ which spring from a cluster of the smaller vessels, *b′*, which form the periphery of the medullary axis. At their medullary extremities the more external of the laminæ, fig. 4, *d*, composing each wedge, bend inwards towards its more central ones, so that each bundle represents an obtuse wedge-shaped group of such laminæ separated from a similar group on either side of it by a primary medullary ray (figs. 1, 2, and 4, *g*). The vessels of each lamina increase in size from within outwards, and between each one or two laminæ (fig. 4, *d*) we find secondary medullary rays (fig. 4, *h*). A cambium layer obviously existed along the lines *i*, *i*, of figs. 1, 2, and 4.

Externally to the xylem zone, B, we have what constitutes the most characteristic feature of this plant, viz., a true phloem zone, C. Each of the phloem-masses, *k*, corresponds in breadth to that of the xylem wedge to which it belongs. In many of these phloem-masses their component tissues are preserved only in a compressed or disturbed condition; but in the figure, Plate 21, fig. 4, *k*, we discover transverse sections of cells and tubular structures of various sizes, which exhibit a strong tendency to arrange themselves, especially at the inner portion of the phloem, in radial lines. In this example the xylem portion of the bundle extends laterally from *g* to *g*. The phloem, *k*, extends upwards and outwards in this figure until its peripheral margin comes in contact with the inner one, *p*, of the true cortex. This illustration is enlarged 48 diameters.

The large primary medullary rays which separate the xylem portions of contiguous fibro-vascular wedges or bundles now expand, as they proceed outwards, into magnificent primary phloem rays (Plate 21, fig. 1; Plate 22, fig. 2; and Plate 21, fig. 4; *n*, *n*). The botanist will at once recognise the remarkable resemblance of these conspicuous phloem rays to those occupying a corresponding position in the phloem of the common Lime, which resemblance has led me to adopt the specific name of *Tiliæoides* for this species of *Heterangium*. Each of these rays, as seen in transverse sections of a stem or branch, fig. 4, *n*, becomes broadly trumpet-shaped as it proceeds outwards from the extremity of the medullary ray, *g*, of which it is an extension. The large, more or less cubical, parenchymatous cells composing it are arranged in irregularly curved lines, the concavities of which are directed towards the medullary axis. Externally these cells merge with those of the inner cortex, *p*. Secondary and smaller phloem rays, extensions of the secondary medullary rays, *h*, can also be traced in all the transverse sections. They are sufficiently distinct in the phloem, *k*, of the isolated wedge, *c*, of fig. 5.

The cortex, D, is separable into two layers, an inner one, *p*, and an outer one, *r*. The inner one (figs. 1, 2, and 4, *p*, *p*) consists of a comparatively uniform parenchyma which presents no special features of interest. The outer cortex, *r*, *r*, transverse sections of which are seen in figs. 1, 2, and 6, is somewhat more complicated. It consists of parenchymatous cells of variable forms and sizes. As seen in figs. 2 and 6, the inner cells, *r*, are much larger than the outer ones, *r′*, *r′*. The orifices, *w*, *w*, of fig. 6 are merely worm-borings and not normal cavities. Two important additional structures exist in transverse sections of the outer cortex. One of these consists of transverse sections of ascending vascular bundles grouped in pairs. In Plate 21, fig. 1, two imperfect examples of these twin arrangements are seen at *u* and *u′*; two such bundles are enlarged 51½ times in Plate 22, fig. 7, *u*, *u*, and a similar pair of still larger ones is enlarged 20 diameters at *u*, *u*, of fig. 8.

The second structure seen in transverse sections of the outer bark consists of masses, of unequal size and shape, of sclerous cells. Examples of these are seen at *t*, *t*, in Plate 21, fig. 1, Plate 22, fig. 2, Plate 21, fig. 6, and Plate 22, fig. 8. The true relations of these masses of sclerenchyma will be seen on examining the vertical sections of the cortex.

Plate 23, fig. 9, represents a vertical section made radially, and passing through the medullary axis at A, the exogenous xylem zone at B, the phloem zone at C, and the innermost border of the inner cortex at D. This section has passed from above downwards in a slightly oblique manner, so as successively to intersect five of the vascular laminæ, *d*, and the intervening secondary medullary rays, *h*, of the fibro-vascular bundle through which the section passes. Each of these alternating layers comes successively into view as we pass from the upper to the lower margins of the Plate. As is so often the case with the fossil Cryptogams, we find the cubical parenchymatous cells of the medullary axis, Plate 23, fig. 9, *a*, *a*, exhibiting a tendency to arrange themselves in vertical lines and with approximately rectangular horizontal septa. The vessels or tracheids, *b*, of this axis vary much in diameter. As already pointed out, those at its periphery and in contact with the inner surface of the xylem cylinder are very small; but the largest of those seen in the isolated bundles (Plate 21, fig. 3, *b*) have a mean diameter of at least $\frac{1}{100} = \cdot 001$ of an inch. More externally we have the vessels of the exogenously developed xylem, the laminæ of which are arranged in parallel radiating series. Their innermost vessels (Plate 23, fig. 9, *e*) are much smaller than the more external ones, *e'*, of the same lamina. The latter have a mean diameter of from $\frac{1}{1200} = \cdot 0008$ to $\frac{1}{1600} = \cdot 00062$.

Alternating with these laminæ of vertically disposed vessels, we have, at Plate 23, fig. 9, *h*, *h*, the secondary medullary rays composed, in these radial sections, of horizontal lines of cells arranged in a mural manner. In tangential sections of this exogenous xylem we find each of these secondary rays composed of one or two vertical series of cells, much compressed laterally. At C we obtain a radial section through the phloem zone of the stem. Here, again, we find numerous long, narrow, vertically arranged tubes (fig. 9, *l*) alternating with murally disposed masses of cells, *n*, constituting the primary or secondary phloem rays. The tubes have a mean diameter $\frac{1}{3200} = \cdot 00031$ of an inch. Of course it is to be presumed that these tubes may be regarded as representatives of the sieve-tubes of the higher Phanerogams, but I can detect in them no traces of transverse septa, or of any structural peculiarities justifying my affirming that they are actually sieve-tubes. It must be remembered that we are equally unable to verify the identity of the similar tubes in the phloem of the Selaginellæ with the true sieve-tubes of Ferns and of the Phanerogams.*

Plate 21, fig. 10, represents a tangential section of the phloem of our plant. We here see that the tubes, *l*, just described, display a tendency towards an undulating arrangement, the spaces between the curves of which enclose horizontally disposed lines of cells. I have already called attention to the fact that transverse sections

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* See De Bary, 'Comp. Anatomy of Phanerogams and Ferns' (Engl. Transl.), p. 182.

like Plate 21, fig. 4, C, seem to indicate some disposition on the part of these phloem tubes to arrange themselves in radial lines.

Radial sections of the inner cortex (Plate 23, fig. 9, *p*) exhibit no peculiarities in the form and arrangement of its parenchymatous cells requiring special notice, except one shortly to be referred to. It is otherwise with the outermost cortex *r*, of part of which a longitudinal section, enlarged 31 diameters, is shown in Plate 22, fig. 11. The peripheral layer is wanting in this preparation. It shows, however, at *r*, *r*, the coarse parenchyma seen in the section, Plate 22, fig. 2. It also exhibits three thick bands of sclerenchyma (Plate 22, fig. 11, *t*, *t*, *t*) corresponding to the detached patches of the same tissue seen in figs. 1, 2, and 8. The cells forming these horizontal bands have a mean diameter of from $\frac{1}{1600}$ = ·00062 to $\frac{1}{2000}$ = ·0005 of an inch. One longitudinal section in my cabinet exhibits one of the twin vascular bundles already described (fig. 8, *u*, *u*) passing upwards and outwards through the cortex.

