D. Sc. Thesis, 1911.

The Fossil Flora of the Pettycur Limestone

by
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Dear Sir,

In presenting the accompanying Thesis for the degree of Doctor of Science I hereby declare that the thesis has been composed by myself, and that, unless expressly stated to the contrary, the results embodied in it have been obtained by myself

Yours faithfully

Professor James Geikie, D.C.L., LL.D., etc
Dean of the Faculty of Science
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be exceedingly rare. And as the fossils seldom occur singly, it is practically impossible to tell whether a particular block would furnish specimens whose stems, roots and leaves were in organic continuity with one another. To leave such a correlation to chance is obviously undesirable and so the observer must either make the necessary preparations or personally supervise the making of them. These preparations consist of thin transparent slices of the petrifactions which are capable of being examined with a microscope. They have frequently to be examined during the process of their manufacture so that whether the investigator does <u>all</u> the work or not he must spend a considerable amount of time in mechanical or manual labour. Cases of course, do occur where no such personal supervision is necessary and then the preparations may be made by a professional man, but I consider that the results obtained and recorded here, have justified my method of personally preparing the thin sections with the occasional help of a laboratory assistant. Indeed had any other method been employed, I am satisfied the results embodied in this thesis would probably never have been obtained. In fact the greater part of the difficulty lay in the accurate cutting and preparation of the slides. In all about 1400 thin sections of the Pettycur plants have been prepared; they were generally cut in series so that any changes in the plant might be gradually followed for long distances. In this way a fairly complete knowledge of several species has been obtained.

A summary of the results may be given here. Five new species have /

have been added to the flora, viz. Lepidophloios Scottii; Lepidostrobus cylindricus; Heterangium Arberi; Heterangium sp. nov.; Physostoma sp. nov.; one genus - Diplolabis - has been recorded for the first time from a British locality; two species of ferns - Diplolabis romeri (Solms) and Metaclepsydropsis duplex (Williamson) - have been carefully examined and their stems, roots and petiolar development discovered; many new points have been noted in the anatomy of the other plants contained in the Pettycur blocks.

The nucleus of the material at my disposal had been collected by Dr. Flett, Assistant Director of H. M. Geological Survey. I was soon able to add greatly to this, and most of the material now in my possession has been obtained since I began my research. Following the custom of former collectors the blocks were, at first, broken into small pieces, but I soon saw the wisdom of removing the blocks in as few pieces as possible. In this way one could follow any specimen more easily than when the material consisted of numerous small pieces.

As very little was known about the mode of occurrence and the nature of the material comprising the blocks I communicated the following paper on that subject to the Geological Society of Edinburgh.

Reprinted from the "Transactions of the
Edinburgh Geological Society," Vol. IX., Part iv., 1909

On the Nature and Occurrence of the Plant-bearing Rocks at Pettycur, Fife. By W. T. GORDON, M.A., B.Sc., Falconer Fellow of Edinburgh University, and Advanced Student Exhibitioner of Emmanuel College, Cambridge.

(Read 17th March 1909.)

THE plant petrifactions obtained at various times from the rocks of Calciferous Sandstone age at Pettycur, on the north shore of the Firth of Forth, have proved exceedingly interesting to the palæobotanist, but hitherto very little attention has been given to the manner of their occurrence from a geological standpoint. When carrying out a special study of plant remains from this locality I became interested in the nature and distribution of the rock-masses containing them. During a visit to the locality in company with Mr Robert Campbell, M.A., B.Sc., we were fortunate in discovering a large mass of the material in the cliff above the shore on the west side of Pettycur Bay; since then I have discovered detached pieces of petrified vegetable remains and also small blocks of calcareous material containing similar plants embedded in the rocks to the east of Pettycur Harbour.

The occurrence of fossil plants at Pettycur has been known since 1871. In that year Mr G. J. Grieve of Burntisland noticed that several blocks of limestone, lying loose on the shore, contained recognisable plant remains in a petrified state. The earliest reference to these plants with which I am acquainted was published in the Transactions of the Botanical Society of Edinburgh[1] on the 11th May 1871. It is there recorded that "Professor [J. H.] Balfour exhibited a specimen of a fossil lately discovered by Mr Grieve near Pettycur."

