XIII. *On the Organization of the Fossil Plants of the Coal-measures.*—Part III. Lycopodiaceæ (*continued*).

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In the last memoir which I laid before the Royal Society I described a number of forms of Lepidodendroid plants from the Coal-measures, without making any material attempt to ascertain the relationship which they bore to each other. I now propose to carry the subject somewhat further, and to show that some of these apparently varied forms of Lycopodiaceæ merely represent identical or closely allied plants in different stages of their growth. The discovery of some remarkable beds in Burntisland, by George Grieve, Esq., and his persistent kindness in supplying me abundantly with the raw material upon which I could work, have enabled me to do this in a manner, at least, satisfactory to myself. Upon the geology of these remarkable beds I will not now enter, beyond saying that they appear to have been patches of peat belonging to the lower Burdiehouse series, which are now imbedded in masses of volcanic amygdaloid. The stratum, where unaltered by contact with the lava, is little more than a mass of vegetable fragments, the minute structure of most of which is exquisitely preserved. The more perfect remains that are capable of being identified belong to but few types. The most abundant of these are the young twigs of a *Lepidodendron*, portions of the stem of a *Diploxylon*, stems of a remarkable Lycopodiaceous plant belonging to my new genus *Dictyoxylon* (but which, for reasons to be stated in a future memoir, I propose to unite with Corda's genus *Heterangium*, under the name of *H. Grievii*), and fragments of *Stigmaria ficoides*. Along with these occur, but more rarely, several other curious Lycopodiaceous and Fern stems, and those of an articulated plant, which I believe to be an *Asterophyllites*; also some true Lepidostrobous fruits and myriads of caudate macrospores belonging to the *Lepidostrobi*.

The first point to be noted is that all the Lepidodendroid branches are young twigs. No one example of a large stem has been found presenting exactly the same structure as these small branches, which, as already stated, are so abundant. On the other hand, all the *Diploxylons* are large branches or matured stems. These facts at once suggested the inquiry whether the two plants referred to might not be complementary to each other. A careful and very extended study of a large number of specimens has convinced me that such is the case. I have made more than a hundred sections of the two forms, and the result has been a remarkably clear testimony that the *Lepidodendra* are the twigs and young branches of the *Diploxylon*-stems. I am also led to the con-

clusion that the *Lepidostrobi*, with their peculiar macrospores and microspores, belong to the same plant. I will examine each of these forms in detail.

Plate XLI. fig. 1 represents a section, rather less than a quarter of an inch in length, of a compressed twig of a *Lepidodendron*. Nearly all the stems found in these beds are thus compressed, the peat and its contents having apparently been heavily weighted by the superimposed volcanic masses. In the case of the larger *Diploxylon*-stem the central woody cylinders have been strong enough to resist the pressure, their thick cortical layers alone having yielded to it. The smaller *Diploxylons* are somewhat more compressed, as is also the case with the Lepidodendroid twigs.

In the section under consideration we have a central vascular cylinder (fig. 1, *c*), in the middle of which is a small vacant space. In other and similar sections this vacant area is occupied by a very delicate form of cellular tissue. The vascular cylinder consists of an aggregation of barred vessels not arranged in radiating lines; it is surrounded by a mass of parenchyma, the innermost portion of which (*g*) is somewhat different from the rest. This parenchyma is continuous with that of the bases of the leaves (*l*), whilst at *l'* we have sections of the free extremities of several of the leaflets. Such are the broad features of the majority of these sections; but a closer study of a large number of specimens reveals differences which it may be well to study in the order of their development.

Plate XLI. fig. 2 represents the extreme tip of a very slender twig, not more than one twelfth of an inch in diameter. In its centre is a small bundle of barred vessels; the rest of the section is composed of cells whose maximum diameter is rarely ·0012, those of the epidermal surface being smaller and more dense than those of the interior of the section. The bases of the leaves (*l*), with the exception of that marked *l'*, exhibit none of the peculiar form which characterizes them when perfect, as seen in fig. 1, *l*. Fig. 3 represents the central vascular bundle of a specimen in all respects similar to fig. 2. It consists of an irregular cylinder of barred vessels of various sizes; but the transverse section of the largest is not more than ·0025 at its greatest diameter, whilst others are even less than ·0005*. In the centre of the bundle is a very small area (*a*) of irregular shape, in which there are no vessels, but which exhibits faint traces of cellular tissue. The entire compressed vascular cylinder has a maximum diameter of about ·015. No traces of vascular bundles appear in the young leaves. The external aspect of these young leaves is represented in Plate XLV. fig. 31. Longitudinal sections of them show that the basal half of each one is turgid and thick, whilst at about half its length it suddenly contracts into a thin and semimembranous form. Advancing from this example we pass through intermediate forms to Plate XLI. fig. 1, where, as we have already seen, the leaves are fully formed, and where there is a slight tendency to differentiation between an inner bark (*g*) and an outer one (*i*). This difference in the transverse sections is scarcely capable of being described, though the eye sees at a glance that the two tissues are not exactly alike. It partly consists in a

* All these dimensions refer, it is scarcely necessary to say, to the standard of an inch.

tendency in the cells of the inner bark to arrange themselves in a line parallel with the larger axis of the section, partly in the more uniform size of the cells, and partly in the less dense character of the tissue. On turning to the central vascular bundle, we find that it has undergone a considerable change. The vessels have become much more numerous, and the transverse sections of the larger ones have a larger axis of ·0033. The vascular and somewhat compressed cylinder itself has a longer diameter of ·022, and an uncompressed circular one belonging to a twig of about the same size as Plate XLI. fig. 1 has a diameter of ·017. Fig. 4 represents a transverse section of one of these larger cylinders, drawn to the same scale as fig. 2.

Vertical sections of specimens in this stage of growth reveal yet more distinctly the changes that have occurred. Plate XLI. fig. 5 represents such a section made across the shorter diameter of an example like fig. 1; figs. 6 & 7 are the radial sections of the bark of two other similar specimens.

Plate XLI. fig. 5 reveals at *a* a slender column of very delicate cells elongated in the vertical direction; these cells are obviously those of a rudimentary medulla. At *d* are the barred vessels of the vascular cylinder; *h*, *h* is a cellular mass considerably disorganized, but of which we shall learn the true structure from other examples; at *i* is a layer of elongated cells with oblique overlapping extremities, a true prosenchyma, the cells of which occasionally become so much elongated as to approach the general condition of bast-tissue*; whilst at *i'* the prosenchymatous cells gradually become broader and shorter, thus passing into a parenchyma (figs. 6 & 7, *k*), which usually forms the exterior of the plant, but which is not well represented in the specimen, fig. 5. I think there can be no doubt that the inner parenchymatous tissue (*h*) represents the *middle* cortical layer of my previous memoir, whilst *i* represents the *outer* bark, and *k* the *epidermal* layer of the same memoir, but which latter may be more accurately termed the *subepidermal* layer. In the present instance *h* appears to be the innermost layer of the bark; but I have previously applied the term *inner* to a very delicate structure, found in some plants (e. g. *Stigmaria*), which I do not detect in the specimens under consideration. The distinctive features of the three layers of bark just described are sufficiently obvious. The cells of the layer *h* are arranged in rather regular vertical columns, each column having a diameter of about ·00022, the entire layer being about ·0025 in thickness. These cells are almost destroyed in fig. 5, but in figs. 6 & 7 their true aspect is well shown. They have square and not overlapping extremities. The longer ones are about ·0008 in length, being about three times longer than broad, but in many of them length and breadth are about equal. The prosenchymatous layer (*i*) is thicker than the more internal parenchymatous one, whilst the largest of its cells are as much as ·0025 in length, mingled, however, with numerous others of much smaller dimensions. The cells of the subepidermal or outer parenchyma (*k*) are of the ordinary character,

* The use of this term is not intended to imply that the part of the bark in which these elongated cells occur is homologous with the liber of Dicotyledonous stems, but that the individual cells are similar to those to which the liber owes some of its chief peculiarities.

exhibiting a tendency to elongation in the surfaces of the leaves (Plate XLI. fig. 5, *l*). I have had the utmost difficulty in determining whether or not vascular bundles were prolonged into the leaves of these young Lepidodendroid branches; I cannot find such in the smaller twigs, but I have detected them in two specimens rather larger than fig. 1; and in some others I trace vacant spaces in the leaves which, I doubt not, were occupied by similar bundles. In one transverse section, like fig. 1, I discover two small bundles at a little distance from the central cylinder.

Various sections in my cabinet exhibit a gradual increase in the size of all the concentric layers of tissue just described. Plate XLI. fig. 8 is a transverse section of one of the larger vascular cylinders, drawn to the same scale as figs. 3 & 4. The cylinder in this instance is nearly uncompressed, and has a diameter of ·0625, whilst the area occupied by the cellular medulla has attained to a diameter of ·03. The barred vessels composing the cylinder have also undergone a corresponding increase in their dimensions, the largest of them having attained to a maximum diameter of ·005. The expansion of the cylinder is but partly due to the increase in the size of the vessels. There has been a simultaneous increase in their number. In the three figures 3, 4, & 8, Plate XLI., every vessel in the respective sections has been copied with geometric accuracy, so that the drawings may be relied upon as correct transcripts of the sections. We find that in fig. 4 there are about eighty vessels in the entire cylinder; in fig. 8 there are more than four times that number. It will also be observed that a large number of very small vessels is developed at the periphery of the cylinder, these being apparently the newest growths of the series.

Plate XLV. figs. 31 & 32 represent the external aspect of the leaves at this stage of the plant's growth. They are ovato-lanceolate, and very closely imbricated. The central longitudinal keel is more or less prominent, as is also shown to be the case in their transverse sections. I have found a few fragments in which this dorsal ridge is impressed with several transverse indentations, as represented in fig. 32: whether this condition represents a distinct species or a mere variety I am unable to say; at all events it is not the common form of these leaves. In their general habit these twigs closely resembled the *Lycopodium Saururus* figured by Brongniart*. Small as these leaves are in this young state, they gradually develop into thick scale-like structures, which ultimately attain to considerable dimensions.

The next step takes us to Plate XLII. fig. 9, where we find the plant assuming the form of the young branch of a *Diploxylon*. The specimen represented is much compressed, so that the cellular medulla is obliterated, or nearly so. The two inner sides of the vascular medullary cylinder (*c*) are thus forced into close contact. The thickness of this cylinder, from its inner to its outer surface, has been about ·044, that of Plate XLI. fig. 8 having been about ·014; hence we see that this portion of the plant has here undergone a yet further increase in the number of its component vessels. But a new element now makes its appearance for the first time. The vascular medullary cylinder

* Végétaux Fossiles, tome ii. pl. i. fig. 1.

is closely invested by a second ring of barred vessels (*d*), arranged in radiating lines, and the products of an exogenous process of growth. The thickness of this exogenous vascular zone, in the specimen under consideration, is about the same as that of the medullary one which it incloses. Each radiating line commences, at its inner extremity, at one of the very small vessels corresponding with those at the periphery of Plate XLI. fig. 8. From this starting-point new vessels have been added to the peripheral end of the line, as occurs in the case of the wood-cells of coniferous plants; but here each succeeding vessel has been somewhat larger than the one preceding it, so that many of the outermost ones of this cylinder have a mean diameter of ·005. Each of the radiating rows consists of from thirteen to seventeen vessels. On making vertical sections of this specimen new elements revealed themselves. Plate XLII. fig. 10 represents a small portion of a radial section crossing the two cylinders. To distinguish these latter from each other I will now employ terms used in my previous memoir, designating the inner one the *medullary* cylinder and the outermost the *ligneous* zone. In fig. 10 part of the former is represented by *c* and the latter by *d*. The drawing shows the gradual increase of size in the vessels of the ligneous zone as we proceed from within outwards. At *d'* we find the very small vessels from amongst which the radiating exogenous series originates; and we now find that large and well-defined bundles of vessels (*m*) spring from the same series, but which curve rapidly outwards so as to proceed horizontally, and at right angles to their original course, to the periphery of the ligneous zone. These vessels are very small, not averaging more than ·0006 in diameter; but as considerable numbers of them are aggregated to form each bundle, the latter attains to conspicuous dimensions. That they are identical in character with those already noticed as observed in the young leaflets I have no doubt; but it is also obvious that the bundles have now become very much enlarged, though no corresponding enlargement has taken place in the individual vessels. This increase in the size of the bundles is explained by the fact, that whilst in the specimen represented in Plate XLI. fig. 1 the largest leaflets are not more than ·055 in diameter, in that under consideration (Plate XLII. fig. 9) they have expanded to more than double that size, or ·12. Medullary rays also now make their appearance in the ligneous zone; but as I propose to describe these more fully when speaking of the matured stem, I will not dwell upon them now. The greater part of the bark has disappeared from this specimen; all the inner parenchymatous layer is gone, and most of the prosenchymatous one. All that remains consists of the parenchymatous subepiderm with its leaf-petioles (Plate XLII. fig. 9, *l*), and with a small portion of the prosenchyma of the outer layer, *i*, attached to its inner surface. In the transverse section the cells of the latter have now begun to assume the radiating linear position which I described in my last memoir as so commonly characterizing this tissue amongst the Lepidodendroid plants.

The specimen last described has obviously been a stem or branch, with a diameter of about 1½ inch; but other examples in my cabinet lead us up from this one to stems of much larger size.

Plate XLII. fig. 11 is a transverse section of a woody cylinder of a large stem. Calculating roughly the proportions which the vascular axis of fig. 9 has borne to the entire stem, I conclude that fig. 11 represents the vascular axis of a stem of about 14 inches in diameter; its central medulla has a mean diameter of about half an inch, whilst that of the entire vascular area is nearly an inch and a half. The medulla (*a*) is present, though considerably disturbed; but sufficient remains in a normal position to show that its cells were arranged in vertical columns, a disposition which is well illustrated by another specimen in my cabinet to which I shall call attention. I pointed out in my last memoir that this disposition to a columnar arrangement of the medullary cells is a common feature amongst the Lepidodendroid plants. The medullary cylinder (*c*) is very narrow in proportion to the diameter of the stem, not averaging more than ·055. The *thickness* of the ligneous zone (*d*), on the other hand, is fully half an inch. On one side the medullary cylinder has been detached from the ligneous zone and forced inwards into the pith by some force that must have acted through one of the two extremities of the specimen, since the ligneous zone is but slightly disturbed at its inner surface, and not in the least so externally. In this specimen the large vessels of the medullary cylinder have a mean diameter of ·0075, a large increase upon the ·0025, which was the maximum diameter in the young twig, Plate XLI. fig. 2. The great thickness of the ligneous zone is due to an enormous increase in the number of vessels in each radiating line, they having increased from the 13 to 17 of Plate XLII. fig. 9 to from 84 to 100. There is not a corresponding increase in the diameter of these vessels; the more peripheral ones are actually smaller than those in the central parts of the woody zone. This may readily be accounted for. The latter have now attained to their maximum development, whilst the former, being younger, have not done so.

Plate XLII. fig. 12 represents a tangential section of a portion of this ligneous zone, magnified 10 diameters. We here see the vascular bundles (*m*) passing outwards to the leaves, arranged in regular quincuncial order. Fig. 13 exhibits a portion of fig. 12, enlarged 40 diameters: we here find that numerous medullary rays (*f*) pass outwards between the barred vessels (*e*); these rays sometimes have but from one to four or five cells in each vertical pile, but in other instances their vertical extension is considerable. The cells of the rays have disappeared, but the spaces they occupied are well marked by the deep indentations which their pressure has made upon the walls of the contiguous barred vessels. In radial sections of the stem these rays are seen proceeding towards the periphery horizontally (fig. 10, *f*), and as straight as if they had been drawn with the aid of a parallel ruler. Enough of their form can be ascertained to demonstrate that they consisted of the mural form of parenchyma. In the centre of fig. 13 we have one of the foliar vascular bundles (*m*) passing outwards through a lenticular space corresponding in all respects, save size, with a medullary ray. Like these latter appendages, the space not occupied by the vascular bundle was occupied by cells identical with those of the medullary rays; and in many instances these lenticular spaces pass into and are continuous with true medullary rays. We

shall afterwards see, from the way in which these spaces are formed, that they do not differ in any essential respect, except in their size and in the number of their cells, from such true medullary rays. The vascular bundles (*m*) are of course divided transversely in these tangential sections, in which they exhibit a diameter of from ·005 to ·0075. Each bundle consists of a large number (rarely less than 100) of minute barred vessels, varying from ·0005 to ·0008. The origin of these bundles amongst the minute vessels which abound at the point of junction of the medullary cylinder and the ligneous zone has already been shown. In the *Diploxylon* originally described by CORDA (Flora der Vorwelt, tab. x. fig. 3, and tab. ii. fig. 1) these bundles are represented as ascending obliquely upwards and outwards; but in the plant before us such is not the case; they wend their way outwards through the ligneous zone, as do also the medullary rays, in a perfectly horizontal plane. The second of CORDA'S figures also represents them as originating *abruptly* at the external surface of the medullary cylinder. Their real origin has been already shown in Plate XLII. fig. 10. CORDA further describes his plant as having no medullary rays. This, as I have pointed out in my previous memoir, is also an error, and has arisen from the circumstances there indicated, viz. that in some species of *Diploxylon* the CELLS of the medullary rays are barred, which caused CORDA to mistake them for true vessels.