Plate 23, fig. 12, is a tangential section through the exogenous xylem of a stem or branch which is giving off a true branch, *w*. We have the xylem zone at B, a little of the phloem at C; the inner cortex at *p*, and the outer cortex at *r*, with three of the horizontal masses of sclerenchyma at *t*, *t*, *t*. The section has not been made exactly parallel with the axis of the main stem; hence it has cut obliquely through the considerable branch at *w*. This branch has evidently originated in a tortuous deflection of the xylem vessels, which have only attained to their normal arrangement in regular radiating laminæ in the more external semi-diameter of the branch. The complete development of these radial vascular laminæ would only be attained at a higher point of the branch where it became entirely free from the parent stem. The identical development of a similar branch of *Kaloxylon Hookeri* is shown in Plates 6 and 7, figs. 32, 33, and 34 of my Memoir, Part VII. ('Phil. Trans.,' 1876). The branch, *w*, of fig. 12 is invested by an imperfectly preserved layer, *p'*, of the inner cortical zone. The figure is enlarged 13 diameters.

The resemblance in the origin of the branch just described to that of *Kaloxylon Hookeri* is also further sustained by the specimen represented in Plate 22, fig. 13. In figs. 32 and 33 of the *Kaloxylon* referred to above, the branch is seen to be given off opposite to a large primary medullary ray; the two vascular wedges bounding that ray on its two sides contributing equally their supplies of vessels and cells to the formation of the branch. Fig. 13 exhibits identical conditions. In it we have the large primary medullary and phloem ray, *n*, bounded on its two sides by the lateral vascular laminæ of the two vascular wedges, *c*, *c'*. A mass of tracheids and vessels, *e*, *e'*, is being given off from the peripheral angle of each of these two wedges; these meet beyond the outer boundary of the primary phloem ray, *n*, where they unite to form the rudiments of the branch, *w*. The abundance of short tracheids at this point reminds us of the similar development of these elements where roots or branches are being given off by the stems of living vascular Cryptogams.

There yet remains to be considered the character of the vessels and tracheids which enter so largely into the composition of this stem. In the twin bundles (Plate 22, figs. 7–8), going off to what, both in this plant and the allied *Heterangium Grievii*, I presume to have been petiolate leaves, the vessels are mainly of the barred or spiral type represented on Plate 22, fig. 14. In the other vascular organs they appear, as represented in fig. 15, to be reticulated; but more careful examinations, aided by higher microscopic powers, show that all these vessels are furnished with the bordered pits seen in Plate 21, fig. 16, the canals of which are all narrow, oblique, and parallel to one another. In the larger proportion of these vessels and tracheids the canals alone remain visible, as in Plate 22, fig. 17; but in fig. 18 we see the transition from the one form to the other in the same tracheid or vessel. At *e* we have in each pit both the central canal and its investing areole; but at *e′* all the areoles have disappeared, I presume during mineralisation, the oblique canals alone remaining; but that each canal was originally surrounded by its own areole is unquestionable.

One more curious feature is presented by this plant. In Plate 22, fig. 5, we have the exogenous xylem zone at B in its normal position relatively to the medullary axis A. But the two fibro-vascular bundles or wedges *c*, *c′*, are being pushed outwards by a mass of parenchyma, *z*, which has developed on the inner side of the two bundles separating them from the medullary axis.

It will further be noticed that each of these bundles carries away with it, on its inner side, a cluster of the medullary vessels *b*, *b*, suggesting the probability that the cellular mass, *z*, has really been an outgrowth from the medullary cells, since it must have originated from the central side of the two clusters of medullary vessels *b*, *b*, which it has been instrumental in pushing outwards. I discover no clue to the destination of these displaced fibro-vascular bundles; but they remind us of somewhat similar conditions seen in the stems of *Lyginodendron Oldhamium*.

Fig. 19 represents a cluster of cortical cells, enlarged 187 diameters. Cells in this condition are extremely abundant in the cortical layers. At the first glance they look like cells with thickened cell-walls, but they are constantly found in close association with cells belonging to the same parts of the plant, the walls of which exhibit no such thickening, hence the effect is possibly due to some condition of mineralisation which has produced deposits of various amounts within the cell-walls.

The next plant requiring further notice is the *Kaloxylon Hookeri*, which I first described in my Memoir, Part VII.* The specimens described and figured on Plates 5, 6, and 7 of that memoir were all obtained from one of the Oldham localities, and, as is not seldom the case with the fossil plants from that quarter, their cellular structures are ill-defined through defective mineralisation. But for several years past we have obtained examples of a *Kaloxylon* from the Halifax beds which are in a very different condition. These specimens long ago showed that the cortical zone possessed peculiarities of structure which the Oldham examples had not revealed to me; but on re-examining those examples, guided by the light thrown upon them by those

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* ‘Phil. Trans.,’ vol. 166, 1876.

from Halifax, I soon found that the cortical tissues of the two forms had been identical.

At the same time, the Halifax specimens had peculiarities of their own which seemed difficult of explanation. The forms most generally met with at Oldham were of the type represented in my earlier memoir by the two figures, Plate 5, figs. 23 and 26, in which six large exogenously developed vascular wedges radiated from what appeared to be a central vascular axis. At that time I was unable to discover any cellular tissue in that axis; I have since obtained three or four examples like those just referred to, from Halifax, one of which is represented in Plate 23, fig. 20, of the present memoir. But most of the Halifax specimens are like those seen on Plate 24, figs. 22 and 27.

That fig. 20 is the *Kaloxylon Hookeri* of my former memoir is unquestionable. In that memoir I called attention to a special development of cells at the free extremity of each of the six radiating vascular wedges (*loc. cit.*, p. 15). The cells occupying the peripheral ends of the six primary medullary rays separating the six radiating vascular wedges were enclosed within a wavy line round, and at a little distance from, the end of each of those wedges, where "they enclose a small semi-lunar area (*g*) co-extensive with the diameter of the wedge, and which is occupied by a distinct form of cellular tissue. I shall shortly give my reasons for believing that this latter tissue is a quasi-cambial meristem layer, which is concerned in the formation of the newest exogenous vascular growth."

More extended investigations into the structure of this curious plant lead me to the conclusion that the above extract embodies a truth, but not all the truth. Plate 23, fig. 20, represents an excellent example of this stem from Halifax. As in the corresponding Oldham examples, the central axis is a bundle of vessels apparently unmixed with any cellular tissue. The radiating wedges, *c* (which are here five, not six, in number), and their five intervening primary medullary rays, *g*, do not differ from those of the Oldham forms. But the semi-lunar areas of the Oldham specimens represented in fig. 15, *g*, of the memoir quoted in the above paragraph are clearly seen in fig. 20, *k*, *k'*, of this memoir, to be the true phloem-masses of the several radiating wedges, and not a quasi-cambium as previously surmised; but which must, when the plant was living, have had a true cambium separating the inner border of each phloem from the periphery of the xylem. Plate 23, fig. 21, represents the phloem of the radial bundle, *k*, of fig. 20, enlarged 62 diameters; at *p'* we have the long narrow cells of the innermost margin of the cortex pursuing their undulating course, sweeping outwards opposite the ends of the xylem-wedges to make room for the phloem-masses, *k*, *k'*, and curving inwards when crossing the outer ends of the primary medullary rays, *g*, *g*, as at *g'*, *g'*. There can be no doubt, therefore, that the *Kaloxylon Hookeri* was a true exogen, having a perfect cambium, which developed both xylem and phloem, but the traces of which cambium are but very imperfectly, if at all, preserved.

