X. On the Organization of the Fossil Plants of the Coal-measures.—Part II. Lycopodiaceæ: Lepidodendra and Sigillariæ. By W. C. Williamson, F.R.S., Professor of Natural History in Owens College, Manchester.

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In 1849, when M. Brongniart published his 'Tableau des genres des Végétaux Fossiles,' he admitted into his series of Acrogenous Cryptogams a family of Lepidodendra, in which he included Lepidodendron, Ulodendron, Megaphyton, Halonia, Lepidophloios, and At the same time he recognized as Gymnospermous Dicotyledons, a family of Sigillariæ, including Sigillaria, Stigmaria, Syringodendron, and Diploxylon. guished these two groups by supposed differences in the structure of the ligneous cylinder surrounding the pith. Speaking of this structure in the Lepidodendroid plants, he says, "Non-seulement il est continu et non divisé en faisceaux par des rayons médullaires, caractère que j'ai indiqué dans plusieurs familles très-diverses des dicotylédonés, mais les éléments qui le composent ne forment pas de rangées rayonnantes. absence de direction radiée dans la disposition relative du tissu ligneux me paraît un caractère très-essentiel, car elle indique la formation simultanée de ce tissu, et non sa formation successive du dedans au dehors, caractère de la zone ligneuse des dicoty-Describing his family of Sigillariæ, he says, "Le caractère essentiel de ces plantes, c'est de présenter, dans l'intérieur de leur tige, un cylindre ligneux entièrement composé de vaisseaux rayés ou réticulés disposés en séries rayonnantes, séparés en général par des rayons médullaires, ou par les faisceaux vasculaires qui, de l'étui médullaire se portent vers les feuilles"†. He further adds, "Les principaux genres de cette famille, ceux qui appartiennent sans aucun doute à de vraies tiges, présentent, en dedans du cylindre intérieur, sorte d'étui médullaire, continu et sans rayons médullaires dans le Diploxylon, divisé en faisceaux correspondant aux faisceaux principaux du cylindre ligneux dans le Siqillaria"‡.

I have long been engaged upon the study of the plants referred to in the above extracts. I have not only had the opportunity of examining numerous specimens in the cabinets of friends, but in nearly every instance I have literally dissected each specimen described, in my own lathe, so as to avoid, as far as possible, all sources of error. The result is that I am now in a position to demonstrate the complete unity of the plants which M. Brongniart has separated so widely, and to show that the transition from one form to another is so gradual as to necessitate the inclusion of the entire series in the Lepidodendroid family.

\* Loc. cit. p. 39. † Loc. cit. p. 55. ‡ Loc. cit. p. 55. MDCCCLXXII. 2 D That the Sigillariæ were Lepidodendroid is a conclusion that has been already arrived at, first by Dr. Hooker and afterwards by Mr. Binney and Mr. Carruthers; but the facts upon which this conclusion was based by these writers appear to me insufficient to furnish a demonstration of this affinity, since no example of a true Sigillaria in which the internal structure is preserved appears to have been hitherto described. Mr. Binney has described some plants\* which he believes to be true Sagillariæ; but I agree with Mr. Carruthers, who has pointed out that one of these † is a true Lepidodendron. Another; is a very curious and distinct plant of which I have sections, but which I have, as yet, failed to interpret; whilst the remaining plates refer to a plant which I shall notice further in this memoir, and which may be a Sigillaria; but I fear that we have not as yet sufficient evidence to render justifiable the conclusion that it is so. Mr. Carruthers informs me that since his several memoirs referring to this subject were published, he has obtained such a Sigillaria, which he is about to describe; but not having seen the specimen I am unable to form any opinion respecting it.

My object in this memoir is to describe and illustrate the structure and affinities of several genera respecting which there is no longer any ground for doubt, and also to demonstrate the successive steps by which we ascend from the lowest type of Lepidodendron to stems which, as Brongniart has truly concluded, are furnished with an exogenous woody cylinder, richly supplied with medullary rays. For this purpose I shall take as my point of departure the Lepidodendron figured by Mr. Binney, already referred to, but which, in his specimen, lacked the outermost epidermal layer. plant has also been described by Mr. Carruthers &, who regards it as identical with the Lepidodendron selaginoides of Sternberg. I owe some apology to the latter gentleman for redescribing a plant which, so far as he went, he has described so accurately; but to do so is indispensable to the object which I have in view, and which includes points not referred to in his memoir, as well as some others on which I am constrained to arrive at a different conclusion from his. He carefully abstains in his memoir from employing the terms medulla or pith, wood or ligneous cylinder, and bark; whereas I am satisfied that these three portions, characteristic of an exogenous growth, are to be discovered in the entire series of these plants. This threefold division is least conspicuous in the type just referred to; but a gradation of forms leads us from that type up to others in which the tripartite distinction is too remarkable to be overlooked. I have no doubt in my own mind respecting the existence of these divisions throughout the entire series; consequently in this memoir I shall speak of the medullary, ligneous, cortical, and epidermal layers, and I shall also always employ the same letters to indicate what I believe to be homologous structures in the various plants described.

‡ Loc. cit. pl. 34. figs. 1, 2, 3.

<sup>\* &</sup>quot;A Description of some Fossil Plants, showing structure, found in the Lower Coal-seams of Lancashire and Yorkshire," Phil. Trans. 1865, p. 579.

<sup>†</sup> Loc. cit. pl. 35. figs. 5, 6.

<sup>§ &</sup>quot;On the Structure of the stems of the arborescent Lycopodiaceæ of the Coal-measures," by W. Carruthers, Esq., F.L.S., F.G.S., Botanical Department, British Museum (Monthly Microscopical Journal, London, October 1869).

Plate XXIV. fig. 1 represents a transverse section of Lepidodendron selaginoides, from the cabinet of Mr. Butterworth, magnified six diameters. The medullary axis (a) consists of a very peculiar admixture of barred cells and vessels also barred. I abstain, as I have already done in my previous memoir on Calamites, from designating these vessels scalariform, because I have not yet found them to be thickened at their angles with continuous deposits of lignine, as is the case with the true scalariform vessels of ferns. Fig. 2 represents a longitudinal section of the same specimen, magnified four diameters. Fig. 3 is a small portion from the centre of the medullary axis of fig. 1, more highly magnified, and fig. 4 is a corresponding enlargement of the same structure, though less highly magnified, of fig. 2. The cells of this structure in the specimen figured exhibit a tendency to diverge into two forms. We have one thick-walled series, arranged in vertical rows (fig. 4, b), the transverse septa of which are sometimes rectangular in relation to their sides, but much more frequently oblique, the obliquity tending sometimes in one direction, and sometimes in another even in the same pile. The sides and ends of these cells are alike richly barred. Sometimes the bars are regularly parallel with each other, and arranged transversely as in the vessels; but very frequently they describe a series of curves as if one, two, or even three of the angles of the cells had been centres from which corresponding series of concentric segments of circles had been drawn. the transverse section these cells also appear barred on their transverse partitions (fig. 3, b), the bars being usually arranged in two opposed systems of curves. These barred cells vary in diameter from .005 to .0015\*. The cells of the other class are much smaller, have very thin walls, and appear to be small masses of ordinary parenchyma intermingled with the other medullary tissues; it is possible, but not probable, that this difference is due to mineralization, a point to which I shall return. The vessels (figs. 3 & 4, c) are often almost undistinguishable from sections of the barred cells; indeed we appear to have here strong evidence of their primarily cellular character. In the specimen figured, those of the centre of the medulla are somewhat widely separated by the two kinds of cellular tissue as shown in fig. 4; but this separation only extends over a small area. In the peripheral portions of the medullary axis they are closely conjoined, the cellular element becoming less abundant, especially the delicate parenchymatous tissue which is so much more copious in the centre of the structure. These vessels range from '0014 to .002 in diameter.

Immediately investing the medullary axis is a thin cylinder (figs. 1 & 2, e) of small barred vessels arranged in parallel series radiating from the medulla outwards. These represent the ligneous zone. The innermost ones are exceedingly minute, and though they increase in size as we proceed outwards, they rarely exceed ·016 in diameter, the great majority of them being very much smaller. It is from the innermost surface of this cylinder that the vascular bundles are given off to the leaves, a point of importance in determining the homologous relationships of the various portions of the Lepidodendroid plants. The radiating arrangement of these vessels suggests, as the quotation already

<sup>\*</sup> All these dimensions refer to decimal divisions of an inch.

made from the writings of M. Brongniart points out, an exogenous mode of growth, a conclusion fully borne out by facts yet to be mentioned; small cells arranged in single or double vertical rows pass outwards, like medullary rays, between these vessels. The tissue immediately surrounding the ligneous zone has almost always disappeared from the specimens of this plant, its place being represented by an almost vacant space; but there are indications, as Mr. Carruthers has correctly pointed out, that it has been a delicate form of parenchyma. In the present example almost every trace has disappeared save a narrow ring (g) of disorganized carbonaceous matter at some little distance from the ligneous zone. The space within this tissue represents the innermost portion of what I regard as the cortical layer. Scattered through this vacant space, as well as the more external one, we find in the transverse sections small bundles of minute scalariform vessels (fig. 1, m) fringed round with delicate parenchyma, and exhibiting a circular or oval section. Their diameter ranges from  $\cdot 003$  in the round sections near the ligneous zone to a longer axis of  $\cdot 007$  in the more peripheral portions.

We now come to the middle bark (h), a dense, well-preserved layer of thick-walled parenchyma, gradually passing into prosenchyma at its outer margin. The rounded cells of the former have a mean diameter of about 003, gradually becoming more oblong, with a longer axis of about 007 and a shorter one of 002. The foliar vascular bundles make their way through this layer, the delicate parenchyma with which each bundle of vessels is surrounded gradually merging with its coarser cells. The delicacy of this parenchyma investing the bundles frequently leads to its entire disappearance, leaving blank spaces (m') channelled through the bark, in the middle of which the barred vessels of the foliar bundles are sometimes conspicuous from their isolation. As the parenchyma of this middle bark becomes converted into prosenchyma at its outer portion, its cells become elongated vertically, and at last pass rapidly into the almost vascular form of prosenchyma (k), constituting the bast-layer of the outer bark. In the transverse section these tubes are seen to be arranged in radiating series proceeding from within outwards. In the vertical section the more external ones become as elongated as in the pleurenchyma of many exogenous barks, the fibres being arranged longitudinally in curving lines having a very regular parallelism. They have a mean diameter of about 00083. Towards the outermost portion of this tubular prosenchyma we find, in these fossils, a tendency to split vertically, and to the consequent detachment of the epidermal layer (1). The innermost portion of this detached layer consists of tubes precisely similar in every respect to those of the outer bark, but which again change rapidly, as we proceed outwards, first into the prosenchymatous form seen in the middle bark, and then into a thick-walled parenchyma which constitutes both the superficial portion of the epidermis and the entire substance of the petioles or bases of the leaves (l). I have here referred the tubular bast-layer partly to the outer bark and partly to the epiderm, because, when the latter becomes detached, the line of separation usually passes through the middle of the layer; but it may perhaps be more correct to regard the whole of these bast-tissues as one subepidermal layer. Fig. 5 exhibits a tangential

section of the outer bark passing through the prosenchymatous layer and immediately underlying the epidermal one; but owing to the cylindrical form of the specimen, on the left hand of the sketch the section has passed outwards through the latter layer (fig. 5, l) and the attached bases of the leaves. The prosenchymatous character of this bark-tissue is well shown in this section. Openings, indicating the points through which the foliar bundles of vessels have passed, are seen to be partly occupied by delicate cells. The section of each opening is oblong in a vertical direction. Fig. 6 is a tangential section made parallel to the last, but through the outermost epidermal layer (l). bases of the leaves are here indicated by large lozenge-shaped spaces (fig. 6, l), arranged, like the corresponding openings in fig. 5, in quincuncial order. These two sections illustrate, with great clearness, the tissue to which two common appearances seen amongst fossil Lepidodendra belong. Fig. 5 represents the Knorria-like forms which are commonly, but erroneously, spoken of as decorticated; whereas they belong chiefly to the outermost surface of the middle cortical layer, the bast-layer and epidermis alone having disappeared: such a surface, in the plant under consideration, is represented in In some larger stems of this, or an almost identical species, belonging to J. B. DAWKINS, Esq., the lenticular projections are rather shorter and broader than those in this figure. Fig. 5 corresponds to the ordinary Lepidodendra.

The sections of the persistent bases of the leaves (l) vary considerably in form, as is shown by figs. 1, 2, 5, & 6. So far as the transverse section is concerned, fig. 1, l'', appears to indicate the characteristic form, since its resemblance to a depressed acuminate leaf reappears with more or less of distinctness in most of the other sections made in the same plane. These petioles consist of coarse thick-walled parenchyma, the cells in some portions not unfrequently appearing elongated in the direction of growth. The cells of the exterior surfaces are small and dense.

I have mentioned that in the medullary axis of the specimen described there is a very distinct appearance of two kinds of cells, but I am far from certain respecting the true signification of this difference. In other sections of the same species of Lepidodendron I find similar appearances, but with more semblance of a transition from the barred and thick-walled to the thin-walled cells; whilst in one specimen, the centre of which, however, is considerably disorganized, every cell, large and small, appears as if it had been equally barred. I have long since learnt that amongst these coal-plants the absence of a barred or reticulated structure from a cell or vessel is no proof that such secondary elements never existed. We frequently find that, during mineralization, the carbonaceous matter, representing the original deposits of lignine, has been diffused in a uniform, granular layer over the walls of the tissues. Hence it is barely possible that the variations in the medullary cells of the plant described are due to such mineralization.

It appears that, in this plant, we start at the centre with a highly vascular axis intermingled with cellular tissue, and that the vessels, though diffused over the entire medulla, exhibit a slight tendency towards a peripheral polarity, being less intermingled with cells at the exterior of the medulla than at its centre. Around this we have a thin layer

of vessels which exhibit an exogenous arrangement, and have, passing outwards between them, thin vertical layers of cells which I believe to be early forms of medullary rays, Mr. Carruthers rejects this interpretation; but I think I shall be able to show, in the course of my descriptions, that they are what I have affirmed them to be. Mr. Carruthers objects to the idea of their being medullary rays, because "the axis of the stem is not occupied with a cellular medullary tissue, but with scalariform vessels" \*; and that consequently "it cannot be interpreted as similar to that of the medullary system of Dicotyledons." Experienced as my friend and co-worker in the field of phytology is, I must venture to differ from him here. He recognizes, in his description, the existence of the scalariform cells which I have also described, though in phraseology different from my own. "Some of those (vessels) in the centre of the axis are divided into chambers by horizontal septa, or rather they appear to be made up of a series of short, obtuse cells, whose transverse as well as longitudinal sides are marked with scalariform bars. Such interrupted vessels are scattered irregularly through the others. I can detect no trace of any other structure in the axis than scalariform vessels". I submit that such tissues as are here so correctly described cannot, in any accepted sense of the term, be called vessels; they are cells, which it is true might by fusion become vessels. In their earliest state they were not barred or scalariform, but simply forms of parenchyma.

In seeking an explanation of the philosophy of these medullary rays, we must not limit our attention to their matured state, but go back to the time when all the tissues associated with them existed as a cluster of undifferentiated parenchymatous cells. One of the first changes to be detected would be the development of a few vessels, and amongst others would ultimately appear those destined to constitute the incipient exogenous ring. The moment these made their appearance, they converted the few cells which separated them into incipient medullary rays. Thus much of a change might occur before the cells deposited in their interiors their bands of lignine which give them their barred or scalariform structure. It would not be necessary that, as growth advanced, all the cells should follow the same course of development. Such we know is never the case in the higher plants; were it so, differentiation of tissues would be impossible. Further, I think Mr. Carruthers must differ from me as to the essential characters and functions of medullary rays. Though in their earliest state their purpose is doubtless to connect the medulla with the more external tissues, such is not their permanent function. As exogenous stems grow, the pith gradually contracts, and what cells remain do so in a final condition that rather represents effete structures than active cells filled with vigorous protoplasm. Yet though the medulla becomes thus altered, and its primary mission a thing of the past, the medullary rays continue to grow and actively fulfil their essential functions, which is to maintain free lateral communication between the inner and outer layers of the wood, and between both these and the bark. If this reasoning is sound, and I believe it to be so, the fact that a matured Lepidodendroid stem has its medullary axis occupied in some cases with barred cells, and in others

<sup>\*</sup> Monthly Microscopical Journal, October 1869, p. 180.

even with barred vessels, in no way militates against the conclusion that the vertical piles of mural cells which separate the laminæ of the vessels constituting the woody zone, and which are constantly extending in a peripheral direction, are true medullary rays. Their earliest genesis, combined with their final functions, rather than the degree of differentiation which the several tissues have finally undergone, determine their nature.

