

XVII.—*On the Primary Structure of certain Palæozoic Stems with the Dadoxylon Type of Wood.* By D. H. SCOTT, M.A., Ph.D., F.R.S., Hon. Keeper of the Jodrell Laboratory, Royal Botanic Gardens, Kew. *Communicated by Professor I. BAYLEY BALFOUR, F.R.S.* (With Six Plates.)

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In a Note published in the *Annals of Botany* for December 1899,* I gave some account of the structure of two stems from the Lower Carboniferous of Scotland, provisionally named *Araucarioxylon fasciculare*, sp. nov., and *A. antiquum*, Kr. (Witham, sp.).

In the present paper these stems are described fully, with the help of illustrations, and others, presenting similar points of interest, are added. The species dealt with are the following:—

Calamopitys fascicularis (*Araucarioxylon fasciculare* of the Note).

Calamopitys beinertiana (*Araucarioxylon beinertianum*, Kr.), (Göpp., sp.).

Pitys antiqua, Witham (*Araucarioxylon antiquum*, Kr. of the Note).

Pitys Withami (*Pinites Withami*, Lindl. & Hutt.).

Pitys primæva, Witham.

Dadoxylon Spencersi, sp. nov.

The reasons for the nomenclature adopted will be given in each case when the structure has been described. It was stated in the Preliminary Note that the two stems there described would certainly require generic separation on the basis of their primary characters (*l.c.*, p. 619). This has now been done, but I have succeeded in avoiding the creation of any new genus, for in the one case the characters appeared to indicate the genus *Calamopitys* of UNGER as the appropriate one, while in the other the use of WITHAM's old generic name, in an emended sense, seemed to meet the case.

Where the old genus *Dadoxylon* or *Araucarioxylon* has to be kept up, I agree with KNOWLTON† and ZEILLER‡ that the former name is to be preferred in the case of Palæozoic woods, restricting *Araucarioxylon* to Secondary or Tertiary specimens, which may more probably be referred to true Araucariæ. The use of the name *Araucarioxylon* for Palæozoic specimens, probably belonging to the Cordaiteæ, or to some other family equally remote from true Araucariæ, is likely to mislead, and though I employed this name in the Preliminary Note, I now think it better to avoid it.

* "On the Primary Wood of certain *Araucarioxylons*," *Ann. Bot.*, vol. xiii, p. 615.

† "A Revision of the Genus *Araucarioxylon* of Kraus," *Proc. U.S. Nat. Mus.*, vol. xii, p. 601, 1890.

‡ *Éléments de Paléobotanique*, p. 279, 1900.

The importance of the fossils now to be described consists in their showing the primary structure of the wood; in all of them there is proof of the existence, within the zone of secondary wood, of distinct strands of primary xylem, resembling more or less closely those which have long been known in the stems of the *Lyginodendreae* and *Poroxyleae*. This structure co-exists with secondary wood of the *Dadoxylon* type, in some cases agreeing exactly with the wood which is known to have belonged to the stems of *Cordaiteae*.^{*} Thus these fossils tend to establish a connection between the stems of Palæozoic Gymnosperms and those of certain Cycadofilices, and so to throw new light on the question of the Filicinean origin of the Gymnospermous Phanerogams. The subject of the course of the leaf-traces is closely connected with that of the primary wood-strands, and is dealt with below so far as the material afforded data. Other characters are considered incidentally. At the close of the paper the theoretical bearings of the structural features in question are discussed.

I. CALAMOPITYS, Unger.

1. *Calamopitys fascicularis*, sp. n.

This is the stem described in my Note of 1899 under the provisional name of *Araucarioxylon fasciculare*. The reasons for now placing the fossil in UNGER's genus will become apparent when the structure has been described. As mentioned in the Preliminary Note, two specimens have been examined; the first which came under investigation is in the collection of Mr KIDSTON, and was found in 1898 by Mr JOHN RENWICK at the Loch Humphrey Burn in the Kilpatrick Hills, Dumbartonshire. The horizon is that of the Calciferos Sandstone Series. Mr KIDSTON very kindly placed his sections at my disposal for investigation, and also allowed me to have some additional sections cut from the remainder of the block.

The second specimen is one of which the sections are preserved in the WILLIAMSON Collection under the generic name *Dadoxylon*. The structure is identical with that of Mr KIDSTON's stem (*cf.* Pl. I. phot. 1 and Pl. III. fig. 1). The WILLIAMSON specimen is described in his MS. catalogue as being derived from the Carboniferous Limestone near Haltwhistle. Thus both specimens are of Lower Carboniferous age. This plant, like the other species to be described, combines an Araucarian type of secondary wood with the presence of distinct primary strands of xylem around the pith. It is characterised by the small diameter of the pith, the small number and relatively large size of the primary xylem-strands, the simple leaf-traces, and the narrow medullary rays, giving the secondary wood a Cordaitean character.

The diameter of the pith is only about 2 mm. in Mr KIDSTON's specimen, and about 3 mm. in the WILLIAMSON example. The whole specimen reaches a maximum diameter

^{*} On the *Cordaiteae*, see GRAND' EURY, *Flore carbonifère du Département de la Loire*, 1877; RENAULT, *Structure comparée de quelques Tiges de la Flore carbonifère*, 1879; *Cours de Bot. Fossile*, t. i., 1881. A general account of the family is given in SOLMS-LAUBACH's *Fossil Botany*, chap. v., Eng. transl., 1891, and in my *Studies in Fossil Botany*, Lecture XII., 1900.

of nearly 3 cm. in the former, and about 2 cm. in the latter, but these dimensions are of no significance, as the wood is manifestly incomplete. In neither specimen is anything beyond the wood preserved.

In Mr KIDSTON's specimen the pith is complete, though somewhat contracted (see fig. 1); consequently all the xylem-strands can be recognised, and their course traced in successive transverse sections. In the WILLIAMSON stem the pith has perished, and the smaller xylem-strands are obscure; for details of the wood and larger primary strands, however, this specimen is rather superior to the other. Fig. 1, from one of the transverse sections of Mr KIDSTON's specimen, gives a good idea of the general structure. The parenchymatous pith, which, owing to shrinkage, has partly separated from the surrounding wood, has, in itself, a very uniform structure; the peripheral cells are narrower and have rather thinner walls than those towards the centre (compare the longitudinal section in fig. 3); some of the larger elements are filled with dense carbonaceous contents, which may indicate that they had a secretory function during life. Around the pith a number of xylem-strands are disposed, forming an irregular ring. Eight of these strands are wholly or partially embedded in the pith; a ninth strand (B), much the largest of all, is passing out into the zone of wood. It is a constant rule, holding good for all the sections of both specimens, that the outgoing bundles are those which attain the maximum dimensions (*cf.* phot. 2, from the WILLIAMSON specimen). A, the next largest strand, is in close contact with the secondary wood, and will be the next to pass out above, as is shown by the comparison of successive transverse sections. Most of the smaller strands are actually embedded in the pith, and are separated from the inner edge of the wood by several layers of parenchyma (*cf.* the longitudinal section, fig. 3). We have here an approach to a condition which we shall find existing, in a much more marked degree, in *Pitys antiqua*.

There are in all eight transverse sections of Mr KIDSTON's specimen. They were cut at different times, and I have no record of their order, but have been able to determine it with practical certainty by careful comparison of the peculiarities of the individual sections as to detailed structure, position and form of cracks, exact state of preservation, etc. The succession of the sections having been thus ascertained, it became possible to determine the course of the xylem-strands. The *camera lucida* diagrams in the text, 1 to 4, prepared for me by Mr L. A. BOODLE, F.L.S., are taken from a series of four consecutive sections, sufficient to fix the essential points in the distribution of the strands. The series is from above downwards. The top section of the four (diagram 1) shows three principal bundles, markedly larger than the rest. One of them, C, is still far out in the secondary wood; another, B, of equal or even greater size, has just reached, with its inner edge, the periphery of the pith; the third, A, which is much smaller, though still far exceeding the other circum-medullary strands in size, has already entered the pith. These three leaf-traces may be taken as fixing the position of the three orthostichies, A, B and C, on which the leaves supplied by these traces were inserted. A, being cut lowest down in its course, belongs to the

uppermost leaf of the three, B to the next, and C to the lowest. In the next section (diagram 2) the same three orthostichies are represented. The bundle C has here moved up nearly to the pith, but is still separated from it by a mass of radially arranged parenchyma. B has moved but little inwards, and has scarcely changed. A is much smaller than before, and has shifted in watch-hand direction, approaching an adjacent small strand (α) on that side. In the next section below (diagram 3) a new bundle, D, makes its appearance out in the wood, between A and B; it evidently comes from a leaf next below C, and thus gives the position of a new orthostichy. C has here just reached the edge of the pith and B is projecting further into it. A is now scarcely

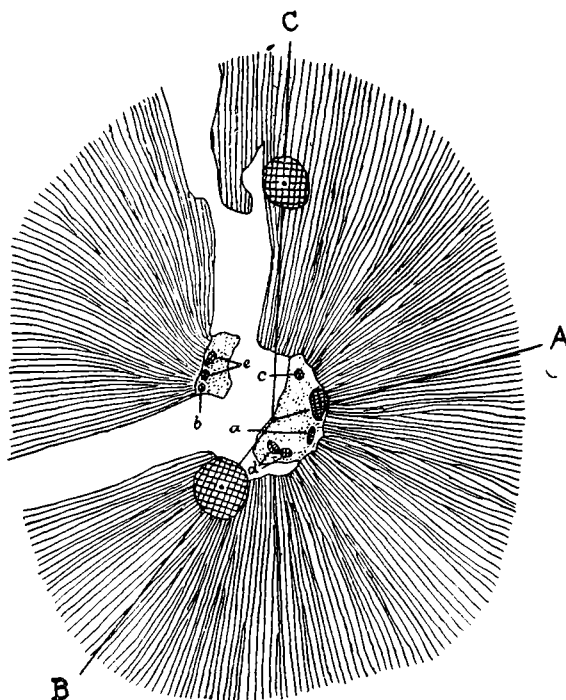


DIAGRAM 1 (K. 788).

larger than its fellow circum-medullary strands; it has shifted a little further and is now joining the adjacent strand, α ; it has also become embedded in the tissue of the pith.

In the lowest section of the series (diagram 4) a new strand again, E, is entering through the wood on the left, between B and C, thus fixing the position of the fifth orthostichy, and clearly belonging to the lowest of the five leaves which are represented by their traces in this series. D has here reached the edge of the pith; C is beginning to enter it, and is somewhat reduced in size; B is much smaller than before, and has entered the pith sufficiently to have been drawn away from the wood by the contraction of the former. A, no longer distinguished by size, is still fusing with the adjacent strand, α .

The whole arrangement clearly points to a $2/5$ phyllotaxis. The three successive traces, which are alone recognisable in diagrams 1 and 2, are separated by angles which

correspond roughly to a $2/5$ between A and B, and B and C, and about $1/5$ between C and A. Where a new trace, D, makes its appearance (diagram 3) it bisects the $2/5$ gap A—B, and again where a fifth trace, E, appears (diagram 4) it bisects in like manner the other $2/5$ gap, B—C. It may be mentioned that all the leaf-traces shown in the other sections, not figured, are likewise referable to the same five orthostichies, A, B, C, D, E, and follow the same order of succession. No other than a $2/5$ arrangement would account for the facts. The irregularities in divergence which occur are easily explained by the distortion due to cracks, and to the contraction of the pith.

The course of the smaller strands, *i.e.*, of the lower ends of the leaf-traces where they have become medullary, has not been completely made out, but some light has

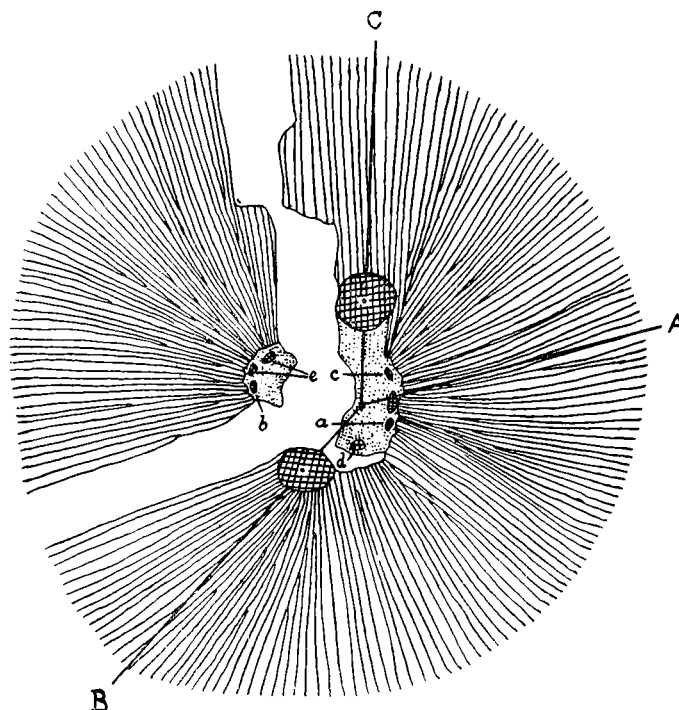


DIAGRAM 2 (K. 628).

been thrown on it. Thus the entering leaf-trace A, after it has become embedded in the pith and has diminished much in size, obviously united with the adjoining bundle (*a*) on the cathodic side (diagrams 3 and 4). The arrangement of the strands indicates that this was a general rule. The last leaf-trace to enter, above A, would have lain on the orthostichy E. In this position we see, in diagram 1, two small bundles (*e*) which may well be the reduced leaf-trace with its reparatory strand. Lower down (diagram 3) these two bundles are fusing, and in the lowest section (diagram 4) they are completely fused.