Plate 24, fig. 22, is a form from Halifax, in which the central axial bundle is in process of development, but in which no exogenous growth has yet taken place. Its thick cortical layer, *r*, from its hypodermal portion to within a short distance from the vascular bundle, has been very uniform in its composition. This structure was, as I have already observed, imperfectly preserved in the Oldham specimens, but soon after my description of the latter was published I obtained from Halifax several of those now described. The parenchyma of this cortex has been thin-walled, and the forms of its cells apparently rather irregular; but scattered amongst the latter are numerous long, narrow, longitudinally arranged canals, *r′*. It is not quite easy to determine whether these canals are true tubes or merely intercellular passages. Plate 23, figs. 24 and 25, demonstrate that each canal is enclosed by a wall, *r′*, within which we constantly find a black substance, evidently moulded upon the interior of this wall, either in the form of a solid rod, as in fig. 24, *r″*, or as a hollow cylinder, as in fig. 25, *r″*. The wall, *r′*, may either be a true one belonging to the canal, or it may only consist of the coalesced walls of the surrounding cells. Seeing how long different opinions prevailed respecting the structure of such organs as the so-called laticiferous vessels, a determination of such a point in the case of fossil plants may well be doubtful. That these passages have been gum or resin canals may be inferred from the large amount of the black carbon which they so often contain. Fig. 26 is a section of a specimen from Halifax, in which five vascular wedges have undergone a considerable development, though much less than fig. 20. The inner ends, *d′*, *d′*, of the vascular laminæ composing each wedge curve away from its centre, converging towards similar laminæ belonging to contiguous wedges to form a series of semicircular curves. I further discover in similar specimens a few parenchymatous cells creeping in amongst the vessels, *e*, of the central axis. Such examples constitute connecting links between the type represented in fig. 20 and others yet to be described. The phloem masses are again visible at *k*, *k*. The epidermal layer, *p″*, so extremely characteristic of this plant, is here thicker than usual, consisting of from three to four cells in breadth, the ordinary number being two or occasionally three.

The specimen just described conducts us to fig. 27, which is an excellent example of the type most frequently obtained from the Halifax deposits. Its medullary axis, which is of large size compared with that of fig. 20, has an undulating peripheral outline of a pentagonal or hexagonal form; some specimens having the former, others the latter contour. The conspicuous bundles of vessels, *e*, are now largely intermingled with a delicate parenchyma, *a*. We find here no exogenous growths, unless the single continuous line of vessels, *e′*, seen bounding each peripheral concavity with more or less regularity, is to be regarded as the first of a series of such growths. This vasculo-cellular axis is completely invested by a zone of extremely delicate parenchyma, *p*, the innermost portions of which, especially where they fill the concavities, *p′*, of the peripheral outline, consist of very minute cells. Other specimens, resembling fig. 27 in most of their features, exhibit a wavy line of cortical cells, indicative of the beginnings of exogenous development by the formation of phloem elements like those of fig. 26, *k*.

The specimen before us possesses additional interest from displaying a longitudinal section of what appears to be a rootlet, *y*, springing from the periphery of the medullary axis at *y*′, and pursuing its outward way through the bark. We see no vessels in this rootlet, since the section has only passed through the cellular zones forming its cortical cylinder; but another similar specimen in my cabinet exhibits such vessels in their normal central position.

I may now call attention to a remarkable series of objects, chiefly from Oldham, which are certainly organs of the plant under consideration. They vary in relative size from that represented at Plate 24, fig. 28, to fig. 37. So far as their general features are concerned, these objects differ but little from each other. In all we have the epidermal layer *p*″ enclosing the cortex *r*, in the centre of which latter is a vascular bundle *e*. The chief interest of these specimens resides in the illustration they afford of the gradual development of this vascular bundle, and the conclusions suggested by that development as to the nature of the objects to which the bundles belong. Being from Oldham, the cortex *r* of each of these specimens is in the same imperfect state of preservation as characterised those figured in my Memoir, Part VII.; but, as the vascular bundle is now the object under consideration, this defect is of no present importance.

In Plate 24, fig. 28, we find the section of the bundle *e* of an oblong form. There are faint traces of small vessels given off from each side of the centre of this bundle, but they are too indistinctly preserved to be relied upon. In Plate 23, fig. 29, we again discover the bundle at *e*, and at Plate 24, fig. 29A, this bundle is enlarged 182 diameters. Most of the structures in this latter figure are certainly vessels or tracheids. A few of those marked *p*, *p*, may possibly be inner cortical cells. We here see the section of the bundle approaching a triangular, if not a quadrangular, contour. In Plate 24, fig. 30, *e*, we have a fine bundle from a Halifax specimen, enlarged 156 diameters, enclosed within a mass of small cells, *p*, which in turn are surrounded by the ordinary cortical parenchyma, *p*′. In this bundle we have a striking resemblance to that of a tetrarch rootlet which had developed centripetally; the vessels at the four primitive points of apparent protoxylem being very small, whilst the central ones, assumably of later growth, are of much larger size. Such was long my interpretation of this and similar specimens, but we shall see that the further study of other examples throws serious doubt upon the accuracy of this determination. Plate 24, figs. 31 and 32, represents transverse sections of two other bundles, the former enlarged 77 and the latter 99 diameters. Both these bundles, which are from Halifax specimens, present the same quadrate form, suggestive of a tetrarch origin, as fig. 30, and each bundle is imbedded in an investment of extremely delicate parenchyma, obviously identical with that (*p*′) surrounding the vasculo-cellular axis of Plate 24, fig. 27.

Plate 24, fig. 33, is a still smaller specimen of the type of fig. 28, from Oldham, enlarged 39 diameters; its vascular bundle is shown, enlarged 187 diameters, in fig. 33A. This example closely resembles a triarch rootlet-bundle. Plate 24, fig. 34, is yet smaller, also from Oldham, and enlarged 39 diameters. Its bundle, *e*, enlarged 187 diameters, is represented in fig. 34A. It now consists of but six vessels. Figs. 35, 36, and 37 are three sections of these root-like structures from Oldham, becoming successively smaller, so that in fig. 37 the epidermal layer, *p''*, now consists only of a single layer of cells enclosing but a very small number of cortical ones. The vascular bundle of fig. 35, seen at fig. 35A, is now distinguished with difficulty from the cells by which it is surrounded. So far as I can determine, it consists of the five vessels marked *e*, *e*. In like manner, the bundle of fig. 36, represented at fig. 36A, seems to consist of the three vessels marked *e*, *e*; whilst that of fig. 37, shown at fig. 37A, seems to consist of the two vessels indicated by the same letters. All the Oldham specimens just described, viz., figs. 28, 29, 33, 34, 35, 36, and 37, belong to one great cluster of root-like examples crowded together in one slide; amongst them are other, more completely developed specimens, showing that the entire series belongs to *Kaloxylon Hookeri*. My first impression was that the whole cluster consisted of a series of rootlets, and the study of such examples as figs. 30, 31, and 32 not only seemed to confirm this opinion, but to show that they were rootlets with a tetrarch development of their several primary xylem bundles. But on tracing the development of those bundles downwards through such examples as figs. 34, 35, 36, 37, it became evident that, if the objects of which they formed a part were rootlets, the bundles had not been developed centripetally in the way characteristic of living rootlet-bundles, and which also was the case with other plants (*e.g.*, *Stigmaria Ficoides*) that lived during the Carboniferous age. Nevertheless, it is difficult to believe that these organs have been other than roots; though the apparently centrifugal growth of their bundles is more suggestive of an axial cauline development than of radicular structures.*

We may now ask: Can any light be thrown upon the systematic affinities of the two plants, *Heterangium Tiliœoides* and *Kaloxylon Hookeri*, described in the preceding

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* [I find amongst the Carboniferous plants other examples of what appear to be branching stems, which diminish gradually in diameter, until, as in the instance described in the text, they become extremely slender. At the same time that they are reduced in size, they rapidly increase in the number of the transverse sections of them that are met with in our slides. The *Rachiopteris Oldhamium*, described in my Memoir, Part VI. ('Phil. Trans.,' Part 2, 1874), presents these conditions. The figures 20–24 on Plate 53 of that memoir show a gradation of diameters of sections from about ·125 to ·006 of an inch; yet none of these sections display the slightest trace of any foliar appendages. Stems thus gradually diminishing in diameter, whilst their numbers are multiplied, must be reduced either to the condition of aërial twigs or of subdividing roots and rootlets. If the former, where are their foliar appendages? If the latter, why do not their fibro-vascular bundles show the symmetrical arrangement telling of the centripetal development so characteristic of the proto-xylems of all roots? Of course the idea suggests itself that these curious objects may have had some relationships with the rootless subterranean branches of *Psilotum*, though many difficulties interfere with our ready acceptance of this explanation.—August 12th, 1887.]

pages? One fact is undeniable, viz.: that certain portions of them, obviously stems or branches, possessed, when living, a true cambium which developed xylem and phloem in a normally exogenous manner. The same statement applies to two other plants described in previous memoirs, and which must be considered along with those just named. These are *Lyginodendron Oldhamium* and *Heterangium Grievii;* besides which close affinities appear to exist between the *Lyginodendron* and *Rachiopteris aspera*, also described in the Memoir, Part VI.