I shall shortly demonstrate that, simple as these rays are in their early form, they become very definite when we ascend to some of the higher developments of the ligneous zone which we shall find amongst these Lepidodendroid plants.

If I am correct in these determinations, no question can arise as to the cortical nature of the thick, investing, and more external layers, with their prevalence of prosenchyma, so characteristic of Lycopodiaceous cortical structures. We also see that the retention on the epiderm of portions of the bases of the leaves hides what should otherwise represent the regularly arranged leaf-scars seen in the common Lepidodendroid stems. Whether, in the species under consideration, these leaf-petioles were persistent, or whether, as the stem advanced in age, they fell off, leaving a natural cicatrix of the forms represented in fig. 6, is doubtful; but my present belief is that the latter was the case, and that the fact explains why we only find such examples as I have figured of comparatively small size.

I have sections of one example of the above type from South Owram, near Halifax, and for which I am indebted to Mr. NEILD of Oldham, in which the cellular element of the medullary axis is reduced to its minimum. The axis consists mainly of barred vessels; nevertheless cells exist in sufficient numbers to demonstrate the identity of the The next modification of the Lepidodendroid type to which I would call attention is one that Mr. BINNEY has included, together with that which I have just described, in his memoir on Sigillaria already referred to, but which I agree with Mr. CARRUTHERS in regarding as a distinct plant. None of the specimens of it which I have had the opportunity of studying exhibit the outermost layer of the bark; consequently I know nothing of its external contour, but the portions which I possess are interesting and instructive. Plate XXV. fig. 8 represents a transverse section of the central axis (a, c), with the ligneous zone (d) and the inner portions of the bark (g, i), of a specimen in Mr. Butterworth's cabinet, besides which I have made numerous dissections of some other specimens of the same type, with which Mr. Butterworth has kindly supplied me. The prominent features in the medullary axis of the specimen figured are the entire absence of vessels from its central portion, and its transverse division into two longitudinal halves, by a line extending on each side from its central cellular portion to its periphery. Mr. Binney has correctly represented this structure\*; but he says respecting it, "The dark line across the axis, as well as the dark space in the centre, both seem to be the result of a disarrangement of the tubes during the process of mineralization, as similar appearances have not been observed in many other specimens examined by me, which in those parts are in a more perfect preservation". I

feel constrained to differ from the above conclusion, to which, I think, Mr. BINNEY has been accidentally led by uniting two plants, which, though very closely allied, are nevertheless distinct, viz. the one which I have just described and that now under considera-The dark central portion of the medulla is a compact mass of cells, as is well seen in Plate XXV. fig. 9, a. No vessels appear in their midst, and the dividing line, extending on each side to the woody zone, is a prolongation of the same cellular tract\*. The cells average from 01 to 0025 in diameter, their length being variable. As in the preceding instance, they are generally arranged in vertical piles, but with great irregularity in the obliquity of their horizontal or transverse septa. This peculiar obliquity of many of these cell-partitions in the cells traversing the long axis of the stem appears to be a characteristic feature of most of the Lepidodendroid plants. All these cells in the plant before us have had barred walls. External to this cellular axis we have a dense ring of barred vessels (figs. 8 & 9, c). At the inner portion of the ring they are detached from one another, masses of the barred cells ramifying between them; but towards its exterior portion the vessels become a compact mass. They have a varying diameter of from ·01 to 0025, but the most peripheral series in immediate contact with the ligneous zone are not more than .0012. The entire series is arranged, in transverse sections, in parenchymatous fashion, being wholly devoid of any linear disposition, and small tubes being packed into the interstices amongst the larger ones.

One of the striking and characteristic features of this plant is its well-developed ligneous zone (figs. 8 & 9, d). This consists of barred vessels, arranged in very regular radiating lines. In the specimen figured, there are not more than seventeen or eighteen of these vessels in each radial series; but in another section, in my cabinet, of a stem which, though deprived of its epidermal layers, has been fully  $2\frac{1}{2}$  inches in diameter, the woody zone has a breadth of 37, and each linear row contains about 80 vessels. As usual the innermost of each series are the smallest, and they increase in size as they proceed outwards. The medullary rays are very abundant (Plate XXV. figs. 9 & 10, f). In the tangential sections (fig. 10) they are easily recognized; but, owing to the delicacy of their texture, a superficial observation easily leads to their details being overlooked in the radial sections. They are nevertheless most distinct, sweeping across the vessels in straight and parallel lines from the medullary to the cortical surface of the ligneous zone; precisely as they would be seen to do in a corresponding section of any exogenous wood. The exogenous growth of this portion of the stem is sufficiently obvious. We have the radiating arrangement, and the regular increase occurring in the number of vessels in each linear row, as the stem enlarges its diameter. The new vessels have not been intercalated, but added to the exterior of each series,—a fact often rendered evident by the circumstance that, from their walls being less strengthened by ligneous deposits than in the case of the older vessels, they are much more liable to be disturbed and disarranged by lateral pressure.

<sup>\*</sup> Other specimens have come under my notice, in which the medullary vessels encroached almost entirely upon the inner parts of the pith; nevertheless there remained the central spot, of which the transverse line dividing the medulla into two halves is the lateral extension.

The next distinctive feature in all the examples of this type which I have examined is seen in the inner and middle bark. Instead of a thick parenchyma, we have here very little of that tissue. I had for some time a difficulty in satisfying myself that any existed; but I think that the crushed and disturbed structures represented in figs. 8 & 9, g, have been parenchymatous. Almost immediately after leaving the woody zone, the tissues of the bark become conspicuously prosenchymatous, the cells, as seen in the transverse section (fig. 8, i), being arranged in radiating lines, and bearing the closest possible resemblance to a corresponding section of the wood of an ordinary coniferous plant. But on turning to the radial and tangential sections (fig. 9, i), we see that this tissue consists of simple prosenchyma, the walls exhibiting no traces of the pits or extensions of the protoplasm through the ligneous cell-layers to the primary cell-wall, seen in the true pleurenchyma of Conifers and of the hard endocarps of fruits. These cells have a length of ·022 and a diameter of ·0025. Their general aspect is represented in Plate XXV. fig. 11. The outer bark is not represented in the figure; but in the transverse section it merely presents a continuation, outwards, of the same linear series of cells as is shown in fig. 8, i, while in the radial sections we find that the prosenchymatous cells are now drawn out into very long tubes, such as are found immediately beneath the epidermal layer of Lepidodendron selaginoides. The entire thickness of the bark in my specimens, deprived of its epidermal layer, is about 62. We have distinct evidence that bundles of vessels are given off from the woody zone of this plant to the leaves. Three such are represented in fig. 8, m; but these are very much less obvious than in the case of Lepidodendron selaginoides. We do not find here regularly disposed channels ploughed conspicuously through the bark; without careful observation the bundles would easily be overlooked.

The next type to be described, and which I believe to be identical with the Lepidoden-dron Harcourtii, leads us in the opposite direction from that just discussed. In its general aspect it approaches nearer to L. selaginoides; but it has its own distinctive features, which lead us further away than any of the other instances from the exogenous type of structure. Plate XXV. fig. 12 represents a transverse section of the natural size, in the cabinet of W. Boyd Dawkins, Esq. It was prepared from a fine specimen collected by J. Aitken, Esq., of Bacup. In Plate XXVI. fig. 13 a small portion of this section is more highly magnified. Plate XXV. fig. 14 is the central axis, with a small portion of the inner bark, yet further enlarged; and Plate XXVI. fig. 15 represents the outer surface of the outer bark on the removal of the epidermal layer, but taken from another specimen of the same type as that from which the sections were prepared, and for which I am indebted to Mr. Butterworth.

The medullary axis (a-c) is about 25 in diameter, of which the central cellular portion (a) occupies about 18. This consists of cells arranged in irregular vertical rows, and frequently with the oblique transverse septa so common amongst the Lepidodendra. I can detect no trace of barred structure in these cells; but, as their walls are thickened with a deposit of brown carbonaceous matter, I think it very possible that this deposit

may represent the disorganized cell-fibres of barred cells. The exterior of the medullary axis is occupied by the usual ring of barred vessels, but it is much narrower than in the previously described types, being not more than .035 in breadth. Yet more remarkable is the almost complete absence, from the transverse section, of the woody zone. In figs. 12 & 13 it is scarcely visible, but it may be represented by the minute barred vessels of the vertical section (fig. 14, d). The inner bark (g) consists of parenchyma, the cells of which are very minute, being rarely more than 0012 in diameter. More externally we have a very thick middle bark, consisting of a coarser parenchyma (h) with larger cells, and about half an inch in thickness. External to this are the radiating lines of a thin subepidermal layer of prosenchyma (i), about .06 to .12 in thickness, the transition from the coarse parenchyma of the middle bark to the elongated prosenchyma being very abrupt. The outermost layer of epiderm is wanting in all the specimens which I have seen of this type. I have not had the opportunity of examining the original specimen in Mr. AITKEN'S cabinet; but Mr. BUTTERWORTH'S example of the same plant, from South Owram, exhibits the subepidermal surface of the outer bark, which is covered, not with oblong projections, as in the case of Lepidodendron selaginoides, but with hexagonal areola about a quarter of an inch in breadth, as represented in fig. 15. This distinction shows that, though in their internal organization the two plants approach very nearly to one another, they are nevertheless different. The aspect of the well-marked vascular bundles proceeding to the leaves (m, figs. 13, 14) is also different. They leave the thin vascular zone, and plunge into the parenchymatous bark with little or none of the perishable investment derived from the delicate cells of the inner bark seen in Lepidodendron selaginoides; hence they appear in all the sections as dark radii of well-defined vessels without any open space between them and the bark itself.

Before leaving these examples of the genus Lepidodendron, I would call attention to some sections which illustrate yet more clearly the nature of the apparently persistent petioles that adhere to the bark of some examples, and also throw light upon the scars that characterize the Lepidodendroid stem. Plate XXV. fig. 16 represents a section kindly lent to me by Mr. DAWKINS, who also obliged me further by placing in my hands half of the specimen from which the section was obtained. It is a radial longitudinal section of the epidermal layer of a Lepidodendron with its attached petioles; 16 k is the layer of tubular prosenchyma constituting the subepidermal tissue in all these plants; i is a fragment of the outer bark, consisting of the ordinary forms of short prosenchymatous cells; whilst at l we have a series of petioles, which, in this section, appear to be turgid and succulent at their bases, but become more shrivelled and thin as they ascend outwards from the bark. The specimen supplied to me by Mr. Dawkins enabled me to make a series of sections of these petioles. Plate XXVI. fig. 17 represents a tangential one made through the bases of the petioles external to the subepidermal prosenchyma, The petioles are here in close contiguity, and of more or less regular rhomboidal The position of the vascular bundle going to each leaf is indicated faintly in a few of the petioles by a rather darker spot (m). Plate XXVI. fig. 18 is a section made

nearly parallel to the last, but a quarter of an inch nearer the free extremities of the leaves. Each petiole is now seen to be deeply indented by a sharply defined groove running along the centre of its upper surface, which appears to have become generally depressed, the lower surface having undergone little change of form; but the two margins of each petiole have become winged or prolonged laterally into broad membranous expansions (18, l'), explaining corresponding appearances seen in the longitudinal section (16, l'). These membranous expansions are mutually disposed with the utmost regularity, the one proceeding to the right, from each petiole, always overlying the margin of that approaching it from the opposite direction. The position of the vascular bundle of each petiole is now very distinctly marked by a small semilunar opening (m), from which the vessels have disappeared. A corresponding section of the specimen represented by fig. 20 displays this sharply defined semilunar orifice yet more strikingly.

The section Plate XXVI. fig. 19 is a transverse one, made in the line x, x of fig. 16, so as to intersect some of the petioles near their extremities, and yet at right angles to their longer axes, as is done at l". They are here seen to have become yet thinner and more flattened at their central portions, though retaining the central groove on each upper surface. The same regularity in the superposition of the thin margins is found here as in fig. 18. Fig. 19, k represents the layer of tubular prosenchyma, and l the turgid bases of three more petioles. That the latter only exhibit the marginal membranous expansion on one side (19, l') is due to the fact that the section has passed obliquely through the petioles, and only crossed in the plane of those expansions on one side. Plate XXVI. fig. 20 is a longitudinal section of a fragment of the same species of Lepidodendron as the last, supplied to me by Mr. Whittaker, of Oldham, and which I have figured because it displays very clearly the somewhat elongated form of parenchyma of which these petioles consist. At their free extremities the latter have become yet more membranous than is the case with those of the corresponding, but less highly magnified, figure 16. This difference indicates that the shrivelling process incident upon the decay of the leaves has been, as might be expected, a gradual one; and that by the time it reached the portions of the petioles represented in the tangential section fig. 17, a natural cicatrix would have been formed at which the decay would be arrested, and which, when the shrivelled portion had fallen away, would exhibit the ordinary lozenge-shaped scars seen in the common examples of Lepidodendron. The generic distinctions that have been drawn between types that retain and others that do not persistently retain their petioles, appear to me to be of more than doubtful value, since, in all probability, they represent temporary rather than permanent conditions. That some species have retained their petioles longer than others is sufficiently probable, but I believe this to be all that is implied by such differences.

Resuming the task of tracing the development of the exogenous type amongst these Lepidodendroid stems, we come to a series of specimens of which that represented in Plate XXVIII. fig. 21 & Plate XXVI. fig. 22 is a marked example. These plants correspond very closely with the *Anabathra* of Witham and with the *Diploxylon* of

CORDA, but they are unmistakably Lepidodendroid in structure. The different examples which I have seen exhibit variations in the development of the medullary rays in the ligneous zone; but I can trace no distinctive feature separating the extreme modifications; consequently the one which I have figured may be accepted as a fair and well-marked example of its class. The characteristic feature of all these specimens is that they have a medullary ring of barred vessels (c) not arranged in linear or radiating order, surrounded by a well-developed woody zone of smaller barred vessels which are arranged in linear series (d), the whole having been encompassed by a parenchymatous or prosenchymatous bark (q). The centre of the axis is vacant, but whether primarily fistular, or occupied by some other tissue, remains to be considered. In the example figured there are as many as 130 vessels in each radiating linear series seen in the transverse section of the woody zone. On making a tangential section of a portion of the same zone (Plate XXVII. fig. 23), we discover that medullary rays (f) abound. Some of these, like that represented near the centre of fig. 23, f', are very large, consisting of a dense mass of vascular and cellular tissue, whilst others (f) are of the smaller cellular type common to all the Lepidodendra. The general arrangement of these rays is well shown in the radial longitudinal section (Plate XXVI. fig. 22, f), which closely resembles, so far as the rays are concerned, a similar section from a living Conifer. In the figures of Diploxylon given by Mr. Binney\* the woody zone is represented as coming into contact with the medullary vascular ring by a series of concentric curves, the convexities of which are directed inwards. Corda represents the examples upon which he based his genus in the same way. But the specimens now under consideration do not exhibit this contour, the line of demarcation between the two tissues being nearly straight. The crenulated outline is also represented in Witham's Anabathra; but in this instance the irregularity is easily explained. It does not correspond with the line of demarcation between the two tissues. I am indebted to the kindness of Professor King, of Galway, for a very fine transverse section of WITHAM'S original plant, and find that the greater part of its area is broken up into a series of small circles, within each of which the tissues of the plant are well preserved, but external to which there is nothing but agatized mineral matter. The line of junction between the medullary vessels and the ligneous zone is similarly affected. Hence probably the existence in this case of the crenulated outline referred to. WITHAM himself correctly refers these appearances to "the crystallization of siliceous matter". At the same time plants of the class under consideration do exist which possess this crenulated inner margin of the ligneous zone. M. Brongniart has represented one in his well-known memoir on Sigillaria elegans, and I will now call attention to another which presents the best illustration of the structure in question that I have yet seen. It was obtained from the lower coal-measures near Oldham, by Mr. NIELD, and its appearance before being cut into sections is represented in Plate XXIX.