The leaf-trace still further above would have been on the orthostichy D. Two small bundles in this position (*d*) are already uniting in the uppermost section (diagram 1), and in the next below (diagram 2) their union is complete.

Considering next the leaf-traces which enter below A, the small strand *b* on the

kathodic side of B is presumably the one destined to unite with that leaf-trace (diagrams 1-3); in the lowest section (diagram 4) it has disappeared, which may be due to its fusion with B, or more probably to mere destruction of tissue; for the fusion, according to the analogy of other strands, would not be likely to take place so high up. Lastly, the remaining small bundle, *c*, which appears in all four sections, is in all probability the reparatory strand ready to unite with C, which it is already approaching in the lowest section (diagram 4). In other words, if we trace the course of the bundles from below upwards, we may say that each circum-medullary strand branches

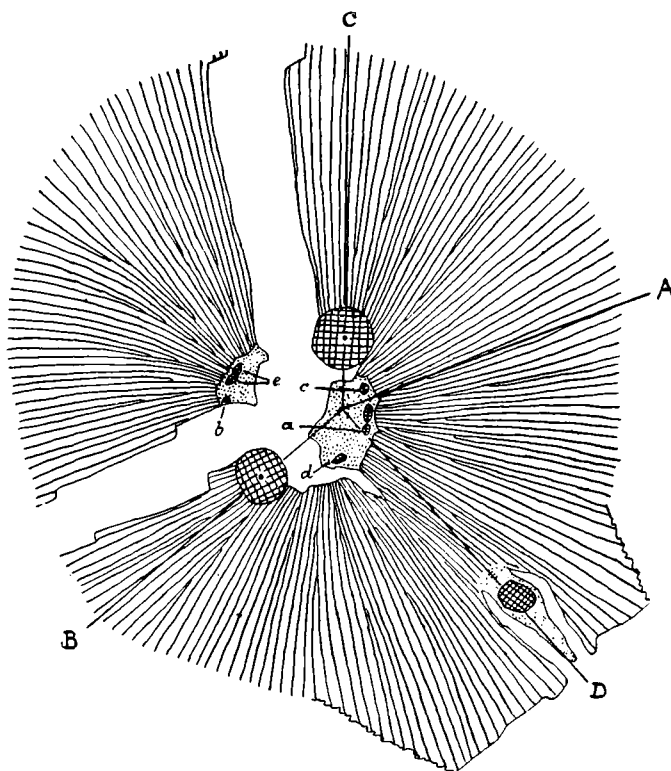


DIAGRAM 3 (K. 629).

at regular intervals; the one branch, that on the anodic side, becomes the leaf-trace and passes out, while the other continues its course up the stem as a reparatory strand, until the next leaf of the orthostichy has to be supplied. It is, however, probable that subsidiary unions between the bundles also occurred.

The course of the bundles, so far as it has been determined, thus appears to be identical with that found in the stem of *Lyginodendron oldhamium*.*

The position of the xylem-strands in the three transverse sections of the WILLIAMSON specimens also points to a $2/5$ phyllotaxis. The order of the sections from above downwards appears to be :—1378, 1380, 1379.

The internodes of the stem were probably short, as is indicated by the rapid succession

* WILLIAMSON and SCOTT, "Further Observations on the Organization of the Fossil Plants of the Coal-Measures." Pt. III. *Lyginodendron and Heterangium*, *Phil. Trans. Roy. Soc.*, vol. 186 (1895), B, p. 711.

of the outgoing leaf-traces. Sometimes, as shown in diagram 3, as many as three successive traces, passing out through the wood, are seen in the same transverse section. In the lower part of its course, as we have seen, the leaf-trace bundle passes very gradually outwards, diverging but little from the vertical direction. When it has once fairly entered the wood, however, it curves more rapidly (owing to the growth in thickness of this zone), so as to assume a more nearly horizontal course, and is consequently cut in an approximately transverse plane when intersected by a tangential section of the wood; such a section, from the WILLIAMSON specimen, is represented in Pl. IV. fig. 7.

From the course of these strands, as described above, there can be no doubt that

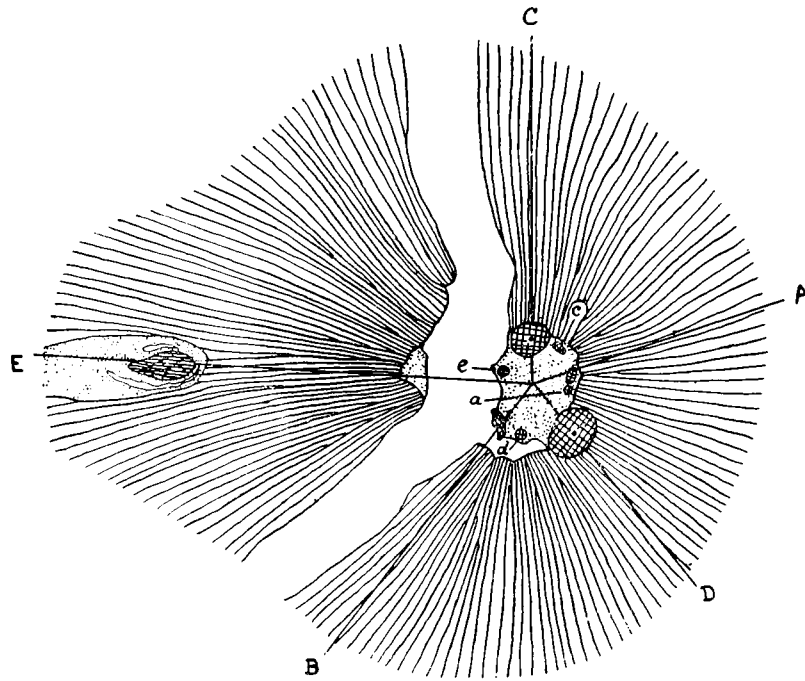


DIAGRAM 4 (K. 540^c).

they represent the leaf-traces, or rather their xylem-constituent, passing out to leaves with a $2/5$ phyllotaxis. On a superficial view, it might perhaps be supposed that the larger strands belonged to branches, but more careful observation shows every grade of transition between the larger and smaller strands, and proves their identical nature (see diagrams 1-4, and figs. 1 and 2). It is evident that the bundle, as it approached its point of exit from the pith, increased rapidly in size, attaining its full dimensions where it began to pass outwards. A similar increase in size, though perhaps less striking, occurs in the outgoing strands of *Lyginodendron** and *Poroxylon*.†

The structure of the primary xylem-strands is most obvious where they attain their

* WILLIAMSON and SCOTT, *loc. cit.*, Pl. 21, fig. 1.

† BERTRAND et RENAULT, "Recherches sur les Poroxytons," *Arch. Bot. du Nord de la France*, 3^{me} Année, 1886, figs. 198, 199, etc.

largest dimensions. The general contour is here nearly circular, and the smallest elements are placed near the centre, where they form a small group, accompanied by a little parenchyma (phot. 2, fig. 1, B). In some bundles the small elements form two distinct groups, separated by parenchyma; this is found chiefly where the strand is well advanced on its outward course, as for example in that shown in fig. 7, from a tangential section, where the strand is seen passing through the secondary wood. Oblique sections show that the small central tracheides are spirally thickened; I have not seen a satisfactory longitudinal section through one of the larger strands, but in the small bundle represented in radial section in fig. 3, the spirals in the interior of the strand are evident. As regards the large strands, there can be no doubt that the structure is *mesarch*, the protoxylem lying about at the centre of the whole strand, and probably separating into two groups as the bundle passed outwards. The tracheides towards the periphery of the primary strand have pitted walls, like those of the secondary wood, but are of larger size, reaching a diameter of 0.1 mm. or more. Between these large elements and the central protoxylem, transitional, scalariform or reticulate forms of sculpturing occur.

As the xylem-strand is followed downwards at the margin of the pith, it rapidly diminishes in size, and its elements become smaller (see A in fig. 1). Lower down, the strand passes deeper into the pith, so as to become separated from the inner margin of the secondary wood by a few (about 2-6) layers of parenchyma (fig. 1). In the lower part of its course, the arrangement of the elements of the bundle undergoes some change; the larger tracheides come to be limited to the outer side of the strand, and the spiral elements lie further inwards. A good example of a bundle fairly low down in its course is shown, in transverse section, in fig. 2. The structure is still *mesarch*; the protoxylem, however, is beginning to approach the inner edge of the strand; the xylem is interrupted at several points by parenchymatous elements. The small strand shown in radial longitudinal section, in fig. 3, has its spiral elements much nearer the inner than the outer side.

A similar structure is seen in some of the smaller bundles in the transverse section represented in fig. 1. Thus, as the bundle is traced downwards, the centripetal part of the xylem diminishes, but it does not appear that a purely *endarch* structure was ever attained. In the bundles of *Poroxylon*, according to Messrs BERTRAND and RENAULT, the centripetal xylem disappears altogether towards the lower end of each bundle.* The change of structure in *Calamopitys fascicularis* is in the same direction, but has not gone so far.

Broadly speaking, the secondary wood has the same structure as in the stem of a *Cordaites*; the medullary rays are narrow, and the pitting of the tracheides is of the usual *Araucarian* type. The structure is well shown in the radial section represented in fig. 4, where the pits are seen to be arranged in three or four rows on the radial walls. A small part, represented more highly magnified in fig. 5, shows the hexagonal bordered

* *Loc. cit.*, p. 306.

pits, with the narrow, slit-like, more or less inclined pore, very clearly. The borders of the pits are sometimes beautifully shown in section, where the wood is cut tangentially, as represented in Pl. IV. fig. 6 (*b.p.*), from the WILLIAMSON specimen.

The medullary rays, which have the usual muriform arrangement of their elements (fig. 4), are, for the most part, one cell only in thickness, but often become two cells thick in places (see figs. 6 and 7). Some are of considerable height (up to sixteen cells or more), while others are only one or two cells high (fig. 6). The outgoing leaf-trace is accompanied by a considerable amount of parenchyma, especially on the upper side* (fig. 7). The medullary rays in the neighbourhood of the leaf-trace are irregular, and generally shorter and broader than elsewhere.

The pits adjacent to the medullary rays are bordered only on the side towards the tracheide—the usual structure in all such cases (see fig. 6, *m.r.*).

The chief peculiarity of the secondary wood is in its innermost region, near the pith, where the elements have an unusual form and arrangement. The tracheides here are broad and short, often with horizontal terminal walls, which thus appear in surface view when seen in a transverse section (*cf.* figs. 2 and 3). Their course is tortuous and irregular; the maximum diameter is usually in the radial direction (see figs. 2 and 3). The pits on their walls, though in more numerous series than elsewhere, are of the usual form; the arrangement of the tracheides, so far as any regularity can be traced, is in radial series, and the medullary rays pass between them; towards the exterior the structure passes over rapidly into that of the normal wood. This peculiarity of the inner zone of wood is common to both the specimens investigated. There seems to be no doubt that the short tracheides in question belong to the secondary wood; they resemble the primary tracheides found by Mr SEWARD in his new genus *Megaloxylon*,† and may probably have served, as he believes to have been the case in that plant, for the storage rather than for the conduction of water.

The chief results arrived at from the investigation of *Calamopitys fascicularis* are the following:—

(1.) The small pith (2–3 mm. in diameter) is surrounded by a ring of distinct primary xylem-strands, eight or nine in number, with mesarch structure.

(2.) These strands are the xylem-constituent of the leaf-traces; they attain their maximum diameter (·8 mm.–1 mm.) when they are about to leave the pith and to pass out through the secondary wood. Below this point they rapidly diminish in diameter, and each unites with the adjacent strand on its kathodic side.

(3.) The outgoing strands are arranged on five orthostichies, corresponding to a 2/5 phyllotaxis. In passing through the wood, each leaf-trace is represented by a single strand.

(4.) The secondary wood has the typical Araucarian or Cordaitan structure, with

* The orientation of fig. 7 has been determined by comparison with a transverse section of the same specimen, in which the parenchyma accompanying a leaf-trace is found on the *inner* (= upper) side of the strand.