Canals, precisely like those in the bark of *Kaloxylon Hookeri*, exist equally in the inner bark of *Lyginodendron* and of *Rachiopteris aspera*. The latter is unquestionably a rachis of a Fern; whilst the former displays a wonderfully clear exogenous development of its xylem zone. I have more than once, in previous memoirs, suggested that the *R. aspera* was the petiole of the leaf of the *Lyginodendron;* and my friend, the Count DE SOLMS, of Gottenburg, who has obtained numerous examples of these two plants from the Westphalian deposit at Pith Vollmond, has arrived independently at the same conclusion. If we are correct in this supposition, we have now, for the first time, in *Lyginodendron Oldhamium*, a Fern of which the stem or rachis exhibits a highly developed form of exogenous growth. This fact in some degree influences our interpretations of the two species of *Heterangium*, in both of which we find in the outermost bark the remarkable horizontal bands of dense sclerenchyma represented in Plate 22, fig. 11, of the present memoir, and in Plate 29, fig. 32, *h'*, and Plate 31, figs. 45, 47, and 49 of the Memoir, Part IV., in which *Heterangium Grievii* was first described. This remarkable peculiarity in the structure of the outer cortex of these two plants has led to a careful search for any fossil stems, with their foliage attached, in which a similar structure seemed to exist. Some months ago Mr. KIDSON sent me some stems which he believed to belong to *Sphenopteris elegans*, the cortex of which displayed an exactly similar series of thickened horizontal parallel bands. Still more recently he received from my friend Professor VON WEISS, of Berlin, and forwarded to me, a beautiful specimen of an exactly identical stem, attached to which are the unquestionable pinnules of *Sphenopteris elegans*. So far as these internally structureless specimens affect the question, they suggest the possibility that both the species of *Heterangium* may also prove to be Ferns. At first sight, remembering the exogenous growth developing both xylem and phloem, as well as the discigerous tracheids of *Heterangium Tiliæoides*, this idea seems to be a most improbable one; but it is no less probable than that *Lyginodendron Oldhamium* belongs to the group of Ferns, which latter conclusion has now made a near approach to certainty.

The extraordinary vasculo-cellular structure of the medullary axis of the two *Heterangiums* finds its parallel in such examples of *Kaloxylon Hookeri* as that represented in Plate 24, fig. 27, of the present memoir. To see anything approaching this structure in other plants, we must go back to the somewhat similar central axis of *Lepidodendron Selaginoides* (Memoir, Part XI., figs. 3, 5, and 10), which presents equally anomalous combinations of internal structure, that remove it far from any known living form of vegetation, though it is an unquestionable Lycopod.

We thus fail, for the present, to reach anything beyond probabilities respecting the true affinities of the plants described in this memoir; but, whatever may be finally determined as to their real systematic position, one thing is certain, viz., that in their internal organisation they present combinations of tissues that find no representatives amongst living plants. Possibly they are the generalised ancestors of both Ferns and Cycads, which transmitted their external contours to the former and their exogenous modes of growth to the latter types. In considering this possibility, we must not forget that in *Stangeria* we have a still living plant in which the stem of a Cycad bears fronds, the leaflets of which retain the dichotomous nervation of a true Fern. The *Stangeria* has retained, not only the primitive exogenous stem of some ancestral type, in common with its other Cycadean relatives, but also the peculiar Fern-like leaflets, which may also have come down to it from Palæozoic times. Hence we have here a combination of Fern-like features and of an exogenous mode of growth. Such being the case, it need not startle us if we have to conclude that a similar combination existed during the Carboniferous age.

In closing this memoir, I have again to thank Mr. SPENCER and Mr. BINNS, of Halifax, for the specimens with which they have so kindly supplied me. But my thanks are most specially due to WILLIAM CASH, Esq. Resident on the spot, his incessant vigilance in seeking for new material and opening out new sources of supply has a value to me of which I can scarcely speak too highly.

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Plates 21 and 22, figs. 1–19.

A, Vasculo-cellular medullary axis.
  a, Medullary cells.
  b, ,, vessels.
B, Exogenous xylem.
  c, Vascular wedges or bundles.
  d, ,, laminæ.
  e, *f*, Vessels or tracheids.*
  g, Primary medullary rays.
  h, Secondary ,, ,,
  i, Cambial line.
C, Phloem zone.
  k, Phloem of the vascular bundles.
  l, ,, tubes.
  m, ,, parenchyma.
  n, Primary phloem rays.
  o, Secondary phloem rays.
D, Cortex.
  p, Inner cortex.
  r, Outer ,,
  s, Cortical cells.
  t, Cortical bands of sclerenchyma.
  u, Double vascular bundles.
  w, Lateral branch.
  x, ,, ,,

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* I have employed these two terms throughout the memoir without attempting to determine which of them may be applicable to the objects described. It is impossible to distinguish vessels from tracheids in these Carboniferous fossil plants.

Figure.	Plate.	*Heterangium Tiliæoides.*
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16	21	A vessel with bordered pits from the exogenous zone of a stem. × 187 diameters. C. N. 1621, p. 293.

Figure.	Plate.	*Heterangium Tiliæoides.*
17	22	A vessel only showing the canals of the bordered pits. × 112 diameters. C. N. 1621, p. 293.
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19	21	Cluster of cells from the cortex having the appearance of sclerous ones. Due probably to mineralisation. Page 293.

Letters of reference to the figures of Kaloxylon Hookeri.

Plates 23 and 24, figs. 20–37A.

A, Medullary axis.
  a, Medullary cells.
  b, Vessels of medullary axis.
B, Exogenous xylem.
  c, Vascular wedges.
  d, ,, laminæ.
  e, Vessels and axial bundles.
  g, Primary medullary rays.
  h, Secondary ,, ,,
  i, Cambial line.
  k, Phloem.
  p, *p′*, Innermost cortex.
  p″, Epidermis.
  r, Outer cortex.
  r′, Canals of outer cortex.
  y, Rootlet (?)