The next reference is in the Report of the British Association Meeting at Edinburgh,[2] also in the same year, recording a paper by Mr G. J. Grieve, "On the Position of Organic Remains near Burntisland," of which, however, no abstract is given. This paper does not appear to have been subsequently published elsewhere, but, in a general account of the meetings of the Geological Section of the British Association at Edinburgh some mention of it is made. I am indebted to Mr Hopkinson, the author of the digest in question, for bringing it to my notice. It is there[3] stated that "Mr Grieve's attention was first directed to the specimens by observing on the shore large masses of

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[1] *Trans. Bot. Soc. Edin.*, vol. ix. p. 168, 1871.

[2] *Sectional Report, Brit. Ass. Edin.* (1871), No. 41, p. 98, 1872.

[3] *Proc. Geol. Ass.* (1871), vol. ii. pp. 309-320, 1872.

limestone which had been polished by drifting sand. These were found to be filled with coal-plants, and the limestone was traced to the cliff above, where it appeared to be intercalated in a mass of volcanic products. Mr Carruthers, in a paper by himself on the vegetable contents of these masses of limestone, said that he considered that the plant remains had been enclosed in a peaty condition from the surface bed on which they were growing when the volcanic ash was ejected, the lime abounding in the bed having subsequently calcified them, preserving all the details of their structure."

The plant remains discovered by Mr Grieve were sent to Professor W. C. Williamson for examination, and at this same meeting of the British Association, the latter read a paper in which he referred to Heterangium (Dictyoxylon) Grievii,[1] one of the Pettycur plants. This plant was subsequently more fully described and figured in the Philosophical Transactions of the Royal Society.[2] In none of his memoirs, however, does Professor Williamson give any account of the lithological character of these plant-bearing blocks.

There is another reference, in the Transactions of the Botanical Society of Edinburgh,[3] to fossil plants from Pettycur. On the 10th April 1873 Mr C. W. Peach exhibited thin sections of fossil plants "from the ash-beds" at Pettycur. These sections are now, I think, in the General Collection of Fossil Plants at the Natural History Museum, London.[4]

As quoted above, Mr Grieve stated that the blocks could be traced to the cliffs, "where they appear to be intercalated in a mass of volcanic products." Mr Peach records that his specimens were obtained from the trap-tuffs. Mr Hopkinson has informed me that he was present at a Geological Excursion to Burntisland after the British Association Meeting in 1871, and he was shown loose blocks on the shore but no pieces *in situ* in the cliff. For the next twenty-nine years no reference was made to these blocks, but in 1900 we get the last record in the Geological Survey Memoir on Central and West Fife, where it states that the blocks "may have fallen out of these basalts," which are seen exposed in the cliff. None of these references gives any very definite information as to the exact position of the masses in the cliff, and the indefiniteness of the early records accounts for the qualification of the statement as expressed in the Geological Survey Memoir. Since 1873 those who have visited Pettycur