† SEWARD, "Notes on the Binney Collection of Coal-Measure Plants." Part II. *Megaloxylon*. *Proc. Cambridge Phil. Soc.*, vol. x, 1899, p. 158.

medullary rays one, or at most two cells in thickness. The inner part of the wood consists of short broad tracheides, with a tortuous course.

The reasons for placing this species in the genus *Calamopitys* of UNGER may now be briefly considered. This genus was established by UNGER on the species *C. Saturni* in 1856,* but our present accurate knowledge of its structure is due entirely to the recent work of Count SOLMS-LAUBACH,† who has further shown that UNGER's *Stigmaria annularis* was also a *Calamopitys*, scarcely distinct from the original species. The generic name *Calamopitys*, which expressed UNGER's view of the Calamarian affinities of his fossil, is entirely inappropriate, and the real relationships of the genus have proved to lie in quite a different direction. The old name is kept up simply in order to avoid burdening the synonymy with a new one.

In the specimens of *Calamopitys Saturni* there is a small pith (only about 1–2 mm. in diameter) surrounded by an irregular tracheal zone, reduced or perhaps wholly interrupted at certain points, and forming enlarged nests between them, each such nest having a central group of small elements, presumably the protoxylem. This zone of primary xylem is surrounded by the secondary wood, the tracheides of which have small narrow circular pits ranged in several rows on their radial walls. The medullary rays are usually pluriseriate. Some remains of the phloem have been found, and the cortex is well shown; in its inner part it consists of parenchyma, while towards the periphery it contains parallel bands of hypodermal fibres, thus having the well-known 'Sparganum' structure. In the cortex the leaf-trace bundles are also found; their course has been followed with great completeness, in successive transverse sections, by Count SOLMS-LAUBACH, who finds that a single bundle leaves the wood, and at first (as in *Lygiodendron*) is accompanied by secondary xylem. The leaf-trace divides into two on entering the cortex, then into four, and finally into six; the six resulting bundles enter one of the leaf-bases which are found attached to the stem. The leaf-stalk has the structure of *Kalymma*, and as *Kalymma* is known to have branched, the inference is that the leaves of *Calamopitys* were compound. Count SOLMS-LAUBACH has shown beyond doubt that the phyllotaxis was 2/5, or extremely near it. In the form referred to *C. annularis*, the primary wood is more extensive, and apparently more continuous; in some of the specimens the pith attains a diameter of 7 mm. In other respects there is no important difference between *C. annularis* and *C. Saturni*, and it is not even certain that the species were really distinct. Both forms belong to the Culm, or Lower Carboniferous, of Central Germany, and are thus of similar horizon to that of the British species.

In comparing the German species of *Calamopitys* with our own fossil, we are unfortunately restricted to characters presented by the pith and wood, for these parts are alone preserved in the British specimens. Count SOLMS-LAUBACH most kindly lent

* RICHTER u. UNGER, *Beitrag z. Palæont. d. Thüringer Waldes*, Denkschr. d. K. K. Akad. zu Wien, math. naturw. Cl. Bd. xi., 1856.

† *Pflanzenreste des Unterculm v. Saalfeld in Thüringen*—Abh. d. K. Preuss. Geol. Landesanstalt, Heft 23, 1896, p. 63, Taf. IV.

me some sections of *C. annularis* for comparison with our own, and on visiting Strasburg I was able to examine a number of other sections both of that species and of *C. Saturni*. Neither of the German fossils is specifically identical with the British form, but I could find no grounds on which to base a generic distinction. A small specimen of *C. annularis* closely resembled Mr KIDSTON'S specimen of *C. fascicularis* in the character of its tissues, and might, on superficial examination of the sections, have been taken for a part of the same stem. It differed, however, in the more continuous primary xylem, and the less marked enlargement of the outgoing xylem-strands, as compared with the others. In this specimen the rays were usually two cells thick, but often one cell only in thickness near the pith. There was thus little difference in this respect from the British form. In the large specimens, both of *C. annularis* and *C. Saturni*, the rays are wider. The pith appeared to present no marked difference from that of *C. fascicularis*. Count SOLMS-LAUBACH has pointed out that in *C. Saturni* a xylem-strand is sometimes found embedded in the pith, without direct contact with the secondary wood, though not far removed from it (*loc. cit.*, p. 72). I have observed the same thing in one of his sections of *C. annularis*, and this, as we have seen, is characteristic of all the smaller xylem-strands in our *C. fascicularis*. *C. Saturni*, in the greater separation of the individual circum-medullary strands, approaches nearer to our species than does the form *C. annularis*. The preservation of the Thuringian specimens is, however, such that the exact limits of the xylem-strands are much more difficult to make out than in the British fossil, especially Mr KIDSTON'S specimen. In the shortness of the internodes *C. Saturni* also agrees with *C. fascicularis*, and, as we have seen, the phyllotaxis and general course of the xylem-strands were the same, so far as the evidence available can show.

On the whole, taking into consideration all the characters available for comparison I feel no doubt that the genus *Calamopitys* is that in which our fossil may most naturally be placed. The form and relative dimensions of the xylem-strands, and the usually uniseriate rays, serve to characterise *C. fascicularis* specifically.

2. *Calamopitys beinertiana* (Goepp. sp.).

The investigation of this species is based on a specimen collected by Mr KIDSTON in September 1900 at Norham Bridge on the Tweed; the horizon (Calcareous Sandstone Series) is similar to that of the Dumbartonshire specimen of *C. fascicularis*. Mr KIDSTON had numerous sections prepared by Mr LOMAX from his specimen, and from these he himself determined the main points in its structure, and identified the species with the *Araucarites beinertianus* of GOEPPERT.* He then very kindly lent me the sections for further investigation, with a view to the inclusion of the species in the present communication.

The specimen is a rather large one, about 4 cm. in diameter in its present incomplete

* This identification has since been confirmed, as will be explained below, by comparison with authentic sections of *A. beinertianus*, for the loan of which I am indebted to Count SOLMS-LAUBACH.

state (see phot. 3); the main stem shows nothing outside the wood, and probably not the full thickness of that, but the transverse sections also contain a detached fragment which has the bark attached, though in a poor state of preservation. The main piece is fairly well preserved, but in places the tissues appear to have suffered from maceration before petrification took place. The most important region—the zone immediately surrounding the pith—is a good deal damaged, but the chief features of its structure are sufficiently plain, as the figures show. The pith, 13–15 mm. in diameter, has a very characteristic appearance, owing to the presence of conspicuous masses of dark-coloured cells, much resembling the ‘sclerotic nests’ in the pith of *Lyginodendron Oldhamium** (see photos. 3 and 4). The nests here consist of rather thick-walled cells, containing carbonaceous matter, which may probably have been derived from the disorganised inner layers of a cell-wall originally much thicker than it at present appears. In the middle of each nest there is a small irregular group of very dark cells; the more peripheral elements of the nest are squarish cells, arranged in series radiating in all directions from the central group. These radial series are continued out into the surrounding thin-walled pith, and are no doubt the result of growth and cell-division subsequent to the first origin of the sclerotic nest. Such a structure is commonly met with in recent plants, around groups of hard tissue differentiated in the midst of an actively growing parenchymatous matrix. Similar cell-divisions occur around the sclerotic nests of *Lyginodendron*, but not to the same extent as in the present species. The general resemblance in the pith of the two plants is sufficiently striking.

The most important point, however, is the presence of a number of primary xylem-strands around the pith, adjoining the inner edge of the secondary wood. The bundles are small compared with the size of the pith, though some of them reach a diameter of about 75 mm. (see Pl. IV. fig. 8). The larger strands are just entering the wood; those which remain at the periphery of the pith are smaller (see fig. 9). It appears, therefore, that here, as in *C. fascicularis*, the strand attained its maximum size just before passing out towards a leaf. As would be expected from the large dimensions of the pith, the xylem-strands are numerous; I was able, in spite of the imperfect preservation, to count seventeen strands which were clear enough for the position of the protoxylem to be recognised. No doubt there were others besides, too obscure to be identified. In parts of the periphery of the pith the primary xylem appears to be almost continuous, for the inner edge of the wood is here formed of irregularly arranged tracheides, larger than those of the secondary zone. This lateral confluence of the primary xylem-groups, though not amounting to continuity all round the pith, recalls the structure found by Count SOLMS-LAUBACH in *Calamopitys annularis*.† The primary strands of *C. beinerianus* bear a strong resemblance to those of *C. fascicularis*, as is evident if we compare the large outgoing xylem-bundle shown in fig. 8 with the corresponding large strands

* WILLIAMSON and SCOTT, *loc. cit.*, p. 717; Pl. 18, photos. 1 and 4; Pl. 21, fig. 1.

† *Loc. cit.*, p. 74.

of the former species represented in fig. 1 and phot. 2; or again, if we compare the smaller xylem-strands of the two species (fig. 9 with fig. 2). In *C. beinerianus*, as in the former species, the outgoing strand has an almost circular transverse section, with the smallest elements towards the centre (fig. 8). As the strand figured is damaged at the back, we cannot be quite certain whether the structure was strictly mesarch, *i.e.*, whether there were tracheides all round the protoxylem. From the evidence of another outgoing strand, however, it is probable that this was the case, so that the resemblance to *C. fascicularis* appears to be complete, so far as these larger strands are concerned. I have also carefully examined all the smaller xylem-strands shown in the transverse sections; some of them, like the outgoing bundles, may be mesarch, but the majority are certainly endarch; some have a structure which may be described as hippocrepiform-endarch (see fig. 9); that is to say, the ring of tracheides is interrupted at the back of the bundle, so that on the side towards the pith the protoxylem is in contact with thin-walled tissue. There is very little real difference between this structure and that of the smaller mesarch strands of *C. fascicularis* (*cf.* fig. 2); there also the xylem, or rather the tracheal tissue, is interrupted, but not so regularly on the inner side of the strand. Similar differences occur among the bundles in the stem of *Osmunda*.*

This partial assumption of endarch structure is of interest, as marking the first step in that disappearance of centripetal xylem which characterises the later types of Gymnospermous stem.

In some of the longitudinal sections the spiral tracheides of the protoxylem are quite distinct, as in the bundle shown in fig. 10. Here the protoxylem is adjacent to parenchyma, but the poorly preserved element still further to the interior is a tracheide. The section, however, as shown by the direction of the medullary rays, was not accurately radial, so most probably this was a 'hippocrepiform endarch' bundle, one of the flanking tracheides appearing on the inner side of the strand in consequence of the deviation of the section from the radial plane. The primary tracheides show the usual transitions through reticulate to pitted structure. The walls of the largest of the primary xylem-elements have numerous rows of hexagonal bordered pits, sometimes beautifully preserved (see fig. 11). The largest primary tracheides are as much as .1 mm. in diameter; those of the secondary wood seldom exceed .05 mm.

The pitting of the secondary wood, usually imperfectly preserved, but well shown at a few places, is limited, as usual, to the radial walls. The pits are most often in two rows only; sometimes they are scattered, and even when in contact do not usually assume a regular hexagonal outline, though sometimes there is an approach to this form. The bordered structure of the pit with a narrow slit-like pore is evident in the better preserved parts of the wood. Examples of medullary rays, as seen in tangential section, are shown in fig. 12. They are nearly always one cell only in thickness; cases where the ray is locally two or more cells thick (as in fig. 12, B) are very rare, and appear to be connected with some irregularity in the course of the tracheides. The great differences in

* ZENETTI, *Bot. Zeitung*, p. 57, woodcut 2, and p. 62, woodcut 3, 1895.

the height of the rays are sufficiently illustrated by the comparison of figs. 12, A, and 12, C. Small rays two cells in height are common, and rays only one cell high also occur. In the rays of greater height there is often considerable variation in the dimensions of the constituent cells (see fig. 12, A). The secondary wood, as a whole, has quite a Coniferous character, and thus offers a striking contrast to the primary structure.

In some of the tangential sections a large leaf-trace bundle, accompanied by parenchyma, is seen passing out through the wood (see Pl. V. fig. 13). The strand is rather obscure, as it is cut obliquely; the smallest elements are central, with some xylem and parenchyma next them, and the structure therefore probably mesarch. The pits on the larger tracheides of the strand can be recognised. It is important to note that in this part of its course the leaf-trace is represented by a *single* strand and not by a pair of bundles, thus agreeing with *C. fascicularis*.

The fragment of stem with bark attached has been already mentioned. The bark, which is about 5 mm. thick, is shown in transverse section, and consists of alternate darker and lighter tangential bands of tissue. The whole mass evidently represents a regular scale-bark; in some of the darker bands radially arranged peridermic cells can be recognised; the intermediate softer tissue may be partly phloem; the larger cells to the outside between the periderm-bands may have belonged to the primary cortex. At one place a broad band of thick-walled periderm is well preserved; at another, a few displaced fibres can be recognised; but, on the whole, the preservation is too imperfect to justify a more detailed description.