In other specimens of *Diploxylon* which I possess I find some variations from that just described, as well as some points which are more fully elucidated by them. In several examples the medullary cylinder is very much thicker than in others, in proportion to the diameter of the medulla. In some its thickness is as much as ·12. One remarkably fine example exhibits the true structure of the medulla; a vertical section of the medulla and medullary cylinder of this specimen is given in Plate XLII. fig. 14. The space between the letters *a a* is occupied by the cells of the medulla, which are arranged in vertical columns with a considerable approach to regularity, when undisturbed by pressure or mineralization. These columns have a mean diameter of ·005 to ·0075. Generally the cells are nearly cubical, allowance being made for the frequent obliquity of the transverse septa, one of which sometimes inclines upwards and the other downwards at the two extremities of the same cell. Fig. 15 represents a small portion from a transverse section of the same specimen, illustrating the relations of the ends of these columns of cells to the intersected vessels of the medullary cylinder. It will be seen that the cells (*b*) can only be distinguished by their colour and their thinner walls from the vessels (*e*). The colour is due to the circumstance that one or both of the transverse cell-walls of each cell appear in the plane of the section, their carbonaceous substance giving a brown colour to the section where they exist. On the other hand, the vessels being long tubes filled with translucent carbonate of lime, transverse sections of them exhibit no such colour. The walls of the vessels also are more sharply defined and thicker, owing to the deposit of lignine forming the transverse bars in their interior; but in every other respect of size and shape the two exhibit no material differences. It is difficult to believe that the very peculiar arrangement of the cells in vertical

piles of uniform width is not a result of the same polarizing tendencies in the primitive tissues as those which led the cells of the latter to arrange themselves in a similar manner to form the barred vessels. In the latter the conversion into vessels has been completed. In the former the cells remained unconverted; but they have not only retained the primary disposition to assume the columnar form, but the same tendency reappears in all the new cells subsequently formed in the enlarging pith.

Whilst the large specimens last described are almost invariably accompanied by some portion of their bark, which surrounds them as a flattened cylinder, I have in no one such instance obtained so perfect examples of this bark as in the specimen represented by Plate XLI. fig. 1; the tissue is usually limited to its outermost part, viz. to the sub-epidermal parenchyma and a small portion of the subjacent prosenchyma. The example Plate XLII. fig. 11 was so surrounded, a small portion of the bark being seen at *i*. Fig. 15[a] represents a vertical section of a fragment of bark from the same specimen; to the left of the figure we have the two tissues (*i* and *k*) just referred to, whilst at *l* are the persistent bases of the petioles, which remain *in situ* in this plant, as in CORDA'S genus *Lomatophloios*. In this figure, which represents the object of its natural size, the leaf-petioles are small, though larger than in the bark of fig. 9; but I have specimens in which they are fully three times the size shown in fig. 11. Thus it will be seen that I have these leaves in every gradation of size, from the imperfectly formed one of Plate XLI. fig. 2, to large ones which, though their extremities have been broken off, have their basal petioles five eighths of an inch in length. But though large stems rarely have the bark *in situ* and in perfect condition, Mr. GRIEVE has sent me several large masses of it, so that it does not appear to be a scarce object. But it usually occurs in a remarkable state, being deeply fissured longitudinally, and partially broken up into long wedge-shaped masses, linked together at their broad bases—a probable result of desiccation.

In the transverse section, that which appears to be identical with the inner parenchymatous bark (*h*) of the young twigs merely appears as an ordinary form of parenchyma; its usual aspect in radial sections is shown in Plate XLIII. fig. 16; it consists of innumerable square cells, slightly elongated vertically, and exhibiting some disposition towards an arrangement in perpendicular lines, reminding us of what is seen in Plate XLI. figs. 6 & 7, *h*. The prosenchymatous layer is easily identified with the layer *i* in the two figures just referred to. It is very thick, and the cells vary in form, being sometimes much larger, as well as more fusiform, than at others; whilst towards the exterior of the layer radial sections exhibit in a very marked manner the arrangement of prismatic cells seen in Plate XLIII. fig. 17. These cells are elongated vertically in a very regular manner, having a uniform diameter from end to end of about ·0025. Their length varies greatly: sometimes, though not often, they are almost square; at others they are so much elongated, especially at the outer portion of the layer, that they almost assume the form of vessels; but what gives them their remarkable appearance is the fact that clusters of them have exactly the same length, and are arranged in the same radial plane, causing

numerous straight lines of transverse cell-walls to traverse the section horizontally from within outwards, as shown in Plate XLIII. fig. 17, *i*. There is no doubt that the walls of the more tubular of these elongated cells are thickened by internal depositions of lignine, and that they thus assume the character of bast-tissues. I have already described thin-walled cells arranged in regular rows which, in outward form, closely resemble those of Plate XLIII. fig. 17, but occurring in the primary and secondary medullary rays of Calamites. The tissue is a very peculiar one. I have not succeeded in discovering any structure absolutely identical with it elsewhere than amongst these Carboniferous plants. I have already referred, both in my preceding memoir (Part II.) and in the present one, to the fact that transverse sections of this prosenchymatous layer of the bark exhibit the cells arranged in regular radiating lines proceeding from within outward, as in the wood of the Coniferæ. On seeing such sections, it is difficult to resist the impression that we are looking at true vascular tissues.

The subepidermal layer differs in no material respect from that of the young twigs, being composed of ordinary parenchyma. The same remark applies to the structure of the persistent petioles, except that in transverse sections of the latter we find the position of the central vascular bundle very distinctly marked, as in the scars of the ordinary *Lepidodendra*. It will be remembered that this was not the case with the leaflets of the smallest twigs. Plate XLIII. fig. 18 represents part of a tangential section of a cluster of these petioles made close to the subepidermal layer of bark. In their disposition and general aspect they remind us vividly of a similar section of Corda's *Lomatophloios crassicaule*, figured by him in his 'Flora der Vorwelt'*.

Having thus completed our review of the ordinary structure of these stems, I would next direct attention to some peculiarities connected with their growth.

In preparing my sections, on one or two occasions I met with small, detached, medullary cylinders corresponding in all respects with those of the young twigs, only instead of being perfect rings of vessels, they were interrupted on one side, giving the transverse section of each the form of a horseshoe. I was long before I succeeded in discovering what this meant. It was obviously a medullary cylinder, and I at length obtained specimens which explained its nature. When one of the stems is about to dichotomize, the central vascular cylinder first becomes elongated laterally in the plane of the approaching bifurcation; it then splits into two halves, each of which is, of course, open at its inner side. Plate XLIII. fig. 19 represents the centre of one of these specimens, belonging to a twig of about the same size as Plate XLI. fig. 1. What takes place subsequently is uncertain; but there is reason to believe that the opening thus made into the interior of the medullary cylinder, bringing the medullary and cortical tissues into direct contact, never closes through any growth of new *medullary* vessels. I am confirmed in this opinion by the fine section shown in Plate XLIII. fig. 20, which reveals similar conditions, only in this example the plant has attained to the *Diploxylon* stage of growth, having developed an ample exogenous cylinder externally to the medul-

* Taf. 1. fig. 1.

lary one. In the minute details of its structure this plant differs in no respect from those already described. But we here see that whilst nature has made no attempt to reclose the vascular cylinder (*c*) and again separate the pith (*a*) from the bark by means of the medullary vessels, she has endeavoured to accomplish the same process, though not yet effectually, through the instrumentality of the exogenous ligneous zone (*d*). In each of the divisions this exogenous zone overlaps the two free central margins of the medullary one, thus gradually filling up the gap between them. I doubt not that eventually such a closure of the vascular ring and isolation of the medullary area would become complete. I presume, from the comparative rarity of specimens with these open vascular cylinders, that after a growing branch had bifurcated, the buds of the two growing twigs have developed their medullary cylinders in the usual way, and that the imperfection of the cylindrical ring is confined to the neighbourhood of point of dichotomization. I have not met with an open ring in a single branch, save when it had obviously been ruptured by violence. The specimen (Plate XLIII. fig. 20) is enclosed within the usual cylinder of bark (*i*).

The last subject brings us to another one on which my views have been criticised by some botanists for whose attainments I have the greatest respect, but who have not had the advantage of being able to study the large series of specimens which my cabinet contains. In both my previous memoirs I expressed my conviction that both in Calamites and in the Lepidodendroid plants the peculiarities of their structure could only be explained by the recognition of an exogenous mode of growth by which these peculiar features had been produced*. My more recent researches have still further strengthened these convictions; so much so, indeed, as not to leave a shadow of a doubt on my own mind as to the correctness of my conclusions on this subject. The specimens represented in Plate XLIII. fig. 20 and Plate XLII. fig. 11, especially the former of the two, afford striking illustrations of this process of growth. The cylinder in the upper half of the former figure exhibits no unusual peculiarity; but the lower one is surrounded by a remarkable zone of half-developed vessels (*d'*), which is evidently of newer formation than the rest of the ligneous zone, and which I can only explain by the assumption that it is the product of some equivalent of a cambium-layer. Plate XLIII. fig. 21 represents a portion of the exterior of the ligneous zone (*d*), with its radiating lines of vessels (*e*) separated by medullary rays (*f*). Externally to these tissues, we have at *e'* a new zone

* My views upon this question having excited so strong an opposition in some quarters, I invited Professor Dickson, of Glasgow, to visit me for the purpose of examining my specimens and giving me his opinion of them. He kindly authorizes me to publish the following significant extract from a letter just received from him, dated March 17, 1872:—"Having examined your sections of stems of *Diploxylon* showing the outermost woody tubes to be of distinctly smaller calibre than the more internal ones, as well as sections of a series of stems of the same, from small to large, affording constructive evidence of a progressive increase of the wedge-like woody plates, I have no hesitation in expressing my belief in a truly exogenous growth in this plant; and I consider that you are quite justified in applying the terms 'medulla,' 'woody zone,' 'medullary rays,' and 'bark' to its parts, as corresponding more or less perfectly to analogous parts in the Dicotyledonous stem."—March 19, 1872.

in process of development; it consists of numerous masses of small vessels arranged, in the transverse section, in a radiating direction, but of which the lines have not yet assumed the orderly disposition that characterizes them when fully developed. Between these vascular laminæ are cellular masses (f'), the positions and structure of which obviously show that they are destined to become prolongations of the medullary rays (f). Plate XLIII. fig. 22 represents part of a tangential section of the new tissue (fig. 21, e', f'), which is very instructive. The right-hand portion of the section dips more deeply into the specimen than that to the left; the latter consequently exhibits the more peripheral aspect of the structure. In the former the vessels are becoming closely arranged, and the medullary rays (f'), though still much more enlarged and containing more cells than characterize the matured rays of the woody zone, are comparatively circumscribed; but in the more peripheral part the vessels (e'') are more widely separated, meandering through large cellular masses (f''), which are scarcely, if at all, distinguishable from the contiguous parenchymatous bark-cells. These young vessels have a diameter of from ·0025 to ·0012, whilst the transverse bars on their walls are from ·0003 to ·0002 apart. In the matured vessels we have a diameter of from ·005 to ·0024, whilst the bars are from ·0008 to ·00035 apart. The comparison of these figures demonstrates that the young vessels under consideration are but half-developed in either direction; both in their diameter and in the longitudinal separation of their bars of lignine they must have attained to double their present dimensions before they corresponded with those of the matured ligneous cylinder which they invest. At this early stage of their growth the walls of these vessels exhibit a crenulated outline, the indentations being caused by the pressure of the contiguous cells upon the half-plastic tissues. This feature disappears as the vessels swell to their full dimensions and are brought into mutual contact by the absorption of the cells which temporarily separate them; but it is permanently maintained where the vessels are in contact with the medullary rays. I have not been able to identify any of the cellular structures that surround them with true cambium-cells: though exceedingly delicate they have the aspect of *formed* tissues; but there is not the slightest room for doubting that both cells and vessels are younger than those of the ligneous zone which they enclose, or that they are the products of an exogenous growth in which the *Xylem* of the German botanists is represented, whilst the *Phlöem* is absent*.

I have called attention to the break in the continuity of the medullary cylinders of Plate XLIII. fig. 20, through which a direct communication is established between the cells of the medulla and those of the bark. The equivalent of the cambium has bent round the two inner horns of the crescent-shaped medullary cylinder and formed the

* I may observe here that since my last memoir was written I have obtained specimens of *Stigmaria* which exhibit conditions very similar to those of the example of *Diploxylon* just described, but in which the growth of the new vessels is rather more advanced. I have noticed that in *Stigmaria* the additional growths are rarely made in complete circles, but rather in layers having crescentic transverse sections; I have found the same conditions in some other plants from the Coal-measures yet to be described.

new vessels in the open space between them, thus obviously being instrumental in repairing the breach in the continuity of the cylinder and closing it up by a succession of exogenous additions. It has not completely effected this object in the specimen under consideration, but apparently would have done so in the course of time had the plant survived sufficiently long for the purpose. Another remarkable circumstance appears in the fact that the two ligneous axes, though growing within the same stem, are not growing in equal ratios. Thus that to the lower part of Plate XLIII. fig. 20 is invested by the new layer just described, showing that in it an additional growth was progressing through the agency of some representative of a cambium-layer; but in the twin axis above no such addition is in progress. I presume we can only infer from this fact that at the particular moment when the living plant was destroyed the former branch was pushing forward in a more active manner than the latter one—a condition common enough amongst recent plants, in which one Lycopodiaceous shoot takes the lead, whilst others are comparatively quiescent.

At the outset of my study of the Burntisland beds my attention was arrested by the prevalence, *in every fragment* of the stratum, of broken-up cellular sporangia, indicating the former existence of very numerous spore-bearing fruits; I also met with immense numbers of the remarkable bodies represented in Plate XLIV. fig. 27, and which appeared to me to be caudate macropores. The abundance of these two objects led me, on visting Burntisland, under the guidance of Mr. GRIEVE, to make special search for *Lepidostrobi*, which we soon succeeded in discovering, and at a more recent period Mr. GRIEVE has forwarded me additional specimens. They are all of one species, which fact is important, since it leaves little, if any, room for doubting that they belong to the same Lepidodendroid plant as that whose stems and branches constitute the great mass of the deposit.

The general aspect of longitudinal sections of these strobili is that common to *Lepidostrobi*. They usually have a diameter of from less than half an inch to nearly an inch; each sporangium extends from the central axis to the periphery, exhibiting in the longitudinal sections the form, so prevalent amongst these fruits, of an oblong parallelogram. In one of these sections now before me I count sixteen vertically disposed sporangia in an inch of the length of the *Lepidostrobus*. These dimensions approximate closely to those of the beautiful cone from Burdiehouse figured by Mr. BINNEY*. Plate XLIV. fig. 23 represents a transverse section of one of these cones. The central axis (*s*) in this specimen is imperfect, its central vascular bundles having partly disappeared; but there remains a thick and well-defined cortical layer composed of elongated forms of parenchyma approaching the prosenchymatous type, and identical with what we find in the external portions of some of the Lepidodendroid leaves. From this central axis are given off thick and robust cylindrical scales or bracts (*t*), consisting of a similar tissue to that of the cortex; they spring from the central axis in the usual spiral order common amongst the

* "Observations on the Structure of Fossil Plants found in the Carboniferous Strata.—Part 2. *Lepidostrobus* and some allied Cones," by E. W. BINNEY, F.R.S., F.G.S. (Palæontographical Society, 1871), pl. x. fig. 26.