Figure.	Plate.	*Kaloxylon Hookeri.*
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21	23	Transverse section of the peripheral end of a vascular wedge of fig. 20, with its phloem enclosed within the wavy outline of the endoderm or inner border of the cortex. × 63 diameters. C. N. 1238, p. 294.
22	24	Transverse section of a specimen from Halifax devoid of any exogenous zone, but with numerous tubular lacunæ in its cortex. × 51 diameters. C. N. 1234, p. 295.
23	. .	By accident no corresponding figure.
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Figure.	Plate.	*Kaloxylon Hookeri.*
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34	24	Another section, yet smaller than fig. 33, from Oldham. × 39. C. N. 1239, p. 297.
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35	24	Transverse section of a still smaller rootlet from Oldham. × 39 diameters. C. N. 1239, p. 297.
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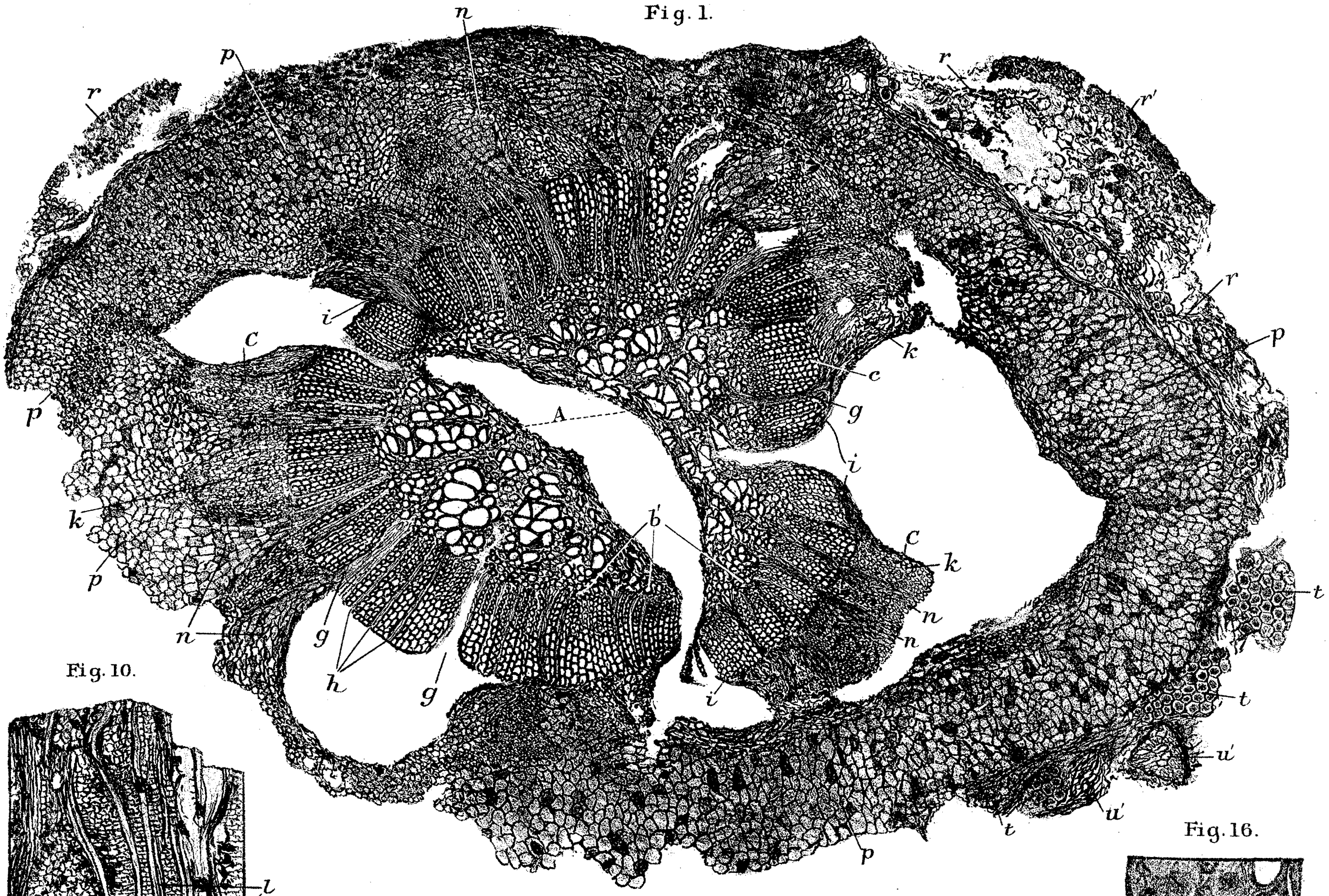
37A	24	The vascular axis and some attached cells of fig. 37. × 187. Page 297.

Fig. 1.



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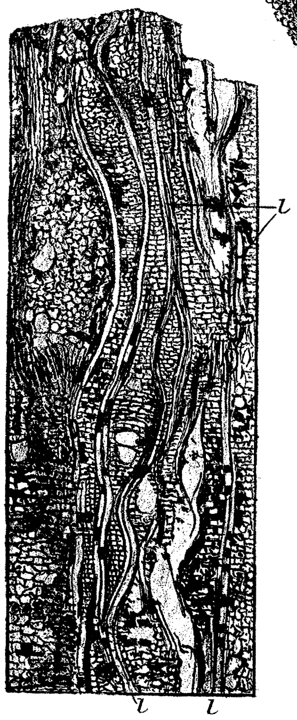

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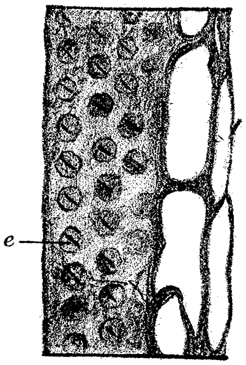

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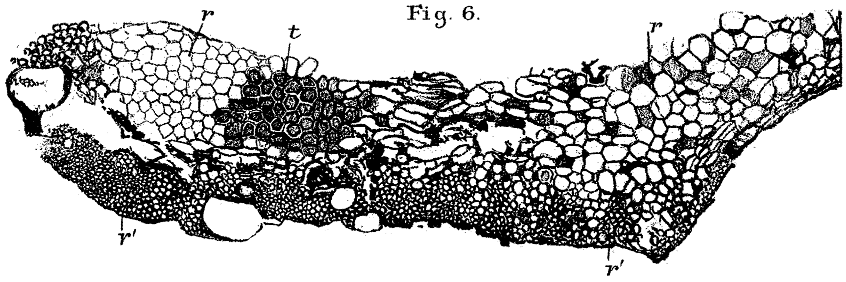

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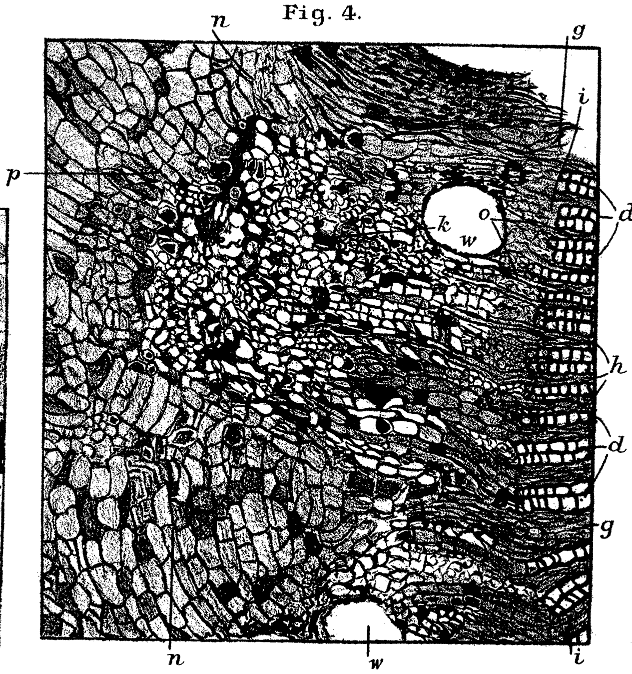

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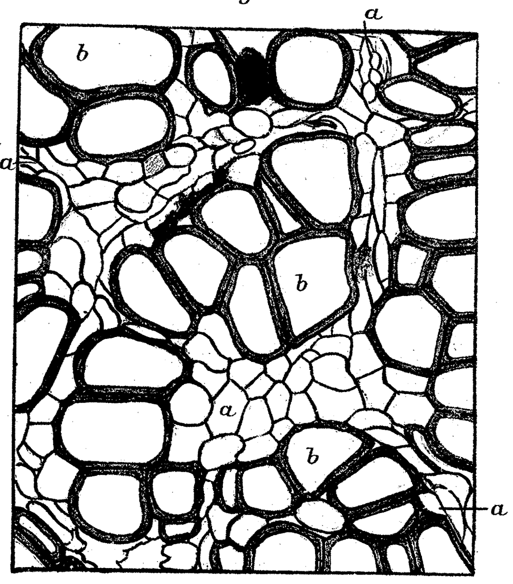

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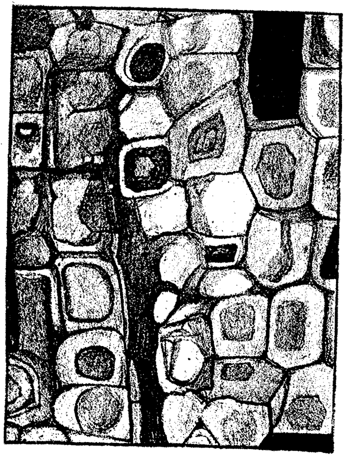