As mentioned above, the specimen just described was identified by Mr KIDSTON with the *Araucarites beinertianus* of GOEPPERT,* with which the characters of the secondary wood agree, as shown by GOEPPERT and STENZEL's diagnosis (1888). "*Ar[auca]riæ ligni, stratis concentricis haud conspicuis, tracheidis amplis punctatis, punctis 1-, 2-, rarius 3-serialibus spiraliter dispositis approximatis aut subcontinguis rotundatis, radiis medullaribus latis 1-, rarius 2-serialibus e cellulis crassis 1-10, rarius pluribus superpositis formatis*" (*loc. cit.*, p. 30). The figures, cited in the footnote, also agree very well with our specimen. On characters of the secondary wood alone, however, one might have hesitated in affirming identity, but Mr KIDSTON's determination has now been fully confirmed by comparison with sections of the Falkenberg plant, very kindly lent me by Count SOLMS-LAUBACH, in one of which the pith and primary wood are included. The section in question is shown in an excellent photograph (Plate VII. fig. 10) among the illustrations to Count SOLMS-LAUBACH's second paper on the Falkenberg Culm-fossils,† though on too small a scale for details to be exhibited. The identity of the

* *Araucarioxylon beinertianum*, Kr. (Göpp., sp.), 1870-72; *Araucarioxylon beinertianum*, Kraus in Schimper, *Traité d. paléont. Végét.*, vol. ii. p. 381, 1850; *Araucarites beinertianus*, Göpp., *Monog. d. foss. Coniferen.*, p. 233, pl. xlii. figs. 1-3; pl. xliii. fig. 1, 1852; *Araucarites beinertianus*, Göpp., *Foss. Flora d. Uebergangs. Form.*, p. 254, pl. xxxv. figs. 1-4, 1888; *Araucarites beinertianus*, Göpp. u. Stenzel, *Nacht z. Kennt. d. Coniferenhölzer d. palæoz. Form.*, p. 30, pl. iv. figs. 36-39; *Araucarites beinertianus*, Göpp., *Revision d. foss. Conif.*, p. 11 (*Bot. Centrabl.*, 1881, vol. v. p. 396).

† "Ueber die in den Kalksteinen des Kulm von Glätzisch-Falkenberg in Schlesien erhaltenen structurbietenden Pflanzenreste. II.," *Bot. Zeit.*, 1893, p. 207.

specimen with the *Araucarites beinertianus* of GOEPPERT was established by Count SOLMS-LAUBACH in conjunction with STENZEL, whom he consulted.

The preservation is decidedly better than that of the Tweed specimen. The pith (about 8 mm. in diameter) contains three sclerotic nests,* and agrees in every respect with that of our plant. At three points distinct mesarch strands of primary wood are present; two of these belong to outgoing leaf-traces, while the third, which is smaller, has not yet begun to pass out. At several other places small strands of tracheides, apparently primary, can be recognised; most of these were no doubt endarch in their development, and they show no clear cases of mesarch arrangement. The secondary wood, in both transverse and longitudinal section, shows essentially the same structure as in the Tweed specimen, except perhaps that biseriate medullary rays are somewhat more frequent.

Mr KIDSTON, who has also examined Count SOLMS-LAUBACH's sections, agrees with me that they remove all doubt as to the specific identity of the British specimen with the *Araucarites beinertianus* of GOEPPERT.

The chief results relating to *C. beinertiana* are the following :—

(1) The relatively large pith contains 'sclerotic nests' resembling those in the pith of *Lyginodendron*.

(2) Around the pith, and in contact with the secondary wood, numerous primary xylem-strands, sometimes laterally confluent with one another, are disposed.

(3) The primary strands attain their largest size where they enter the wood; at this point they resemble the corresponding bundles in *C. fascicularis*, and are of mesarch structure.

(4) The small strands are more usually endarch, and sometimes of a horse-shoe form, the opening being turned towards the pith, and the protoxylem lying in the concavity of the strand.

(5) A single strand constitutes the leaf-trace, where it enters the secondary wood.

(6) The secondary wood has a regular Cordaitan structure, with medullary rays seldom more than one cell thick.

(7) A scale-bark was formed on the older stems.

The reasons for placing this species in the genus *Calamopitys* are apparent at once from the foregoing description. The detailed structure of both primary and secondary wood is so closely similar in the two species, that if *C. fascicularis* is rightly placed in UNGER's genus, it is impossible to doubt that the other species must accompany it. Naturally, both determinations, though resting, as it seems to me, on good grounds, must be regarded as provisional until the characters of the cortex and leaf-bases are known. In the meantime, it is interesting to note that in the same beds which yielded the specimen of *C. beinertiana*, Mr KIDSTON found a petiole—provisionally named by him *Rachiopteris multifascicularis*—which presents very much the same structure as the small *Kalymma*-like leaf-bases borne on the stem of *Calamopitys Saturni*.

* SOLMS-LAUBACH, *loc. cit.*, p. 208.

Distinctive specific characters of *C. beinertiana* are to be found in the large size and peculiar structure of the pith, the relatively small extent of the primary xylem, the frequent endarch structure of the smaller primary strands, and the usually somewhat scattered arrangement of the pits on the secondary tracheides.

II. PITYS. Witham, emend.

1. *Pitys antiqua*, Witham.

The structure of this stem has been investigated principally in a specimen from Mr KIDSTON's collection (sections 598A-598H), collected by Mr B. N. PEACH, F.R.S., at Lennel Braes in Berwickshire, in 1883. The specimen, like those already described, is of Lower Carboniferous age (Calcareous Sandstone Series). Its specific identity has been established by comparison with WITHAM's type-specimen, as will be explained below.

In this case, also, I am indebted to Mr KIDSTON for calling my attention to the peculiarities of the fossil, and lending me his sections for investigation.

The stem is remarkable for its large pith, which in the specimen collected by Mr PEACH, has a diameter of 22 mm. (phot. 5). In a section from another specimen, also from Lennel Braes (No. 221 in Mr KIDSTON's collection) the pith as preserved is as much as 34 mm. in diameter, and may be incomplete. The structure of the pith is characteristic; it consists of large, but very short cells, their width, which usually exceeds their height, being from .15 to .2 mm. (see figs. 14, 15, and 16). Many of the pith-cells are filled with dense carbonaceous contents, suggesting that they may have been secretory elements. Although they do not differ in form from the surrounding, comparatively empty cells, yet their somewhat regular arrangement, and the fact that their relative frequency is unaffected by the state of preservation, may indicate that some real differentiation existed during life.

A conspicuous feature of the pith is the presence of large, horizontal, lenticular gaps in its tissue (see phot. 6). These gaps are largest in the outer part of the pith, though they are present to some extent all through it. They appear to be due to a shrivelling of the tissues, for the cells between the larger gaps are flatter than elsewhere, and have a collapsed look. The gaps extend out into the principal medullary rays. Their presence gives the pith, as seen in radial section, an appearance not unlike that of the well-known discoid pith of *Cordaite*s, but much less regular. It may be doubted whether the resemblance is more than a superficial one. The Cordaitean discoid structure, as shown, for example, in *Cordaite Brandlingi*,* is strikingly regular, and appears to have been due to rupture during a normal process of growth; the gaps are strictly limited to the middle part of the pith, the peripheral zone being uninterrupted; neither do the cells show any signs of collapse. In all these points the pith of *Pitys antiqua* is different; here the imperfectly discoid structure has much

* SCOTT, *Studies in Fossil Botany*, fig. 137, A; RENAULT, *Cours de Bot. Fossile*, vol. i. pl. 12, fig. 12.

more the appearance of having been caused by unequal contraction of the tissue, perhaps after death.* Where the specimen is badly preserved, the gaps are much exaggerated. The pith has evidently undergone dilatation, as shown by the increase in width of the medullary rays at their inner ends, and by the marked horizontal elongation of many of the pith-cells (Pl. II. photos. 8 and 9, Pl. V. figs. 14–16). The latter feature is especially conspicuous around the primary xylem-strands, from which the dilated medullary cells usually radiate out in all directions (photos. 8 and 9, figs. 14 and 15). This is a familiar phenomenon wherever lignified strands occur in the midst of an actively-growing cellular tissue, as, for example, in fleshy roots.

The chief point of interest in the stem of *Pitys antiqua* is the presence of numerous strands of primary xylem around the pith, and for the most part embedded in its tissue. Their distribution is shown in diagram 5, prepared by Mr L. A. BOODLE, in which all

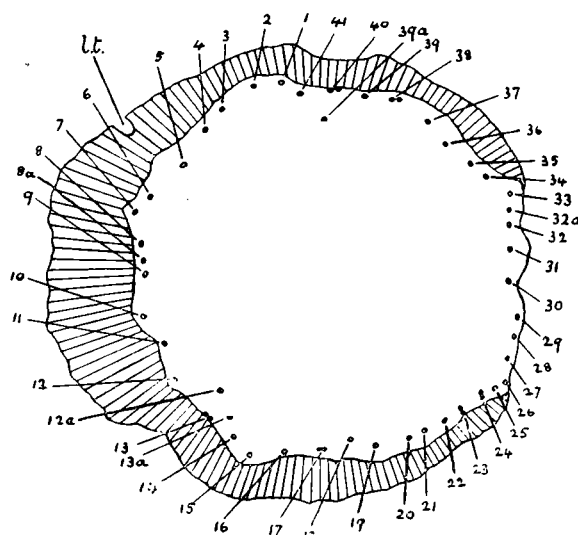


DIAGRAM 5.

the strands shown in a transverse section have been accurately plotted, in their exact position, with the aid of the *camera lucida*. The total number of xylem-strands present in this section was 46. It will be noticed that, with few exceptions, they are separated by an appreciable interval from the inner edge of the secondary wood. Actual contact is only shown at three points, namely, in the case of the strands numbered 13, 23, 40. All the others are separated from the wood by distances ranging from .3 mm. to 1.8 mm.† The xylem-strands themselves vary in diameter from about .15 mm. to about .3 mm., so their distance from the wood almost always exceeds their own diameter, and is often many times as great. Strands 13 and 40 are double (*cf.* Pl. V. fig. 14 for strand 13); we know, from the evidence of successive transverse sections, that strand 13 passed

* Similar lacunæ are present in the central tissue (primary wood) of *Megaloxydon*. See SEWARD, "Notes on the Binney Collection of Coal-Measure Plants"; Part ii., *Megaloxydon*. *Proc. Cambridge Phil. Soc.*, vol. x., 1899.

† Of course only that part of the section in which the secondary wood is present is taken into consideration.

out into the secondary wood a little higher up the stem. The gap shown at *l.t.* on diagram 5 (see also phot. 5), clearly marks the course of another outgoing leaf-trace. The strand 23 also seems to be double, but here the tissue is damaged. From the somewhat slender evidence available, it seems probable that contact between a primary strand and the secondary wood only occurs at points where the former is about to pass outwards, presumably on its way to a leaf. It also appears that, at the point of exit from the pith, the leaf-trace was a double strand, but its two branches, as we shall see, re-united in passing through the wood. Double or paired strands may also occur elsewhere, independently of outgoing leaf-traces (see, for example, phot. 8, representing strand 38 in diagram 5). The diagram is taken from a section higher up the stem, where the two strands have approached nearer to each other.

Before further considering the distribution of the xylem-strands, it will be well to describe their structure. The strands, as already mentioned, are small, indeed very small in comparison with the size of the pith. Most commonly their maximum diameter is about .25 mm.; the sectional form of the strand is usually elliptical, the major axis lying in the tangential direction. A good typical example is shown, in transverse section, in fig. 15, which represents the strand numbered 3 in diagram 5. The smallest elements (*px*) lie near the middle of the strand; towards its periphery the tracheides become considerably larger, about equalling the innermost elements of the secondary wood in size. A few parenchymatous cells occur among the primary tracheides, especially near the middle of the group. Phot. 8 shows the same structure in each strand of the paired bundle numbered 38. Of the two strands shown in phot. 9, one (No. 14) shows the usual arrangement of the elements; the other (13A) is less regular. Longitudinal sections show the nature of the elements. Fig. 16 is from a tangential section (shown as a whole in phot. 7) which passes through the periphery of the pith, and here cuts through the middle of a xylem-strand. The more central tracheides have an evident spiral thickening; the narrowest among them are no doubt the actual protoxylem. The peripheral tracheides of the strand are larger, and their cells definitely reticulated, the lines of reticulation having a spiral course (fig. 16, *r. t.*). Close examination shows that, in the outer tracheides, each mesh is bordered, so that the reticulation is passing over into a system of spirally arranged, bordered pits. Similar elements, one of which is shown in detail in fig. 17, occur at the inner margin of the secondary wood, where, however, no true spiral tracheides have been detected.*

Fig. 16 also shows the xylem-parenchyma, with possible secretory sacs, within the primary bundle.