Lycopodiaceæ, having a thickness at their respective bases of about ·022; but they soon subdivide into smaller branches, which generally proceed to different sporangia. Though the latter are very much more numerous than the primary bracts, each sporangium rests upon its own special branch of a bract. The sporangia (*u*) exhibit in this section a wedge shape. The small peripheral sporangia (*u'*) seen in the figure are merely the tips of the next contiguous ones rising up from below, in consequence of their slightly oblique and ascending plane not corresponding with the horizontal one of the section. Plate XLIV. fig. 24 is a tangential section of another specimen, which exhibits the oblique spiral arrangement of the sporangia characterizing the taxis of these fruits. At *t* we have the free extremities of the subdivided bracts. Fig. 25 represents a small portion of fig. 24 more highly magnified, and exhibits with remarkable clearness the shape of the subdivided bracts, and the way in which the latter are attached to their respective sporangia. The perfect sporangium (*u*) occupying the centre of this figure may be accepted as a type of the structure of these organs and of their relations to the bracts. Each sporangium is enclosed in a cellular sporangium-wall (*v*), which, when viewed superficially, appears composed of ordinary parenchyma, but when seen in section exhibits these cells elongated vertically, the structure closely resembling a corresponding section of a piece of honeycomb. Sometimes one cell extends from surface to surface, at others two cells of equal diameters are piled linearly upon each other. The average thickness of these sporangium-walls is ·0075. The shape of the transverse sections of the secondary bracts is shown in the three dark-coloured objects (fig. 25, *t*), especially in that supporting the central sporangium. The upper surface is rounded and prominent, fitting into a corresponding depression in the under surface of the sporangium. On each side of this the bract spreads out into a thin horizontal expansion, concave superiorly; at its inferior surface a deep thin keel runs along the entire length of the bract and dips down between the two contiguous sporangia of the series immediately below, as if designed to steady the several segments of the strobilus. From the interior of the raised dorsal surface a similar but smaller and thinner vertical lamina rises, the upper part of which ascends into the sporangium and is imbedded amongst the spores; its uppermost margin is bifid, the two diverging parts being recurved in opposite directions outwards and downwards. This ascending portion, obviously the true sporangiophore, is of so delicate a texture, especially at its upper part, that it can only be distinguished from the surrounding spores by its denser aspect. The delicate lines *t'* in fig. 23, which appear as continuations of the large bracts, are longitudinal prolongations of the same sporangiophores, which appear to be coextensive with the entire length of the sporangium. The sporangium-wall is inserted into the bract close to the base and at each side of the sporangiophore. It first arches upwards as it approaches the latter organ, and then, suddenly descending, it plunges vertically into the bract, with the parenchyma of which its own cells become intermingled. It thus appears that each sporangium is not only sustained by its own bract, but is united to that bract throughout its entire length in the firmest manner. I have not been able to ascertain the actual forms of the peripheral extremities

of the bracts. In every instance they have been too much disorganized to display their true contours; but both figures 23 & 24, Plate XLIV., show that they are prolonged so as to form a thin investment to the exterior of the strobilus.

The sporangia of the upper part of this fruit are densely filled with innumerable microspores, whose mean diameter is about ·0007. Sometimes they are tetrapartite (Plate XLV. fig. 26, *w*), and at others tripartite (fig. 26, *w'*). In the lower part of the strobilus the sporangia are occupied by the remarkable macrospores represented in Plate XLIV. fig. 27, *x**. These vary considerably in their form, owing to pressure or shrivelling; but they appear to have been more or less spherical. The one figured, the length of which exceeds its breadth, has a longer diameter of about ·027; and from this to ·05 appears to have been nearly the average size of these objects. The characteristic peculiarity of these macrospores is the projection from every part of their external surfaces of numerous caudate appendages, and which appear to be actual prolongations of the investing layer of the spore. These appendages vary in length from ·003 to ·0055, whilst their diameter is about ·0006. They are rather thicker at their bases than nearer their extremities; but the extreme tip of each one is slightly capitate. They have evidently been very flexible, since they are twisted into varied positions. I detect in them nothing resembling elaters, their texture, like that of the external spore-wall, being perfectly homogeneous. When the strobilus is viewed either by transmitted or by reflected light, all the spores, whether large or small, appear of a rich brown colour, a condition which has been noticed by Mr. Binney and Professor Morris as characterizing certain spores which have come under their observation†. I have not succeeded in discovering any structure in the interior of these objects. I have only obtained these macrospores in actual connexion with two strobili. In one they occupy the lower part of the fruit as already described, four sporangia of which fruit are represented in Plate XLIV. fig. 28. It will be seen from the latter figure that most of these spores (*x*) are torn and distorted. In another fruit the numerous shrivelled sporangia remain; but they have all shed their macrospores, with the exception of three, the spores of which closely resemble those shown in fig. 28. In all these examples the rich brown colour resides in the spore-wall, and not in its contents, whatever those may have been.

That we have in this fruit a new example of that remarkable class of fossil strobili to which attention was first called by Robert Brown and Professor Brongniart is obvious; and I think the reasons I have already given justify me in connecting it with the stems and branches with which I find it associated. No plant of the Lepidodendroid family occurs in the deposit other than those which I have described, save one or two small fragments of a Lepidodendroid bark of the ordinary type, and which very possibly belong to the lowermost parts of the stems now described. In many recent Cycads we find that, immediately below the cluster of perfect leaves, we have a considerable part of the stem

* In this figure the macrospore (*x*) and the microspores (*w*) are drawn to the same scale, showing their relative sizes.

† Binney's "Observations on the Structure of Fossil Plants, &c.," part ii. pp. 44 & 45.

retaining the bases of the petioles after the fronds have fallen; whilst yet lower down on the stem these petioles have disappeared, revealing characteristic lozenge-shaped scars, rendered visible less by the disarticulation of the petioles than by a process of weathering which has disintegrated them down to the level of the cortical layer. It appears to me exceedingly possible that similar phenomena may have occurred in the case of the plants under consideration. In the few fragments of true Lepidodendroid scars which I have met with these scars are long and narrow, corresponding very closely with what I observe on some of the smaller twigs described, from which the leaves have become accidentally detached. These circumstances combine to remove all doubt as to the relationship subsisting between the stems and branches described in the earlier part of this memoir and the strobilus last considered: either as fragments of sporangia and detached spores on the one hand, or as leaves and portions of stems and branches on the other, the two classes of vegetative and reproductive organs are represented in every square inch of the rock I have examined; and as every strobilus which I have obtained is of one species, and that one identical with the innumerable distinctive macrospores referred to, it appears to me that we have every proof of their identity that palæontology can furnish, unless we could discover the tree in its integrity, which is impossible.

I have stated that the central axes of these strobili are commonly imperfect. In one of them we have the usual central bundle of barred vessels partly preserved; but I have obtained one larger specimen, represented in Plate XLIV. figs. 29 & 30, which I think may possibly belong to the same fruit. If so, it has been part of the base of the axis of a somewhat larger strobilus than those described. Fig. 29 represents a transverse section of it, in which is seen a central star-shaped cluster of barred vessels (*s*), surrounded by a vacant space from which delicate cellular tissue, corresponding with the inner or middle bark of the Lepidodendroid twigs, has doubtless disappeared. External to this is a thick cortical layer of parenchymatous and prosenchymatous tissue, the peripheral portion of which has broken up into thick divergent bracts, each of which has again divided into secondary ones, as described in the preceding pages. This divergence is demonstrated by the subdivisions of the vascular bundles seen at *t'*, *t'*. On turning to the longitudinal section (fig. 30) we see that the vascular bundles of the bracts have, as was to be expected, sprung from the central axis (*s*) at *s'*, and after traversing the clear area (*g*) have proceeded upwards and outwards through the thick cortex, as shown by the numerous vacant spaces (*m*) from which the vessels have disappeared. Peripherally the bark breaks up into main or primary bracts, which again subdivide, as in the transverse section, into secondary ones, demonstrating that each primary bract does not merely dichotomize but subdivides, both horizontally and vertically, into a cluster of bracts—a condition corresponding with what I have already observed in the smaller strobili described. The external surface of the central vascular axis (*s*) has evidently been deeply sulcated longitudinally, the vascular bundles having sprung from the intermediate ridges. In the transverse section the vessels of the outermost portions of these ridges exhibit a radiating arrangement, as if the axis had made a

slight effort to strengthen its buttresses by exogenous additions to their exteriors. In tangential sections of the cortical layer the vascular bundles exhibit the regular arrangement characterizing the taxis of all Lepidodendroid stems.

Before attempting to draw any general conclusions from the preceding facts, I would call attention to two interesting modifications of the same Lepidodendroid type that have recently come under my notice. One of these, represented in Plate XLV. figs. 33 & 34, I found in one of the Oldham nodules; the other is in the cabinet of Mr. NIELD, of Oldham.

Plate XLV. fig. 33 represents a transverse section of the first of these plants; it is a young Lepidodendroid shoot a little more advanced in growth than Plate XLI. fig. 1; in other respects the general appearances of the two closely correspond. The chief difference lies in the centre of the medullary axis, which in Plate XLV. fig. 33 is very large and well defined. On turning to the longitudinal section of the medullary cylinder (fig. 34) we see that this medulla (*a*) is a cellular structure; but instead of the cells being nearly cubical, they are elongated vertically and almost fusiform; still they retain much of the disposition to arrange themselves in vertical columns that is so common a feature of the Lepidodendroid plants. Mr. NIELD'S plant, represented in fig. 35, is a very different one; its central axis is of the usual type, consisting of a medullary vascular cylinder (*c*) enclosing a cellular medulla; but whilst the latter is very small, approximating to the condition of Plate XLI. fig. 4, the former is comparatively large, being composed of very numerous vessels of nearly uniform size. The most remarkable feature of the plant is seen in the large size of the bases of the leaves (*l*), which must have approximated in form to thick scales. They are composed of the usual slightly elongated parenchyma. Unfortunately the importance of this remarkable specimen was not appreciated when it was found, and I have seen no vertical section that was made from it; hence I am ignorant of the shape which the leaves assumed in a vertical direction. The maximum diameter of the transverse section is nearly three quarters of an inch*.

* It appears that Mr. BUTTERWORTH prepared other sections of the above specimen, which he recently sold, through Mr. CARRUTHERS, to the Trustees of the British Museum. Mr. CARRUTHERS has described these specimens in a paper which he read before the Royal Microscopic Society since the above descriptions were penned. In this paper he describes the vascular medullary cylinder, but does not refer to the vacant space in the centre of his own figure, which I believe was originally occupied by medullary cellular tissue. I think that the section which I have represented in Plate XLV. fig. 35 displays indications of this cellular medulla. Speaking of the *vascular* cylinder, Mr. CARRUTHERS says, "Professor WILLIAMSON, in his recent investigations into the organization of *Lepidodendron*, proposes to call this axis a medulla." This is certainly not an exact representation of the idea put forth in my last paper; I spoke of the vessels in the centre of *Lepidodendron selaginoides, where they are intermingled with cellular tissue*, as belonging to a *medullary axis* in contradistinction to the exogenous ring which enclosed them, and I then proceeded to show how, in other species, these vessels receded from the centre to the periphery of that medullary axis, where they formed in every Lepidodendroid plant, except *L. selaginoides*, a distinct cylinder, and which I described not *as a medulla*, but as being homologous with *the medullary sheath* of the higher Exogens, which is a very different thing. The true medulla is the cellular element. All my subsequent researches have tended to confirm these views. I never doubted for a moment that these axial vessels represented the vascular bundles of living Lycopods.

If I have correctly interpreted the facts just described, and I believe I have done so, the life-history of this plant throws an important light upon many of those described in the last, or second, of this series of memoirs. How far the numerous plants there referred to may prove to be different states of a few species is not easy to determine, because we do not obtain them in that condition of stratigraphical isolation which has afforded such an important help in the case of the Burntisland examples. In that memoir I pointed out how closely some of the Lepidodendroid forms resembled CORDA'S *Diploxylon*, and how the absorption of the cellular medulla of some of them would actually convert them into examples of the latter genus. It is necessary to remember that hitherto none of the authors who have written on *Diploxylon* have seen either its pith or its bark. The last description of *Diploxylon* published, so far as I am aware, with the exception of my own memoir, was that by Mr. BINNEY, who says of his specimen, "although it shows the so-called medullary sheath in a very perfect state, there is nothing to indicate the former existence of a pith of cellular tissue"*; and he adds, "the part which remains undisturbed shows that the whole of the central axis was formerly composed of hexagonal vessels arranged without order:" "this view is confirmed by another and more perfect specimen of *Anabathra* in my cabinet, and enables me to speak with positive certainty, and to show that these plants had a similar structure in the central axes to the specimens of *Sigillaria vascularis* described by me in my paper published in the Quarterly Journal of the Geological Society"†.

Considering the imperfection of the materials at his disposal, no more discriminating account of these plants has been published than is contained in Professor KING'S memoir entitled "Contributions towards establishing the general characters of the genus *Sigillaria*"‡. In this memoir the author examines carefully the *Anabathra* of WITHAM, which is a true *Diploxylon*, and concludes that it is undoubtedly a Dicotyledonous plant; but notwithstanding this mistake he correctly points out some of the features in which the genus approximates *Lepidodendron*, quoting BRONGNIART'S suggestion as to the possibility of *Diploxylon* being the stem and *Lepidodendron* the branches of the same type of tree. With equal accuracy Professor KING insists upon the truth, recently challenged by some of our younger botanists, that the vascular medullary cylinder and the exogenous ligneous zone are independent systems.

In my previous memoir I also called attention to some of the observations of BRONGNIART and CORDA on *Diploxylon*, especially to an error into which the latter writer fell when he determined that no medullary rays existed in this genus. At the same time I explained the source of CORDA'S mistake, viz. his ignorance of the fact that the medullary rays of these plants *sometimes* consist of scalariform cells, but which he mistook for vessels§. BRONGNIART has made this supposed absence of medullary rays (which he only

* "On some Lower-Coal-seam Fossil Plants," Philosophical Transactions, 1865, p. 584.

† *Loc. cit.* p. 584.

‡ Edinburgh New Philosophical Journal, No. 71.

§ It is an interesting circumstance that I have recently obtained from the Oldham Coal-measures a *Stigma-*

accepts on CORDA's authority) one of his distinctions between *Diploxylon* and *Sigillaria*; but this distinction must now be abandoned as non-existent. WITHAM had described the large openings represented in my figures 12 & 13, *m*, Plate XLII. of the present memoir as medullary rays. Professor KING, on the other hand, correctly discerned that these openings transmitted foliar bundles, also recording his conviction that the vacant spaces surrounding the bundles had probably contained cellular tissue, which I have now proved to be the case.

But, relying upon LINDLEY'S declaration that no vascular tissue was ever found in a medullary ray, he denied the correctness of WITHAM'S application of the term to the spaces in question. Mr. BINNEY, referring to this subject, does not speak very definitely. He says that his specimen "distinctly confirms WITHAM'S opinion as to the occurrence of medullary rays *or bundles* dividing the woody cylinder"*; but he does not define what he means by bundles. At p. 600 of the same memoir he again speaks of "medullary rays or bundles of barred vessels," from which I infer that bundles *of vessels* are also referred to in the previous sentence. So far as I can ascertain, none of those observers who preceded me have distinctly recognized the true secondary medullary rays described both in this memoir and in the preceding one.

BRONGNIART, CORDA, and KING agree in considering the Diploxylons to be Gymnospermous Exogens, associating them in that great group with the true Sigillariæ.