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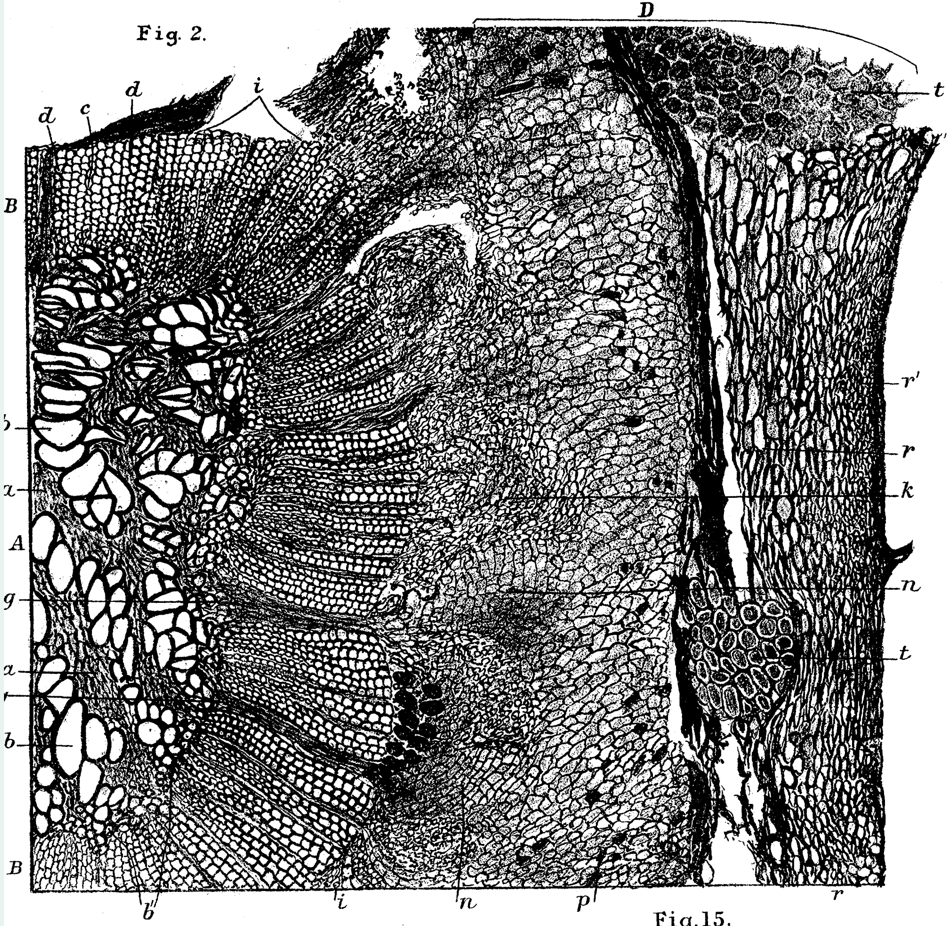

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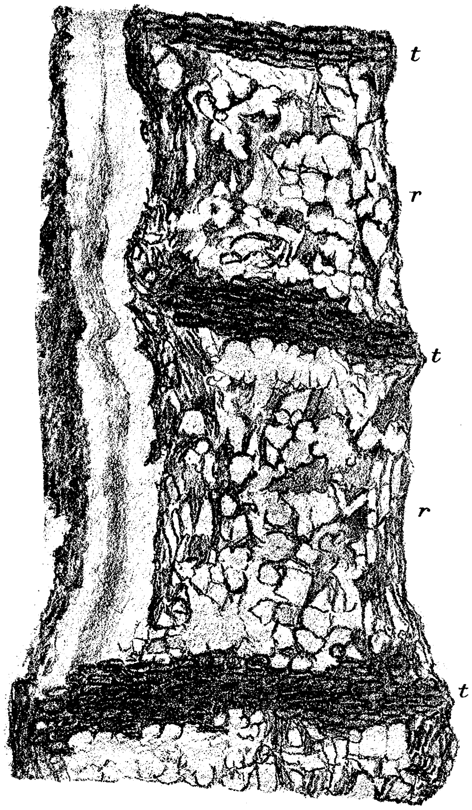

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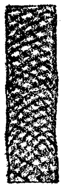

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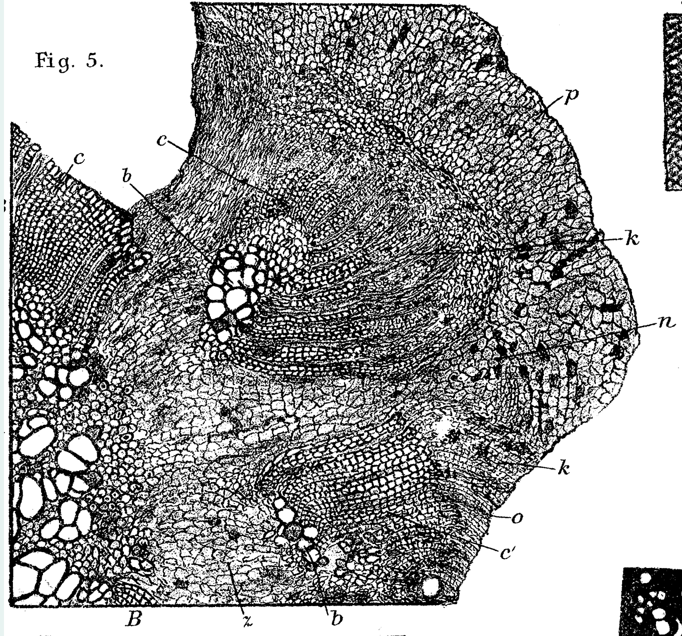

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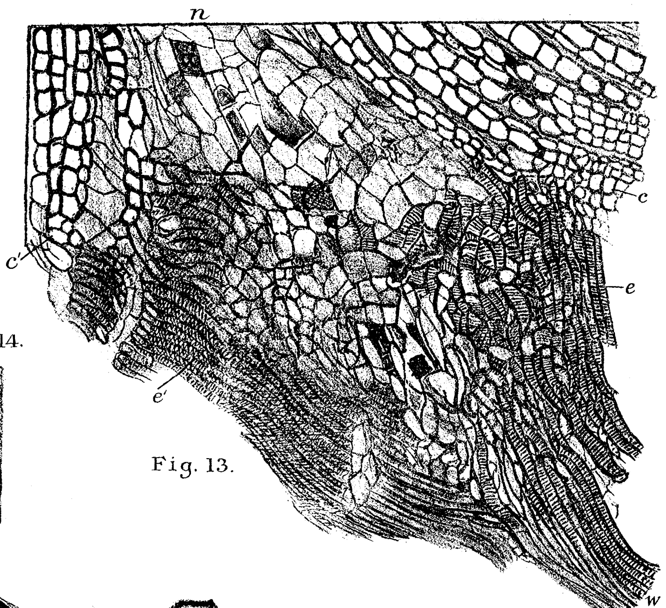

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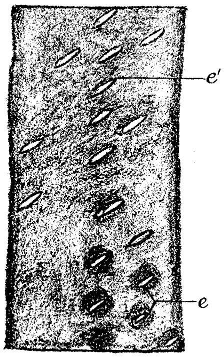

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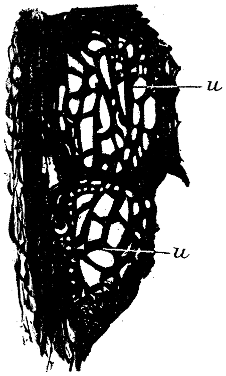
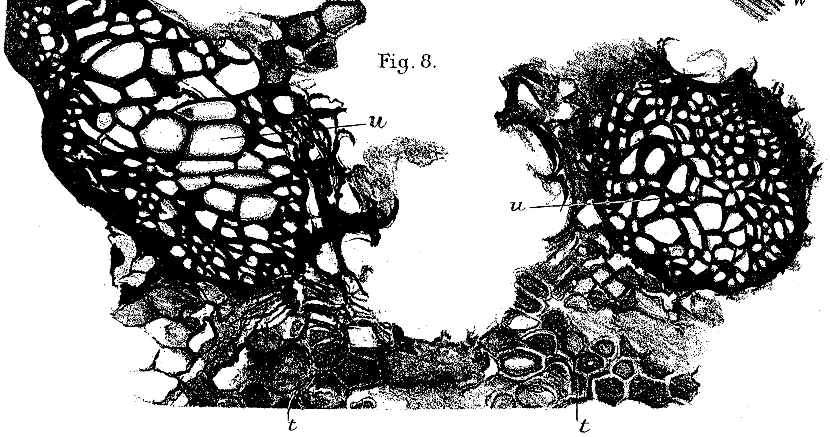


Fig. 7.