The evidence thus indicates that the primary xylem-strands of *Pitya antiqua* have a mesarch structure, differentiation having begun at a point near the middle of the strand, as indicated by the position of the spiral tracheides. The mesarch structure holds good

* I find that perfectly similar elements have been described by ROTHERT, in recent Conifers, under the name of "Gemischte Gefässe." See his "Tracheiden u. Harzgänge im Mark von *Cephalotaxus*-Arten," *Ber. d. Deutsch. Bot. Gesellsch.*, Bd. 17, 1899, p. 284.

for the great majority of the strands; in a few of the smallest the protoxylem may lie on one side or the other (*e.g.*, the strand 13A shown in phot. 9).

At the point where a double bundle comes into contact with the secondary wood previous to passing out into the latter, the structure is less regular. Fig. 14 shows this in the case of the double strand numbered 13. The smallest elements of the two xylem-strands are here directed towards each other, and some of them abut directly on a wedge of secondary wood. In a section cut a little further up the stem, where this bundle is shown entering the wood on its outward course, it appears as a single strand, the two half-bundles having re-united. It is possible that their temporary separation may have been due merely to the intrusion of dilated parenchyma.

The similar outgoing strand between bundles 5 and 6 (*l.t.* in diagram 5 and phot. 5), though obscure, and difficult to distinguish from the adjacent secondary wood, is clearly a single one. It is remarkable how small were the dimensions of the leaf-trace (as we must assume it to have been), at least as regards its primary xylem. Possibly it was supplemented on its outward course by an arc of secondary wood, as was the case in *Poroxydon*,* but at present we have no information as to any of the external tissues of our fossil. It will be noticed that behind each of the outgoing strands 13 and 40 (diagram 5) there is a small xylem-bundle deeply embedded in the pith (12A and 39A respectively); the strand 5 stands in a similar relation to the leaf-trace, *l.t.* The strand 12A is shown in detail in fig. 14. In this case there is a second deep-seated strand near by (13A, shown in phot. 9). In the uppermost of the five successive transverse sections of the stem which we possess, where the strand 13 is beginning to enter the wood, the two deep-seated strands, 12A and 13A, are approaching each other as if about to fuse, but there is no evidence to show whether such a fusion was of general occurrence. In any case it is natural to regard the deep-seated strand behind the leaf-trace as a reparatory strand, destined to constitute or contribute to the next outgoing bundle of the same orthostichy.

The phyllotaxis was no doubt a spiral one, and very probably complex, as suggested by the large number of primary strands.

There is evidence that the primary strands occasionally branched and anastomosed with one another. This is best seen in a tangential section, passing through the outer part of the pith, and touching in places on the secondary wood, represented in phot. 7. Several of the primary xylem-strands are shown; the double strand, which corresponds almost exactly in size and position with some of those shown in transverse section (*cf.* fig. 14), is in contact with the innermost tracheides of the secondary wood, and may probably represent a leaf-trace about to pass out. An oblique anastomosis between the strands of this pair is present.

Another strand appears to be branching, and at several places single tracheides are seen diverging from the xylem-strands in various directions, probably to form a connection with others.

* *Cf. Pitys Withami*, below, p. 355.

Such isolated tracheides, either between two xylem-strands, or between a xylem-strand and the secondary wood, are not infrequently met with in the transverse sections, as shown in phot. 9, between the strands numbered 14 and 13A in diagram 5. It is probable that these elements served to keep up communication between different strands, though in some cases their separation from the bundle to which they belonged may have been an accidental effort of the dilatation of the adjacent parenchyma.

The wide separation between most of the primary xylem-strands and the secondary wood presents a considerable difficulty, which exists also, though in a less degree, in the case of *Calamopitys fascicularis*, and probably other species of that genus. In *Pitys antiqua*, as mentioned above, the actual distance ranges from about a third of a millimetre to almost two millimetres. The average interval, it is true, is only about half a millimetre, but this is equal to twice the average diameter of the xylem-strand itself. Cases of contact are rare, and probably limited to bundles approaching their exit. Apart from these special cases, we find that the number of pith-cells intervening between a primary strand and the wood varies from one up to about twenty, averaging five or six.

The question arises: What could have been the primary structure of a stem in which such an arrangement prevailed? If, as all the evidence indicates, the process of secondary growth was of the normal type, the secondary wood being intercalated between the primary xylem and the phloem, it follows that in the primary condition the xylem and phloem of each bundle must have been widely separated, and that to a very unequal extent in different bundles, unless indeed the isolation of the xylem-strands can be explained by subsequent dilatation of the parenchyma. We have already seen that this took place to a considerable extent; in some cases the apparent doubling of a xylem-strand has evidently been brought about by tangential dilatation of its own fascicular parenchyma, and the isolation of single tracheides may sometimes have been due to a similar cause. But I have found no evidence that in *Pitys antiqua* the dilatation was greater between the xylem-strand and the secondary wood than elsewhere. It rather appears that the *relative* position of the two has remained approximately constant, though the *absolute* distance between them has no doubt been increased by the general extension of the parenchyma. If this were so, there must have been from the first an unusual separation, varying in different bundles, between xylem and phloem, and the cambium must have arisen towards the phloem-side of the intervening tissue, thus leaving the primary xylem more or less isolated. The tissue between primary and secondary wood would, on this view, have originally been fascicular, but have become assimilated to the pith by subsequent dilatation. The position of the specially deep-seated xylem-strands, behind the outgoing leaf-traces, remains a difficulty, and I do not think that the whole question will be solved until young stems are discovered. Some analogy for the separation of primary from secondary wood is afforded by the peduncles of certain Cycads (especially *Stangeria*) where the centripetal

is often rather remote from the centrifugal wood.* A similar separation is of common occurrence in roots, especially those of Gymnosperms.

Two other explanations are theoretically possible, though I believe really untenable. We might suppose that the cambium was extrafascicular, the xylem-strands thus representing complete vascular bundles. I have not, however, found the least indication of phloem in connection with them, and the preservation is sufficiently good to leave little doubt that none existed, and that the xylem-strands were surrounded on all sides by parenchyma only.

The other possibility is that the xylem-strands may not have constituted the primary xylem of the leaf-trace system, but may have formed a merely accessory system of medullary strands, remotely comparable to the medullary bundles of *Encephalartos*, *Macrozamia*, or even, as some might suggest, to the star-rings of *Medulloseæ*. The absence of phloem is an obvious objection to this view also, and even apart from this, the facts that the xylem-strands pass out through the secondary wood, and that they are the only part of the wood where spiral elements occur, seem fairly decisive for their primary nature, as part of the main leaf-trace system of the plant. The very remarkable medullary xylem found by ROTHERT in a Conifer, which he refers to *Cephalotaxus Koraiana*, offers a certain analogy with that of our fossil, but, in the case of this recent plant, no spiral elements occur among the medullary tracheides.†

The general structure of the secondary wood of *Pitya antiqua* has long been known,‡ but as Mr KIDSTON's specimen (No. 598) is probably the best-preserved of any hitherto investigated, a short description may be given, more especially as the existing accounts are inaccurate in various points.

The chief generic character of *Pitya*, as at present defined—the wide medullary rays—is well exhibited. The principal rays are usually much wider at their inner ends than elsewhere. A ray .3 mm. in tangential width at its junction with the pith may diminish to a tenth of that width in a distance of little more than a millimetre (fig. 14, phot. 8). The difference depends more on the width of the individual ray-cells than on their number, which remains nearly constant, and is evidently due, in great part, to dilatation occurring during the early stages of wood-formation. The gaps in the pith, referred to above (p. 346), run out for some distance into the principal medullary rays. Close to the pith, where the rays are wide, the nature of these gaps, as mere tears in the tissue, is evident; further out, as the rays become narrower, the gaps assume a more regular form, and sometimes strongly suggest the resin-canals in the rays of *Abietinæ* (see Pl. VI. fig. 20, g). This appearance is in all probability

* SCOTT, "Anatomical Characters presented by the Peduncle of Cycadaceæ," Pl. XX. figs. 1-5, *Ann. Bot.*, vol. xi., 1897.

† ROTHERT, *l.c.* It is interesting to find (p. 285), that ROTHERT's "gemischte Gefässe" occur in the medullary as well as in the normal wood of his *Cephalotaxus*, just as is the case in *Pitya antiqua*.

‡ WITHAM of Lartington, *Internal Structure of Fossil Vegetables*, Edinburgh, 1833, pp. 25-27, 37, 38, 71, pl. iii.; pl. iv., figs. 1-7; pl. vii., figs. 9-12; pl. viii., figs. 1-3; pl. xvi., figs. 9, 10. Little appears to have been added by later writers.

deceptive, and the spaces due simply to the contraction of the surrounding tissue. Traced out into the wood, the rays soon assume the ordinary structure; their tissue, as seen in radial section, has the usual muriform character (see Pl. V. fig. 18). The cells usually retain some remains of their contents, often in the form of definite granules. Secondary rays appear between the principal ones, as best shown in specimens where the wood attains some considerable thickness.

Seen in tangential section (Pl. VI. fig. 19) the larger rays are found usually to reach a width of four cells, sometimes five or even six, and are often of great height, seventy cells or upwards in some cases. Among the large rays, however, much smaller ones occur, only one cell thick, and of small height, sometimes reduced to a single cell. At one or two places an isolated strand of xylem-parenchyma was observed, consisting of a row of vertically elongated cells, at least three times as high as those of the rays. This tissue is, however, extremely scanty, and in most sections is not shown.

The tracheides are exquisitely preserved. Those at the inner edge of the secondary wood are transitional between the reticulated and pitted forms; the spirally arranged reticulations are distinctly bordered (fig. 17). Further out in the wood, the spiral arrangement becomes less marked, and the pits assume the characteristic hexagonal form (fig. 18). They are ranged in four or five ranks, on the radial walls of the large tracheides, and are usually in contact with one another throughout. Occasionally, however, especially near the ends of the tracheides, the pits are more scattered, as WITHAM described them,* and may be even reduced to a single row, leaving the rest of the wall bare. The border of each pit is, as a rule, perfectly preserved, enclosing a narrow slit or pore, usually in an inclined position (fig. 18). A more perfect example of typical '*Araucarioxylon*' structure than that presented by this wood could not be imagined.

The tangential walls of the tracheides are, as a rule, without pits, but exceptions occur, especially in the inner layers of the wood. A good example is shown in fig. 20, where a number of pits (*t.p.*) are seen on the tangential wall of a tracheide. Where they occur, they are less crowded than those on the radial walls, and do not cover the whole surface. Tangential pits are of common occurrence in the wood of the Coniferæ, especially in the first-formed layers, and in the tracheides of the autumn wood.†

We may sum up the chief anatomical characters presented by the stem of *Pitys antiqua* as follows:—

(1) The pith is large (22 mm. to 34 mm. or more in the specimens examined) and consists of short-celled parenchyma, interrupted by extensive horizontal lacunæ, probably due to shrinkage of tissue.

(2) Around the periphery of the pith, and usually at some little distance from the inner edge of the secondary wood, are a large number (40–50) of small primary xylem-strands, which occasionally anastomose with one another. The central elements of each strand are spiral tracheides, indicating a mesarch structure.

* *L.c.*, p. 38.

† *L.c.*, STRASBURGER, "Leitungsbahnen," *Histologische Beiträge*, iii. p. 9, 1891.

(3) At certain points the primary xylem-strands come into contact with the secondary wood, and pass out through it; these outgoing strands no doubt represent the leaf-traces.

(4) The secondary wood is traversed by numerous medullary rays, the larger of which are usually four cells or more thick. The principal rays are much dilated towards their junction with the pith. In addition to the rays, vertical strands of xylem-parenchyma occur, but very sparingly.

(5) The secondary tracheides have, on their radial walls, several rows of bordered pits, usually contiguous and hexagonal. Tangential pits also occur not infrequently. No true spiral elements are present at the inner edge of the secondary wood.