I think the facts now published finally settle this primary question. It being admitted by all authors that the *Lepidodendra* are Cryptogams, the Diploxylons can no longer be regarded by any one as Gymnospermous Exogens; and as the close identity of BRONGNIART'S *Sigillaria elegans* with *Diploxylon* is equally obvious, we must accept the entire group as Lycopodiaceous. Dr. DAWSON, in his recent memoir on *Sigillaria*†, arrives at a different conclusion; but whatever may be the case with Transatlantic specimens, there is not the slightest room for doubt about our European ones: they are all modifications of the Lepidodendroid type. The distinction drawn by BRONGNIART between the *Sigillariæ* which have medullary rays and the *Lepidodendra* which have not, I have now shown to be merely due to difference of age. In its young state the Burntisland *Diploxylon* is an ordinary form of *Lepidodendron*. As it develops it passes through successive stages of growth, all of which appear to be more or less permanently represented amongst other matured *Lepidodendra*, though within what limits has yet to be ascertained, since, as I have already suggested, some of the forms described in my last memoir may be parts of the same plant at different ages, though in several of the examples there described this is certainly not the case. Long before attaining to the dimensions and stage of growth in

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ria, identical in every other respect with *S. ficoides*, but in which the medullary rays are similarly composed of scalariform cells. Remembering the fact that a *Diploxylon* from the same locality, which I described under CORDA'S name of *D. cycadeoides*, possessed the same features, the question arises, how far may these similarly constructed plants have borne the mutual relations of root and stem?

Loc. cit. p. 583.

† Quarterly Journal of the Geological Society, May 1871.

which it becomes a true *Diploxylon*, this plant possesses a well-defined *cellular* pith. Its central axis is *not* composed of bundles of vessels, but of vertical piles of true cells. As soon as the outer ligneous cylinder makes its appearance, true medullary rays also present themselves. Simultaneous with the formation of these true medullary rays is that of my primary rays, or cellular spaces through which the vascular foliar bundles pass outwards through the ligneous zone, and which differ from the others in no respect, either of structure or of origin, save in the circumstances that they are larger and that the foliar bundles are lodged within them. The specimen from which Plate XLIII. fig. 22 is taken clearly proves this. The vascular bundles proceeding from the interior of the ligneous zone to the leaves, when once formed, evidently became permanent structures, undergoing neither increase nor diminution of number; but as the diameter of the stem steadily increased, these bundles obviously became lengthened, by some process as yet unascertained, so as to accommodate themselves to the altered dimensions of the tree, especially of its bark. It follows that when the pseudo-cambium-layer commenced its work of producing new vessels, which were added exogenously to the exterior of the preexisting vascular cylinder, it was penetrated by these leaf-bundles, and the arrangement of the newly formed vessels was modified by their preexistence. On studying these tissues in the original of Plate XLIII. fig. 22, where the arrangements of the new growths are very distinct, no essential difference can be observed between those intervascular areas filled with cells through which a vascular bundle passes, and which are destined to become what I have designated *primary* medullary rays, and those which ultimately assume smaller dimensions and become *secondary* ones. It appears to me that as the new, longitudinally arranged vessels of the young growth increased in size, the intermediate cellular tissue seen in Plate XLIII. fig. 22 was gradually absorbed to make room for them. In the secondary medullary rays this absorption was carried so far, in consequence of the pressure occasioned by the steady growth of the vessels, that nearly all the cells disappeared; whereas in the primary rays, where a vascular foliar bundle interposed between two adjacent enlarging vessels, the bundle resisted their pressure, protecting the cells immediately above and below it from its effects. Hence a lenticular space was left permanently occupied by unabsorbed cells; but at the upper and lower angles of this space it contracts to the dimensions of the true secondary medullary rays. If this explanation is correct, it establishes my conclusion that these large spaces, seen in Plate XLII. figs. 12 & 13, *m*, are but modified medullary rays, and that they are so modified, not for the purpose of transmitting the vascular foliar bundles, but as an effect of their presence, which is a very different thing.

In my last memoir I called attention to the fact that the foliar bundles originated from the line of junction between the vascular medullary cylinder and the ligneous zone*.

* I have to correct an error into which I fell on this point in the text of my previous memoir. I had clearly ascertained that the foliar bundles sprang from small vessels occupying the plane where the outer surface of the vascular medullary cylinder and the inner one of the ligneous zone were in contact, and I came to the conclusion that they belonged to the latter rather than to the former; but I now see that this was a mistake. I

This statement is confirmed by my more recent researches, as is also another observation made in the same memoir, viz. that the *crenulated* outline described by BRONGNIART and BINNEY as characterizing the line of junction between the vascular medullary cylinder and ligneous zones of *Sigillaria* and *Diploxylon* is not a constant feature in the latter genus. In the variety which I described under the name of *Diploxylon cycadeoideum*, believing it to be identical with CORDA'S plant so named, I pointed out, as already stated, that the cells of the medullary rays had a barred or scalariform structure; and I showed how these cells started from an interrupted layer of similar ones located between the inner and outer vascular cylinders. Nothing of the latter kind exists in the plant now described. The cells of the medullary rays have very thin and delicate walls, differing but little, save in form, from those of the innermost bark, with which latter those of the outermost extremities of the medullary rays become actually merged. The exogenous growth of the ligneous zone which I have so long recognized, but which has been objected to by some botanists, is now more clearly demonstrated than before. Decided as were my previous convictions on this point, they have received fresh strength, so that I am less than ever inclined to abandon them. We have in these plants the three distinct tissues of pith, wood, and bark, in addition to the vascular medullary cylinder, which latter I am still inclined to suspect may typically represent the medullary sheath of the true Exogens. The specimens described in the memoir demonstrate two facts bearing upon the question of the growth of these plants:—1st, that the formative layer, whether we designate it cambium or give it some other name, has been substantially parallel with the exterior of the previously formed vascular tissues; 2nd, that this layer has displayed an intermittent activity, periodic resumptions of vigorous growth alternating with times of rest. The facts detailed in the memoir clearly demonstrate that the ligneous zone was gradually built up by a succession of such growths. The pith, primarily small, ultimately attained to considerable dimensions through the fissiparous multiplication of its cells. Possibly it may have been the pressure occasioned by this multiplication that caused the continued expansion of the medullary cylinder.

But before attempting to discuss either the physiological questions suggested by this inquiry, or the homologous relations of the various tissues of the *Lepidodendra* to those of the living Lycopods, it will be necessary to call attention to a few features in the latter objects which require to be considered.

Considerable variations exist in the structure of the living *Lycopodia* and *Selaginellæ* but an essential unity pervades the entire group. If we take a matured stem of a *Selaginella Martensii* as a simple type, we find in the centre a single large fibro-vascular bundle. In the transverse section this bundle is elliptical, consisting of a central line of vessels which are scalariform, spiral, and annular, all the three modifications occurring

fell into it from the circumstance that the small size of these vessels was in exact correspondence with that of the innermost series of the exogenous growth, and very different from that of the large vessels constituting the bulk of the medullary cylinders. Having now traced the origin of this vascular cylinder, the question appears to be set at rest.

in the group. This cluster is surrounded by a ring of very small woody fibres, the *Phlöem* of the German botanists, the innermost cells being the smallest and the outer ones the largest in the series. Around this central bundle is a cylindrical air-cavity traversed by numerous detached columns of cells, which ascend as they pass inwards from the cortical layer to the fibro-vascular bundle, to which latter they serve as a series of flying buttresses, sustaining it in its position. Externally to this air-cylinder is the bark, which varies in its composition in different Lycopods. In *Selaginella Martensii*, *denticulata*, and *Wallichii* the inner part of the bark consists of a dense mass of parenchyma, with large cells and thin transparent walls, and with a few large chlorophyl-grains in each cell. Yet more externally this parenchyma gradually passes into a thin-walled fusiform prosenchyma, the walls of the cells becoming thicker as we proceed outwards, until at their external surfaces they present a woody structure, forming the outermost envelope of the stem. But on turning to the leaves we find something more: the substance of each leaf is parenchymatous, besides which it has a true epidermal layer of sinuous cells and stomata on its under surface*.

In *Lycopodium chamæcyparissus*, though the central fibro-vascular mass is more complex than that just described, it is, as SACHS justly points out, essentially the same; but the air-cylinder of the *Selaginellæ* is absent, as is also the inner parenchyma of the bark. The prosenchymatous layer is very thick, and closely embraces the fibro-vascular bundle; its component cells also are much more thickened by ligneous deposits in their interiors than in *S. Martensii*. Another important difference exists in the fact that the parenchyma of the leaves now extends itself over the entire stem, forming an outer cortical layer; but this is not invested by any true epidermis, such as is seen covering the leaves.

If we turn from these general features to some special points in the development of these plants, we shall find that new light is thrown upon the fossil forms. The young growing bud at the tip of a Lycopod is composed externally of ordinary parenchyma; but in its interior we find formed at the earliest period a central column of what SACHS designates *procambium*, a solid cylinder of very delicate, vertically elongated cells, the transverse section of which has in most species an elliptical outline. I have carefully traced the development of these procambial tissues in many Lycopods, and can thoroughly confirm the accounts given of them by SACHS. Where the first pair of leaves is given off in *S. Martensii*, a slender spiral or scalariform duct passes from each leaf into this procambial layer, through which the two vessels descend vertically into the stem at points corresponding, as SACHS correctly indicates, with the two foci of the ellipse, where it joins some vessels already formed in the stem itself. The second pair of leaves contributes a second set of vessels, which in like manner enter the procambial cylinder. We thus obtain, partly from the stem itself and partly by successive additions from the various leaves, two parallel columns of fibro-vascular tubes separated by the central mass of procambium. Descending still lower into the matured parts of the stem, we find that,

* *Selaginella denticulata* appears to have the same structure as *S. Martensii*. See SACHS's 'Lehrbuch,' fig. 89 A.

by successive centripetal growths, these vessels have so increased in number as to cause the two bundles to meet in the middle of the procambial cylinder, through the longer axis of the transverse section of which they now form a continuous line. The central vessels of this linear series are now the largest. A further distinction appears in the circumstance that the central vessels are generally more perfectly scalariform, whilst the outer vessels are spiral ones. Whilst these changes have been going on, corresponding ones have connected the remaining procambial cells into an interrupted ring of prosenchyma with somewhat thickened walls, or, in other words, into a ring of limiting tissue, making the whole axis a closed bundle. The cortical layers appear to be composed of meristem; that is, they do not grow from any true cambial structure, but by the division of the preexisting cells of all the parts, until the normal dimensions of each stem are reached. The central vascular bundle of the axis thus represents the Xylem, and its investing prosenchyma the Phlöem, whilst the bark derives its existence from an independent source, originating in the primitive cellular tissue. In the plant quoted most of the vessels of the fibro-vascular bundles appear to be derived from the leaves. The outer vessels of these bundles are smaller in size as well as more spiral in structure than the inner ones. These facts have an important bearing upon the interpretation of our fossil forms. NÄGELI has argued that the fibro-vascular bundles belong to the stem and not to the leaves, because he finds such bundles in *Psilotum*, in which the leaves are deprived of them; but the *Psilotum* is altogether so exceptional a form that it can scarcely outweigh the evidence afforded by the *Lycopodia* and *Selaginellæ*.

Guided by these examples, I think we can ascertain the homologies of the fossil stems so far as their tissues are represented in the living types. It is clear that the central bundle of Plate XLI. fig. 2 corresponds substantially with a young state of the central fibro-vascular bundle of *Selaginella Martensii*, only here some of the central primitive tissue has remained to form the basis of a future pith which has no existence in the living forms. In the latter we have no central axis preserved which can, by the utmost stretch of the imagination, be identified with a pith; their primary central axis of procambium is wholly converted into or replaced by the central vessels (Xylem) and the investing zones of prosenchyma (Phlöem). Parenchyma has no longer an existence in this part of the plant; hence we must conclude that the preservation of a central portion of primitive parenchyma, capable of very considerable increase by cell-division, is peculiar to the fossil types.

We have seen that the number of the vessels in the central vascular bundles of living types increases, up to a certain point, with age, and also that each foliar vascular bundle unites with those of the central axis, at least where the first two come in contact and for some distance down the stem, at the external surface of the central bundle. The fossil and recent forms agree in this point; but we now face a difficulty. The number of the vessels in such a cylinder as I have represented in Plate XLI. fig. 8 represents, doubtless, the aggregation of the bundles of a yet larger number of leaves than there are vessels; and if each leaf of the upper part of the stem added its quota to the whole externally

to all previously formed ones, it is difficult to understand why we do not find the lower ones traversing tangential sections of the medullary cylinder, as we do in corresponding sections of the exogenous zone (Plate XLII. fig. 12). I think there can be no doubt that the large inner vessels of the vascular medullary cylinder belong directly or indirectly to leaves located at points of the stem inferior to those smaller ones belonging to the periphery of the circle. Yet in radial sections we witness the anomalous arrangement represented in Plate XLII. fig. 12, where the leaf-bundle (*m*) joins the cylinder (*c*) at a point external to the larger vessels of *c*, but which latter is connected with leaves higher up the stem than that supplied by the vessels *m*. At *m'* we still find the foliar bundle retaining its position external to the cylinder. I can only conclude that as they descend into the stem the vessels of each foliar bundle pass inwards, but do so obliquely and slowly, thus preventing their altered direction from being conspicuous in tangential sections of the cylinder. This peculiar difference in the arrangement of the upper and lower extremities of the foliar vessels may explain the sinuous course which those of the medullary cylinder pursue. They never exhibit the mutual parallelism seen in those of the ligneous zone, but twist about, so that they rarely preserve such parallelism, for any distance, either with each other or with the plane of the section*.

But supposing this peculiarity in their arrangement to be explained by what I have stated above, there yet remains another problem to be solved. We have seen that, in the first instance, these medullary vessels are few in number, and exhibit scarcely any central medullary area, whilst at later periods of growth opposite conditions prevail in both these respects. The pith becomes larger as the branch increases in size, involving a corresponding enlargement of the vascular ring composing its peripheral boundary. This could only be accomplished either through the pressure of the growing pith causing *displacement* and *rearrangement* of the surrounding vessels, or by producing *absorption* of the inner ones, the loss of which must, in that case, have been antagonized by a constant addition of new ones at the periphery. But after what I have seen of the displacement of older vessels through the pressure occasioned by the growth of newer ones, I have no hesitation in adopting the former of these explanations; the more so, since I have not in any instance seen such ragged irregularity in the vessels in contact with the medulla as continuous absorption would produce. Plate XLII. fig. 15 demonstrates that the real condition of things is precisely the reverse of this, the cells of the pith and the vessels of the cylinder adapting themselves to one another with geometric regularity. After the development of the foliar bundles and their aggregate product the vascular medullary cylinder went on for some time, an altogether new set of vessels began to be formed laying the foundations of my exogenous growths. These differ from those of the cylinder in almost every respect, whether of origin, structure, or function. 1st, as to origin: they are not, directly or indirectly, associated with the leaves; hence the foliar bundles have had nothing to do with their production. They have been formed in unequal concentric rings, in immediate contact with the inner layer of the bark. It

* These peculiar arrangements are represented in the diagram, Plate XLV. fig. 36.

must not be forgotten that the homologue of the vascular bundles of the living Lycopods, *i. e.* the vascular medullary cylinder, is not encased within a ring of prosenchymatous cells, or Phlöem, as in the recent plants: hence they remain throughout their entire development open and not closed bundles, which is a very important distinction. So far as I can judge, the appearance of this exogenous growth possibly corresponded with the period at which the leaves ceased directly or indirectly to produce further increase in the number of the vessels of the medullary cylinder. I can discover no reason for supposing that the number of the vessels of that cylinder subsequently received further additions, or that any further enlargement took place in the diameter of the cylinder. I can only account for the development of the exogenous layers by supposing the existence of some equivalent of a cambium-layer surrounding and parallel to the cylinder. The fact of these growths taking place as I have already described is beyond all question. The only debatable points refer to the source whence these exogenous layers were derived, and to the relations which they bear to the similar structures of other plants.