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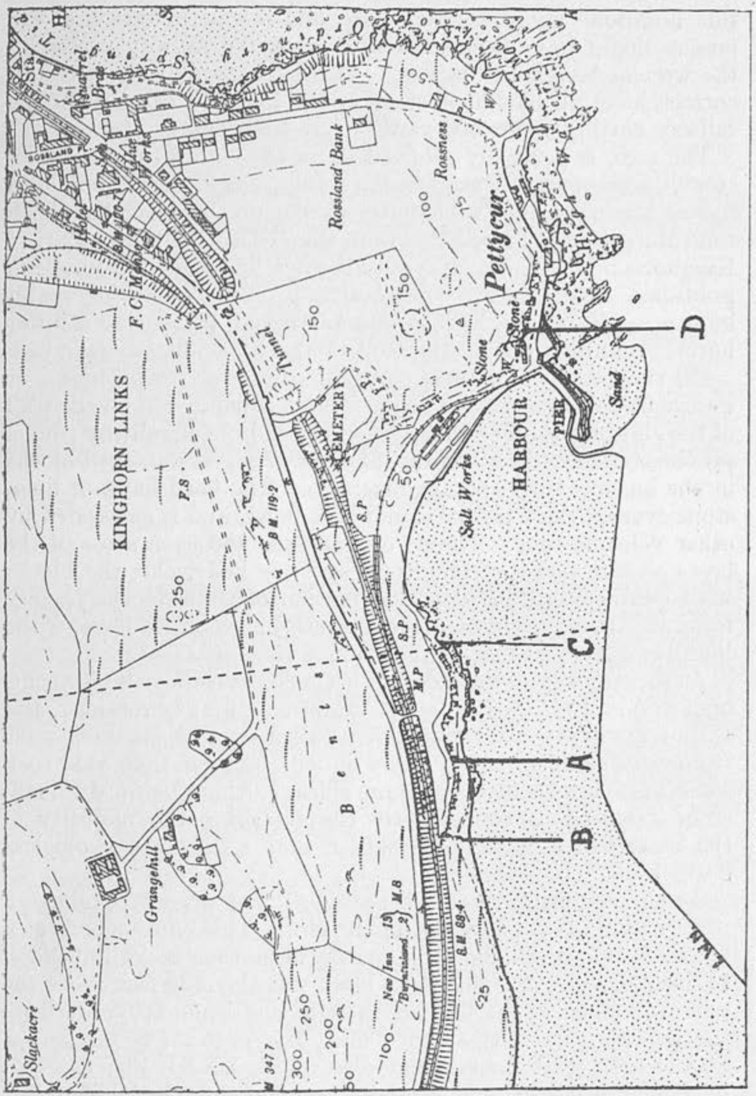
[1] "On the Structure of the Dictyoxylons of the Coal Measures." *Sectional Report, Brit. Ass. Edin.* (1871), No. 41, p. 111, 1872.

[2] *Phil. Trans. Roy. Soc. London*, p. 277, 1873.

[3] *Trans. Bot. Soc. Edin.*, vol. ix. p. 505, 1873.

[4] They are numbered V. 8890 and V. 8893.



Map of Pettycur and District, showing positions from which the limestone is obtained. Scale 6 in. to 1 mile.

to obtain specimens of fossil plants have collected them from the loose material on the shore. At one time a large accumulation of this limestone lay on the foreshore, and it was thought that the masses might have been excavated from the railway tunnel to the west of Kinghorn Station. This is probably only partially correct, as in all likelihood some of the material came from the railway cutting about 400 yards west of the tunnel.

The rock is generally referred to as the "Burntisland Limestone," and sometimes even as the "Burntisland Coal," but both names are misleading. The blocks occur much nearer Kinghorn than Burntisland, indeed Pettycur, the exact locality, is a part of Kinghorn. That the rock is not always a limestone, the analyses published below clearly demonstrate. The limestone band known locally as the Burntisland Limestone belongs to a lower horizon and outcrops on the Golf Course at Dodhead Quarry.

On the other hand there are two calcareous rocks found at Pettycur, one a hard and fairly continuous band seen on the wall of the cliff just before entering the west end of the railway tunnel previously referred to, and the other occurring as detached blocks in the igneous tuffs and agglomerates. The hard band of limestone overlies thick tuff beds and lava flows, and is succeeded by other volcanic beds. These volcanic tuffs and even some of the lavas contain pieces of limestone, and one bed yields the blocks with petrified plants. The distribution of these blocks is very local, and their occurrence has never been recorded beyond the limits of a stretch of shore about half a mile in extent.

As the majority of the blocks contain 80 per cent. to 90 per cent. of calcium carbonate the name "limestone" may be retained, and I think it will save confusion if it is called the *Pettycur Limestone*. From the analyses given below it will be seen that this rock sometimes consists of almost pure silica, so that the word "limestone" is used as conveniently characterising the majority of the masses of this material, rather than as a strict geological designation.