The identification of Mr KIDSTON's specimen, No. 598, on which the description above is based, with the *Pitys antiqua* of WITHAM, rests on a comparison with sections of WITHAM's type-specimen, kindly lent me by Prof. BAYLEY BALFOUR, F.R.S., and Mr KIDSTON. The specimen from which these sections were cut is the large stem shown in transverse section, reduced to half natural size, in WITHAM's *Internal Structure*, Plate III. The two sections sent me from Edinburgh are originals of WITHAM's, while those lent by Mr KIDSTON (Nos. 217-220 in his Collection) are better and more modern preparations from the same specimen. In all these only the secondary wood is shown. The preservation is not equal to that of the stem (No. 598) collected by Mr PEACH, but, allowing for this difference, the structure essentially agrees. The locality, Lennel Braes on the Tweed, is the same. The medullary rays in WITHAM's specimen are more scattered, and sometimes broader than in No. 598, attaining an extreme width of seven cells, as against five, or rarely six, in the latter, but these differences may well be due to the much greater size of the WITHAM stem. The dimensions of the elements agree very nearly. Where the pitting is well shown in radial section, the arrangement corresponds with that in No. 598. At many places the pits are in 3-5 rows, covering the whole wall of the tracheide, closely packed and hexagonal in outline, quite like those shown in fig. 18, except that, as the preservation is not so good, the outline of the borders is less sharp. In other places the pits are more scattered and rounded in outline, as also occurs in the other specimen. There is a section in Mr KIDSTON's collection (No. 221) which, he tells me, may be from a different specimen. This is the section referred to above (p. 346) as showing a pith at least 34 mm. in diameter. The state of preservation is similar to that of the type-specimen, with which its secondary wood exactly agrees. The pith is lacunar, and primary strands of xylem are present, just as in No. 598. A transverse section of a branch, figured by WITHAM (Pl. VII., fig. 11), with a pith more than 3 cm. in diameter, has quite the anatomical habit of our fossil (*cf.* phot. 5).

Considering the identical locality, I feel no doubt that the specimen on which the description given in the preceding pages is based, is referable to WITHAM's species, *Pitys antiqua*, his 'Lennel Braes Tree.'

2. *Pitya Withami* (Lindl. et Hutt., sp.).

I take this species to include the *P. medullaris* of LINDLEY and HUTTON, which WITHAM himself regarded as probably identical with the former.* There seems no object in keeping up the two specific names, as the characters on which *P. medullaris* was separated—the large pith, and the appearance of concentric markings (probably not annual rings) in the wood, are common to many stems of the *Dadoxylon* group, and of no diagnostic value. Both were included in the old genus *Pinites* of LINDLEY and HUTTON, which, as employed by those authors, has long since been abandoned. The distinction drawn by WITHAM† between *Pinites* and *Pitya*, and based on the round, separate pits in the case of *Pitya*, and the hexagonal contiguous pits in that of *Pinites*, has no value, as both conditions are found in different parts of the same specimen. *Pitya Withami* is, in fact, a closely-allied species to *P. antiqua*. The pitting on the tracheides is identical (if equally well-preserved specimens are compared), and there is no constant difference in the size of the elements. The medullary rays are, however, on the whole narrower in *P. Withami* than in *P. antiqua*, rarely exceeding four cells in width in the former. The point of interest for our present purpose is that *Pitya Withami* shows the same primary anatomical structure as *P. antiqua*, having, like that species, a ring of primary xylem-strands disposed round the pith. My observations were made on an original section of WITHAM'S (figured in *Internal Structure*, Pl. VI., figs. 5–8), lent me by Professor BAYLEY BALFOUR. This section was from the branch to which LINDLEY and HUTTON gave the name of *P. medullaris*; it is represented as a whole in Pl. II. phot. 10. The pith, which measures 19×10 mm., shows essentially the same structure (so far as exhibited in transverse section) as that of *P. antiqua*, but much of the tissue is altered in appearance by the infiltration of some dark-brown substance. The preservation is tolerably good, but towards the wood, where the cells become smaller, the structure is obscure, partly owing to the section not being sufficiently thin. Yet at several places small strands of thick-walled elements can be distinguished lying near the outer margin of the pith, a little within the ring of secondary wood. These groups agree so closely, in appearance and position, with the primary xylem-strands of *P. antiqua*, that we cannot doubt their identical nature. The strand figured (Pl. VI. fig. 21) appears to be a double one.

The secondary wood is described by WITHAM (*l.c.*, p. 32) as showing “decided indications of five concentric layers.” The layers are marked by tangential bands of somewhat flattened elements (see WITHAM, Pl. VI., fig. 8),‡ and the bands, so far as the section extends, are fairly, though not completely, continuous. There is thus a certain resemblance to the annual rings of recent Coniferæ, but very much less marked and regular in the fossil, so that (considering the inconstancy of such markings in Palæozoic

* *Internal Structure*, pp. 36 and 42. *Pitya Withami* was founded on the well-known Craighleith trees discovered in 1826 and 1831 in the Craighleith Quarry, near Edinburgh.

† Who, however, himself had some doubts as to the generic value of the distinction. *L.c.*, p. 39.

‡ This figure gives a fair idea of the relative forms of the elements, but the dark shading makes the rings appear more conspicuous than they really are.

stems) it would be extremely rash to draw any inference as to a seasonal periodicity of growth.

At one place a bundle, no doubt a leaf-trace, is clearly shown, passing out through the wood (see phot. 10, *l.t.*). A very definite arc of secondary wood forms part of the outgoing leaf-trace, and is sharply marked off from the general wood of the stem. This observation confirms the conclusion, drawn from *Pitys antiqua*, that in this genus the leaf-traces, on leaving the pith, were single strands.

So far as the evidence extends, there was thus a complete agreement in the primary structure of the stem between *Pitys Withami* and *P. antiqua*.

3. *Pitys primæva*, Witham.*

This species, one of WITHAM'S Tweed Mill fossils,† is a very distinct form, as shown by the great width of the medullary rays, which are commonly seven cells in thickness and often more, and of a decidedly broader and shorter form, in tangential section, than those of *P. antiqua* or *P. Withami* (see fig. 22). The tracheides, also, are larger, and the pitting slightly different, the pits of *P. primæva* being less crowded than those of the other species. Hence the hexagonal form is less marked and a circular outline more frequent in the pits of *P. primæva* than in those of its congeners.

As regards the question of primary xylem-strands, the material at my disposal was not favourable, as I have seen no sections passing through the pith of a main stem. In one case, however, a tangential section happens to cut transversely across the base of a lateral branch (Pl. II. phot. 11). The pith of the branch is only partly preserved; what remains of it resembles that of *P. antiqua*. At two places in the pith, near the wood, I observed a group of small, rather thick-walled elements, similar to the tracheides of the secondary xylem. At one point the spiral band of a tracheide could be recognised. The pith-cells are elongated radially around the groups in question, and the whole appearance (allowing for the imperfect preservation) is in all respects similar to that of the primary xylem-strands in *P. antiqua*.

The same tangential section is also of interest from another point of view, for it appears to throw light on the problematic fossil described by WILLIAMSON under the name of *Lyginodendron* (?) *anomalum*.‡ In the section of *P. primæva* (phot. 11), the medullary rays near the lateral branch have a form very different from that which characterises them elsewhere (see fig. 23, and compare with fig. 22). They are shorter than usual, and at the same time much wider, so as sometimes to assume a nearly circular form, as seen in the tangential section. These exaggerated medullary rays constitute in this region the great mass of the wood, the strands of tracheides merely forming a sinuous network between them. The appearance is almost identical with

* Sections of two specimens, one from the River Irthing, Northumberland, the other from Juniper Green, Midlothian, were lent me by Mr KIDSTON for investigation. Both are from the Calcareous Sandstones.

† *L.c.*, pp. 38, 71, pl. viii., figs. 4-6.

‡ "Organization of Fossil Plants of Coal-Measures," Part IX., *Phil. Trans.*, 1878, pt. ii. p. 352, pl. 25, figs. 90-92.

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that presented by the tangential section of *Lyginodendron anomalum* (WILLIAMSON, *loc. cit.*, fig. 92), except that in the latter the dilated medullary rays are on a still larger scale.

In *Pitya primæva* the dilated rays are limited to the neighbourhood of the lateral branch, becoming normal at a greater distance from it.

The puzzling structure of *Lyginodendron anomalum*, which is only known as a fragment of calcified wood from the volcanic ash of Arran, was correctly interpreted by WILLIAMSON, who says (*l.c.*, p. 352): "These cell-masses are in fact huge medullary rays of a most extraordinary form." No stem, however, has hitherto been known, presenting the same peculiarity in so extreme a degree. Mr SEWARD, who observed a somewhat similar enlargement of the rays near the outgoing leaf-trace, in the stem named by him *Lyginodendron robustum*, made the following suggestion: "Such a comparison suggests the probability that the shorter and broader medullary rays and the more irregular course of the tracheides may not represent the normal character of the stem from which the Arran fragment was obtained, but that these appearances may be the result of some disturbing influence in the secondary wood."* In the specimen of *Pitya primæva* just described, we have a striking confirmation of Mr SEWARD's suggestion. Under the 'disturbing influence' of the presence of a lateral branch, the wood of this plant assumes the same peculiar structure which characterises the Arran fragment, while elsewhere retaining the ordinary organisation.

In other respects, and notably in the pitting of the tracheides, there is a close, though not an absolutely exact agreement between the wood of *Pitya primæva* and that of the Arran fossil, which is of similar Lower Carboniferous age. It is possible that the two are specifically identical, the specimen known as *Lyginodendron anomalum* being simply a fragment of a large stem of *Pitya primæva*, from a part affected by the presence of some bulky appendage. Until further evidence is obtained, it may be well to keep up WILLIAMSON's specific name, but the genus is presumably *Pitya* rather than *Lyginodendron*.

The Genus *Pitya*.

Apart from the doubtful fragment last mentioned, all the species of *Pitya*, as limited by GOEPPERT,† prove to be characterised by the presence of small primary strands of xylem around the pith. GOEPPERT enumerates four species, *P. Withami*, *P. medullaris*, *P. antiqua*, and *P. primæva*. The first two are not really distinct,‡ and the name *medullaris* therefore disappears from the list. The remaining three, *P. Withami*, *P. antiqua*, and *P. primæva*, have all been found to possess the primary xylem-strands, which I propose to make a character of the genus.

* SEWARD, "A Contribution to our Knowledge of *Lyginodendron*," *Ann. of Bot.*, vol. xi. p. 81, 1897.

† GOEPPERT, "Revision meiner Arbeiten über die Stämme der fossilen Coniferen, etc.," *Bot. Centralbl.*, Bd. v., 1881, p. 403.

‡ GOEPPERT, *l.c.*, p. 404, conjectures that all four may have to be united. This, however, is not borne out by comparison of the specimens; *P. primæva* is a very distinct form, and *P. Withami* and *P. antiqua*, though allied, are not identical.

Taking, with free modification, the more essential parts of GOEPPERT'S generic diagnosis,* and adding the newly discovered primary characters, we may define the genus as follows:—

Pitys, Witham, emend.

Trunks arboreal, with wood resembling that of recent *Araucariaceæ*.

Trunks composed of a large central medulla, and a zone of wood, in which the presence of concentric layers is inconstant.

Medulla surrounded by numerous small strands of primary xylem, which pass out through the wood. Tracheides with bordered pits; pits in three or four series, on the radial walls, spirally arranged, usually contiguous and hexagonal; sometimes occurring on the tangential walls also. Larger medullary rays formed of 2, 3, 4, or more series of cells.

The old genus *Pitys*, rightly revived by GOEPPERT, turns out to be quite neatly characterised by its numerous small mesarch strands of primary xylem, as well as by the large pith, and multiseriate rays, which have hitherto served to distinguish it.

III. *Dadoxylon Spenceri*, sp. nov.

This stem was found by the late Mr JAMES SPENCER in the Horse Bridge Clough at Hebden Bridge, about six miles to the west of Halifax.† I am only acquainted with one specimen of importance. A second specimen, from the same locality, appears to have a similar structure, but the preservation is too imperfect for determination.

Sections of the good specimen are preserved in the WILLIAMSON Collection, and also in Mr SPENCER'S private collection, which, since his death, has come into my possession. The horizon is given by Mr SPENCER as that of the Yoredale Rocks, while WILLIAMSON, who described the specimen in 1879, speaks of it as derived from "the Marine Ganister Bed near Halifax."‡ This apparent contradiction, involving a doubt whether the fossil belonged to the Lower or Upper Carboniferous, led me to make inquiries of my friend Mr KIDSTON, who referred the question to Dr E. D. WELLBURN, of Sowerby Bridge, who has made a special study of the Geology of the district. Dr WELLBURN'S conclusion is that the rocks at Horse Bridge Clough are not the equivalents of the Yoredales of Phillips, but are a newer group of rocks belonging to the Upper Carboniferous division. It thus appears that the true horizon of the specimen cannot be very different from that assigned to it by WILLIAMSON; *Dadoxylon Spenceri* is consequently the only stem of Upper Carboniferous age dealt with in the present paper.

WILLIAMSON, in his description of the specimen, calls attention especially to the

* *L.c.*, p. 403.

† The discovery of the prolific plant-bed in which the *Dadoxylon* occurred is recorded by Mr SPENCER in his paper on "The Yoredale and Millstone Grit Rocks," published posthumously in the *Proc. Yorkshire Geol. and Polytechnic Soc.*, New Series, vol. 13, 1898 (see p. 378).