Professor M'NAB, who objects to my views on this point, lays much stress upon the distinction between a layer of "*meristem*" tissue and a cambium-layer. The distinction between these structures was made by NÄGELI and further illustrated by SACHS (Lehrbuch der Botanik, p. 75). The characteristic feature of a *meristem* structure is that all or most of its cells are capable of spontaneous division or multiplication by fission, as is the case with the first-formed elements of every plant; whilst such cells as are no longer capable of undergoing such divisions become *permanent* tissues. SACHS points out that these meristem tissues were formerly comprehended in what was generally termed cambium; but he urges the advisability of limiting this latter expression "to that meristemic (*merismatische*) layer in the tissues of the older parts of the plant by which is effected the lateral growth (*Dickenwachsthum*) of the Dicotyledons and Coniferæ." Hence, as cell-fission occurs in the true cambium-layer as well as in meristem layers, one chief peculiarity of the former lies in its position relative to the older parts of the stem—or, in other words, to its location, in the case of Dicotyledonous plants, between the wood and the bark. HENFREY describes some of the peculiarities of the Dicotyledonous stem as follows:—"When the buds open to produce new shoots, cell-division recommences in the cambium-region of the old bundles, and an additional layer of wood is added gradually during the season to that formed the year before. Season after season this process is repeated" (Elementary Course of Botany, p. 521, 2nd edition). "The medullary rays which separate the primary bundles are developed in the cambium-region with the yearly layers of wood, and always extend to the cortical parenchyma" (*loc. cit.* p. 523). HENFREY also points out, as other writers have also done, that one chief peculiarity in an exogenous stem resides in the parallelism of the cambium-layer to the previously formed fibro-vascular bundles (*loc. cit.* p. 518), and in the periodic resumption of activity in the bundles (*id.* p. 519). If all these conditions are not fulfilled in the specimens which I have described and especially illustrated by Plate XLIII. fig. 20, I know not where to seek for such a fulfilment in any living plant. But SACHS

further says, "das echte Cambium der Dicotyledon dagegen erzeugt sowohl nach aussen als nach innen fibro-vasale Gebilde, nach aussen Phlöem, nach innen Xylem" (*loc. cit.* p. 397). If this determination that a cambium-layer must develop tissues on both its inner and outer surfaces is to be accepted, there is no further room for discussing the matter. We shall see directly that I find no reasons for believing that the bark increased its inner surface by *prosenchymatous* additions from a true cambium-layer, and we have nothing in the interiors of these stems corresponding with the ordinary wood-cells of the Dicotyledons and Coniferæ. I have never for a moment pretended that we find in these arborescent Cryptogams all the features of a highly developed exogenous Dicotyledon. Primarily seeking to show the absurdity of applying the term *acrogens* to these plants, I have done so by demonstrating that they grow by the addition of new layers to the periphery of the old ones, that their woody wedges are disposed in radiating laminæ, as in the Coniferæ, and that these laminæ are separated by medullary rays of which the cells exhibit a mural arrangement. Whatever name may be given to the genetic material out of which these new investing layers develop, whether we choose to term it cambium or meristem, we have here very manifestly a form of exogenous growth.

That this exogenous structure belongs, as Professor KING long ago pointed out, to a system of vessels wholly independent of and distinct from the medullary cylinder is clear. What its functions may be is not equally clear. It undoubtedly gave strength to the trunk and branches of the tree, but it contributed nothing *directly* to the nutrition of the leaves. The leaf-bundles pass through it, but they clearly have no further connexion with it than results from that positional relationship. When I wrote the second memoir of this series I had not ascertained so clearly as I have since done the relations of these foliar bundles. Two facts, however, require further notice. One is that in that memoir I described a unique bit of a *Diploxylon*-stem in which some vascular bundles *were* given off from the ligneous zone, but whether or not they were foliar I cannot say*. The other relates to *Stigmaria*. That this is the root of a Lepidodendroid plant is unquestionable. It is also well known that the vascular medullary cylinder is not represented in it. The pith, which is large, is in direct contact with the inner surface of the exogenous woody zone. Remembering the apparent origin of the medullary cylinder from the leaf-bundles, we can understand the possibility that the downward prolongations of them would not reach the roots. But, as I have illustrated in my last memoir, the exogenous woody axis of *Stigmaria does* give off the vascular bundles to the rootlets. Hence it would appear that the nutritive fluids were absorbed by the rootlets and transmitted up the stem primarily by the vessels of the exogenous zone; but in order that those fluids should reach the leaves, they had to be transferred, by some lateral movement, to the vessels of the medullary cylinder. I do not propound this otherwise than as an hypothesis; but I can see no other way in which the end could be attained.

* I think it more than probable that this curious specimen may belong to that part of the base of the stem where the medullary vascular cylinder of the latter and the woody zones of the roots with their peculiar Stigmarian structure somewhat overlap one another.

There yet remains to be considered the relations which subsist between the respective cortical layers of the extinct and living Lycopodiaceæ.

In the former we have substantially three layers—an inner one of parenchyma composed of cells having a tendency to become arranged in vertical lines, an intermediate layer of prosenchyma, in which, in old stems, a peculiar, vertically elongated tissue tends to develop itself, and an outer parenchyma of the ordinary type, and which also constitutes the principal tissue of the leaves. If we combine what we find in the cortical investments of the recent Lycopods *Selaginella Martensii* and *Lycopodium chamæcyparissus*, we shall be furnished with all that we require to illustrate the identity between these tissues in the living and the extinct forms. In *Selaginella Martensii* we have an inner layer of parenchyma enclosed in an outer one of prosenchyma, which latter becomes more compact, in consequence of the increasing thickness of the ligneous deposit within its cell-walls, as we proceed from within outwards. No true epiderm invests the stem. In *Lycopodium chamæcyparissus*, on the other hand, we have no inner parenchyma, but the prosenchymatous layer, very much thickened*, closely invests the central vascular axis. External to this prosenchyma we have a distinct parenchymatous layer, which Sachs describes as being an extension of that composing the leaves. Thus these two living plants combine to furnish us with the three layers of bark found in the fossil ones. It is interesting to remember that in one of the fossil Lepidodendroid stems from Lancashire and Yorkshire described in my last memoir, I found the very thick prosenchymatous layer apparently in close contact with the vascular tissues, as in *Lycopodium chamæcyparissus*. It will be noted that no true epiderm invests the stems of either of these recent species, but it exists in the leaves in a well-defined form and with the usual stomata. In that position it rests immediately upon the foliar parenchyma, which, as we have seen, extends over the entire stem of *L. chamæcyparissus*, as it does over the fossil stems. Hence in the latter I have designated this superficial parenchyma the *subepidermal* layer, though I have seen no trace of true epidermis investing it; but this term assists us in maintaining correct relationships between the nomenclature of the recent and fossil types.

I have hitherto said nothing about the probable roots of the plant described in this memoir; but since the Burntisland beds are permeated in every direction by Stigmarian rootlets, specimens of the thick roots also being far from rare, I have come to the conclusion that they belonged to the same plant as the Lepidodendroid stems and branches. I am the more inclined to adopt this conclusion from the circumstance that I have not yet seen in this deposit a single fragment of a true *Sigillaria* to which these numerous roots could have belonged. Mr. Binney has more than once affirmed the probability that *Lepidodendron* had a Stigmarian root, which opinion I fully endorse.

Having satisfied myself of the soundness of these conclusions, I venture to suggest that Plate XLV. fig. 37 may be regarded as a diagrammatic representation of a vertical section of a typical Lepidodendroid tree, drawn in accordance with the various details described

* Sachs, 'Lehrbuch,' fig. 89 B.

in the preceding pages. At its upper portion we have on the left hand the leading shoot, and on the right the lateral branch of a *Lepidodendron*, with their leaves *in situ* and the central vascular axis of each limited to a medullary cylinder (*c*) enclosing a true pith (*a*). Lower down we have the later-formed layers of the exogenous zone (*d*). The leaves are here represented by their petiolar bases (*l'*), whilst yet lower we find that these have disappeared, leaving only the ordinary Lepidodendroid scars (*y*). Below the level of the black ground-line we have the Stigmarian roots, with their rootlets (*o*) and their rootlet-bundles of vessels (*n*), derived from the exogenous zone (*d'*).

In my last memoir I described a very peculiar variety of bark which I frequently found associated with the Lancashire forms of *Diploxylon*. Nothing resembling it occurs in the bark of the Burntisland type. In one of the Lancashire types, as I have already stated, I found the cells of the medullary rays thickened by internal bands of lignine, rendering them scalariform. No such cells appear in the Scottish plant. These are probably specific distinctions, to learn the exact value of which will require prolonged research.

I have now brought together the representatives of four distinct genera. The young twigs which I have described, whether we are guided by their outward forms or their internal structure, are true *Lepidodendra*. The older and larger branches and stems have the internal organization of a *Diploxylon* with the external bark and persistent petioles of a *Lomatophloios*, whilst the branching stems, with their double ligneous axes, are unmistakably identical with the *Leptoxylon* of Corda*. The broad features of resemblance in the cortical and petiolar portions of my plant to Corda's minutely described *Lomatophloios crassicaule* are too manifest to require that I should dwell upon them. The disciform Sternbergian pith of Corda's species does not recur in any of our British forms. All such modifications of pith that have come under my notice continue to be correctly located where I placed them many years ago, viz. in the woody cylinders of Dadoxylons. But the possession of a disciform pith is not recognized as constituting a generic distinction amongst recent plants, and we need not give it that value amongst fossil ones. Corda's genus *Leptoxylon* was founded upon a single decorticated axis, which, so far as it remains, displays no single feature differing from those of *Diploxylon*, except in the double character of the axis. Brongniart has already shown that this feature was but a result of the branching of the stem, and I have further illustrated the same truth in the preceding pages. Of the above names, the most appropriate one to be retained would be that of *Lomatophloios*, were it not clear that this is also a synonym of Sternberg's older term *Lepidophloios*†: Brongniart has already adopted the latter name, uniting with it Corda's genera *Lomatophloios*, *Leptoxylon*, and *Calamoxylon*, Sternberg's *Cycadites columnaris*, and Goeppert's *Pachyphyllum*‡, all of which generic terms except *Cycadites* he abandons. It is obvious that *Anabathra* and *Diploxylon* must

* Flora der Vorwelt, tab. 15, p. 21.

† Dr. Dawson further considers *Ulodendron* to be merely a synonym of *Lepidophloios*.

‡ Tableau des genres de Végétaux Fossiles, pp. 43, 44.

share the same fate, there being no longer any independent grounds for their retention. I propose therefore to adopt the generic term *Lepidophloios* for the plant which is the chief subject of this memoir. The necessity for the destruction of several genera just indicated suggests the probability that a number of specific names will have to suffer in like manner. I am satisfied that all attempts to apply specific names to the plants of the Coal-measures can but be provisional, until we learn more than we at present know of the effects of age upon their form and organization. Still, though they may not have any permanent value, such names are necessary for working purposes. I would therefore provisionally distinguish the subject of this memoir as *Lepidophloios brevifolium**.

I cannot close this memoir without expressing my obligations to Dr. Dawson, of Montreal, who first directed my attention to the Burntisland deposit, and yet more to G. Grieve, Esq., of Burntisland, by whom the deposit was discovered. I am not only indebted to the latter gentleman for his personal guidance to the locality whence the fossil plants are derived, but he has laboured most indefatigably to keep me supplied with abundance of raw materials upon which to pursue my investigations. The deposit itself is a very remarkable one, apparently consisting of detached masses of peat imbedded in volcanic amygdaloid. Here and there fragments of the fossil plants occur charred to the extreme of blackness, but such is not their ordinary condition; they are usually of a rich brown colour, and the perfect way in which their most delicate organization is preserved leaves little to be desired.

Appendix.

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Since the remarks on page 306, relative to the growth of the new vascular layers of the ligneous zone of the *Lepidodendra* were penned, I have endeavoured to satisfy myself yet more thoroughly respecting the relations which this subject bears to the views of modern botanists on the general question of new vascular growths. Some years ago physiologists would have agreed to regard the new vascular layers described in this memoir and its predecessor (Part II.) as the products of a cambium-layer. Latterly,

* In a letter from Dr. Dawson, dated Nov. 28, 1872, that observer informs me that he regards the Burntisland plant as identical with *Lepidodendron Veltheimianum*. Mr. Carruthers, on the other hand, rejects this identification. Until the very characteristic macrospores of my plant are shown to exist in some of the localities in which the *Lepidodendron Veltheimianum* is common, I think it best to retain my proposed provisional name. I find these macrospores associated with a section of Witham's original specimen of *Anabathra pulcherrima*, for which I am indebted to Professor King, and have not a doubt that the latter is identical with the Burntisland plant; but I have not sufficient proof to establish this point with the certainty requisite for a scientific determination. I trust that the Geologists of the Scotch Survey will succeed in obtaining from Witham's locality of Lennel Braes the decisive evidence which I doubt not will some day be forthcoming. Professor Geikie kindly informs me that he regards the Burntisland deposits as belonging to the upper part of the calciferous sandstones of the Burdiehouse series, and that the Lennel Braes rocks belong to nearly the same stratigraphical horizon.

however, the German botanists especially have restricted the application of this term to a more special set of phenomena than was previously done. They now limit the expression cambium to a cellular layer which originates in a peculiar way, and which develops new tissues in a manner equally special, both processes being illustrated by what occurs in the majority of Dicotyledonous and Gymnospermous Exogens. In these plants the young aërial buds and the tips of the young leaves and roots severally contain the special homogeneous parenchyma to which SACHS has given the name of "procambium." The foliar fibro-vascular tissues are developed, in the first instance, in this procambium; and on tracing each bundle so formed down into the stem we find, in Dicotyledons and Gymnosperms, that its fibro-vascular elements are produced on both the central and the peripheral sides of the procambial mass. For those tissues which are produced on its inner or medullary surface, corresponding with the new wood of English botanists, some Germans assign the name of Xylem; whilst to the tissues formed on the outer or peripheral side they give the name of Phlöem, which is the equivalent of our English liber or endophlœum. These two elements of permanent tissue are developed centripetally, so far as each isolated string of procambium is concerned, until they almost meet in the centre, having used up in their growth a considerable portion, if not all, of the procambial cells. At this stage the detached fibro-vascular bundles are separated from each other by some of the primitive cells constituting the primary medullary rays. The growth of the second year commences by the extension of the cambium-tissue, as interfascicular cambium, across the outer ends of these primary rays by the usual process of cell-fission, to which the German botanists give the general name of Meristem. Instead of the cambium continuing as a circle of isolated vertical strings, it now forms a continuous cylinder, which repeats, on an enlarged scale, the operations of the previous year, with the addition of lengthening the preexisting medullary rays by adding new mural cells to the outer extremities of those in the Xylem layer, as well as to the inner ends of others separating the Phlöem bundles. The Germans designate the latter the Phlöem rays, in contradistinction to the Xylem rays separating the growing wedges of true wood.

As I have already shown, nothing that exactly corresponds with the details of these processes has taken place amongst the fossil Cryptogams which I have described; hence I cannot affirm that the latter possessed a cambium ring in the sense to which I have just referred. But that a process of new cell-growth has led to the development of a succession of enlarging woody zones, each in its turn enclosing more or less completely the preexisting ones, is certain.

But there are many obscurities which make it difficult to ascertain what are the exact analogies subsisting between the growth-processes in the recent Dicotyledons and fossil Cryptogamic plants. In the former, the primary ring of vascular bundles in the stem consists of an aggregation of individual leaf-bundles. The equivalents of this foliar series, as I have shown in the preceding pages, are to be found in my medullary vascular cylinder, which in the fossil Lycopodiaceæ is mainly, if not wholly, composed of prolongations of the true foliar bundles. So far as origin and position are concerned, this

medullary cylinder appears to correspond with the pith-crown (Markkrone) or pith-sheath (Markscheide) of the Germans; only it lacks, in the fossil forms, all the multiplied wood-cells of various kinds which enter into the composition of the Xylem portion of that structure, whilst the Phlöem layer has no true representative either at this or any subsequent stage of growth.