Fig. 17.

Fig. 8.



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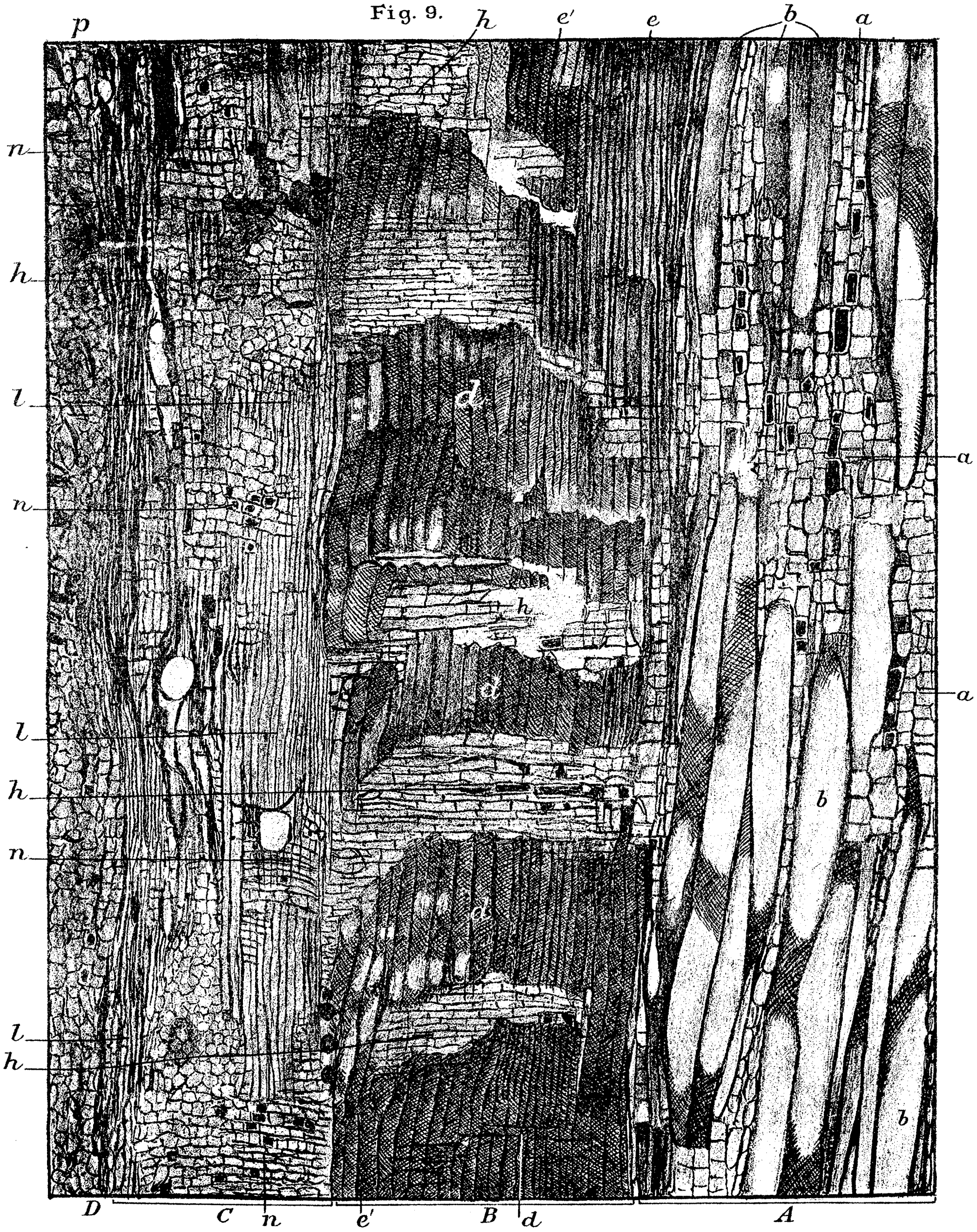

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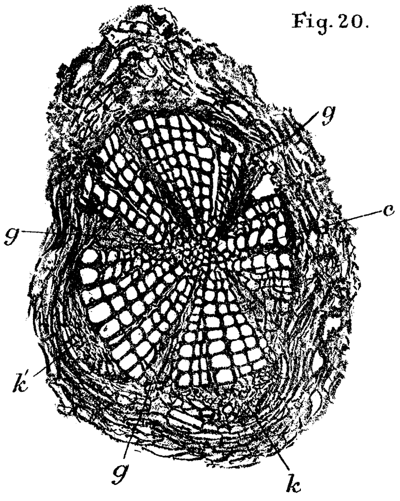

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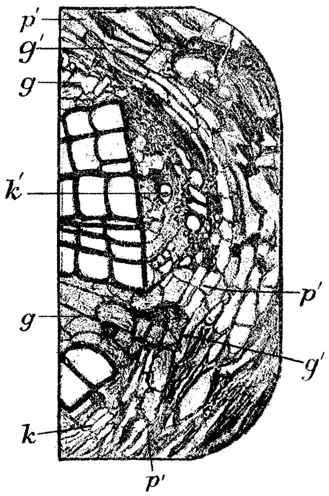

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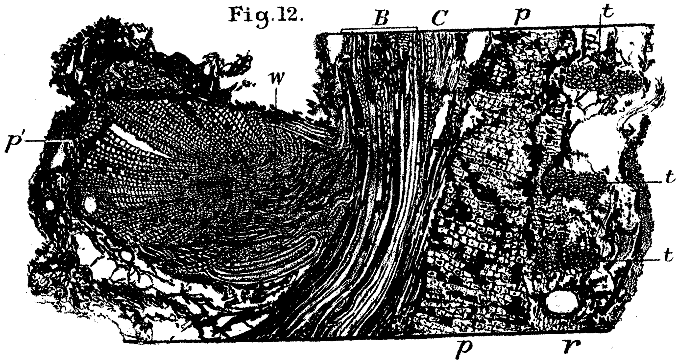

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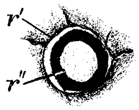

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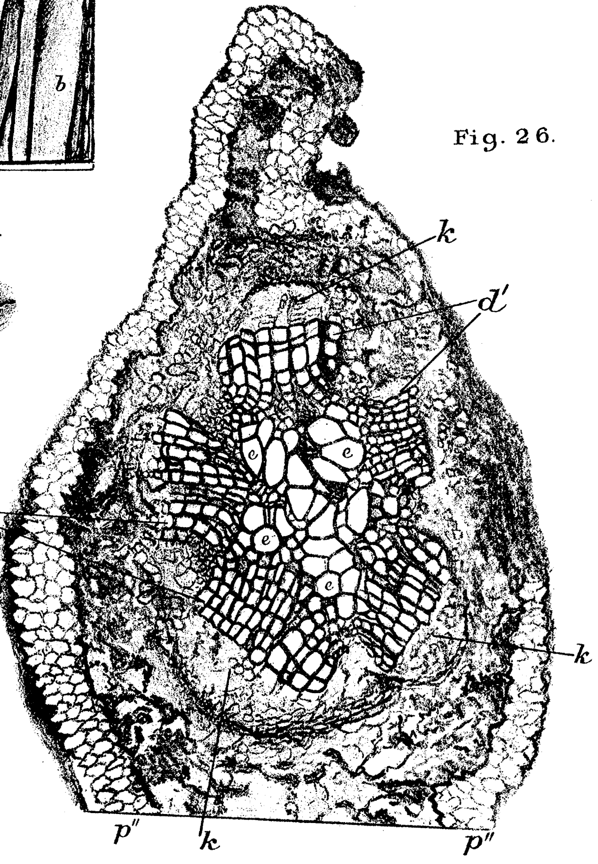