‡ "Organization of Fossil Plants of Coal-Measures," Part X., *Phil. Trans.*, 1880, pt. ii. p. 516, Pl. 20, fig. 60.

pairs of vascular bundles which pass out, almost horizontally, through the woody zone (WILLIAMSON, *l.c.*, fig. 60; *cf.* Pl. II. phot. 12 in the present paper). He was at that time inclined to believe that they supplied paired branches of the stem (*l.c.*, p. 517), though in a previous Memoir, in discussing similar structures in other *Dadoxylons*, he said "either two bundles went to one leaf with a double midrib, or the leaves were arranged in pairs."* On a later occasion, WILLIAMSON† compared these paired strands in *Dadoxylon* with the closely similar double leaf-traces of the recent *Ginkgo*. There can be no doubt that in the fossil, as in the recent stem, each pair of bundles represents the trace of a single leaf.

The stem, as preserved, is about 1·8 cm. in diameter; nothing beyond the secondary wood is shown. The pith, which has a diameter of from 5 to 6 mm., is obtusely pentagonal, the prominent angles evidently corresponding to the points of exit of the paired leaf-trace bundles. At two places in photograph 12, the dark bands, marking the position of a double leaf-trace, are seen passing out from the two sides of a truncated angle of the pith.

The pith, which is not very well preserved, consists of a fairly uniform parenchymatous tissue, the cells averaging about ·07 mm. in diameter, but becoming smaller towards the periphery. They are for the most part filled with dark, carbonaceous contents; at some places a larger carbonaceous mass is seen, suggesting the presence of a secretory space, but this appearance may merely be due to disorganisation.

The secondary wood is very dense, and has typical *Dadoxylon* characters. The tracheides are narrow, averaging ·025 mm. in radial and rather less in tangential diameter. Their radial walls bear multiseriate bordered pits, closely packed. The medullary rays are small, one to eight cells in height, and hardly ever more than one cell thick. In rare cases a ray two cells thick in the middle may be met with. The absolute width of the ray is from ·01–·015 mm. Fig. 25 gives a fair idea of the aspect of the wood in tangential section.

The interest of the specimen lies in the fact that distinct strands of primary xylem occur at the inner margin of the secondary wood, and in contact with it. In one of the transverse sections (No. 1381 in the WILLIAMSON Collection) five of these strands are present; the other transverse section (now No. 1504 in my collection) only shows four, the tissues having been destroyed where the fifth would lie. Some of these strands are double, others single. Phot. 13 represents a double strand; the two groups are each about ·15 mm. in tangential width, and are separated from each other by a space nearly equal to their diameter. The smallest elements lie towards the middle of each strand. Fig. 24 represents on a larger scale another bundle, in which the two strands are partly fused, the whole having a diameter of about ·3 mm.; the smallest elements are in two groups, accompanied by parenchyma, and no doubt represent the protoxylem. Towards the outer side the irregularly grouped primary tracheides pass over gradually

* Part VIII., *Phil. Trans.*, 1877, vol. 167, part i. p. 231.

† Part XII., *Phil. Trans.*, 1883, pt. ii. p. 469.

into the radial series of the secondary wood. I have not been able to observe a longitudinal section showing these xylem-strands, but in one case a displaced tracheide, belonging to the more external part of the group, showed a spiral thickening.

The xylem-strands, being both small and few in number, form only an inconspicuous feature in the general structure, but none the less they are perfectly distinct, especially where approaching their exit from the pith, and here represent mesarch primary wood-strands, quite comparable to those of *Lyginodendron*, though on a smaller scale.

Although there is no series of successive sections in which the course of the bundles could be followed, there is little doubt that the distinctly double strands are those near their exit, preparing to furnish the twin-bundles of a leaf-trace, while the fused or single strands are cut lower down in their course. The arrangement of the bundles indicates a $2/5$ phyllotaxis as probable. The stem differs from *Lyginodendron* in the fact that the leaf-trace divides into two before leaving the pith, and that it passes out almost horizontally. In the former point our fossil resembles *Poroxydon*, in the latter it agrees with some of the other *Dadoxylons* figured by WILLIAMSON.* The elements of the outgoing leaf-traces are seen in one of the transverse sections, and have spiral or reticulated sculpturing. The leaf-traces are also seen in pairs in the tangential sections; the small strand of transversely cut tracheides, constituting the trace itself, is accompanied by contorted elements belonging to the secondary wood, such as are usually associated with outgoing bundles. In some cases the irregular secondary elements have insinuated themselves among those belonging to the leaf-trace.

A *Dadoxylon* from Brazil, probably of Permian age, described by ZEILLER† under the name of *D. Pedroi*, bears some slight resemblance to our fossil. The pith, as shown in transverse section, has three prominent angles, recalling the five similar projections in our specimen, and, like them, marking the lines along which lateral appendages were inserted. The medullary rays are usually uniseriate, and the secondary wood agrees fairly well with that of *D. Spenceri*. The pith, however, is enormously larger than in our fossil, having a diameter of 37 or 38 mm. as against 5 or 6 mm. The structure appears to have been purely endarch, as the author shows the spiral elements on the inner edge of the wood. There is thus little to connect *D. Pedroi* with our fossil, except a certain general similarity in the transverse section.

The stem of *Metacordaites Rigolloti* of RENAULT‡ is at once distinguished from that of our plant by the fact that each leaf-trace, in passing through the wood, consisted of five bundles, not to mention other differences.

I have named the Hebden Bridge stem *Dadoxylon Spenceri*, in commemoration of the discoverer, to whom we owe so many valuable contributions to Carboniferous Palæobotany. I have not thought it necessary to found a new genus for its reception, as the primary xylem-strands are much reduced, and the stem in other respects agrees

* *L.c.*, Part viii., Plate 9, figs. 44 and 46.

† "Note sur la Flore fossile des Gisements houillers de Rio Grande do Sul," *Bull. Soc. Geol. de France*, Sér. 3, t. 23, 1895, p. 619. Text-figs. 8-19; pl. ix., fig. 4.

‡ B. RENAULT, "Note sur le Genre *Metacordaïte*," *Soc. d'Hist. Nat. d'Autun*, 1896.

closely with that of other *Dadoxylons* in which primary wood has not yet been distinguished.

The pentagonal pith, double leaf-traces, small and few primary xylem-strands, and dense wood, with almost wholly uniseriate medullary rays, may serve to characterise the species.

The importance of *Dadoxylon Spencersi* lies in its being, on the one hand, a typical *Dadoxylon*, with the type of secondary wood which we know to have belonged to *Cordaite*s, while, on the other hand, it shows, in a reduced form, primary xylem comparable to that of *Lyginodendron* or *Poroxyton*. It suggests, perhaps more strongly than any of the other species described, a truly Gymnospermous stem, which may well have belonged to one of the *Cordaiteæ*, but which still retains the last relics of the primary wood-structure characteristic of the *Poroxytonæ* and *Lyginodendronæ*.

SUMMARY AND CONCLUSIONS.

The principal result of the present investigation has been to show that in a number of stems of Palæozoic age (most of them from the Lower, but one from the Upper, Carboniferous) with secondary wood of the well-known *Dadoxylon* structure, distinct, usually mesarch, strands of primary xylem, forming the downward continuation of the leaf-traces, were present around the pith. Thus the anatomical structure, of which we may take *Lyginodendron oldhamium* as the type, proves to have been widely distributed among Palæozoic plants, and to have extended to stems which, on the basis of other characters, would have been referred with some probability to the *Cordaiteæ*.

The stems examined appear to range themselves naturally in three groups, as indicated by the generic names employed.

The *Calamopitys* group is characterised by the relatively large dimensions and distinct mesarch structure of those primary xylem-strands which are about to pass out from the pith, while the same strands, lower down in their course, are reduced in size, and in some cases assume endarch structure, owing to the dying out of the centripetal wood. A single strand passed out from the pith to form the leaf-trace. The pith is solid, with no trace of discoid structure; it is very variable in size; in *C. fascicularis* and in some species of *C. Saturni*, it is remarkably small (1-3 mm. in diameter). The secondary wood has the typical *Dadoxylon* structure; the medullary rays are in many cases one, or at most two cells in thickness (*C. fascicularis*, *C. beinertiana*; some specimens of *C. annularis*); in *C. Saturni* pluriseriate rays appear to prevail.

The characters of the cortex and leaf-bases are known in *C. Saturni* and *C. annularis*, but not as yet in the species occurring in Britain. The repeated subdivision of the leaf-trace in passing through the cortex is one of the most important characters exhibited by the Thuringian specimens. The reference of *C. fascicularis* and

C. beinertiana to the genus, though I think highly probable, must be regarded as provisional until the structure of these species is more completely known.

In the *Pitya* group the numerous small xylem-strands disposed around a large pith are characteristic. The strands, except the outgoing ones, are more or less deeply embedded in the pith; as a general rule their structure is mesarch. Here also a single strand passed out through the wood, though it may appear as a double bundle immediately below its exit from the pith. The pith is large in all known specimens (1–5 cm.)*, and may show some approach to discoid structure (*P. antiqua*), but is probably not really comparable to the *Sternbergia* pith of the true Cordaiteæ. The secondary wood has the typical characters of the *Pissadendron* sub-genus of *Dadoxylon*, with rather wide elements; the larger medullary rays are always pluriseriate (4–7 cells or more thick). Nothing is known as yet of the cortical structure or of the appendages.

Lastly, there is the type of *Dadoxylon Spenceri*. In the one specimen known there are a few small primary xylem-strands scattered at the margin of the pith, and closely applied to the secondary wood. When clearly seen, these strands are found to be of mesarch structure. They pass out *in pairs*, each pair presumably constituting a single leaf-trace. The pith is of moderate dimensions (5–6 mm. in diameter), and probably not discoid. The secondary wood is once more of the usual *Dadoxylon* character, but very dense, consisting of small tracheides, with very narrow medullary rays, scarcely ever more than one cell in thickness. In this form—at present isolated—the primary bundles are less conspicuous features than in either of the previous groups. The double leaf-trace is a striking character shared with other stems, both fossil and recent (*Ginkgo*), in which no such primary strands appear. For these reasons I have not thought it well at present to found a new genus for the *D. Spenceri* type.

We have now to consider the probable affinities of these various groups.

The stems referred to *Calamopitys*, even on the characters shown in the incomplete specimens by which the British species are represented, are strongly suggestive of Cycadofilices, owing to the great development of the primary xylem-strands, and the marked similarity to the structure of *Lyginodendron*.

The additional characters present in the Thuringian specimens of the forms described by Count SOLMS-LAUBACH seem decisive on this point. The cortical structure, the large leaf-bases, with the characters of *Kalymma*, the course and structure of the leaf-trace bundles, all point in the same direction. The petioles, known as *Kalymma*, were no doubt those of compound, fern-like leaves. As mentioned above, it is extremely probable that the petiole, named *Rachiopteris multifascicularis* by Mr KIDSTON, belonged to one or other of our *Calamopitys* stems.

The genus *Calamopitys* has clear affinities with *Lyginodendron*, but differs in the structure of the petiole, which shows some approach to that of a *Myeloxylon*. As, however, I have no new observations to record on this part of the structure, I will pass on to one or two points on which the British species have thrown additional light. It is

* A specimen of *Pitya antiqua*, with a pith two inches in diameter, is mentioned by WITHEAM, *l.c.*, p. 27.

interesting to find that, while the bundles approaching their exit are so distinctly mesarch in structure, those lower down in their course tend to lose their centripetal wood, so that, in *C. beinertiana*, most of them become actually endarch. These facts may indicate that the *Calamopitys* group had advanced rather further towards the usual stem-structure of Gymnosperms than was the case with *Lyginodendron* or even *Poroxyton*. Another point is the narrow-rayed secondary wood, quite Cordaitean or Araucarian in structure, co-existing with primary characters pointing to the Cycadofilices. The width of the rays, however, varies a good deal within the genus, and sometimes even within a single species (*C. annularis*) and is clearly a character on which too much stress has been laid by palæobotanists. On the whole, *Calamopitys* may be regarded as decidedly the most primitive of the three groups dealt with.

The *Pitys* stems are known to have belonged to tall branching trees.* We know of no Cycads or Cycadofilices with at all a similar habit, nor is there any evidence that the Coniferæ existed at so early a period. The only known family to which these trees could be referred is that of the Cordaiteæ, leaves of which have been found at a similar horizon.† The species of *Pitys* differ from stems, traced with certainty to true Cordaiteæ, in the broad medullary rays, the non-discoid pith (for the slight approach to discoid structure which they exhibit is of doubtful value), and in the presence of the primary xylem-strands. On the whole, I am disposed to regard the genus *Pitys* as a primitive member of the Cordaitean family, retaining some of the characters of an earlier stock. The mesarch xylem-strands, in spite of their reduced size, and the peculiarities of their arrangement, are evidently comparable to those of *Lyginodendron* or *Calamopitys*. Thus the *Pitys* trees appear to afford a new link, so far as stem-structure is concerned, between the Cycadofilices of the family Lyginodendreae and the true Cordaiteæ. Such a connection was already indicated by the structure of *Poroxyton*, but that genus, from its later horizon (Permian), has a less direct bearing on the question of the origin of the Cordaiteæ.