<sup>\*</sup> Description of some Fossil Plants, &c. loc. cit. pl. 30. fig. 4.

<sup>†</sup> The Internal Structures of Fossil Vegetables found in the Carboniferous and Oolitic Deposits of Great Britain, by Henry T. M. Witham, of Lartington, Edinburgh, 1833, p. 40.

fig. 33\*. It is of precisely the same type, so far as its general organization is concerned, as Plate XXVIII. fig. 21, consisting of a hollow central cavity surrounded by a ring of medullary vessels (c). The line of demarcation between these two tissues is crenulated with great regularity; not only so, but at c', where the ligneous zone has been broken away from the zone of medullary vessels, we see that the exterior of the latter is fluted like the medullary cast of a Calamite, for which the specimen might very easily be mistaken. The more minute details of the transverse section are shown in the enlarged segment of it represented in Plate XXIX. fig. 34. In this figure it will be seen that the woody zone presents the convexities of its outline (d') towards the medullary axis; whilst the vessels of the latter, filling up the angles (c') between the convex projections of the former, are very small compared with those composing the rest of the medullary zone (c). The cellular tissue of the medullary rays has disappeared, but the cavities which mark their position are almost identical with those of fig. 21. In both this specimen and that previously described, vascular bundles (m) pass outwards to the leaves.

We must now pass to some allied genera of the Lepidodendroid family. One of the most interesting of these is a very small specimen of *Ulodendron*, for which I have been indebted to Mr. Nield, of Oldham. Plate XXVI. fig. 24 represents a transverse section of this stem, magnified two diameters. Plate XXVII. fig. 25 is a longitudinal section of its central axis, enlarged twelve diameters. Plate XXVII. fig. 26 is a transverse section of the same portion, and Plate XXVIII. fig. 27 is a longitudinal section of the outer bark and epidermis, with the bases of its petioles attached.

The structure of the central axis (figs. 25, 26) is identical with that of the Lepidodendron represented in figs. 12, 13 & 14. We have at  $\alpha$  the same vertical piles of cells, devoid of any indication of spiral structure, their transverse septa being, as before, sometimes rectangular and sometimes oblique. The transverse diameter of each of these piles varies from .0025 to .005. The cavity (a') in the centre of this medulla is clearly not fistular, but a mere rupture, the result of desiccation. Surrounding this is a circle of barred vessels (c) with about eight or nine tubes, counting radially; these are not arranged in rows, but represent the medullary vessels of the Lepidodendra. ligneous zone (figs. 25, 26, d) is very feebly represented. A great portion of its circumference has disappeared through disorganization, but it remains at one or two points; nowhere, however, in such measure as to present a lineal arrangement of its small barred vessels. It is chiefly in the longitudinal section that they can be distinguished by their small size. External to the central axis is a large space from which the tissues have wholly disappeared, comprehending most of the inner and middle portions of the bark. Externally we meet with some of the latter in the shape of coarse parenchyma, the cells of which have a diameter of .003. This passes through an exceedingly narrow layer of common prosenchyma (Plate XXVI. fig. 24 & Plate XXVIII. fig. 27, i), but a few cells in thickness, into the tubular prosenchyma (Plate XXVII. fig. 25 & Plate XXVIII.

<sup>\*</sup> I have more recently obtained a second fine example of this species from Mr. James Whittaker, of Watersheddings, near Oldham.

fig. 27, k) of the subepidermal layer, whilst beyond this again the outermost epidermal parenchyma reappears and composes the bases of the leaves (Plate XXVI. figs. 24 & 27, l). These petioles present the usual appearance of such appendages. Plate XXVIII. fig. 28 represents a tangential section of them, close to the surface of the epidermis. The transverse diameter of each cicatrix is fully three times its vertical one; in other respects these petioles are undistinguishable from those of the Lepidodendra already described. Fig. 24, l', shows that the extremities of the petioles are compressed and membranous, whilst their bases (fig. 24, l) are turgid. One striking feature of this plant is the great apparent thickness of the mass of persistent petioles, as indicated by the lower portion of fig. 24, all external to the dark line of tubular prosenchyma (k) being an aggregation of these appendages. So far as all these portions of its organization are concerned this Ulodendron resembles the lowest types of Lepidodendron.

The remarkable circular areolæ of *Ulodendron* arranged in two vertical rows, one on each side of the stem, are sufficiently distinct in this specimen; they have each a diameter of more than an inch. But sections through them exhibit no peculiarity of structure beyond the circumstance that, in this specimen, the epidermal layer is absent from their superficial area\*. The margin of the band of tubular prosenchyma (k) forms their outer boundary line, whilst their superficies is occupied by the middle bark. In one instance I have discovered indications of a vascular bundle running to the centre of the areola, but it is too indistinct to be of much value. It seems probable that these scars sustained objects which were chiefly developed from the epidermal layer, and whose bases rested upon the outer bark; they certainly were not roots or branches, and I incline to the belief that they were organs of fructification.

Amongst numerous other specimens for which I am indebted to Mr. WHITTAKER, of Oldham, is a small but very well-marked fragment of Favularia, with the characteristic square cicatrices of full size and remarkably prominent. The specimen had been subjected to great pressure; consequently the subepidermal layers of the two sides had been brought into the closest contact, whilst the central axis, along with detached fragments of the prosenchyma, had been squeezed out from between the contiguous cortical layers. Unfortunately I did not obtain a good transverse section of the medullary axis and ligneous zone, having only discovered their presence by finding them in two of my longitudinal sections. The latter, however, show them with some distinctness. Plate XXVII. fig. 29 exhibits a longitudinal section of three of the epidermal leaf-scars (l) with a fragment of the central axis in almost its normal position, the greater part of the cortical prosenchyma, which ought to have intervened between the two, having been forced out of its place. Plate XXVIII. fig. 30 is a transverse section of two of the leafscars and the subjacent prosenchyma. Fig. 31 is a radial longitudinal section of one portion of the central axis to the right hand of fig. 29, including part of the medulla, all the ligneous zone, and a little of the cortical parenchyma. Fig. 32 is a longitudinal section of the epidermal layer, showing the transition from the regular paren-

<sup>\*</sup> The specimen has been weathered or watered over, which may possibly account for the absence.

chyma (l) of the leaf-bases into the tubular prosenchyma (k) adjoining the inner layer of the epiderm.

The medullary axis has been ruptured, leaving a cavity (fig. 29,  $\alpha'$ ) filled with carbonaceous matter; it has consisted of cells (fig. 31, a) arranged in somewhat regular vertical piles, many of these cells having a quadrate shape with a diameter of .005, whilst others of the same form have only about half that diameter. Many others, again, are elongated vertically to a length of .012. Of the diameter of this axis I have no means of judging, owing to the derangement of these parts of the plant. This axis has been surrounded by a cylinder of barred vessels (figs. 29 & 31, d), which may have been disposed in radiating series, though I cannot be quite certain respecting this point; since it is possible that this vascular zone may comprehend both medullary and ligneous vessels, the difference between them being masked by imperfect mineralization. But the opinion that some of them were arranged in a radiating series is further sustained by the circumstance that, in parts of the woody zone, there are straight lines of cells, having a muriform arrangement, but the cells are elongated vertically as in the medullary rays of Calamites. I only meet with these in certain portions of my longitudinal sections; but they look exceedingly like medullary rays, and are of course suggestive of a radial arrangement of the vessels between which they pass outwards. They may, however, belong to The vessels have a diameter of 0012; in many of them the transverse bars have disappeared through imperfect mineralization, but in others they are sufficiently distinct to demonstrate their nature. Immediately external to the vascular zone, I discover patches of oblong, fusiform prosenchyma (fig. 31, g); but we now come to a hiatus (fig. 29, h) from which the tissues have been displaced, but which has been occupied by the middle bark. Small patches of the outer bark appear (fig. 29, i') attached to the inner surface of the epidermal layer. All these patches consist of the same oblong fusiform prosenchyma as that adhering to the exterior of the ligneous zone. Coupling these facts with the additional one that all the numerous detached fragments of bark seen in the specimen consist of beautiful examples of the same tissue of uniform size, unmixed with any other; and arranged in parallel lines with the greatest regularity, I arrive at the conclusion that the entire bark has closely resembled that of the plant indicated by Plate XXV. fig. 8. At the junction of the outer bark (k) with the epidermal layer (l) we find the usual transition of the fusiform into the tubular form of prosenchyma (Plate XXVIII. fig. 32), which, as is seen in fig. 30, k, is still arranged in radiating lines, until it suddenly passes into the parenchyma of the external epiderm and of the bases of the leaves (figs. 30 & 32, l). This parenchymatous structure is one of the most regular and beautiful that I have met with. On making a tangential section of the bases of the leaves, we find that they consist entirely of parenchyma, but with a point in the centre of each scar, marking the spot where the vascular bundles penetrated the leaf, and where the parenchyma is much more dense, consisting of much smaller cells than elsewhere. The same conditions exist at the outer surface of each scar or petiole. I have not discovered any traces of the vascular bundles passing from the woody zone to the

epiderm in the longitudinal section, but I find them in the tangential section of the latter tissue.

From the above description it will be obvious that though Favularia has its own peculiarities, especially as seen in the varied character of the cells constituting the medullary axis, and in the apparent though not certain absence of all medullary vessels, its general structure indicates its close affinity with the Lepidodendroid plants; we have in both the same thick prosenchymatous bark with its thin tubular layer at the inner surface of the epiderm passing into the regular parenchyma of the petioles. These facts are important because of the obscurity which yet rests upon the history of the true Sigillariæ. No one has questioned the close affinity of Favularia and Sigillaria: the very prominent cicatrices of the former are but exaggerated representatives of the slightly projecting leaf-scars of the latter.

A remarkable specimen of *Favularia*, which appears to have borne cones, will be described in the sequel of this memoir.

Considering the abundance of Sigillariæ in the Coal-measures, it is marvellous that indisputable specimens displaying their internal organization should be so rare; but such is the case. After years of search I have only met with three specimens, of the Sigillarian character of which there can be no doubt. One of these is a portion of the epidermal layer, with five of the parallel flutings that characterize the genus, each of the depressed ridges having a breadth of nearly three eighths of an inch, the distance between the central point of one areola and of that adjoining it being rather more. On the external surface the grooves separating the prominent ridges follow a slightly wavy course, as in the Sigillaria contracta of Brongniart and several other species; but at the inner surface of the epiderm, where there are corresponding longitudinal projections, the latter are in straight lines, explaining the difference so commonly observed in the Sigillariæ found in the coal-shales between the outer surfaces and the so-called decorticated portions; the latter are, as I have already shown to be the case among the true Lepidodendra, casts of the inner surface, not of the bark, but of its epidermal portion, which has been held together by the firm layer of bast-tissue that occupies its inner surface.

The structure of what remains of this specimen is very similar to that of the one last described. Plate XXIX. fig. 35 is a transverse section, enlarged four diameters, of four of the ribs, the outer surfaces of which project into the stone. Fig. 36 represents one of these, magnified thirteen diameters. The external portion (l) consists of very regular parenchyma, which becomes exceedingly dense at its outer surface; but internally these cells assume a radiating linear arrangement, a circumstance to which I shall again call attention when speaking of the structure of Stigmaria. Still more internally (i) we have smaller prosenchyma arranged in the usual radiating lines. On turning to the longitudinal sections, Plate XXVIII. figs. 37 & 38, the latter of which is a more highly magnified representation of a portion of the former, we have precisely the outline which a corresponding section of an ordinary Sigillaria would present. The depressions (l) in the outline represent the lozenge-shaped scars left by the deciduous petioles, whilst l' are

the sloping surfaces running from the inferior margin of one cicatrix to the base of the upper prominent edge of the next below it. The inner surface of the section exhibits the prosenchymatous layer (i), which occupies about one half of the section; part of this prosenchyma consists of cells of the usual fusiform type, whilst other portions are prolonged into tubes, as amongst the Lepidodendra. I found the above specimen amongst the Lower Coal-measures near Oldham.

Though there is no question that the specimen last described is a true Sigillaria, it belongs to a type intermediate between the true Favulariæ and the Syringodendra. But Plate XXIX. fig. 39 represents three of the longitudinal ribs of a true Syringodendroid Sigillaria, from a specimen for which I am indebted to Mr. NIELD, of Oldham. The figure is of the natural size. A transverse section of a portion of this specimen, also of the natural size, is seen in fig. 40. Plate XXXX. fig. 41 represents a segment of fig. 40, magnified 15 diameters, and Plate XXIX. fig. 42, which is also enlarged 15 diameters, is a radial longitudinal section which passes through part of one of the leaf-scars.

I cannot identify this Sigillaria with any of Brongniart's species; but it unmistakably belongs to the group of S. Saullii, Schlotheimii, and scutellata, and of which his Syringodendron cyclostigma has merely been a narrow-leaved example.

The transverse section (fig. 41) merely exhibits an external layer of parenchyma (l) with an inner one arranged in regular radii, and which consists of an elongated tubular form of prosenchyma (i), an arrangement almost identical with that of the corresponding section of Favularia (Plate XXVIII. fig. 30). The longitudinal section (Plate XXIX. fig. 42) is much more interesting: at l we again have the parenchyma, the cells of which tend to an arrangement in lines which incline upwards and outwards. Immediately below each leaf-scar the cells are purely parenchymatous, but lower down, in the space between two leaf-scars, they become more elongated and fusiform than in the portion figured.

The elongated prosenchyma (i) of the inner epiderm and outer bark is very regularly arranged in elongated tubuli; but as the very thin radiating laminæ of these elongated cells do not exactly run parallel with the plane of the section, they are intersected at intervals by lines, k', giving rise to the appearance of medullary rays, an appearance also represented in the corresponding portion of Brongniari's Sigillaria elegans. That author describes this tissue as "formé de cellules allongées, très-serrées terminées par des extrémités coupées obliquement, et dont plusieurs contiguës correspondent à la même hauteur, de manière que leurs terminaisons forment des lignes transversales en zigzag"\*. The last portion of the sentence which I have italicised is, I believe, a mistake. I have no question that, in my specimen at least, the appearance is due to the cause just specified, viz. to a want of exact parallelism between the planes of the radiating laminæ of prosenchyma (seen in the transverse section, fig. 41, k) and that of the vertical section. Of course whenever the latter passed obliquely through one of the former, which it does continually, it would cut off a number of tubes in the same line, and give them the

appearance of terminating at that line, which certainly is not the case\*. The arrangement of the parenchymatous and prosenchymatous tissues in this section again corresponds very closely with that seen in the similar one of Favularia (fig. 32). But the most instructive part of the specimen is exhibited by the vascular bundle (fig. 42, m), consisting of several very minute barred vessels, and obviously surrounded by a thick mass of very delicate cellular tissue, which is parenchymatous, but with a tendency on the part of the cells to become elongated in the direction taken by the vascular bundle. Near the outer surface of the epiderm these cells become merged with the ordinary epidermal parenchyma. Where this cellular mass, in passing through the epiderm, comes in contact with the prosenchyma of the latter (fig. 42, i), the tubes of the prosenchyma all bend inwards in the line of the vascular bundle: this is the case in each instance where my sections cross a leaf-scar. It will also be seen from fig. 42, that, at these points, the prosenchymatous tissue projects (k) into the subjacent bark.

The entire thickness of this double layer has been fully a quarter of an inch. In the interior of the stone that of the opposite side is also preserved; but every portion of the intervening bark, as well as of the central vascular cylinder and medullary axis, has disappeared. The specimen is in the condition in which all the flattened stems of the Sigillariæ so common in the coal-shales doubtless have been, viz. a mere cylinder of epiderm, rendered tough and resisting decay through its inner layer of elongated fibrous prosenchyma, and having its two opposite inner surfaces brought into near proximity as soon as sufficient pressure was applied to the sides of the stem.

It is a remarkable circumstance that after the publication of the valuable and clearly illustrated observations on the structure of *Stigmaria* made by M. Brogniart, there should have been, in later years, so much misapprehension respecting this well-known plant.