As already mentioned, Mr Campbell and myself obtained a piece of the material *in situ* in the cliff. This cliff consists of a volcanic tuff containing large masses of igneous rocks imbedded in the finer ash. The limestone block was about 10 feet above the path which skirts the base of the cliff and some 60 yards from the western extremity of the cliff. The position is marked A on the map (text figure), and also in Pl. XXXI. Fig. 1. This particular specimen was partially removed by Dr Kidston, Mr Gwynne-Vaughan, and myself, and it contained the typical Pettycur plants. Pl. XXXI. Fig. 2 shows a near view of this block before its removal.

Since this specimen was discovered I have been able to obtain

rans. Geol. Soc. Edin., Vol. IX., p. 356, Plate XXXI.

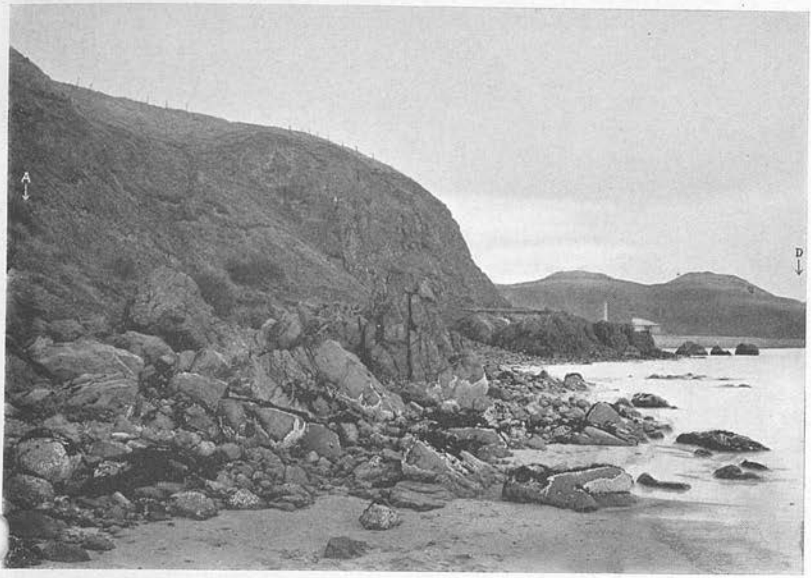


Photo by A. G. Stenhouse, F.G.S.

FIG. 1.

Photo by A. G. Stenhouse, F.G.S.

FIG. 2.

other pieces from a position about half-a-mile east of this place. It is on the east side of the hill marked D in Pl. XXXI. Fig. I, and the exact position is shown at D (text figure). The occurrence is at Pettycur House, where a tuff is exposed by the side of the road. Overlying the tuff are lenticular patches of black shale which are very much contorted. Above the shale there is a mass of basalt, but it is from the tuff below the shale that the plant petrifactions are obtained. This bed is referred to in the Survey Memoir on Central and West Fife as a basalt, and a Lepidodendron is noted as having been obtained from it. Dr Kidston has identified this Lepidodendron with his Lepidodendron Pettycurense.

The peculiarity of the specimens from this place is that they occur sometimes without any matrix, petioles of Diplolabis Römeri—a genus new to Britain, which I hope to describe shortly—and stems of Lepidodendron lying quite bare in the tuff. At the same time masses of calcareous material containing plants are also found, and as the plants are petrified in both cases, any explanation of their occurrence must account for the presence of the matrix in one case and its absence in the other.

I have obtained the following plants from this locality :—

Diplolabis Römeri, *Zygopteris Duplex*,
Heterangium Grievii, *Lepidodendron Brevifolium*,
Lepidodendron Pettycurense.

The loose material which I have almost entirely removed from the shore for examination occurred in quantity near both ends of the railway cutting (these positions are marked B and C in text figure), while the specimens at Pettycur Harbour (position D) are on the same horizon as the beds pierced by the tunnel. It is thus probable that the plant remains have been excavated both from the cutting and from the tunnel. The rock from which the limestone masses are derived lies above the lower basalts of King Alexander's Crag, and is a volcanic tuff of coarse texture containing large blocks of igneous rocks both rounded and angular. The presence of such large masses indicates close proximity to the centre of eruption. The tuff at Pettycur House does not contain so many blocks, and they are all much smaller.