With the exogenous peripheral extension of the wood some new differences present themselves. In the case of the Dicotyledons and Gymnosperms, the fibro-vascular bundles of the medullary sheath, or "pith-crown," consist of elongated, annular, spiral, and reticular vessels, mingled with long wood-fibres; whilst in the new layers of secondary wood no spiral or annular vessels appear, their places being taken by what SACHS terms "short-membered, wider, pitted or dotted vessels"*. In the fossil Lycopods, as we have seen, the first exogenous zone is developed immediately around the vascular medullary cylinder, just as the first layer of secondary wood is developed immediately around the medullary sheath in the Dicotyledons and Gymnosperms. But instead of a change occurring in the nature of the vessels in such new layers of these Lycopods, corresponding with that just referred to in the living Exogens, the vessels of the new zone of the former are mostly identical in character, except in their smaller size, with those of the medullary vascular cylinder. If the former are barred, so are the latter; if the former are reticulated, so are the latter. But with this exception, the further development of these new zones proceeds so as to produce results substantially representing those seen in living Exogens. Thus a ring of detached vascular bundles first surrounds the vascular medullary sheath with definite vertical layers of mural cells between them, constituting the beginning of as many medullary rays. New bundles are added to the exteriors of the preexisting ones, as well as new cells to the peripheral margins of the medullary rays. As this intercalation of additional radiating vascular laminæ increases the tangential diameter of these bundles, new, and yet more peripheral, medullary rays become intercalated, as in living Exogens; so that, though these exogenous zones have attained, in many of the fossil Lycopods, to very large dimensions, no material increase takes place in the diameter of the individual woody wedges as they progress from within outwards. I have also shown in the preceding pages that these exogenous layers neither contribute to nor receive from the leaves any portion of their vascular elements; whilst, as shown in the case of the *Stigmaria*, they do furnish the vascular bundles going to the rootlets, and consequently act as the channels through which the crude sap has ascended from the roots to the upper portions of the tree. It appears to me that we have here an analogy of the utmost importance in relation to the problems under discussion. We seem to have here an identity of function which overrides all secondary differences of origin in its bearing upon the nature and homologies of these several structures, and which, when superadded to the structural resemblances existing between the exogenous ligneous zone of a Diploxyloid Lycopod and that of a recent Dicotyledonous tree, justifies my hypothesis as to the relations subsisting between the two in no slight degree, viz. that

* Lehrbuch, p. 540.

they foreshadow the cambial growths of a later age. But another question arises, viz. What is the genetic relation subsisting between the innermost cellular layer of the bark of a *Lepidodendron*, through the agency of which these new exogenous growths have been developed, and the cambium ring, which has accomplished a similar end in living Exogens?

I have already stated that the entire cortical layer of the fossil Lycopods corresponds much more closely with that of the recent ones than it does with that of any living Exogens. We find in it nothing identical with the endophlœum or liber of English botanists, the Phlöem of German ones. It is essentially a meristem tissue, the result of successive cell-fissions, and usually divisible into from three to four layers. We have, first, an outer parenchyma, which I have termed subepidermal, within which is a variously modified prosenchymatous layer. This is succeeded by an inner parenchyma, the innermost portion of which is usually more or less differentiated into a reproductive layer in which the successive exogenous zones are developed. I have got some magnificent specimens of bark which show that the two outer layers, viz. the subepidermal parenchyma and the prosenchymatous one, but especially the latter, increased in thickness through a meristem action which from time to time developed an abundance of new cells along the line of separation between the two tissues, and which process is illustrated by the curious specimens of bark described and figured in my second memoir (Phil. Trans. 1871, p. 220, Plate XXXI. figs. 54 & 57). The growth of these two outer layers being thus apparently accounted for, we have further to ascertain the corresponding process in the history of the inner parenchyma. That it also increases *enormously* in thickness with the increased age of the stem is quite certain; but though I have examined it in numerous specimens, I have wholly failed to detect any trustworthy traces of a *diffused* cell-fission or meristem process acting simultaneously throughout the entire substance of the layer. Such facts as I have observed seem to me to render it more probable that the new cell-divisions have taken place near its inner surface, and that, whilst these divisions were ultimately instrumental in adding to the thickness of the vascular ligneous zone on their inner side, they also increased the diameter of the parenchymatous bark-layer to which they belonged in the opposite direction. If this idea proves to be correct, it will follow that this meristem action of the innermost bark ends in the production of two kinds of permanent tissue—an inner vascular one, belonging to the vascular axis, and an outer cellular one, belonging to the true bark.

These meristem processes have evidently taken place interruptedly. There seem to have been periods of intense activity alternating with periods of rest. The latter state is illustrated by specimens of *Stigmaria* in my cabinet like that represented in Plate XXXI. fig. 52 of my second memoir*, where the outer parenchyma (*l*) passes suddenly and abruptly into the prosenchymatous layer (*k*), the peculiar meristem structures seen in figs. 54 (*h*) and 57 of the same Plate being entirely wanting. But these latter evidences of vigorous action are very conspicuous in other specimens which I have discovered since

* Philosophical Transactions, 1872, Part I.

the publication of that memoir, and the identity of which with those represented by fig. 52 is demonstrated by their possessing *in situ* the peculiar rootlets so characteristic of *Stigmaria*. I have not obtained similarly conspicuous proofs of this intermittent cell-action in the *innermost* bark; but the periodic additions made to the exterior of the exogenous vascular zone, as illustrated by fig. 21 of the present memoir, demonstrate that similar alternations of activity and rest must have occurred in this region. Hence we appear to have in these Cryptogamic Lepidodendroid stems two concentric vertical zones in which these alternations occurred,—one in the same region as is occupied in Dicotyledons and Gymnosperms by the true cambium-layer, and the other in the same plane as that which contributes to the growth of the cork-layer of the bark in the same plants*; and whilst fully recognizing the differences between the details of the physiological phenomena in the two classes of instances thus compared, I cannot believe that the coincidences referred to are wholly accidental. Be that, however, as it may, we are brought to the conclusion that though the *accessory* phenomena attending the exogenous growth of the stems of these fossil Cryptogams differ from those seen amongst the recent Dicotyledons, that process of growth practically leads to similar results in both cases, so far as the lateral expansion of the woody zone is concerned. The most striking difference between them lies in the entire absence of ligneous prosenchyma or wood-cells from the exogenous zone of the fossil types; but this is not more remarkable than the equally complete absence of the other, or vascular, element from the corresponding zones of a coniferous stem. In a letter which I recently received from Professor Sachs, referring to this subject, he says:—"The main point seems to me to be whether or not, in the case of Cryptogams, subsequent growth in thickness (Dickenwachsthum) occurs. Whether this takes place by means of cambium or merely by means of meristem, is manifestly a question of secondary importance." That such a growth does occur is now put beyond all possibility of doubt.

But the difficulties which surround these efforts to ascertain the homologies subsisting between the Carboniferous Lycopods and living plants are not confined to the exogenous zone. A somewhat similar difficulty attends the attempt to establish true homologies between the vascular medullary cylinder of the plants described in this and the preceding memoir and the central fibro-vascular bundles of the living Lycopods. That these two structures *are* homologous I have no doubt, nor, so far as I am aware, has any other observer. Professor Sachs agrees with this conclusion. He writes, "I consider that your medullary axis of fibro-vascular bundles consists of several such fibro-vascular bodies as I have depicted in fig. 310 in the second edition of my 'Textbook,'"—which figures represent sections of the stems of living Lycopods. But more than one difficulty presents itself when we try to work out the details of this relationship.

Our fossil *Lepidodendra* do not exhibit any thing which exactly corresponds with what I have described on pages 303 & 304 as occurring in the living Lycopods. I have already

* See M. Rawenhoff "On the Formation of the Cork-bark in Dicotyledons," Annales des Sciences Naturelles, 5ième serie, vol. xii. p. 34.

shown that, as each branch grew, a rapid and very large increase took place in the number of the vessels constituting the medullary cylinder of the Lepidodendroid plants; but I have been unable to satisfy myself whether these new additions were developed centrifugally or centripetally as in living Lycopods. The difficulty of determining this point arises from a circumstance which marks an additional distinction between the living and the extinct forms. In the former, the vessels first produced in the procambial axis retain their relative positions permanently: the new vessels added to them merely occupy, in succession, the spaces intervening between older ones, without either disturbing the latter or enlarging the area which the entire bundle occupies. The case is wholly different with the Lepidodendroid plants: in them we have no evidence that the vascular elements developed in this manner. However we regard my medullary cylinder, whether as exclusively composed of foliar bundles or of a combination of foliar and stem-bundles as in living Lycopods, there is no perfect parallelism between its arrangements and those of the recent plants. Beginning in the fossil form at the tip of a twig as a small vascular bundle, we have seen that it gradually enlarged its area until it became a cylinder of considerable dimensions. Some of the primitive cells out of which the vessels were developed, and which I presume have been procambial, obviously increased by a prolonged meristem action until they produced a central axis of permanent parenchymatous tissue representing a medulla, the pressure occasioned by the growth of which was probably the cause of the centrifugal movements of the vessels composing the rudimentary vascular medullary axis. But whilst we may thus account for the displacement of the vessels, it is difficult to explain the origin of the numerous additions to their number in the vascular ring taking place coincidently with the growth of the stem. We find no traces of reproductive procambial cells interspersed between the vessels of this vascular zone. Were these additional vessels produced through the cells of the pith-meristem *within* the cylinder, or through those of the cortical one *external* to it? We must look to one of *these* sources for their origin; and my own impression is that their true source was the innermost layer of the cortical cells. If so, their development was centrifugal, or in the opposite direction to that of their living allies. But there is yet a further distinction to be recorded. We have seen that in the vascular bundles of the recent Lycopodiaceæ each central vascular bundle is flanked on either side by a layer of prosenchymatous fibre. I find no trace of any such tissue occupying a similar relation to the vessels of the fossil plants. In the latter these vessels are either unmixed with any cellular tissue whatever, as in the Diploxyloid forms of the cylinder, or they are distributed through a mass of mere parenchyma, which appears to be a permanent tissue, as in the medullary axis of *Lepidodendron selaginoides**. Thus we find that even in those structures which are generally accepted as the representatives of the vascular bundles of the living Lycopods, the fossil forms differ very widely from the recent types, both genetically and in their composition.

Such differences occurring in the central vascular axis (so universally accepted as

* Philosophical Transactions, 1872, Part 1, Plate xxiv. fig. 1.

representing the same structure in the fossil and living Cryptogams) demonstrates that we must not expect to find in the primæval types exactly the same genetic phenomena as those with which we are familiar at the present day, when the differentiation of Cryptogams from Phanerogams has progressed so far by the degradation of the former and the elevation of the latter types. When no true Dicotyledons existed, their places being taken by an arborescent type of Cryptogams, the differences to which I have called attention prepare us for recognizing without surprise the possibility of other genetic distinctions, such as we find in the exogenous growth so generally characteristic of the Carboniferous plants.

Description of the Plates.

PLATE XLI.

Fig. 1. Transverse section of a young Lepidodendroid twig, enlarged 20 diameters.
Fig. 2. Transverse section of the tip of a yet younger twig, enlarged 24 diameters.
Fig. 3. Transverse section of the central vascular cylinder of fig. 2, enlarged 54 diameters.
Fig. 4. Transverse section of the central vascular cylinder of fig. 1, enlarged 54 diameters.
Fig. 5. Longitudinal section of a similar twig to fig. 1, enlarged 50 diameters.
Figs. 6, 7. Radial sections of the bark of specimens like fig. 1, enlarged 50 diameters.
Fig. 8. Transverse section of the vascular cylinder of a branch larger than fig. 1, enlarged 54 diameters.

PLATE XLII.

Fig. 9. Transverse section of a young branch which has reached the *Diploxylon* form, enlarged $2\frac{1}{2}$ diameters.
Fig. 10. Radial section of a portion of the vascular medullary cylinder and ligneous zone of fig. 9, enlarged 55 diameters.
Fig. 11. Transverse section of the central axis of a large Diploxyloid stem, natural size.
Fig. 12. Tangential section of part of the ligneous zone of fig. 11, enlarged 10 diameters.
Fig. 13. Tangential section of part of the ligneous zone of fig. 11, yet further enlarged 32 diameters.
Fig. 14. Vertical section of the medulla and vascular medullary cylinder of a Diploxyloid stem, enlarged 12 diameters.
Fig. 15. Transverse section of a portion of fig. 14, exhibiting the junction of the vessels (*c*) of the cylinder with the cells (*b*) of the pith, enlarged 50 diameters.
Fig. 15[a]. Radial section of the outermost layers of the bark with leaf-petioles attached, natural size.

PLATE XLIII.

Fig. 16. Radial section of the inner parenchymatous bark in its matured state, enlarged 50 diameters.

Fig. 17. Radial section of the outer part of the prosenchymatous bark in its matured state, enlarged 40 diameters.

Fig. 18. Tangential section of the leaf-petioles close to the outer surface of the bark, enlarged 2 diameters.

Fig. 19. Transverse section of the centre of a young Lepidodendroid twig, about to branch dichotomously, enlarged 28 diameters.

Fig. 20. Section of a large Diploxyloid stem branching like fig. 19, enlarged 2 diameters.

Fig. 21. Transverse section of part of the ligneous zone of fig. 20, enlarged 40 diameters, exhibiting the young vascular growths.

Fig. 22. Tangential section of some of the young vessels of fig. 21, enlarged 50 diameters.

PLATE XLIV.

Fig. 23. Transverse section of a *Lepidostrobus*, enlarged 7 diameters.

Fig. 24. Tangential section of a *Lepidostrobus*, enlarged 4 diameters.

Fig. 25. Small portion of fig. 24, enlarged 45 diameters.

Fig. 27. *x*, Section of a macrospore, enlarged 70 diameters; *w*, cluster of microspores, enlarged to the same scale.

Fig. 27*. Single macrospore, external aspect, as an opaque object, enlarged 35 diameters.

Fig. 28. Cluster of four sporangia from the base of a *Lepidostrobus*, and containing macrospores, enlarged 32 diameters.

Fig. 29. Transverse section of the central axis or peduncle of a large *Lepidostrobus*, enlarged 10 diameters.

Fig. 30. Longitudinal section of fig. 29, enlarged 10 diameters.

PLATE XLV.

Fig. 26. Microspores of fig. 25, magnified 800 diameters.

Fig. 31. External surface of a young Lepidodendroid twig of the common type of fig. 1, enlarged 3 diameters.

Fig. 32. External surface of a young Lepidodendroid twig of a rarer variety, enlarged 3 diameters.

Fig. 33. Transverse section of a young Lepidodendroid twig from Oldham, enlarged 8 diameters.

Fig. 34. Longitudinal section of the medullary axis of a young Lepidodendroid twig from Oldham, enlarged 46 diameters.

Fig. 35. Transverse section of a young Lepidodendroid branch from Oldham, with large leaves, enlarged $4\frac{1}{2}$ diameters.

Fig. 36. Diagram representing the arrangement of the foliar bundles and vessels of the medullary sheath.

Fig. 37. Diagram representing a typical vertical section of a Lepidodendroid tree with Lepidodendroid branches, Diploxyloid stem, and Stigmarian roots.

The letters of reference employed in the above figures are applied as follows, the application being as nearly as possible identical with that of my previous memoir; I have given the list complete, though several of the letters refer to root-structures and other parts not described in detail in this memoir, and some additional ones are employed.

a. Medulla.
b. Medullary cells.
c. Medullary vascular cylinder.
d. Ligneous zone.
e. Vessels of ligneous zone.
f. Medullary rays.
g. Innermost parenchymatous bark (rarely if ever present in these Burntisland plants as a distinct layer).
h. Inner parenchymatous bark.
i. Prosenchymatous bark.
k. Subepidermal parenchymatous bark.
l. Leaf-petioles and leaves.
m. Foliar bundles of vessels.
n. Root-bundles of vessels.
o. Rootlet.
p. Cups for rootlets (not present).
r. Cone-scars (not present).
s. Axis of strobilus.
t. Bracts of strobilus.
u. Sporangium.
v. Cellular sporangium-wall.
w. Microspores.
x. Macrospores.
y. Leaf-scars.

Fig. 6.

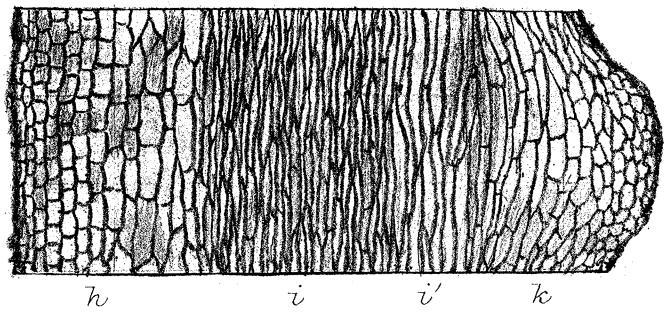


Fig. 8.