The first movement in the wrong direction originated with Professor Goeppert, who described a Stigmaria ('Genres des Plantes Fossiles,' tab. 13) with vascular bundles passing longitudinally through the pith, and from which he believed the vascular bundles going to the rootlets were supplied. In this he was followed by Dr. Hooker (Memoirs of the Geological Survey of 'Great Britain),' who clearly affirmed the existence of medullary rays and bundles, but adopted Goeppert's idea as to their origin. At this stage of the inquiry a very fine pyritized specimen came into my possession, a figure of which was given by Mr. Binney in the 'Quarterly Journal of the Geological Society of London' (vol. xv. pl. iv. fig. 1, a). This specimen, and others subsequently found by Mr. Binney, made it clear that the woody axis had been surrounded by a thick, but as yet unknown

<sup>\*</sup> The mistake is mine. I have more recently obtained evidence that, even in my specimens, these long, parallel-sided cells are bounded at their extremities by the horizontal lines, k', as described by the French botanist.—May 5, 1872.

<sup>† &</sup>quot;Observations sur la structure interne du Sigillaria elegans comparée à celle des Lepidodendron et des Stigmaria et à celle des végétaux vivants. Par M. Adolphe Brongniart," Extrait des Archives du Muséum d'Histoire Naturelle, tab. 5. figs. 6, 7, & 8.

bark. In the memoir just referred to\*, Mr. BINNEY recognizes the medullary rays, but again adopts Goeppert's explanation of the origin of the vascular rootlet-bundles, and gives a figure of a specimen which he supposed afforded confirmation of this explanation, having ten or twelve large vessels, as he believed, in the pith, "each of about one tenth of an inch in diameter." The largest vessels which I have seen in the woody stems of Stigmaria do not exceed .005 in diameter, whilst those going to the rootlets are generally much smaller. I have elsewhere called attention to the way in which the rootlets of Stigmaria have penetrated every thing within their reach that was penetrable; and I have no doubt that in both Professor Goepperr's and Mr. Binney's specimens, these supposed medullary vessels were really Stigmarian rootlets that had found their way into the interior of the cavity left by the decay of the medulla, and been mistaken for a part of the plant into which they had intruded themselves †. Mr. BINNEY, in 1857, discovered the structure of the rootlet of Stigmaria, and also gave the first insight into the nature of the outer bark. In some specimens supplied to him by Mr. Russell, of Airdrie, he found remains of an outer radiating cylinder, at a considerable distance from the inner one, and upon which the rootlets were planted. This outer cylinder Mr. BINNEY described as consisting of "wedge-shaped masses of tubes or elongated utricles". With this discovery progress virtually ceased. The subsequent history has mainly been one of retrogression. Notwithstanding the clear statements of Hooker, and the equally accurate figures of Brongniart, it has become the fashion to deny the presence of medullary rays in Stigmaria. This has been done on several occasions by my friend and fellow labourer in this field of research, Mr. CARRUTHERS; but I think I shall be able to demonstrate that, for once, his usually accurate powers of observations have failed him, owing partly to his not having seen the best specimens, and partly to his general objection to the recognition of medullary rays in the stems of these Palæozoic Cryptogams. Mr. Carruthers states that he has met with one specimen in which the central axis exhibits elongated scalariform cells. Not one of my numerous specimens contains a trace of any such structure. I speak with hesitation as to the cells of the central part of the medulla, because even when present these cells are almost always disintegrated; but so far as the more peripheral ones of the pith of the true Stigmaria were concerned, I have the clearest proofs that they never were barred.

I am convinced that one cause of the discrepancies that exist amongst writers on this subject has been the want of an exact definition of a *Stigmaria*, several very distinct roots having been included in the term. But the plants described by Brongniart,

<sup>\*</sup> Some observations on Stigmaria (loc. cit. pl. iv. fig. 2).

<sup>†</sup> I have before me at the present moment a section of a large Lepidodendron of which the woody axis and its medullary centre have disappeared, the thick cortical layer alone remaining. A large Stigmarian root has found its way into the cavity and filled it up, giving off its peculiar rootlets within the Lepidodendroid cylinder. Such a specimen would inevitably mislead even a botanist, whose eye was not familiar with the appearances of the two plants.

<sup>‡</sup> Philosophical Transactions, 1865, p. 593 and woodcut 4.

HOOKER, and BINNEY have such distinctive features that they ought not to be mistaken for any other. I shall now proceed to show what those features are. I must add that for some of the most remarkable specimens which have enabled me to throw additional light upon this subject, I have been indebted to Messrs. NIELD and WHITTAKER, of Oldham. Others have either been furnished by Mr. Butterworth, or found by myself. Of the figures accompanying this memoir, Plate XXX. fig. 43 is a portion of a longitudinal radial section of a part of the woody cylinder at its inner or medullary surface. In this figure, n is a vascular bundle passing outwards through a large medullary ray. Plate XXIX. fig. 44 is a corresponding section of the outer part of a similar cylinder. Plate XXIX. fig. 45 is a tangential section from the interior of the woody cylinder, revealing one large or primary, and numerous smaller or secondary medullary rays. Fig. 46 is a still more enlarged section of part of fig. 45, with two vessels and several secondary medullary rays. Plate XXX. fig. 47 is a transverse section of part of the medullary or inner portion of the woody axis, with a primary medullary ray and a vascular bundle going off to one of the rootlets. Fig. 48 is part of the external surface of the ligneous cylinder. Fig. 51 is a transverse section of part of the epiderm with the attached bases of three rootlets. Plate XXXI. fig. 52 is a further enlargement of another rootlet with the epidermal layer from which it springs, and fig. 53 is a diagrammatic restoration of the entire plant. Each of these structures requires to be examined in detail.

Several of the specimens which I have examined exhibit more or less of the medullary axis, especially one given me by Mr. Whittaker, of Oldham. It consists of delicate parenchyma, which is better preserved where it is in contact with the ligneous zone (Plate XXX. figs. 43 & 47, a) than in the more central portions, where it has been more liable to become disorganized from some unknown cause. The cells have a diameter of from .005 to .0025. There is not a trace of any spiral or barred structure in the cell-walls, nor of any medullary vessels such as are common in many of the Lepidodendroid stems.

The woody zone consists, as is well known, of a cylinder of radiating wedges which increase in size from within outwards. These wedges are composed of large barred vessels arranged in radiating lines, and in the most regular order. The external surface of the zone, as seen in one of Mr. Whittaker's fine specimens, is represented in Plate XXX. fig. 48, which exhibits a disposition of the structures recurring in every tangential section made from any part of the woody cylinder, and which disposition is one essential characteristic of a true *Stigmaria*. The woody wedges (fig. 48, e) alternately approximate and diverge, leaving, in the latter case, large lenticular spaces (f') filled with muriform cellular tissue passing straight through the entire ligneous zone, and which are the medullary rays of Brongniart and Hooker. The vessels (e) have a diameter which varies from 0025 to 005. On making a tangential section like Plate XXIX. fig. 45, we see that the lenticular orifice is a large medullary ray (f'), which may be distinguished by the name of primary. It consists, as seen in the section,

of ordinary but very delicate parenchyma, which gradually thins out, upwards and downwards, into a single interrupted row of cells. This latter part connects these larger medullary rays with a multitude of smaller or secondary ones (f) seen in the same section. Sometimes these consist only of one single cell: more frequently we see two or more arranged in a single vertical series; and from time to time still larger ones occur with two or even more parallel vertical rows of these cells, thus approximating their arrangement to that of the primary rays. The cell-walls of these secondary medullary rays are so exceedingly delicate and thin that it is not easy to trace them through the radial longitudinal sections of the ligneous axis; nevertheless careful manipulation of the light enables the observer to do so. At their inner or medullary extremity all these rays, primary and secondary, take their rise in, or rather are merely prolongations of the cellular medulla, the parenchymatous cells of the latter (Plate XXX. figs. 43-47, a) being unaltered in shape or arrangement in the immediate neighbourhood of these radial prolongations of the pith; but on entering the medullary ray they soon become mural, being elongated in the direction of the ray. This elongation is seen equally in transverse sections (fig. 47, f') and in radial ones (Plate XXX. fig. 43, f', & Plate XXIX. fig. 44, f'). At their outer extremities (fig. 44, g') they merge in a corresponding manner in a delicate cellular tissue (fig. 44, g), which constitutes the innermost layer of the bark.

We see in the transverse sections of the woody cylinder very clear evidences of successive and interrupted exogenous growths. At each of these lines the continuity of the radiating lines of vessels becomes wholly interrupted and a new series commences. These new vessels are at first very small and irregularly disposed, but, as we proceed outwards, they soon resume their regular arrangement and size. In one of my sections I have clear evidence of a new circle of these small and irregularly disposed vessels forming externally to the entire cylinder, as if in a cambium layer. These additional layers are not always added equally to the entire circumference of the Stigmaria; they sometimes only surround some two thirds of that circumference, as is not unusual amongst living Exogens. But the most remarkable feature of the woody zone is supplied by the vascular bundles given off to the rootlets, and which reach them exclusively through the primary medullary rays. On making a tangential section of any portion of the woody cylinder, we discover appearances which are virtually repetitions of what is seen in Plate XXX. fig. 48, the latter being merely the external surface of the ligneous zone, which exhibits the same arrangement of tissues in all sections made parallel to that surface. The bundles of vessels (e), which are really the external surfaces of the radiating woody wedges seen in the transverse sections, alternately separate and reunite, leaving the large lenticular areas (f') constituting the primary medullary rays already described. As one of these rays proceeds outwards, the vessels bounding its sides at the upper angle detach themselves from the wedges to which they severally belong, and combine to form what, in the tangential sections, appears as a tongue-like projection hanging down (Plate XXIX. fig. 45, n, & Plate XXX. fig. 48, n) into the ray. A radial

section made in the plane of this tongue, shows us that the vessels composing it are deflected outwards (Plate XXX. fig. 43, n') at right angles to their previous course. the section fig. 43 the cells of the part of the medullary ray bounding the remoter side of this mass of deflected vessels are seen at f''. Fig. 47 is an oblique transverse section passing through the inferior keel-like edge (n) of this vascular mass at the innermost part of its course, and exhibiting the derivation of its component tissues from the two vascular wedges (e, e) bounding the medullary ray through which it ploughs its way outwards. Plate XXIX. fig. 44 is a radial section from the external portion of the ligneous cylinder, where we still find even the outermost of the vessels (e) contributing their share to this vascular root-bundle (n), the letters f in this section indicating the external portion of the medullary ray just previous to its becoming merged with the inner bark (g). follows that an enormous number of the vessels directly vertical and superior to each primary medullary ray have their lower extremities bent outwards; but when we examine the ultimate bundles (Plate XXXI. fig. 52, n') that leave the exterior of the woody cylinder and pass through the bark to the rootlets, we find that the number of vessels composing them is very limited, rarely reaching twenty. Hence it is evident that the greater part of the deflected tubes never reach the rootlets, but successively disappear in the tongue-like projections seen in Plate XXIX. fig. 44, n, & Plate XXX. fig. 43, n.

With the exception of the portion of the exterior noticed by Mr. Binney, the cortical layer of *Stigmaria* has not yet been described; but a series of specimens in my cabinet, and in those of my coadjutors, enable me to fill up this hiatus in the history of the plant.

I have already pointed out that the exterior of the ligneous cylinder is invested by a thin layer of very delicate cellular tissue (fig. 44, g), the cells of which are somewhat elongated vertically (Plate XXX. fig. 49, g)\*. In other respects they are almost identical with those of the pith, and wholly so with those of the medullary rays, save in the direction of their longer axes. In a large majority of the examples which I have seen this tissue is the only representative of the bark that is preserved; but I have several specimens which, when combined, give me its entire substance. The thin layer of delicate cells seen in fig. 49, which is not above 015 in thickness, soon passes into a thin stratum of equally delicate parenchyma, which in its turn passes into a very thick layer consisting of an irregular and variable mixture of prosenchyma and parenchyma, but principally the former. In transverse sections these tissues are seen arranged in very narrow but regular radiating lines, each of which usually has a breadth of about The appearance in this section is that of a coniferous wood with very delicate fibres; but on making either a radial or a tangential section, the tissues forming this part of the bark usually appear as represented in Plate XXXI. fig. 50. It will be seen from this figure that whilst some of the cells have pointed and overlapping extremities, others have slightly oblique, and others, again, square ends. The tissue has evidently

<sup>\*</sup> It is impossible to overlook the close resemblance which this tissue bears to that seen investing the vascular bundles of the living Lycopods, and to which Nägell and Sachs have given the appropriate name of procambium, —May 6, 1872.

been prosenchymatous in its general character, but of a very corky form. This is not only shown by the large amount of parenchyma which enters into it, but also in its extreme liability to compression. In one of my specimens this compression from without has given the transverse section an appearance of numerous concentric bands arranged parallel with the surface of the ligneous zone; an appearance which puzzled me the more, since this was the first example in which I found the entire bark. Other examples subsequently coming into my hand threw light upon the perplexing arrangement. Numerous little apertures exist in this bark, through which, I doubt not, the vascular bundles passed to reach the rootlets.

The portion of the bark which is most frequently preserved is the epidermal layer, the structure of which is interesting because of its relation to that of the rootlets long since described by Mr. Binney. Plate XXX. fig. 51 represents a transverse section of this epiderm with the bases of three of the rootlets implanted in it, whilst Plate XXXI. fig. 52 represents the same tissue yet further enlarged, from another specimen lent to me by Mr. Boyd Dawkins. As will be seen from the latter figure, the epiderm consists of a very regular form of thick-walled parenchyma (1), the cells of which become very much smaller and more dense as they approach the outer surface. Internally this parenchymatous layer is continuous with a more delicate one (k') of the same character but with thinner cell-walls, and the cells of which soon become vertically elongated and arrange themselves in straight lines radiating inwards, as in Sigillaria. This is doubtless the radiating cylinder seen by Mr. Binney in Mr. Russell's specimens previously referred to, only instead of being arranged in wedge-shaped masses, as represented by Mr. Binney, a result of the imperfection of his specimen, it is a perfectly continuous layer, and doubtless represents the exterior of the bast-layer of the Lepidodendroid type. The thickness of this outer bark is unequal, in consequence of the depressions (Plate XXXI. fig. 53, p) that receive the proximal extremities of the rootlets, whose bottle-like bases, when perfect, as in fig. 51, o', are implanted in concave depressions of unequal depths, displacing both parenchyma and prosenchyma. The external cellular cylinder of the rootlet (o) is merely an extension of the thick-walled outer epiderm k, and is not in any way articulated to the prosenchymatous tissue. Within this is a space (Plate XXX. fig. 51, o', & Plate XXXI. 52, o') in which I have never seen the tissue preserved in rootlets which could be proved to be Stigmarian. Myriads of rootlets exist in the calcareous nodules from which our Lancashire specimens are obtained, of which all the cellular structures are preserved from their central vascular bundle to their periphery; but these, I am convinced, belong to other plants than that under consideration. In the centre of the vacant space we have the vascular bundle (n), which, though always intersected in some part of the section, can rarely be traced far in one plane because of the flexures of the rootlets. The central axis of about twenty barred vessels is always surrounded by a thin cylinder of delicate cellular tissue. Wherever we see these vascular bundles in the bark between the woody cylinder of Stigmariæ and the epiderm, we inva riably find this cellular ring surrounding the vessels, as at fig. 52, n'; it is continuous with

the innermost bark and with the cells of the primary medullary ray through which the bundle emerged. It appears at fig. 51, n'', where the bundle is entering the rootlet, and it equally reappears if we intersect the latter at its extreme tip. The epidermal tissues immediately subjacent to each rootlet are always dense, consisting of small parenchymatous cells, which show a tendency to arrange themselves in radial lines (fig. 51, k). When the vascular bundles are intersected between the woody zone and the epidermal layer, their outline is usually that of a triangle with convex sides, as seen at fig. 52, n'. Plate XXXI. fig. 53 is a restored diagram, exhibiting what I believe to have been the structure and form of Stigmaria in its integrity. The several parts of this diagram will be easily identified with the details of the preceding description, because the same letters have been employed in both to represent corresponding tissues.