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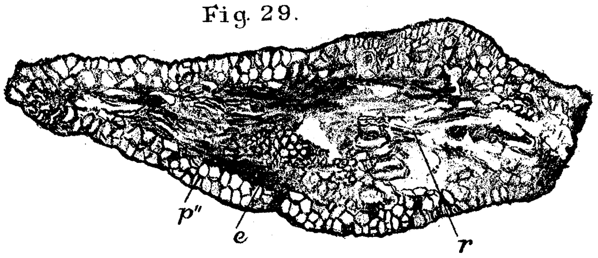

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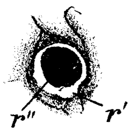

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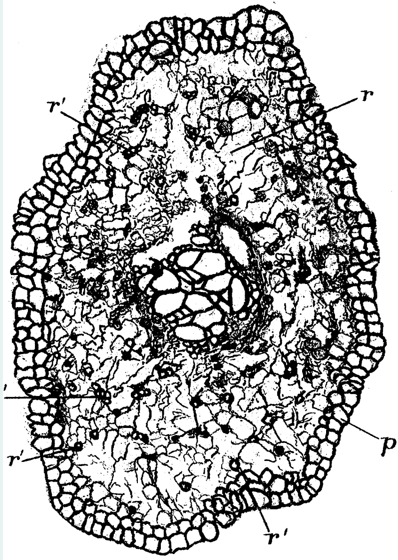
Fig. 22.



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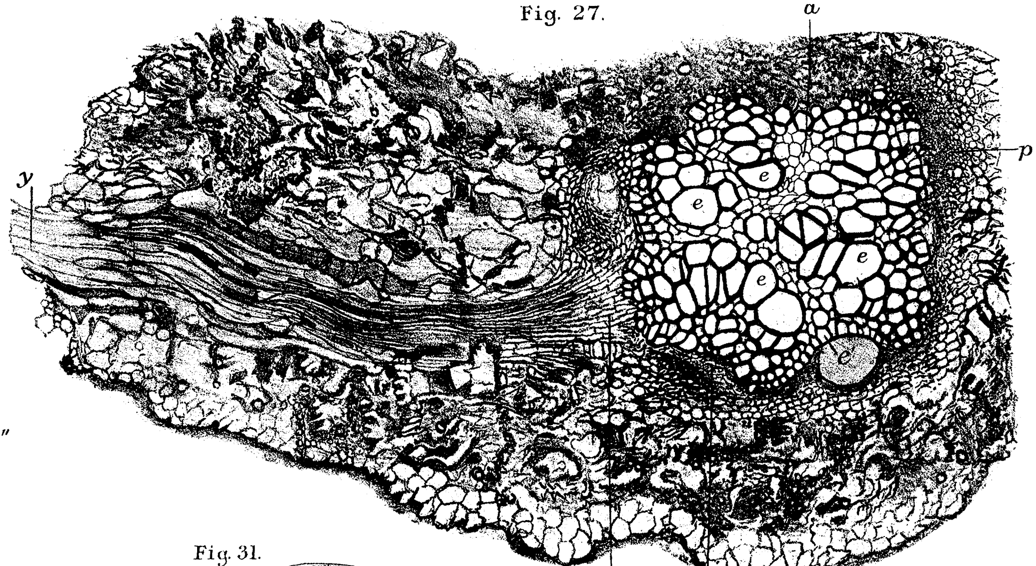

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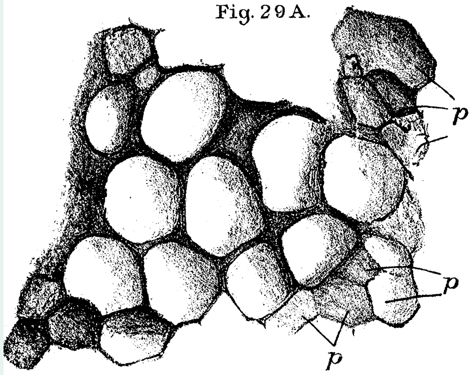

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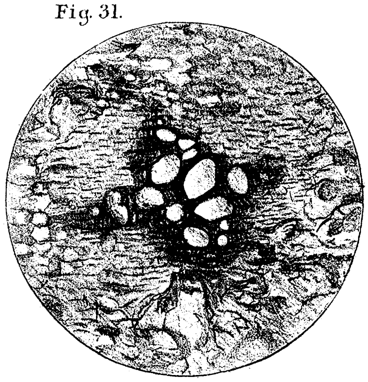

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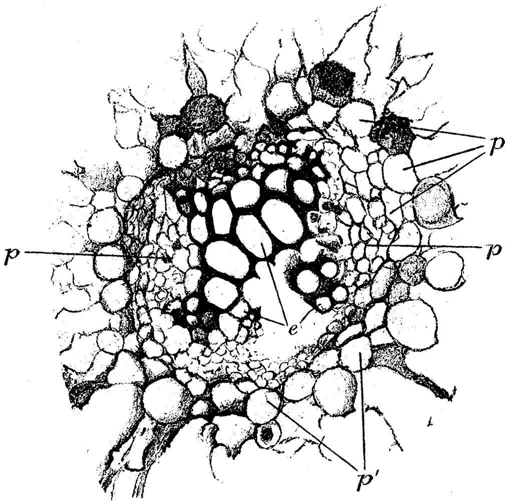

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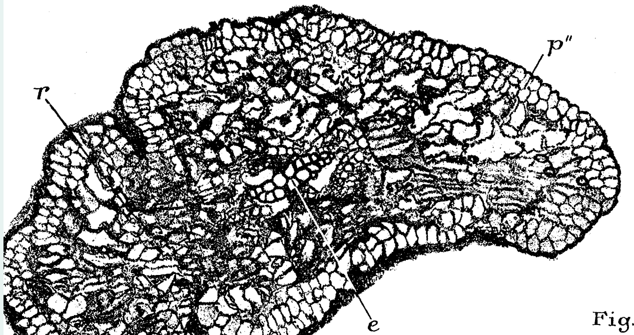

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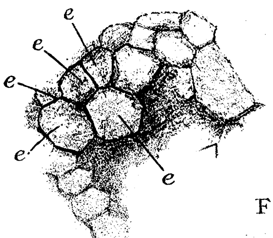

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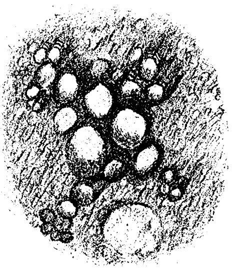

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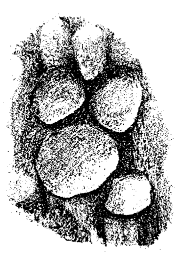
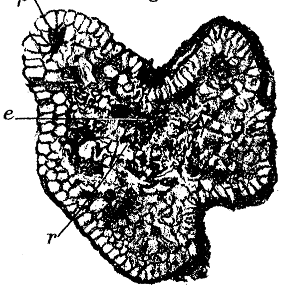


Fig. 33 A.

Fig. 33.



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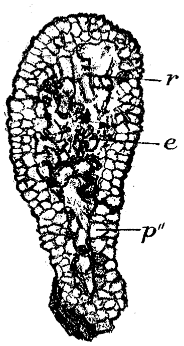

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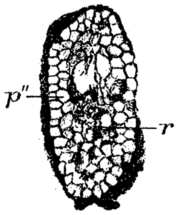

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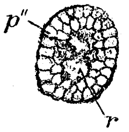

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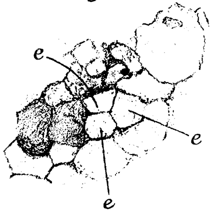

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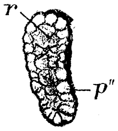

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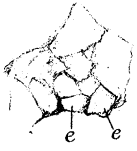

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