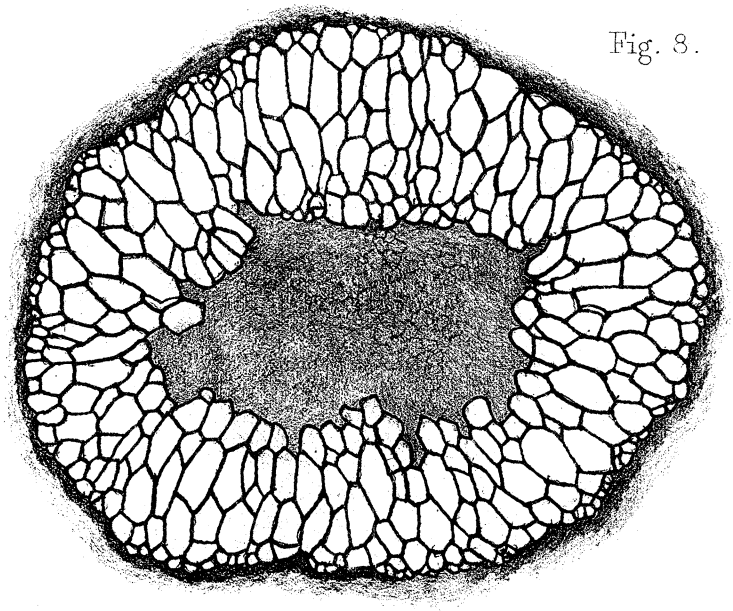
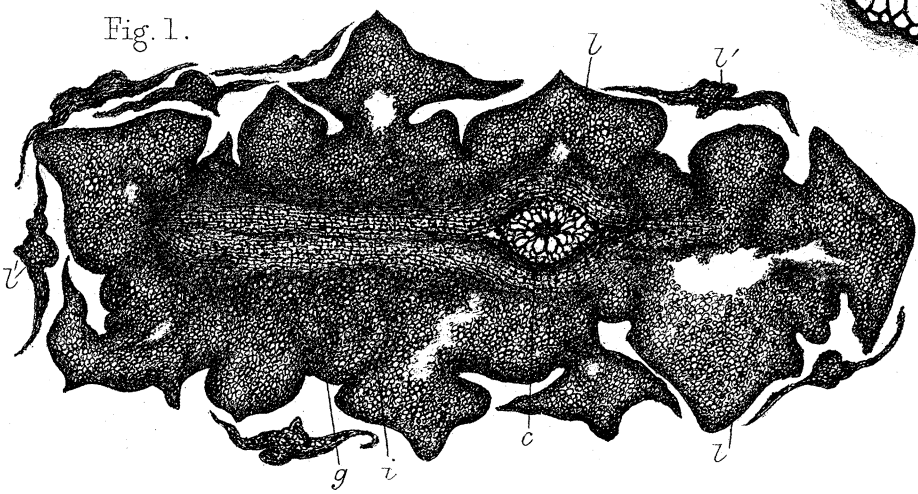


Fig. 1.



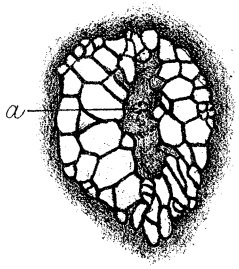
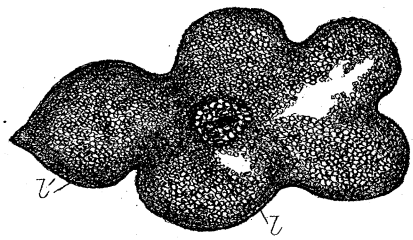


Fig. 3.

Fig. 2.



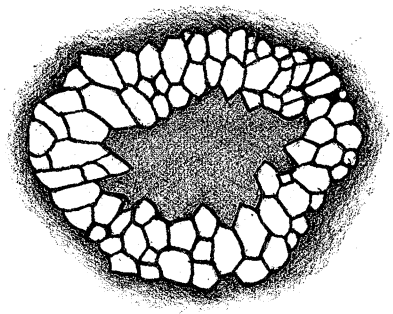
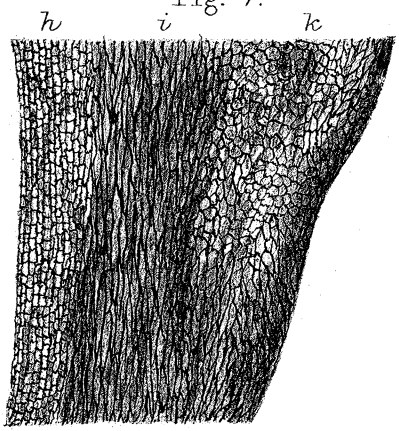


Fig. 4.

Fig. 7.



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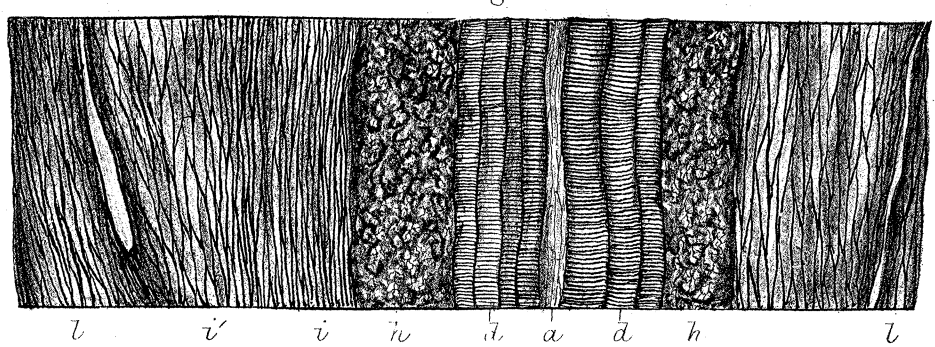

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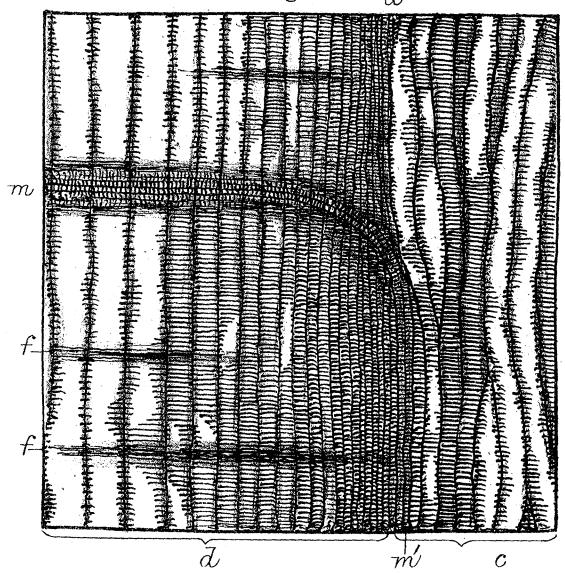

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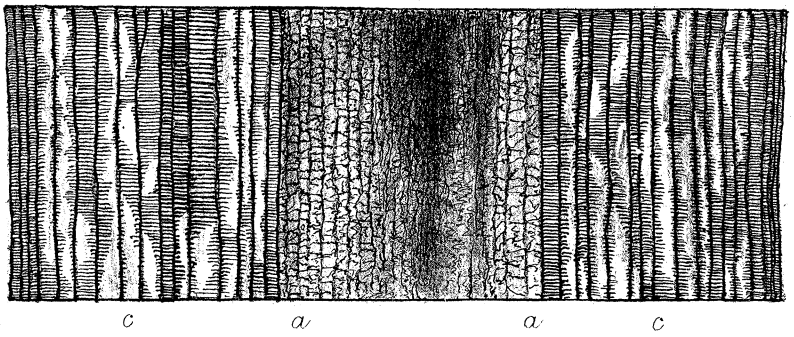


Fig. 15a.

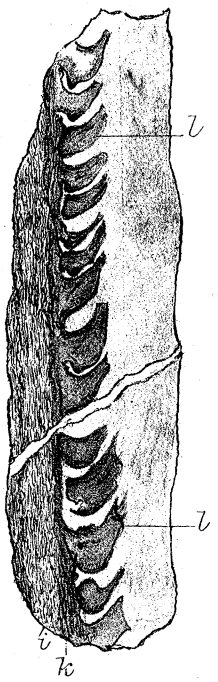
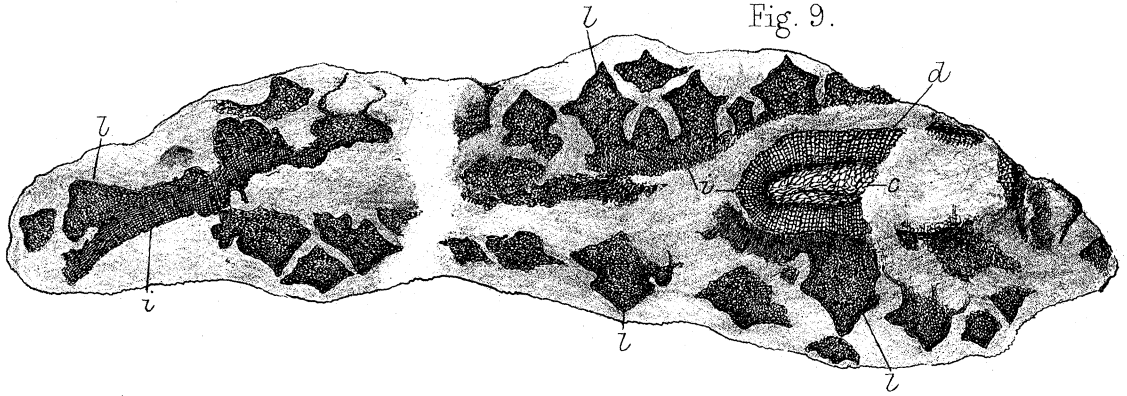


Fig. 9.



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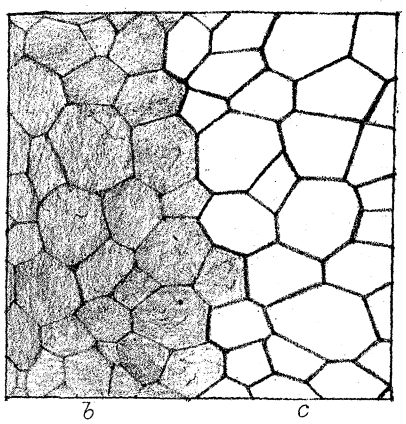

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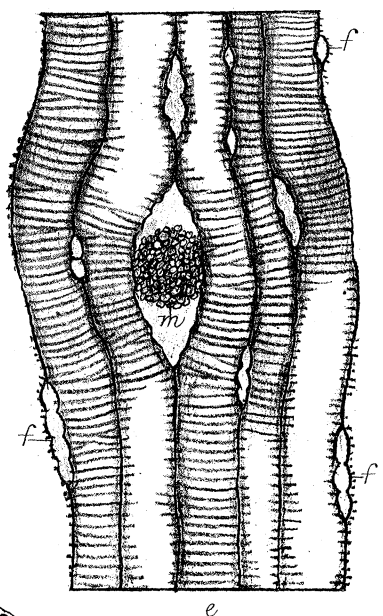

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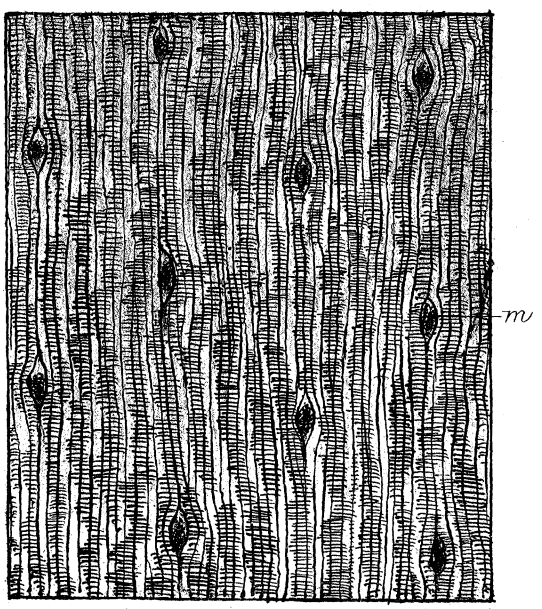


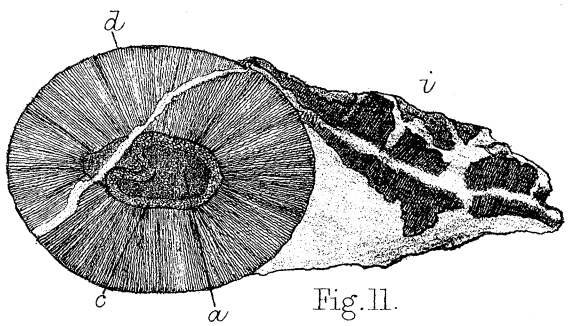
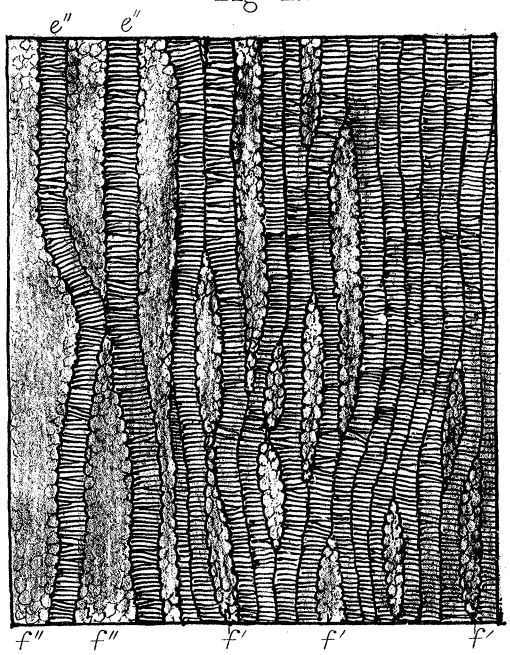


Fig. 11.

Fig. 22.