I have frequently found in the Lower Coal-measures at Oldham fragments of a very curious bark that long perplexed me, because I was unable to discover it in association with any woody axis. In one example it appeared partially to surround a Diploxylon; but as the portion on one side of the ligneous cylinder appeared to be in a reversed position to that on the other side, I both hesitated to connect them and was unable to decide which was the inner and which the outer surface of the bark. On cutting vertically through a part of the specimen represented in Plate XXVIII. fig. 33, and which is essentially a Diploxylon, I again found the anomalous bark associated with this type of ligneous cylinder, and under such circumstances as left me little room to doubt that it belonged to the same plant. The general appearance of these fragments, when cut transversely, is shown in Plate XXXI. fig. 54. Spaces of a lenticular form (h) radiate towards the periphery\*; these are filled with cells, whose parallel sides cross the short axis of each space. The long axis of each cell is often as much as '0075 in length and ·005 in the opposite direction. At one extremity these lenticular masses show a disposition to converge at irregular projecting points; at the other they gradually pass into regularly disposed lines of narrow prosenchyma (h'). The lenticular masses of cells exhibit nearly the same appearance in the radial section that they do in the transverse one; but a tangential section exhibits the cells in fasciculi (fig. 56), where small clusters of them are seen enclosed within dark and strongly defined areas of a doubtful nature. In the regularly arranged prosenchymatous portions the tangential and radial sections are very different from the transverse ones, and, indeed, they vary in different specimens. Fig. 55 is a radial section of a strongly marked type, in which the prosenchymatous cells appear to be of nearly equal lengths and with square ends, so much so, indeed, as to resemble some varieties of mural tissue common amongst the Calamites; but in the tangential section (fig. 56) we see that they are prosenchymatous, but of a very sharply defined geometric type, with straight walls and very distinct angles. But in many other speci-

<sup>\*</sup> I have just met with an example of Stigmarian bark, with its characteristic rootlet attached, in which the structure represented in fig. 54, h, occurs, intermediate in position between the outermost parenchyma and the more internal radiating prosenchymatous layer, blending the two: whether it is merely a variety, or belongs to the Stigmarian root of some distinct species of Lepidodendroid plant, has yet to be ascertained.—Aug. 6th, 1872.

mens which I have dissected, this geometric character is less obvious, the prosenchyma assuming in them the aspect so common in the bark of Stigmaria. On a fragment of the specimen fig. 33 there are indications that the bark has been very thick\*, and that the portion represented by fig. 54, n, has not been far removed from the woody cylinder, though not being actually the innermost bark. The more external parts consist of radially arranged prosenchyma, but with an appearance of a second row of lenticular masses of large cells external to, and of smaller size than, that first described. I have noticed an approach to all these peculiar arrangements in some specimens of the bark of the common Stigmaria, which has evidently varied in the details of its structure, the variations possibly representing different genera and species of Lepidodendroid and Sigillarian plants.

The only specimen which remains to be described is a very important one which I discovered in the cabinet of Mr. NIELD. It is a cast or impression of the outer surface of a Favularia (Plate XXXI. fig. 58), of a very strongly marked type and with very prominent leaf-scars. But its value consists in the exhibition of a transversely disposed verticil of lozenge-shaped scars (fig. 58, r) of a very remarkable character. The figure is enlarged to double the size of the original, in which, being a cast, what are now prominences represent corresponding depressions on the surface of the original bark. The centre of each lozenge-shaped disk consists of a small but prominent circular area; this is surrounded by a ring of much smaller tubercles. Each disk is located at a point where the vertical continuity of the lines of leaf-scars, always so regular in ordinary specimens, is broken, those below the disks being arranged in an alternating series with those above them. It is evident that we have here an hitherto undescribed feature in Favularia; but, on discovering the specimen, it occurred to me that I had frequently observed, in the ordinary examples of the so-called "decorticated" Favularia, transverse bands crossing the stems, along which the regularity of the leaf-scars was interfered with and their distinctness blurred. Brongniart has represented a specimen of this kind in tab. 155 of his 'Histoire des Végétaux Fossiles,' though in his plate the break in the continuous lines of leaf-scars is less marked than is often the case. On examining the Favularia in my cabinet, I found one in which the subepidermal surface displayed the same interruption, but over a part of which there remained the usual layer of coal representing the superficial tissues. On the exterior of the latter I found several scars similar to those of fig. 58. I think there can but be one conclusion respecting these cicatrices. They did not bear leaves, because these are represented by the usual scars above and below them. They are much too small for ordinary branches, besides which, verticils of branches are unknown things amongst these Sigillarian and Lepidodendroid plants. I conclude, therefore, that they supported a row of cones. Now it so happens that one of

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<sup>\*</sup> I have more recently met with another example in which the outer prosenchymatous structure was nearly  $1\frac{1}{2}$  inch thick; it was of the type containing a mixture of ordinary and fusiform cells, the latter elongated vertically and having a length of about 015. The arrangement exhibited irregularly alternating concentric layers of prosenchyma and parenchyma, the one gradually passing into the other.

the most common of the Lepidodendroid strobili in the Lower Coal-measures of Oldham is a small one, of the central axis of which I have given a representation in fig. 59, enlarged two diameters, or in the same proportion as fig. 58. Of course I cannot affirm that the two are actually portions of the same plant; but it is enough for my present purpose to indicate the possibility of such a relation. The correspondences of size, the similar central area in each, and the vascular ring surrounding that area present coincidences too striking to be overlooked.

It will have been observed that I have said nothing about that remarkable form of Lepidodendroid plant, the *Halonia*. The fact is, I have not been able to obtain specimens throwing any light upon this subject beyond what has already been done by Mr. Dawes. His figure and description, given in the Proceedings of the Geological Society of London for March 22, 1848, are so clear that there can be no difficulty in locating the plant in its proper place. The central axis consists of cells arranged as in my Plate XXVI. fig. 13, Plate XXV. fig. 14, & Plate XXVII. fig. 25, this is surrounded by a cylinder of barred vessels, as in fig. 13, from the outer surface of which the vascular bundles going to the bark are given off.

The late Mr. James Wilde, of Oldham, published a notice in the 'Geologist' for 1863, p. 266, in which he states that a specimen of *Lepidodendron* with an *Halonia* attached settles in the affirmative the question whether or not the latter is the root of the former. Through the kindness of Mr. Nield, in whose cabinet the specimen now is, I have had the opportunity of examining it, and conclude that it does no such thing; it merely shows, what we knew before, that *Halonia* is part of a Lepidodendroid plant.

A fragment of an *Halonia* furnished to Mr. Dawkins by Mr. Whittaker, of Oldham, shows that the projecting tubercles which characterize *Halonia* are of the same nature as the scars of *Ulodendron* which I have already described, viz. that they consist of the outer bark which has here pushed up into the epidermal layer, the latter being deflected along their sides. I have little doubt but that the *Halonia* was a fruit-bearing branch of a *Lepidodendron*, and that from each of the tubercles there was suspended a cone \*.

\* Since the above was written, I have obtained a considerable amount of information on this subject. Two fine specimens in the Museum of the Manchester Geological Society, not only throw light upon the condition just described, but also upon the relations of Halonia and Ulodendron. One of these specimens is a fine Halonia regularis, of the usual type, but which is further invested with a thick bark, showing that the examples of this plant so commonly seen are semidecorticated ones, and that the characteristic tuberculated surface is not the outermost one. I may premise that my more recent investigations have compelled me to alter some of the terms applied in this memoir to the several parts of the bark, in order to bring them into harmony with what I find in recent Lycopodiaceæ; consequently in a third memoir, recently laid before the Royal Society, I have designated the middle bark (h) of this paper the parenchymatous layer. The outer bark (i and k) I have termed the prosenchymatous layer, and what I have called the epidermal (l), I now designate the subepidermal layer. The detailed reasons for employing these terms will be given in the memoir referred to, meanwhile they may be applied to the specimens under consideration. In the new Halonia, the conical mammilliform tubercles evidently projected entirely through the prosenchymatous layer, and through a great part of the subepidermal one, a thin expansion of the latter alone appearing to invest the apex of the tubercle; and even here there is a small central mucro which exhibits every indication that it accompanied something which projected entirely

Having thus reviewed all the principal facts that have come under my personal observation, and I have almost entirely confined myself to such, it now remains to be seen what general conclusions can be drawn from them. We began with a Lepidodendroid plant, L. selaginoides, in which we found the medullary axis largely occupied by a great number of scalariform vessels; but we saw that these were not arranged in radiating order, neither did they give off any vascular bundles to the leaves. These bundles were confined to the inner surface of a very narrow, but nevertheless distinct, enclosing circle of somewhat smaller vessels, between which, and passing radially outwards, were vertically disposed rows of cells, which I believe to be true representatives of medullary rays, whilst the thin cylinder through which they pass is the woody zone separating medullary from cortical structures. The bark we found to be thick, consisting of varying elements of parenchyma and prosenchyma, but chiefly the latter; and near the outer surface we discovered a layer of prosenchyma, where the cells are so elon-

through the bark, being, in fact, an investure of the vascular tissue accompanying the latter to whatever organism the tubercle helped to sustain.

It thus appears that these outer layers of bark, having an aggregate thickness of from three eighths to half an inch, filled up the deep valleys separating the conical hillocks of the *Halonia*, and almost reduced the entire surface of the plant, when living, to a uniform level. These determinations bring the minute and geometrically arranged punctations covering the surface of the *Halonia* into homological relations with similar markings seen on other semidecorticated Lepidodendroid plants.

The other specimen to which I have referred is a very large example of one of the round or oval scars so characteristic of *Ulodendron*, but which, instead of being more or less depressed, as is commonly the case, stands out as a projecting cone at least 3 inches above the semidecorticated surface from which it rises. If this cone represents, in *Ulodendron*, the mammillary protuberance of *Halonia* (and that it does so I entertain no doubt), its height gives us a measure of the extreme thickness of the prosenchymatous and subepidermal layers of the plant to which it belonged.

The above specimens having again drawn my attention to *Halonia*, I gladly availed myself of some specimens collected and placed in my hands by my friend W. Boyd Dawkins, Esq. On making sections of these I discovered that the vascular axis consisted of a very distinct vascular medullary cylinder enclosing a well-marked cellular medulla; there was no exogenous zone around the cylinder, but in its place a circle of remarkably numerous and closely disposed vascular bundles, each one of which originated from a groove in the exterior of the medullary cylinder, and which in the transverse section formed a little bay, with the corresponding section of the bundle in its concavity. The cortical tissue consisted of the parenchymatous layer (h), with here and there slight traces of the more external prosenchymatous one (i), the remaining tissues having disappeared.

It is thus clear that, as I have already suggested, the specimens of *Halonia* with which collectors are familiar are branches which have lost the two outer layers of their bark. It is also obvious that the structure of *Halonia* and that of the branch represented in Plate XXVI. fig. 24 are identical; only in the latter specimen the exterior of the vascular medullary cylinder is not quite perfect, since throughout the greater part of it the external indentations with their enclosed vascular bundles have almost all disappeared. A few, however, remain showing that they were originally present, as in my sections of *Halonia*. On the other hand, fig. 24 & Plate XXVII. fig. 25 exhibit the prosenchymatous and subepidermal layers of the bark, which are deficient in Mr. Dawkins's specimen.

Still more recently specimens of the greatest importance, and of most exquisite beauty, have been supplied to me by Mr. Whittaker. From these I can easily make out almost the entire structure of the stem of *Halonia*. The cellular pith and investing medullary cylinder are arranged in our new examples as already described. The vascular foliar bundles appear as in Mr. Dawkins's specimen; but we further learn from them the exact

gated as to constitute a distinct bast-layer, which has exhibited a constant tendency to separate itself from the other subjacent cortical tissues. Outside this bast-layer we have the superficial epidermis, consisting of thick-walled parenchyma, which also constitutes the tissue composing the bases of the leaves.

These arrangements are repeated with variations of detail throughout the entire Lepidodendroid series. In Mr. Binney's Sigillaria vascularis (Plate XXV. fig. 8) we find the vascular part of the medullary axis retreating towards its periphery, but with an undefined inner margin. In Diploxylon there is reason to believe that it had become altogether peripheral, and had a sharply defined inner boundary line, though this latter fact cannot be absolutely affirmed until a specimen is found with the whole of the medullary tissues preserved. In the same two plants we find a corresponding advance in the thickness of the radiating woody cylinder and in the development of the medullary rays. The other genera allied to Lepidodendron exhibit structures of the same type. In

structure of the entire bark, as well as some other important points in their history. Immediately surrounding the medullary vascular cylinder is a layer of delicate parenchyma, the cells of which average about ·166 in diameter; these cells are arranged in columns which proceed obliquely upwards and outwards, diverging from the perpendicular at an angle of about 35°. The entire thickness of this innermost parenchyma is about the eighth of an inch (·125). Externally to it is the ordinary coarser parenchymatous layer, invested in its turn by the prosenchymatous one, which again is enclosed in what I have recently designated the subepidermal parenchyma. Thus we here see distinctly exhibited the four layers of bark of which I have spoken in other parts of this memoir. The ordinary foliar vascular bundles, given off in great numbers from the outer surface of the medullary vascular cylinder, ascend upwards and outwards at the same angle as the cells just referred to (35°), until they reach the exterior boundary of the innermost parenchyma, when they suddenly bend outwards in a horizontal direction, describing a slight curve as they do so, the concavity of which is directed upwards. Each vascular bundle is invested with a delicate cellular sheath, which is a prolongation of the innermost parenchyma of the bark.

But in addition to these bundles, I have now obtained the larger ones, which proceed to the tubercles characteristic of Halonia, and which are very different from the ordinary foliar ones. In the first place, the former are very much larger, consisting of many more vessels than is the case with the latter; they are accompanied in their outward course by a yet thicker investment of the cells of the inner bark-layer. But the most remarkable difference is seen at their point of departure from the vascular medullary cylinder; they are not merely derived, like the foliar bundles, from the exterior of that cylinder, but the entire mass of the vessels of the latter, immediately below the bundle, are absorbed into it. The consequence is that directly above the bundle there is a slit in the medullary cylinder unprovided with vessels, and where the parenchyma of the pith and that of the innermost bark blend their cells into a continuous tissue. This slit ascends for some little distance up the stem, but the vessels on each side of it gradually converge and ultimately close it up. These peculiarities in the origin of the vascular bundle in question appear to me to be of great physiological importance; they can only be understood when compared with conditions connected with the branching of Lepidodendroid plants that I have described in the third memoir of this series read to the Royal Society on the 7th of March last. I there showed that, prior to dividing into two branches, the vascular cylinder split into two halves, bringing the cells of the pith and of the bark into direct contact. It is evident to me that the arrangements in the Halonia just described are of the same nature, only instead of half the entire cylinder being split off, but a small portion of it is so separated. I infer, therefore, that the vascular bundle, thus originated, proceeded to some modification of a branch -but which modification was of smaller dimensions than branches usually attained to, and which, consequently, required a less abundant supply of vascular tissue than ordinary branches needed. Such a modification would,

Ulodendron the innermost surface of the vascular ligneous cylinder is present, though very small compared with the large medullary one, approximating very closely, in this respect, to the Lepidodendron represented in Plate XXVI. fig. 13, Plate XXV. fig. 14. Not having a transverse section of the central axis of Favularia (Plate XXVIII. fig. 31), I cannot be certain about its details; but we have in the longitudinal section evidence of a vascular mass, though whether it be medullary or ligneous I am not able to affirm; but Brongniaria elegans, which is a true Favularia, demonstrates the close resemblance which its central axis bears to that of a Diploxylon. Wherever we are able to trace the origin of the vascular bundles going to the leaves, in Diploxylon, we

I imagine, only be found in a strobilus, which must be regarded as a branch that has undergone an arrested development at a very early stage of its growth.

Guided by these new observations, I have reexamined the curious specimen found by the late Mr. James Wilde and referred to on p. 222. This is a semidecorticated branch of an ordinary Lepidodendron, having a diameter, as it appears in its stony matrix, of about  $2\frac{1}{2}$  inches. This stem divides into two smaller branches, one of which is also that of an ordinary Lepidodendron; the other displays the same Lepidodendroid features on its upper half, but what constituted its underside, when a growing plant, exhibits rows of the characteristic tubercles of Halonia. We here learn two things:—First, that Halonia belongs to the upper branches of a Lepidodendroid tree, consequently it cannot be a root. This may be regarded as finally settled. The same truth is demonstrated by Mr. Whittaker's specimens: in these the large vascular bundle going to each tubercle bends upwards and outwards in the same way as the foliar bundles with which it intermingles. This fact alone would be a conclusive one against the root hypothesis. Secondly, we learn that Halonia is a specialized branch of a Lepidodendroid tree that is not itself an Halonia; and as I have already given reasons for believing that each tubercle sustained an abortive branch, it appears to me that we are shut up to the conclusion that these arrested developments could only exist in the form of strobili.