Lastly, *Dadoxylon Spencersi*, with its dense wood and double leaf-traces, appears to stand near the typical Cordaiteæ (though its pith seems not to have been discoid), and also, as WILLIAMSON pointed out, strongly suggests the recent genus *Ginkgo*, which itself may have Cordaitean affinities.‡ The primary xylem-strands of this species are small in size and few in number, but though so much reduced, have essentially the same structure as in *Lyginodendron*. The fossil indicates that in the period of the Upper Carboniferous deposits, stems which in other respects had attained a typically Gymnospermous character, had not quite lost the primitive form of wood, which we can trace back, through the Cycadofilices, to the Ferns.

* The trunk of the Craigleith tree (*P. Withami*) found in 1830 was 47 feet in length, and at the top still had a diameter of about 1½ feet. WITHAM, *Internal Structure*, p. 29.

† KIDSTON, "On the various Divisions of the British Carboniferous Rocks," *Proc. Roy. Phys. Soc. Edin.*, 1894, p. 255.

‡ SEWARD and GOWAN, "The Maidenhair Tree, *Ginkgo biloba*," *Ann of Bot.*, vol. xiv., 1900, pp. 137 and 146.

EXPLANATION OF PLATES I.-VI.

Plates I. and II., Photographs, taken direct from the sections, by Mr L. A. BOODLE, F.L.S.

PLATE I.

Photographs 1 and 2. *Calamopitys fascicularis*.

Phot. 1. Transverse section, showing the pith (only preserved in its outer portion) and the surrounding secondary wood. A, B, C, arrows pointing to the principal primary xylem-strands. A, rather small xylem-strand, at the border of the pith; B, large strand (shown in detail in phot. 2) just entering the secondary wood; C, strand passing out through the wood. (See p. 332.) \times about 10. From the WILLIAMSON specimen. (W.* 1380.)

Phot. 2. Transverse section, showing the xylem-strand B, more magnified, with its central protoxylem; *p*, part of pith. (See p. 338.) \times about 30. (W. 1380.)

Photos. 3 and 4. *Calamopitys beinertiana*.

Phot. 3. General transverse section, showing the large pith, containing several sclerotic nests, and the surrounding wood. (See p. 342.) \times about $2\frac{1}{2}$. (K. 677.)

Phot. 4. Radial section, showing the pith, *p*, and part of the wood, x^2 . The pith contains several sclerotic nests. (See p. 342.) \times about 4. (K. 677^v.)

Photos. 5-7. *Pitya antiqua*.

Phot. 5. General transverse section, showing the large pith, surrounded by secondary wood. *lt.*, a leaf-trace, passing out through the wood. (See p. 346.) \times about 3. (K. 598^A.)

Phot. 6. General radial section, showing the pith, *p*, with horizontal gaps in its tissue, and on one side the secondary wood, x^2 . *v.b.*, a primary xylem-strand. (See p. 346.) \times $3\frac{1}{4}$. (K. 598^E.)

Phot. 7. General tangential section, passing through the outer part of the pith, and the inner secondary wood, x^2 . x^2 , wood in oblique section; $x^{2'}$, portion of wood in tangential section. Six primary xylem-strands, *v.b.*, are shown; *v.b.*', a double strand in contact with the secondary wood, $x^{2'}$. *v.b.* 2, the primary strand shown in detail in fig. 16. (See p. 349.) \times $4\frac{1}{2}$. (K. 598^B.)

PLATE II.

Photographs 8 and 9. *Pitya antiqua*.

Phot. 8. Transverse section, showing part of pith, *p*, and secondary wood, x^2 . *v.b.*, *v.b.*, double primary xylem-strand, embedded in the pith, numbered 38 in diagram 5, in the text. (See p. 347.) \times 35. (K. 598^C.)

Phot. 9. Transverse section showing pith, *p*, and wood, x^2 . *v.b.* 13^a, and *v.b.* 14, two primary xylem-strands, indicated by arrows, and numbered as in diagram 5, with isolated tracheides between them. (See pp. 348 and 350.) \times 350. (K. 598^C.)

Phot. 10. *Pitya Withami*. General transverse section, showing large pith, surrounded by secondary wood. *lt.*, arrow pointing to outgoing leaf-trace bundle. Note the concentric rings in the secondary wood. (See p. 354.) \times about 3. From one of WITHAM's original sections in the Edinburgh Botanical Collections, marked "Craigleith, 1831," and figured in his *Internal Structure of Fossil Vegetables*, pl. vi., figs. 5-8.

Phot. 11. *Pitya primæva*. Tangential section through secondary wood, showing base of a branch, *br.* *m.r.*', region in which the dilated medullary rays, shown in detail in fig. 23, occur. In other parts the rays show the ordinary structure, as shown in fig. 22. (See p. 355.) \times about 4. (K. 216.)

Photos. 12 and 13. *Dalorylon Speneri*.

Phot. 12. General transverse section, showing the obtusely pentagonal pith, and the surrounding wood. *lt.*, *lt.*, two double leaf-traces passing out almost horizontally through the wood. *v.b.*, arrow pointing towards the angle of the pith where the double xylem-strand shown in phot. 13 is present. (See p. 358.) \times $4\frac{1}{2}$. (S. 1504—from SPENCER Collection.)

Phot. 13. Transverse section showing secondary wood, and outer border of pith, *p*. *v.b.*, pair of mesarch primary xylem-strands, in contact with the secondary wood. (See p. 358.) \times about 50. (S. 1504.)

* The letter W. indicates the WILLIAMSON Collection, K. Mr KIDSTON's Collection, and S. that of the author.

PLATES III.-VI.

Original drawings, made, under the author's supervision, by Mr G. T. Gwilliam.

PLATE III.

Calamopitys fascicularis.

Fig. 1. Transverse section, showing the contracted pith, primary xylem-strands, and inner part of the secondary wood. From a section adjacent to that from which diagram 1, p. 334, was drawn, and showing practically identical structure. The strands are lettered as in the diagram. A, large xylem-strand in contact with secondary wood, x^2 ; px , protoxylem; B, still larger strand, beginning to pass out into the wood; px , protoxylem; C, direction of outgoing leaf-trace shown in diagram 1; a , b , c , reparatory strands of the outgoing bundles A, B, and C; d , strands of the orthostichy D, cut low down in their course; e , similar strands of the orthostichy E. (See p. 333.) $\times 24$. (K. 540^A.)

Fig. 2. Transverse section, showing one of the smaller xylem-strands, $v.b.$ (this is the larger of the two marked e in diagram 2, p. 335); px , protoxylem. x^2 , secondary wood, showing pits on the horizontal walls of the dilated tracheides (*cf.* fig. 3). (See p. 338.) $\times 140$. (K. 628.)

Fig. 3. Radial section, from the border of the pith and wood. p , pith; $v.b.$, primary xylem-strand; px , its protoxylem; p' , circum-medullary tissue; x^2 , inner elements of secondary wood, showing the short, irregular tracheides (*cf.* fig. 2). (See pp. 338 and 339.) \times about 100. From a new section of Mr KIDSTON'S specimen.

Fig. 4. Radial section of the secondary wood, showing the tracheides, with multiseriate bordered pits, and the medullary rays. (See p. 338.) about $\times 120$. (K. 540^I.)

Fig. 5. Tracheides in radial section, more enlarged, to show the hexagonal pits, with slit-like pores. (See p. 338.) \times about 300. (K. 540^I.)

PLATE IV.

Figs. 6 and 7. *Calamopitys fascicularis*.

Fig. 6. Tangential section through the secondary wood, showing tracheides and medullary rays, $m.r.$ $b.p.$, bordered pits of the tracheides in section. (See p. 339.) \times about 120. From the WILLIAMSON specimen (W. 1392.)

Fig. 7. Tangential section through the wood, showing an outgoing leaf-trace. px , protoxylem of the leaf-trace; pa , parenchyma, accompanying the leaf-trace; $m.r.$, medullary rays. (See p. 337.) \times about 30. (W. 1392.)

Figs. 8-12. *Calamopitys beinertiana*.

Fig. 8. Transverse section, showing a large primary xylem-strand, $v.b.$, just entering the secondary wood, x^2 , from the pith. px , protoxylem of the primary strand. (See p. 342.) $\times 60$. (K. 677.)

Fig. 9. Transverse section, showing a smaller xylem-strand, $v.b.$, at the inner margin of the wood, x^2 . px , protoxylem of the strand, which is here of the "hippocrepiform-endarch" type. (See p. 343.) $\times 60$. (K. 677.)

Fig. 10. Somewhat oblique radial section of a primary xylem-strand. px , spiral protoxylem-element of the strand. The ill-preserved element to the right is a tracheide. (See p. 343.) $\times 100$. (K. 677^M.)

Fig. 11. Part of a large primary tracheide, showing the numerous rows of hexagonal bordered pits. (See p. 343.) \times about 200. (K. 677^N.)

Fig. 12. Tangential sections from the secondary wood—

A, showing part of a long medullary ray. $\times 70$. (K. 677^K.)

B, showing a 2-3-seriate ray with irregular adjacent tracheides. $\times 90$. (K. 677^K.)

C, showing several short rays. $\times 90$. (K. 677^M.) (See p. 343.)

PLATE V.

Fig. 13. *Calamopitys beinertiana*.

Approximately tangential section of the secondary wood, passing obliquely through a large outgoing leaf-trace, accompanied by parenchyma. (See p. 344.) \times about 50. (K. 677^L.)

Figs. 14-18. *Pitya antiqua*.

Fig. 14. Transverse section, showing part of the pith and secondary wood, x^2 . *v.b.* 13, double primary xylem-strand, in contact with the secondary wood; *v.b.* 12a, xylem-strand, deep in the pith, perhaps a reparatory strand. (Of. diagram 5 in text, p. 347.) $\times 40$. (K. 598^c.)

Fig. 15. Transverse section. *v.b.*, primary xylem-strand, embedded in the pith; *px*, protoxylem of the strand; x^2 , part of secondary wood, with broad medullary rays, *m.r.* The xylem-strand is that numbered 3 in diagram 5. (See p. 348.) \times about 110. (K. 598^a.)

Fig. 16. Tangential section, passing medianly through a primary xylem-strand (numbered *v.b.* 2 in photograph 7) embedded in the pith. *px*, protoxylem-elements of the strand; *r.t.*, a reticulated tracheide; the meshes of the reticulation are bordered, in reality, as in the element shown in fig. 17. (See p. 348.) $\times 140$. (K. 598^b.)

Fig. 17. Part of one of the innermost tracheides of the secondary wood, showing transition from reticulations to bordered pits. (See p. 348.) $\times 200$. (K. 598^e.)

Fig. 18. Radial section through the secondary wood, showing a medullary ray, and tracheides with multiseriate, hexagonal, bordered pits. (See p. 352.) $\times 120$. (K. 598^e.)

PLATE VI.

Figs. 19 and 20. *Pitya antiqua*.

Fig. 19. Tangential section through the secondary wood, showing tracheides, and medullary rays of various dimensions. The large ray to the right has gaps in its tissue. (See p. 351.) $\times 32$. (K. 598^e.)

Fig. 20. Tangential section, from inner part of secondary wood. *m.r.*, medullary rays; the larger of the two contains a definite lacuna, *l.*; *t.p.*, bordered pits, on the *tangential* wall of a tracheide. The pits to the right are on radial walls seen obliquely. (See p. 352.) $\times 200$. (K. 598^h.)

Fig. 21. *Pitya Withami*. Transverse section, showing a primary xylem-strand, *v.b.*, embedded in the pith. x^2 , inner part of secondary wood. (See p. 354.) \times about 130. From WITHAM's original section, shown in phot. 10.

Figs. 22 and 23. *Pitya primæva*.

Fig. 22. Tangential section of the secondary wood, to show the ordinary form of the medullary rays, large and small. (See p. 355.) $\times 36$. (K. 211.)

Fig. 23. Tangential section of the secondary wood near the branch (represented in phot. 11), to show the dilated form of the rays, and tortuous course of the tracheides, in this region. (See p. 355.) $\times 36$. (K. 216.)

Figs. 24 and 25, *Dadoxylon Spenceri*.

Fig. 24. Transverse section showing a double primary xylem-strand, *v.b.*, in contact with the secondary wood, x^2 ; *px*, one of the protoxylem-groups of the primary strand. *p.p.*, pith. (See p. 358.) $\times 150$. (W. 1381.)

Fig. 25. Tangential section through the secondary wood, showing the tracheides, *t*, and the narrow medullary rays, *m.r.* (See p. 358.) $\times 120$. (W. 1382.)