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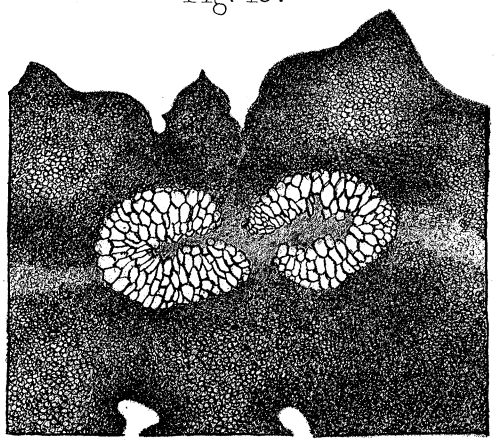

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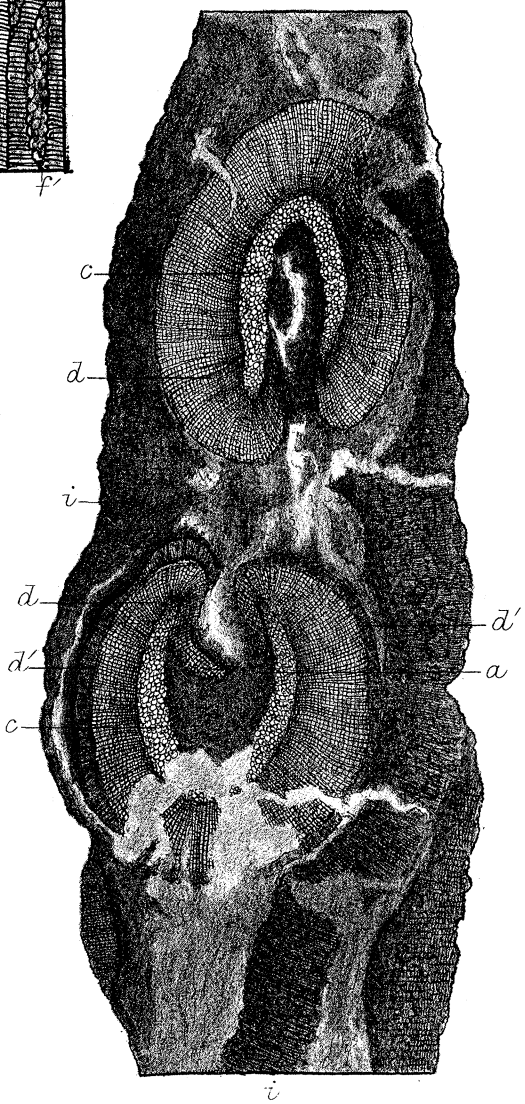

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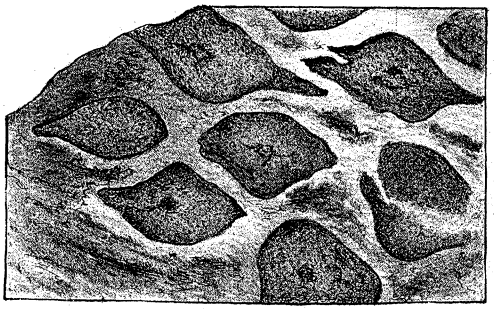

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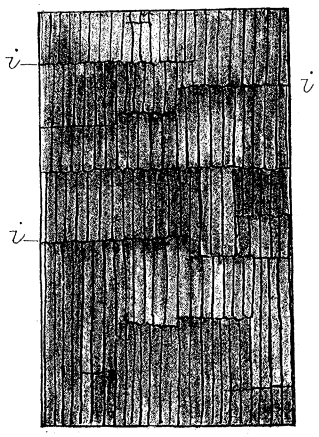

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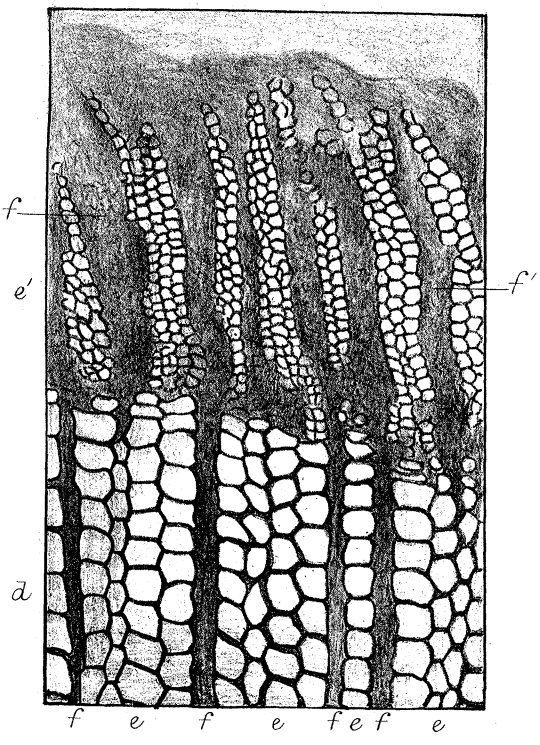

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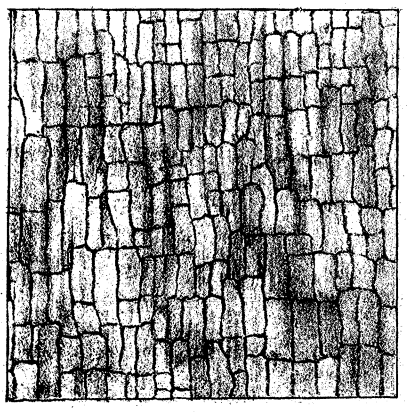

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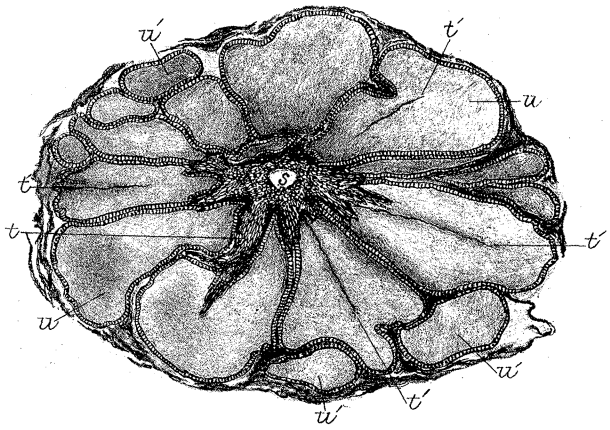

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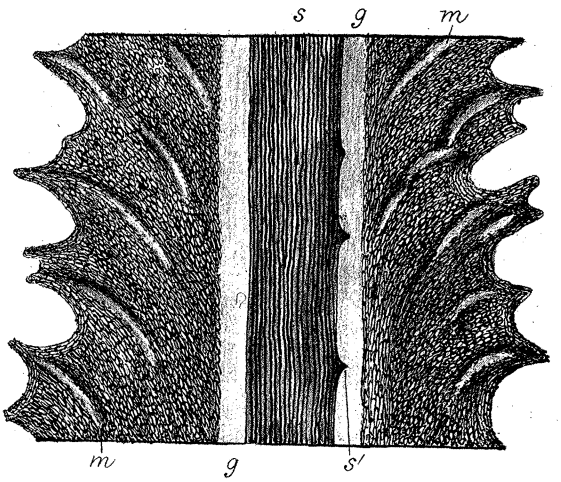

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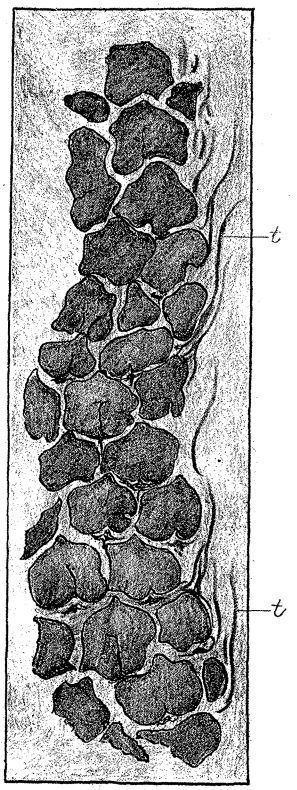

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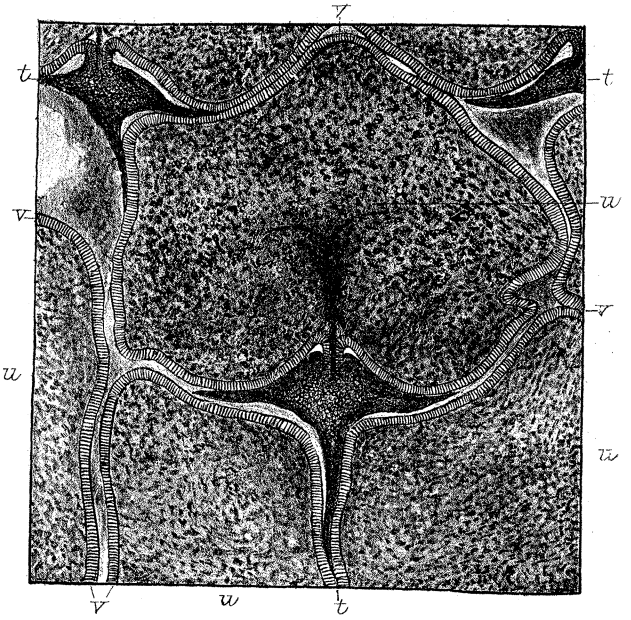
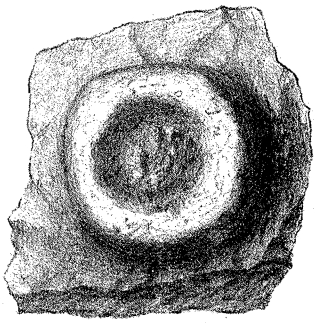


Fig. 27.



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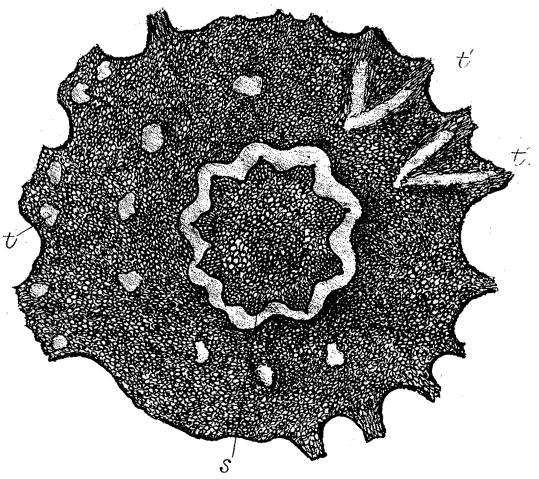


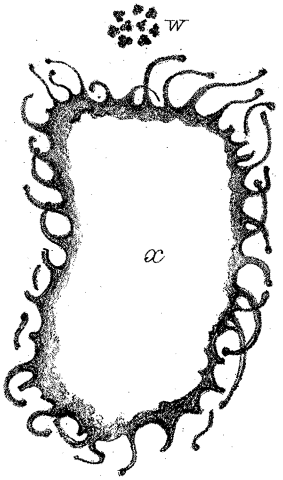
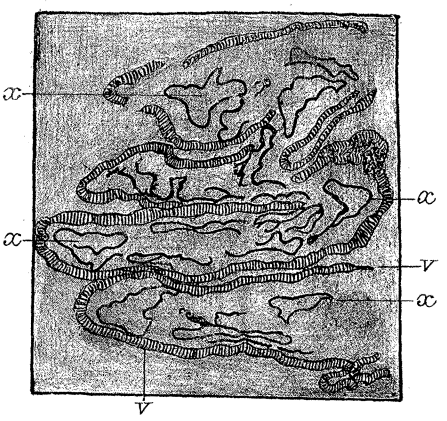


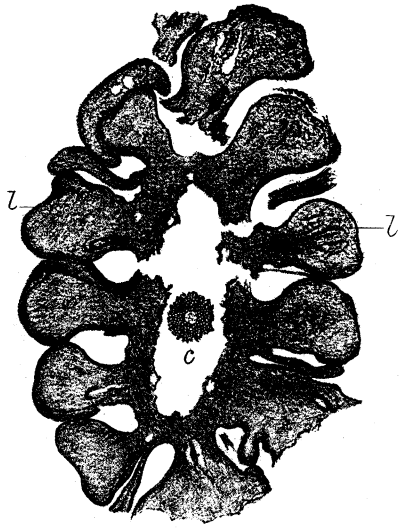
Fig. 27.

Fig. 28.



Whiteman & Bass, Photo-Litho

Fig. 35.



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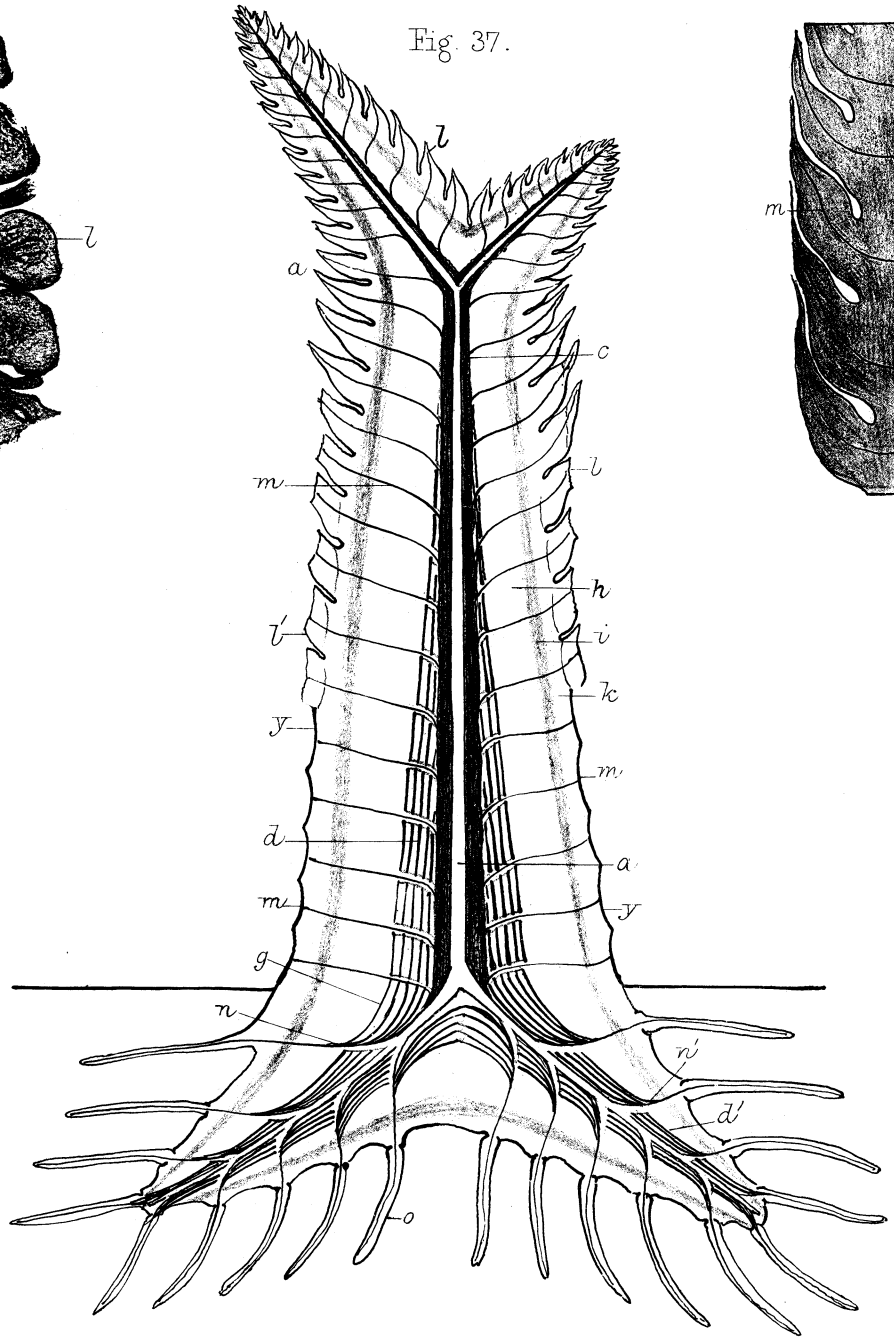

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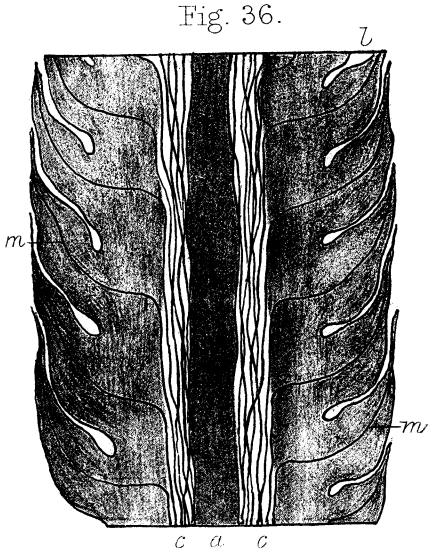

Fig. 31.

Fig. 32.

Fig. 26.

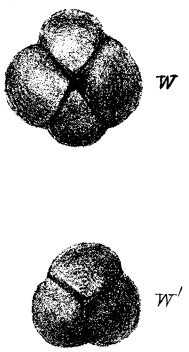

Fig. 34.

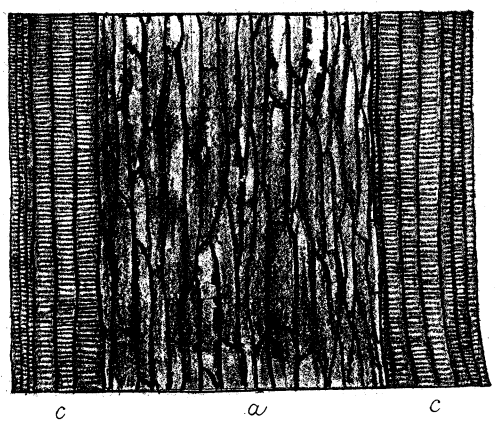

Fig. 33.