I think there can be little doubt that the innermost cortical layer, prolongations of which invest *all* the vascular bundles proceeding from the medullary vascular sheath to the periphery, must be regarded as the homologue of what Sachs, following Nägeli and Leitgeb, has termed the procambian layer in living Lycopods, and which, as we shall see, reappears in *Stigmaria*.

The important truth demonstrated by the specimen in the Manchester Museum, and one with which all the other specimens that I have mentioned appear to harmonize, is, that the projecting tubercles of Halonia and Ulodendron were confined to the inner prosenchyma of the bark, of which they were conical extensions surrounding and accompanying a fibro-vascular bundle on its way outwards to the surface, but that they did not appear in any marked form, if at all, save as a scar, on the exterior of the plant. No such tubercular provision was made for the very numerous leaf-bundles, and we have abounding proofs that the tubercles had nothing to do with the ordinary branches of the plant. It appears to me that nothing remains with which we can associate them but strobili, and with these I believe them to have been connected. Every new fact that we  ${\it discover\ appears\ to\ me\ to\ bring\ the\ two\ genera\ \it Halonia\ and\ \it Ulodendron\ into\ nearer\ relationship\ than\ has\ hitherto}$ been recognized. I have very little doubt that the Halonia were young branches sustaining rows of cones: after the cones fell off, they would leave permanent cicatriculæ impressed upon the bark, and which would enlarge as the stems increased in magnitude, the latter process being probably accompanied by the development of an exogenous zone around the medullary cylinder. Specimens of these old and matured fruiting stems may exist among what we have hitherto termed *Ulodendra*. This explanation would give us the reason why we never find cones or other appendages of a magnitude corresponding with the cicatricula of Ulodendron. The chief argument against the idea that the cicatriculæ of Ulodendron may be those of Haloniæ enlarged by age and growth, lies in the fact that the leaf-scars of Ulodendron do not appear to have undergone any corresponding enlargement.—April 15, 1872.

invariably find that they proceed from the inner surface of the outer or ligneous cylinder, and not from the larger vessels of the medullary one, and it is in the same radiating cylinder that we find the medullary rays\*. I have already stated my reasons for insisting upon the recognition of the medullary character of these rays, and pointed out the necessity for considering their primary origin in the nascent structure, prior to any material differentiation occurring in its tissues, if we are to arrive at a philosophical opinion respecting their nature. All these circumstances combined lead me to the conclusion that in the radiating vascular cylinder we have the representative of the woody zone of exogenous plants. This zone is at its minimum of development in such Lepidodendra as Plate XXIV. fig. 1 & Plate XXVI. fig. 13, whilst it attains to a maximum in some of the Diploxylons, the former bearing some such relation to the latter as the half-developed woody zone of a Cycad does to that of a hard-wooded Pinus or Araucaria. This opinion receives further support from the unmistakably exogenous growth of this zone. The radiating arrangement of its vessels is suggestive of the conclusion; but we can further see, in many of the stems, clear evidences of interruptions to growth succeeded by periods of renewed vital activity. If this reasoning is sound and the conclusion arrived at correct, the latter gives us an unmistakable clue to the remaining tissues. The thick parenchymatous and prosenchymatous structure investing the woody zone is clearly a bark, although not, it is true, divisible into the three layers of epiphlœum, mesophlœum, and endophlœum; but in the enormous development of elongated prosenchymatous fibres or bast-tissues in the inner layer of the epidermis, we have a manifest foreshadowing of that prevalence of the same tissue in the bark of living Exogens. M. Brongniart has already called attention to the close resemblance which the thick cylinder of medullary vessels found in his fragment of Sigillaria elegans bore to the ordinary medullary sheath of an Exogen, and I cannot resist the conclusion that these are homologous structures. It appears to me that these specimens of fossil Cryptogams explain the development of the exogenous medullary sheath, through the gradual separation of the vessels from the parenchymatous elements of the pith, until they constitute a distinct ring; the light thus thrown upon their origin further explaining why the ring of spiral vessels never recurs in the newer woody layers as they ought to do, if, as has been generally supposed, they belong to the inner part of the first formed ligneous zone, rather than to the pith which that zone incloses. It appears to me that this reasoning is justified by the facts upon which it is based. The principal weak point in it lies in the circumstance that in Exogens the spiral vessels supplied to the ribs of the leaves are derived from the medul-

<sup>\*</sup> M. Brongniart, in his various writings, distinguishes the Lepidodendra from the Sigillariæ by the supposed absence from the former of the radiating woody cylinder; but his knowledge of the structure of the Lepidodendra was limited to the one specimen of Lepidodendron now become historically famous under the name of L. Harcourtii. The series of specimens which I have described demonstrates a gradual transition from the one type to the other, with which the French savant was necessarily unacquainted. He concluded that the vascular cylinder of L. Harcourtii solely represented the inner vascular cylinder of Diploxylon, which is certainly not the case. M. Brongniart had not seen the thin outer ring of small barred vessels occurring in plants of the type of L. Harcourtii as seen in my Plate XXV. fig. 14.

lary sheath, whilst in these fossil Cryptogams they are given off from the more external woody cylinder\*; but this difference may be explained by the fact that in the former plants the spirals of the medullary sheath are altogether different from the non-spiral ones in the woody zones, whilst in the latter the two classes of vessels have the same structure, and differ only in size. Hence in the Cryptogams the one set may be substituted for the other, which could not be done in the ordinary Exogens.

My supposition respecting the relations subsisting between the inner vascular ring of Lepidodendron and the medullary sheath of Exogens receives fresh support from the structure of Stigmaria. In the latter plant, now well known to be a Sigillaroid root, we find no inner or medullary cylinder of vessels. The ligneous zone receives a wonderful development; it is furnished with an abundance of medullary rays, and gives off numerous vascular bundles which are supplied to the epidermal rootlets that here occupy the place of leaves. We have here a parallel state of things to that seen in the roots of Exogens, in which in like manner the medullary sheath is wanting. This curious coincidence has not escaped the observant eye of M. Brongniart, who calls attention to it in his memoir on Sigillaria elegans.

My specimens throw no direct light upon the structure of the vascular and medullary axis of the true Sigillariæ as distinguished from the Favularian type; but the cortical portions of all the plants, including the true Sigillariæ, exhibit what is practically an identity of structure. In all we have a remarkably thick spongy bark, reminding us in many of its features of that found in the living Cycads. This consisted either of parenchyma, prosenchyma, or of both combined, enclosed externally in a bast-layer of elongated prosenchymatous tubes, which in turn is invested by a layer of cellular parenchyma supporting the bases of leaves, the latter invariably consisting of the same form of parenchyma as the epiderm. M. Brongniart's specimen of Sigillaria (Favularia) elegans exhibits a central axis, the structure of which is nearly identical with that of my Plate XXVIII. figs. 33, 34. This, in its turn, only differs from the more ordinary forms of Diploxylon, in the crenulated outline which separates the ligneous zone from the cylinder of medullary vessels, giving to the exterior of the latter a fluted aspect like that of a Calamite, but without the transverse nodal constrictions of the latter genus. Diploxylons again, as I have already shown, shade off into the ordinary forms of Lepidodendron, and are undoubtedly Lepidodendroid plants which have lost the central portions of their medullary axes. Remove the cellular tissues from the centre of the plant which I have represented in figs. 8 & 9, and we have, at once, the closest resemblance to WITHAM'S Anabathra and Corda's Diploxylon, as well as to those now under consider-That WITHAM's plant is identical, in type, with mine, is further indicated by his tab. 8. fig. 12, where he exhibits one of the large compound medullary rays shown in my Plate XXVII. fig. 23. The cellular tissues have not been preserved in the medullary rays of Brongniart's Sigillaria elegans; but tab. 4. fig. 2 of his memoir shows that his plant

<sup>\*</sup> The reverse proves to be the case, hence this objection disappears. See note on page 237.

<sup>†</sup> Loc. cit. p, 433.

possessed similar ones to those which Witham and I have figured. Further, the description which M. Brongniart has given of the structure of the outer bark and epiderm of his plant, these being the only cortical elements remaining in his specimen, would apply with little or no alteration to several of my Lepidodendroid and Sigillarian types; so that whilst a really indisputable Sigillaria, like my Plate XXIX. fig. 39, but in which the woody axis is preserved in situ, is still an important desideratum, I have very little doubt that, when discovered, it will be found to correspond with one of the several varieties of Diploxylon. Most probably also my Plate XXV. fig. 8, representing one of the extreme of the two types figured by Mr. Binney under the name of Sigillaria vascularis, will also be found to belong to the same subtype of the same genus. Yet my indefatigable friend informs me that his cabinet contains specimens in which the most gradual transition can be traced from the plant just referred to to the Lepidodendron selaginoides, the oppositely divergent form of the same group; hence his inclusion of both under one common name.

Of the form recently described by Dr. Dawson\* I know nothing, having seen nothing like it amongst our Lancashire Coal-measures. He describes a coniferous type of glandular prosenchyma as occurring in the woody axis of his Sigillaria. I have not seen a single fibre of this kind in any of our Sigillarian or Lepidodendroid forms, neither have I met with any trace of a Sternbergian pith such as he describes in the same plant, which evidently belong to a different type from those of our English Coal-measures, assuming it to be what Dr. Dawson supposes, viz. a true Sigillaria.

If, then, I am correct in thus bringing the Lepidodendra and Sigillariæ into such close affinity, there is an end of M. Brongniart's theory, that the latter were Gymnospermous Exogens, because the Cryptogamic character of the former is disputed by no one; we must rather conclude, as I have done, that the entire series represents, along with the Calamites, an exogenous group of Cryptogams in which the woody zone separated a medullary from a cortical portion. The Cryptogamic type of structure remains in the universal, if not even exclusive, prevalence of barred vessels, a modification of that scalariform type so characteristic of living Cryptogams. The medulla in some cases fails to attain to the simple parenchymatous condition common amongst Exogens; nor does the bark, as already observed, exhibit the division into epiphlœum, mesophlœum, and endophlœum. But neither can these divisions be traced in the Cycads, with which, in some respects, the carboniferous stems exhibit remarkable affinities.

The semivascular bast-layer of the epiderm of these Lepidodendroid and Sigillaroid plants has played an important part in their preservation; it has arrested the decay which appears to have usually commenced in the inner bark, simultaneously perhaps with that of the cells of the medulla, though the latter not unfrequently remain after the former have disappeared. From the not unfrequent occurrence of the vascular woody cylinders deprived of bark, I suspect that they have not been so often involved

<sup>\* &</sup>quot;On the Structure and Affinities of Sigillaria, Calamites, and Calamodendron, by J. W. Dawson, LL.D., F.R.S., &c., Principal of M'Gill University," Quarterly Journal of the Geological Society, London, May 1871.

in the decay that has overtaken the cellular structures as that they have become loosened from their attachments by that decay, and floated out when water reached them. this as it may, it is the bast-layer, with its investment of thick-walled epidermal cells, which has furnished, in nearly every case, the carbonaceous film that covers the stems of the Lepidodendroid plants so abundant in the shales and sandstones of the Coal-measures. The differences so obvious between the aspect of the outer surface of the thin film of coal and that of the subjacent shale are too well known to require further reference. When the carbonaceous matter is detached, the specimens are spoken of as being decorticated; and there may be no objection to the retention of a convenient term provided we distinctly understand the sense in which it is used. In all such instances the entire woody and inner cortical structures equally disappeared. The part which remained was, as I have already pointed out, the epidermal layer, with the semifibrous portion of the prosenchymatous one, which I have invariably found in every specimen that I have examined in which the structure is preserved. This bast-layer evidently gave to the bark the faculty of resisting the decay which so effectually cleared out all the more It was this double layer which constituted the cylinder, the two sides central tissues. of which were brought together and flattened by superimposed pressure when the stems were prostrated, and which constituted the hollow mould into which mud and sand were poured when they remained erect. We thus learn that very large trees were flattened into a thin layer, not because their stems were succulent, but because these hard woody and cellular cortical tissues broke up or were floated out of their epidermal sheath; whilst the latter, though strong and tough, was sufficiently flexible to yield to the superincumbent pressure, often without any material degree of disturbance of its integrity through fractures. Hence the fine flat masses of Sigillaria and Lepidodendron not unfrequently met with under the conditions which I have described.

It is a remarkable circumstance that whilst the woody zone is the part that has so frequently disappeared amongst the larger specimens of Lepidodendroid plants, and especially amongst the Sigillariæ, it is the part which is the most frequently preserved in the Stigmarian roots of the latter plant. I presume that this fact is to be explained by the different circumstances surrounding the two structures. The stems overthrown by storms were equally exposed to the decomposing influences of a warm humid atmosphere, whether they were prostrated on the ground or stood up as decapitated stumps. Such atmospheric influences would speedily destroy all but the tough superficial layers. The roots, on the other hand, imbedded deeply in wet mud, would be preserved from all atmospheric action; hence the beautiful preservation of their vascular tissues: these are often compressed and displaced, but rarely destroyed. The cellular bark, on the other hand, with the exception of the epidermal layer, and also the medullary cells, have yielded much more frequently to the decomposing influences that surrounded them even though protected by the soil.

What we know of the origin of the leaf-scars in living plants has left little room for hesitation respecting their nature in the fossils under consideration; but some of the MDCCCLXXII.

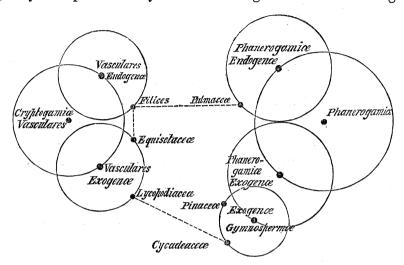
observations which I have recorded place the matter beyond doubt. Such examples as figs. 15, 17, 18, & 19, taken in connexion with figs. 5 & 6, make plain what are the portions of the stem which furnish the appearances so commonly found in fossil examples. The only question that is doubtful refers to the way in which the bases of the petioles of the fallen fronds have become detached. They evidently withered into membranous laminæ, as in some living Cycads and many tree-ferns; but whether they became detached bodily, leaving a well-defined cicatrix marking their base, as in ordinary deciduous trees, or whether the shrivelled stump of the petiole was worn down gradually by atmospheric decay, as in *Encephalartos caffre* and other allied Cycads, is not easy to say. I am inclined to conclude that the latter was the true process; but in either case a surface was reached, corresponding with the outer surface of the epiderm, at which a well-defined cicatrix of parenchymatous cells, of small size and with thickened walls, arrested further decomposition. Our knowledge of the relations of fruits to stems is too vague to enable us, as yet, to arrive at any definite conclusions respecting those of Halonia; but if the scars which I have referred to in Ulodendron and Halonia really supported cones, they were planted upon the subepidermal surface of the outer bark, and, like the leaves and rootlets, only received a vascular bundle to supply them with nutriment. What I mean is, that there appears to have been no deflection to these scars of any large portion of the vascular axis, which would have been the case had these curious organs given origin to branches.

It appears to me that, connecting the preceding observations with those made in my previous memoir on Calamites, we are called upon to make some change in the generally accepted views respecting the classification and nomenclature of the living vascular Cryptogams.

To apply the term Acrogens to plants which grew up into magnificent forest trees, the structure and growth of whose stems was essentially exogenous, whilst those stems exhibited so many of the internal features of exogenous organization, is surely an error. Until the close affinities of the Lepidodrendra with the Sigillariæ was established by actual observation, I do not wonder that M. Brongniart insisted upon his belief that the latter were Gymnospermous Exogens. I do not see how this Gymnospermous theory can be entertained any longer; but to make the facts upon which it was based accord with our systems we must alter the latter.

In the discussion which followed the reading of my memoir on Calamites before the Royal Society in January 1871, Dr. Carpenter threw out a suggestion which accords with my own conclusions on the question. One great distinction between the Exogens and Endogens is to be found in the fact that, when a formation of vessels is made in the woody zone of the former type, the clusters of vessels are left uninclosed, and consequently capable of receiving any amount of addition to their number without interference with the continuity of the series. On the other hand, the opposite is the case with the Endogens. Here each cluster of vessels is incased in a dense cylinder of woody prosenchyma, which latter always interferes to interrupt all continuous additions to the former tissues. If we turn to the Cryptogams, especially as illuminated by the study of

the fossil forms, we find that the stems of the Calamites, the approximate representatives of the Equisetaceæ, and those of the Lepidodendra with their extreme Sigillarian modifications, are of the exogenous type, whilst those of ferns are, in the points referred to, as obviously endogenous. The respective affinities of these plants, so far as the stems are concerned, may be represented by some such diagram as the following.



It will be observed that in this memoir I have paid but little attention to generic distinctions and none to specific ones, because I am satisfied that we are not yet in a position to define either the one or the other. My object has been to ascertain, as far as I could, what are the principal types of structure, and what the ranges of their variation; but, on the latter point especially, very much remains to be done which can only be accomplished by the cooperation of multiplied observers, and especially of such as are investigating distinct localities where new varieties may be expected to obtain. By such observations alone can our mutual errors and oversights be corrected. Where examples of plants in which structure is preserved are rare, we are in danger of drawing general conclusions from individual varieties which happen to be sharply defined: hence it is most important that independent observers should not be deterred from again going over the ground by an idea that it is preoccupied or that the work is done. The present contribution, however, carefully executed as far as it goes, is but that of a pioneer in a very wide and almost unexplored field.

It only remains for me to acknowledge the assistance which I have received either in the loan of sections or, what has been of even greater value to me, of specimens for dissection. The gentlemen to whom I have been thus indebted are W. Boyd Dawkins, Esq., F.R.S., of Manchester, Mr. J. Butterworth, of Shaw, and Mr. Whittaker and Mr. Nield, of Oldham. The scientific liberality of my two last-named auxiliaries demands special notice. They have not only given me the freest access to their cabinets, but have allowed me to cut into fragments some of the choicest specimens which they contained, when the interests of scientific truth seemed to demand the sacrifice. Such a spirit is too rare not to merit the thanks of all investigators whenever it is met with.

## DESCRIPTION OF THE PLATES.

The same letters are employed throughout to represent, as far as possible, what appear to be homologous parts, in accordance with the following plan:—

- a. Medullary axis.
- b. Cells of medullary axis.
- c. Vessels of medullary axis.
- d. Ligneous zone.
- e. Vessels of ligneous zone.
- f. Medullary rays.
- g. Innermost part of the bark.
- h. Middle parenchymatous part of the bark.

- i. Outer or prosenchymatous part of the bark.
- k. Tubular portion of i.
- d. Bases of leaves or petioles, detached or coalesced into an epidermal layer.
- m. Bundles of vessels going to the leaves.
- n. Bundles of vessels going to the rootlets.
- o. Rootlets.
- p. Indentations of epiderm in which rootlets are planted.
- r. Scars or cicatrices from which cones are supposed to have fallen.

Where not otherwise specifically mentioned, the specimens represented are in the author's cabinet. The collectors from whom some of the fossils were received are named, but the sections, in these examples, are also in the author's cabinet.

## Plate

- XXIV. fig. 1. Lepidodendron selaginoides, a young branch, transverse section, magnified 6 diameters. Mr. Butterworth's cabinet.
  - ,, fig. 2. Lepidodendron selaginoides, longitudinal section of fig. 1, magnified 4 diameters. Mr. Butterworth's cabinet.
  - " fig. 3. Lepidodendron selaginoides, part of medullary centre of fig. 1, magnified 200 diameters.
  - ,, fig. 4. Lepidodendron selaginoides, part of medullary centre of fig. 2, magnified 70 diameters.
  - ,, fig. 5. Lepidodendron selaginoides, tangential section of outer bark immediately below the epiderm, magnified 7 diameters. Mr. Butterworth's cabinet.
  - ,, fig. 6. Lepidodendron selaginoides, tangential section of outer layer of epiderm at the base of the petioles, magnified 7 diameters. Mr. Butterworth's cabinet.
- XXV. fig. 7. Lepidodendron selaginoides, subepidermal surface of outer bark, nat. size.
  - "fig. 8. Transverse section of central axis, woody zone, and part of the inner bark of one form of the Sigillaria vascularis of Mr. Binney's memoir, magnified 10 diameters. Mr. Butterworth's cabinet.
  - " fig. 9. Longitudinal section of fig. 8, magnified 10 diameters. Mr. Butterworth's cabinet.
  - " fig. 10. Tangential section of the woody zone of the same type as fig. 8, showing the medullary rays.
  - " fig. 11. Prosenchyma of the bark of fig. 10, magnified 400 diameters.
  - ,, fig. 12. Lepidodendron, transverse section, nat. size. Mr. W. B. DAWKINS'S cabinet.

Plate

- XXVI. fig. 13. Lepidodendron, segment of fig. 12, magnified 8 diameters.
- XXV. fig. 14. Lepidodendron, vertical section of the centre of the same plant as fig. 12. Mr. W. B. DAWKINS.
- XXVI. fig. 15. Lepidodendron, subepidermal surface of the bark of the same species as fig. 12. Mr. Butterworth's cabinet.
- XXV. fig. 16. Lepidodendron, vertical section of epidermal layer and petioles of leaves,  $2\frac{1}{2}$  diameters. Mr. W. B. Dawkins's cabinet.
- XXVI. fig. 17. Lepidodendron, tangential section through outermost layer of epidermis, magnified 3 diameters. Mr. Dawkins.
  - ,, fig. 18. Lepidodendron, tangential section of the same specimen as fig. 17, but nearer the extremities of the intersected leaves, magnified 3 diameters.
  - ,, fig. 19. Lepidodendron, oblique transverse section of fig. 17, magnified 3 diameters.
  - ,, fig. 20. Lepidodendron, vertical section of another specimen similar to figs. 16-19, magnified 4 diameters. Mr. Whittaker.
- XXVIII. fig. 21. Diploxylon, transverse section, nat. size. Mr. Butterworth.
  - XXVI. fig. 22. Diploxylon, vertical section of fig. 21, magnified 5 diameters.
- XXVII. fig. 23. Diploxylon, tangential section of some of the vessels of the ligneous zone and medullary rays of fig. 21.
  - fig. 23 a. Radial section of fig. 21 at the inner surface of the ligneous zone.
  - " fig. 23 b. Radial section through the ligneous zone of Diploxylon stigmarioideum.
  - XXVI. fig. 24. Ulodendron, transverse section, magnified 2 diameters. Mr. NIELD.
- XXVII. fig. 25. *Ulodendron*, longitudinal section of the central axis of fig. 24, magnified 12 diameters.
  - " fig. 26. *Ulodendron*, central axis of fig. 24, magnified 12 diameters.
- XXVIII. fig. 27. *Ulodendron*, longitudinal section of outer bark, epidermis, and petioles of fig. 25, magnified 3 diameters.
  - ,, fig. 28. *Ulodendron*, tangential section of bases of petioles close to the epiderm, magnified 6 diameters.
  - XXVII. fig. 29. Favularia, longitudinal section, magnified 6 diameters. Mr. Whit-
- XXVIII. fig. 30. Favularia, transverse section of the bases of two petioles of fig. 29, magnified 6 diameters.
  - " fig. 31. Favularia, portion of fig. 29, showing the medulla, woody zone, and a trace of the inner bark, magnified 30 diameters.
  - ig. 32. Favularia, portion of the epidermis of fig. 29, showing the outer parenchyma and the bast-layer, enlarged.
  - ing. 33. Diploxylon, aspect of the specimen before it was cut up into sections, nat. size. Mr. Nield.

Plate

- XXVIII. fig. 34. Diploxylon, segment of a transverse section of fig. 33, magnified 15 diameters.
  - XXIX. fig. 35. Sigillaria, transverse section of the epidermal layer of the bark, magnified 4 diameters.
    - fig. 36. Sigillaria, one rib of fig. 35, enlarged 13 diameters.
- XXVIII. fig. 37. Sigillaria, radial section made along the centre of one of the raised longitudinal ribs of fig. 35, magnified 4 diameters.
  - fig. 38. Sigillaria, portion of fig. 37, enlarged 12 diameters.
  - XXIX. fig. 39. Sigillaria, part of the surface of the specimen. Mr. NIELD.
    - ,, fig. 40. Sigillaria, transverse section of the epidermal layer of fig. 39, natural size.
  - XXX. fig. 41. Sigillaria, a segment of fig. 40, enlarged 15 diameters.
  - XXIX. fig. 42. Sigillaria, vertical section through the centre of a part of one rib of fig. 39, showing the vascular bundle going to the base of the petiole, magnified 15 diameters.
  - XXX. fig. 43. Stigmarian root, radial section of the innermost part of the woody zone, with a medullary ray and vascular bundle going off towards a rootlet, magnified 13 diameters. Mr. WHITTAKER.
  - XXIX. fig. 44. Stigmarian root, radial section like fig. 43, but of the outermost part of the ligneous zone, with medullary ray and vascular bundle, magnified 10 diameters.
    - " fig. 45. Stigmarian root, tangential section of part of the ligneous zone, with one primary and numerous secondary medullary rays, magnified 13 diameters.
    - " fig. 46. Stigmarian root, part of fig. 45, with secondary medullary rays, magnified 50 diameters.
  - XXX. fig. 47. Stigmarian root, transverse section of the innermost part of the woody zone, with a medullary ray and vascular bundle going to a rootlet, magnified 15 diameters.
    - ifig. 48. Stigmarian root, outer surface of the ligneous zone, with the peripheral extremities of the primary medullary rays and vascular bundles of the rootlets, magnified 4 diameters. Mr. Whittaker's cabinet.
    - " fig. 49. Stigmarian root, radial section of the innermost bark, magnified 120 diameters.
  - XXXI. fig. 50. Stigmarian root, tangential section of the middle bark, magnified 100 diameters.
  - XXX. fig. 51. Stigmarian root, bases of three rootlets, with the epidermal layer upon which they are implanted, magnified 3 diameters.
  - XXXI. fig. 52. Stigmarian root, base of one rootlet, magnified 6 diameters. Mr. Nield, fig. 53. Stigmarian root, diagram representing a restoration of the entire root, with the surfaces of the pith, wood, and bark successively displayed in the

Plate

centre and to the left of the diagram, and with a section of the wood and bark, the latter with the rootlets in situ, on the right. The latter section is supposed to have passed directly through the centres of the bases of two of the rootlets, and tangentially through the remaining three.

- XXXI. fig. 54. Transverse section of a fragment of bark, apparently of *Diploxylon*, magnified 16 diameters. Mr. Butterworth.
  - " fig. 55. Radial section of the prosenchymatous portion of a similar specimen to fig. 54, magnified 65 diameters.
  - " fig. 56. Tangential section of fig. 55, magnified 65 diameters.
  - ,, fig. 57. Tangential section of the large cells(h) of fig. 54, magnified 60 diameters.
  - ,, fig. 58. Cast of the external surface of a *Favularia*, with cicatrices of cones, enlarged 2 diameters. Mr. Nield's cabinet.
  - ,, fig. 59. Central axis of a small Lepidodendroid cone, enlarged 2 diameters.

Received September 3, 1871.

## SUPPLEMENTARY OBSERVATIONS.

Since reading the preceding memoir I have been seeking further information on some portions of the subject which are as yet very obscure, especially in connexion with the forms represented by the Diploxylon cycadeoideum of Corda. In his 'Flora der Vorwelt' he gives both the generic and specific characters of this plant. The essential features of the former are that the plants belonging to the genus have an inner cylinder surrounding the medulla composed of large scalariform vessels arranged without definite order. This is invested by a second cylinder, also consisting of scalariform vessels, but of smaller size, arranged in radiating fasciculi, and "radiis vasorum ligni interni percursum." In his specific description of D. cycadeoideum he affirms "Radii medullaris nulli" (loc. cit. pp. 5, 6). In his tab. xi. fig. 1 he represents a radial longitudinal section in which three sharply defined vascular bundles, unaccompanied by any other tissue, proceed upwards and outwards across a field of vertical, barred vessels, which are disposed with rigid straightness and perfect parallelism. I think I shall not be venturing too far if I doubt the perfect accuracy of this figure. But what is of chief importance at present is the fact that he believes these vascular bundles to spring from his inner or medullary rings of vessels, and not from any part of the outer or ligneous zone, and that he discovers no traces of cellular medullary rays in his specimen.

M. Brongniart, as we have seen, found a very similar general arrangement in his Sigillaria elegans, only in this plant the inner or medullary vascular cylinder was interrupted, at intervals, instead of being a continuous ring. He also found a profusion of what he unhesitatingly affirms to be medullary rays; but the tissues which composed them being destroyed, he cannot speak with confidence as to their histological character. Besides these he found traces of larger openings in the woody cylinder; and he correctly surmises that these were passages through which the large foliar vascular bundles, seen

penetrating the bark, had emerged from the ligneous zone. He expresses himself very doubtfully as to the source of these bundles; but observing what he deems to be indications of them in the transverse section of the *outer* ligneous cylinder, *close to the inner one*, he thinks they may possibly have originated in the latter.

The third writer whose observations bear upon the question is Professor King, whose able and lucid paper\* contains an admirable account of all that was known of these plants at the time when his memoir was published. In it he discusses the structure of the Anabathra of Witham, having had in his possession a number of that distinguished observer's original specimens. In this plant, as I have already mentioned in the preceding memoir, we have the inner medullary cylinder and the outer ligneous zone of vessels arranged as in Brongniart's Sigillaria and in Diploxylon; only, as in the latter plant, it constituted a continuous instead of an interrupted ring. Professor King calls attention to the large lenticular openings, seen in the tangential sections of the woody zone of Anabathra, figured and described by Witham as medullary rays. He says respecting them, "Mr. Witham described these openings as containing the medullary rays, which is not the case, because what has probably been mistaken for cellular tissue is, in reality, a bundle of small vessels, similar to those which occupy the outer part of the medullary sheath. Although the longitudinal sections do not exhibit any of these bundles springing from the vascular cylinder, their proximity in some transverse sections, together with the fact just stated, leave no room to doubt their having constituted the leaf-cords of the plant." This writer further adds, "from these passages being in part vacant, it may reasonably be supposed that the cords were accompanied in their course with a portion of cellular tissue"†.

It thus appears that all three of the above writers inclined to the idea that the foliar vascular bundles arise from the vessels of the vascular medullary sheaths of the plants which they severally describe. In the previous pages I pointed out that whilst in some Diploxylons the line of demarcation between the medullary sheath and the ligneous zone was a crenulated one, in others it appeared to be straight. Having recently prepared and examined a large number of additional sections, I find that even in some of the examples in which I thought the line was a straight one I can detect a series of small crenulations. This I have especially found to be the case with the specimen represented in figs. 20-23. In this plant the crenulations resemble those seen in fig. 34, though much more minute. The latter figure shows at c' what appear to be angular projections of the medullary sheath penetrating between the large convex, inner extre-projecting angles are not wholly occupied by medullary vessels, but contain a remarkable arrangement of barred cells. Fig. 23 a represents a small portion of a radial longitudinal section of this part of the plant, in which c represents the outermost vessels of the medullary sheath, e the inner vessels of the woody zone, and the cells b the structure

<sup>\* &</sup>quot;Contributions towards establishing the generic characters of the fossil plants of the genus Sigillaria, by William King, Esq.," Edinburgh New Philosophical Journal, Nos. 71 et seq.

<sup>†</sup> Loc. cit. p. 124.

It will be observed that some of these cells are nearly cubical in shape, others more elongated; some have square ends, others oblique ones; but it is important to notice that towards the exterior of this cellular mass (b') the cells exhibit a strong tendency to become prosenchymatous. All these cells, where mineralization has not altered their structure, are more or less regularly barred. Where the convex inner extremity of each fasciculus of the woody zone encroaches upon the medullary sheath, this cellular layer almost disappears, though not altogether so. The large lenticular radii to which allusion has been made take their rise in this cellular tissue. My specimens show that the longer axis of each cell becomes suddenly deflected in the horizontal direction. That such is the case is shown, not only by their general aspect, but by the reversal of the direction of their transverse bars, which are now vertical, and not horizontal as before. Many of these deflected cells are perfectly muriform, but others are more or less prosenchymatous. In the immediate neighbourhood of the cellular tract there is a considerable disturbance of the parallelism of the small contiguous barred vessels, so that the origin of such of the latter as contribute to the formation of the foliar bundle is not easily traced; but, however originated, some of them accompany the deflected cells to constitute that bundle. In no case do any of the inner and larger vessels of the medullary sheath take any part in the formation of these bundles; and my present impression is that all those which do so should rather be regarded as belonging to the innermost part of the woody zone than to the exterior of the medullary cylinder\*. Whichever is the fact, I am convinced that these vessels are the exact equivalents of those furnishing the foliar bundles in the true Lepidodendra. These bundles were needed, in the very earliest stage of the growth of the young shoot, to sustain the developing leaves; and though at this stage of its development the woody zone was obviously represented in a very feeble manner, it nevertheless fulfilled its functions in contributing its quota to the foliar nutrition. But there remains to be explained the supposed absence of true medullary rays mentioned by Corda as characterizing his Diploxylon, but which were observed by Brongniart in his Sigillaria elegans. None of these writers were aware of the existence of barred or scalariform cells in the medullæ of these plants. Consequently when Corda found barred tissues running horizontally, not only in the large lenticular spaces separating the ligneous fasciculi, but also in the smaller ones separating individual laminæ, he concluded that all these were necessarily bundles of barred vessels, and in consequence denied the existence of medullary rays. Since, however, all the medullary cells of many of these Lepidodendroid plants (see figs. 1 & 3) are barred, it follows that some of those in other portions of the ligneous zone would, in all probability, be the same; and such proves to be the case. In the example which I am now describing it is difficult in some places to say which are sections of fusiform cells, and which of parts of contorted vessels; but in a large number of specimens

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<sup>\*</sup> Later researches amongst the Burntisland plants have enabled me to clear up this very obscure point, and to determine that the vessels in question do belong to the outermost surface of the medullary cylinder. See Proceedings of Royal Society, vol. xx. p. 199.—May 7th, 1872.

there is no difficulty in establishing the conjoint existence of the two tissues; hence I venture to affirm that, in *Diploxylon cycadeoideum*, we have two distinct forms of medullary rays: 1st, the larger lenticular ones, which are primarily composed of barred cells, but through which the vascular bundles escape to the surface of the woody zone; and 2nd, of smaller ones, in which similarly barred cells are chiefly, though not invariably, arranged in tangential sections in single vertical rows, often not containing more than two or three cells in each vertical series, but which constitute true medullary rays.

In the preceding memoir I have designated the large lenticular spaces primary medullary rays, to distinguish them from the smaller or secondary ones. Those botanists who, like Mr. Carruthers, wholly repudiate the existence of any parallelism between these fossil Cryptogams and the more highly developed Phanerogamic Exogens, consistently deny that any of these cellular horizontal communications between the interior and exterior of the woody zone are representatives of or entitled to be called medullary rays; but Brongniart, than whom it would be difficult to quote a higher authority, so designated both the larger and the smaller ones in Stigmaria ficoides, as well as illustrated them by what are found in Zamia integrifolia and other Cycads ("Observations sur le Sigillaria elegans"), and I am convinced that he is right in so doing. It is as impossible to separate these Cryptogamic forms of medullary rays from those of the Cycadeæ on the one hand, as it is to disjoin the latter from those of the higher Conifera on the other. Professor King quotes the late Dr. Lindley's opinion that no vascular bundles ever issued through medullary rays. This may be true in the case of Phanerogamic Exogens, but it does not follow that it must be equally true of these Cryptogamic modifications of the exogenous type of woody zone. One thing is clear, viz. that the large lenticular spaces (my primary medullary rays) are but modifications of the smaller or secondary ones, enlarged to serve a special teleological purpose; i. e. the transmission of vascular bundles to the leaves and rootlets. At their upper and lower extremities these large elliptical cellular rays are undistinguishable from and merge in the smaller ones. However large and thick in their central portion, they diminish in size upwards and downwards, both in the Diploxylons and in Stigmaria, until they contract into laminæ consisting of a single thin vertical layer of cells. Such teleological modifications are universal amongst animals; and I fail to see why we should refuse to recognize their existence amongst plants. At all events until some better reasons for doing so are furnished by those who differ from me than they have hitherto advanced, I shall continue to follow the example of M. Brongniart, and employ the terms adopted in the preceding pages.

Having thus obtained additional light respecting the Diploxylons, I again turned to the more highly organized of the stems described by Mr. Binney under the name of Sigillaria vascularis, and which I have already represented in Plate XXV. figs. 8–11. I made a fresh series of carefully prepared dissections, and succeeded in demonstrating the existence in this plant of a series of primary and secondary medullary rays, the former containing large foliar bundles, precisely identical with those of Diployxlon cycadeoideum. I have not succeeded in discovering in the former plant the cellular layer

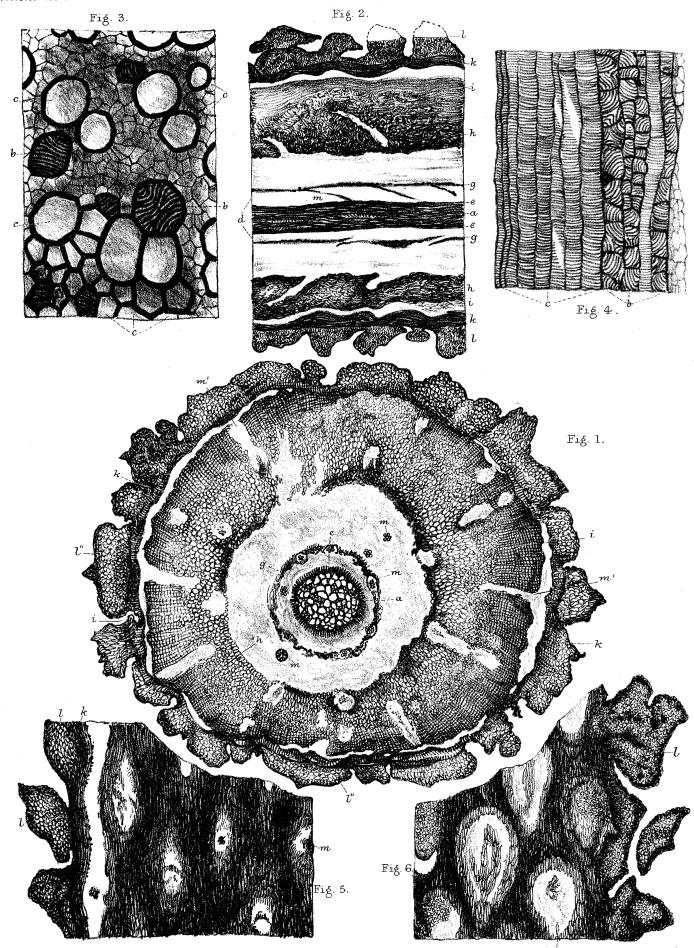
intervening between the medullary vascular cylinder and the woody zone of the latter The large primary medullary rays are composed of barred cells, which are sometimes mural, but more frequently prosenchymatous; through the upper part of each of these large rays there proceeds a bundle of true barred vessels. I have not succeeded in tracing one of these bundles to its medullary extremity, consequently I cannot yet affirm how it originates; but I have seen sufficient to confirm what I have already stated in the body of the memoir, that we need only remove the central cellular medulla of the plant in question to convert it into a true Diploxylon; the identity of the two, so far as structural type is concerned, is as close as it can be, even in its minuter details. Such being my conviction, I propose to designate the plant represented in figs. 8-11 Diploxylon vasculare, and to apply Corda's name of D. cycadeoideum to figs. 21-23. The plant represented by figs. 33, 34, distinguished by its large medullary axis and by the deeply fluted aspect of the interior surface of its ligneous zone, I propose to designate Diploxylon cylindricum, whilst a fourth form, exhibiting some different features yet to be noticed, I would term D. stigmarioideum. So far as the general structure of the stem is concerned the last-named plant does not differ from the other Diploxylons. The cellular medulla has disappeared, but there remains the medullary ring of barred vessels, surrounded by the exogenous ligneous zone. The primary and secondary medullary rays also appear; but neither of them occurs so abundantly as in the other species. Moreover, in the radial vertical sections, the vascular bundles occupying the primary rays exhibit a different aspect to those of the other species described, and approach nearer to what exists in Stigmaria ficoides. This is represented in fig. 23 b. The vascular bundle (m) appears to be derived from the body of the ligneous zone and not from its medullary surface. is composed of smaller vessels than those seen at e; but we find that at e' these vessels diminish in size and approach in magnitude those of the bundle m; not only so, but whilst the upper extremities of the small vessels of m exhibit the perpendicular arrangement indicating that they belong to the part of the woody zone in which they occur, the lower extremities of the large vessels (e) are deflected in the direction of those of the foliar bundle, which is never the case with the corresponding ones of the other forms of Diploxylons. The lower margin of the foliar bundle is cut off in this section by an oblique, sharply defined line; this indicates that the large vessels at e'' have been sharply deflected to the right and left of the bundle to allow the latter to pass between them. All these appearances correspond so closely with what we find in Stigmaria, that for a long time this plant seriously perplexed me; but it appears to be a true Diploxylon, since it has the vascular medullary cylinder of that genus as well defined as in any other species. This cylinder is never found in Stigmaria ficoides. It has been more especially in connexion with this species of Diploxylon, though not exclusively, that I have found the peculiar bark represented in figs. 54-57. It is possible that this plant may, like Stigmaria, prove to be the uppermost part of a root of some of the other forms, though I have never yet found it associated with any rootlets; or it may be a fragment from the base where stem and roots united.

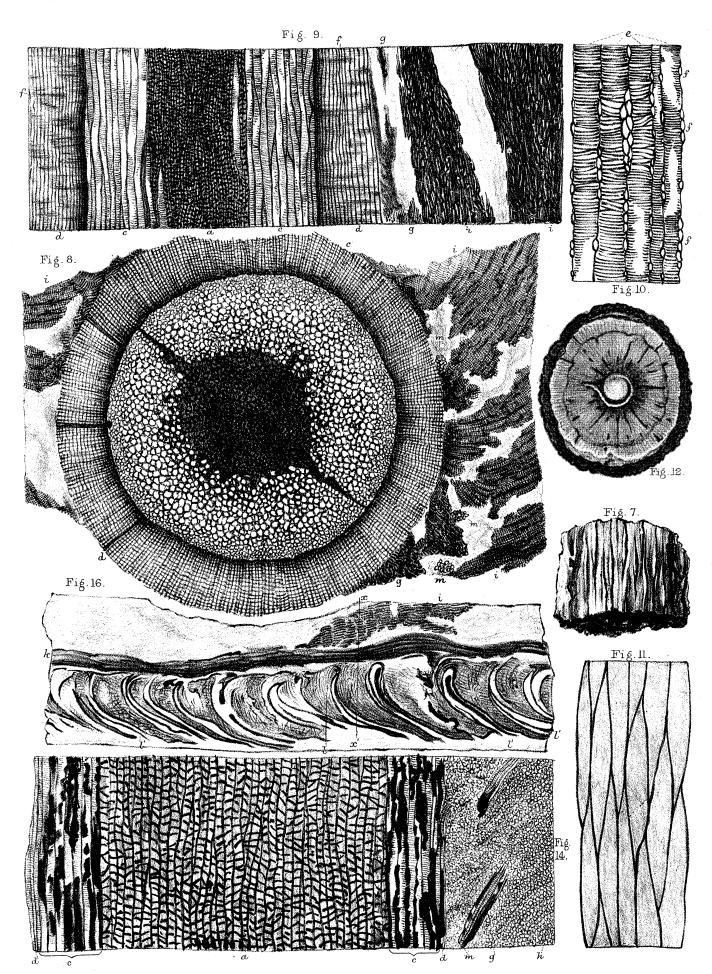
Amongst the numerous other interesting plants for which I am indebted to G. GRIEVE, Esq., of Burntisland, in Fifeshire, is a well-marked Diploxylon closely allied to D. cycadeoideum. Like the rest of Mr. Grieve's specimens, it is from the deposit of lower carbo niferous age which occurs imbedded amongst trappean rocks at Pettycur Bay. specimen is an instructive one, since, though abundantly furnished with primary and secondary medullary rays, or rather with the spaces which they occupied, all the cellular tissues have disappeared from both, whilst the vascular foliar bundles are well preserved. We are thus enabled to distinguish the respective areas occupied by the two tissues in a manner that I have not succeeded in doing so distinctly in the other specimens described. Each bundle is cylindrical, occupying the centre of the lenticular section of the ray when cut at right angles to its direction, and consisting of very small barred vessels. Above and below the vessels are open spaces, but which were originally occupied by the cellular tissues of the ray, the forms of the cells being strongly impressed upon the indented walls of the contiguous longitudinal vessels of the ligneous zone. I have not discovered in this plant the cellular layer intervening between the medullary vascular cylinder and the woody zone; in this respect it appears to approach nearer to the D. vasculare than to the other forms. The vascular medullary cylinder or sheath is strongly marked; but all the medullary cellular tissues have disappeared. I pointed out some time ago\* that some of these Lepidodendra exhibited a feature not previously noticed; viz. the vessels were not only barred transversely, but, in addition, the transverse bars of lignine were connected by a delicate series of threads of the same material, running parallel with the longer axis of the vessel. I find this feature in all the Diploxylons; but in the Burntisland specimen it is so faint that it can only be discovered under the microscope by a careful adjustment of the light. The coarser transverse bars are also much more irregular in size, number, and direction than is usual amongst the Diploxylons of the Upper Coal-measures.

The Diploxylon of Corda is so obviously identical, generically, with the Anabathra of Witham, that the latter name ought to be adopted in preference to the former one. But ere long, in all probability, both these names will have to be abandoned, since there appears to be little doubt that they represent the woody axes of some of the common Lepidodendroid plants of the Coal-measures; and as soon as the identification of these internal axes with their correlate external forms is indisputably accomplished, the yet older names of the latter must become the adopted ones. Under these circumstances it is scarcely desirable to disturb a widely accepted nomenclature, since any day may furnish the required connecting link.

The general conclusion towards which all these additional observations point is the same as that of the preceding memoir, which they strengthen and confirm, viz. that all these varied plants are constructed upon a common type, and belong to one Lycopodiaceous family.

<sup>\*</sup> Monthly Microscopical Journal, August 1, 1869, pl. xx. fig. 10.





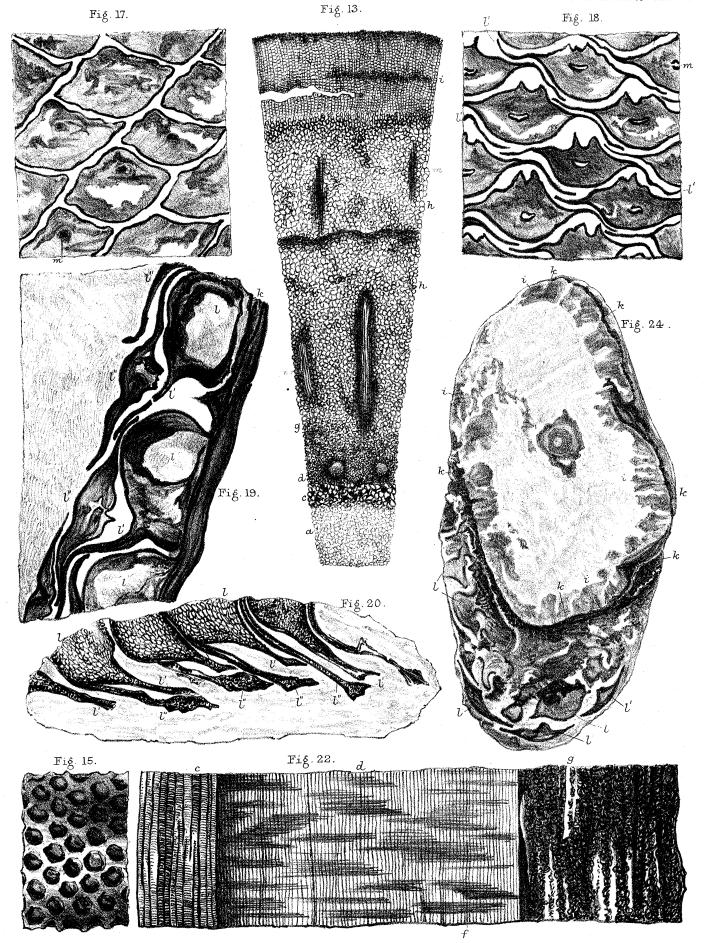


Fig. 25. Fig. 26. <sub>b</sub> Fig. 23 a. Fig. 23 b. Fig. 29