The chemical nature of the plant-bearing blocks is exceedingly varied, and its composition as given by Stopes and Watson[1] cannot be taken as typical. I have made analyses of three specimens (they were parts of the blocks I had been examining for petrifactions), which in tabular form are as follows :—

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[1] *Phil. Trans. Roy. Soc.*, B, vol. cc., p. 167, 1908; also Scott, "Studies in Fossil Botany," 2nd Edit., p. 11, 1908.

	SPECIMEN 1	SPECIMEN 2	SPECIMEN 3
SiO_2	17·71 %	1·7 %	94·09 %
Fe_2O_3, Al_2O_3	·97 %	1·4 %	·56 %
$CaCO_3$	72·2 %	90·1 %	traces
$MgCO_2$	6·64 %	3·56 %	1·17 %
Carbon and water	Undetermined.	Undetermined.	Undetermined.

The analyses were made to determine the chief constituents, so that the water and carbon were not estimated.

With regard to the origin of these petrifactions, we find that Mr Carruthers' opinion as quoted above appears to imply that the plant tissues were not petrified until after their enclosure in the tuff. The Geological Survey Memoir conveys the same idea and also suggests that the whole mass was really a land surface over which a lava flowed. Thus there should be one or more large sheets of plant-bearing rock. None of the specimens collected is in the least lenticular but on the contrary they are irregularly cuboidal, and this applies also to the mass *in situ* in the cliff. In my opinion it is much more probable that the plant remains were petrified before being enclosed in the tuff. Pieces of petrified wood are quite common in the tuffs of Fifeshire, but these are in general very much charred and by no means well preserved; other specimens from North Berwick in similar rocks are in the same charred condition, and so also are the specimens from Laggan Bay, Arran. The presence of masses of brecciated limestone containing small angular pieces with plant petrifactions enclosed in them still further strengthens the idea that these fossils were petrified before enclosure in the tuff. In many cases the brecciation is well marked and the fragments have been recemented either by calcite or silica, the latter in the form of amethystine quartz (Pl. XXXII. Fig. 1).

Taking into consideration the varied chemical constitution of the blocks, it seems highly improbable that they can be classed as comparable with the coal-balls of the coal measures. The amount of silica present is very considerable in some cases, and in others constitutes the main mass of the rock, while the amount of magnesium carbonate does not bear any relation to that of calcium carbonate. The only explanation which can satisfy all the observations must, to my mind, be one involving the action of thermal springs containing dissolved mineral matter, and the whole condition of this part of the Carboniferous Series undoubtedly favoured the occurrence of such springs. To enumerate the observations, we find that the specimens are

(a) Composed of material varying from nearly 95 per cent. silica to 95 per cent. carbonates.

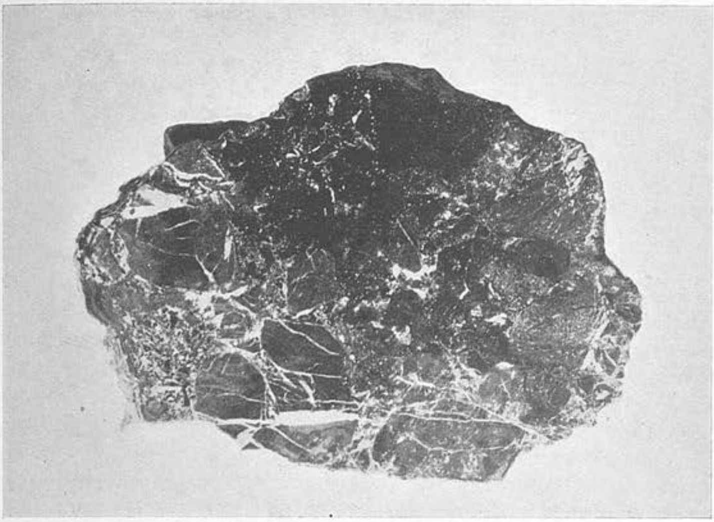

FIG. 1.

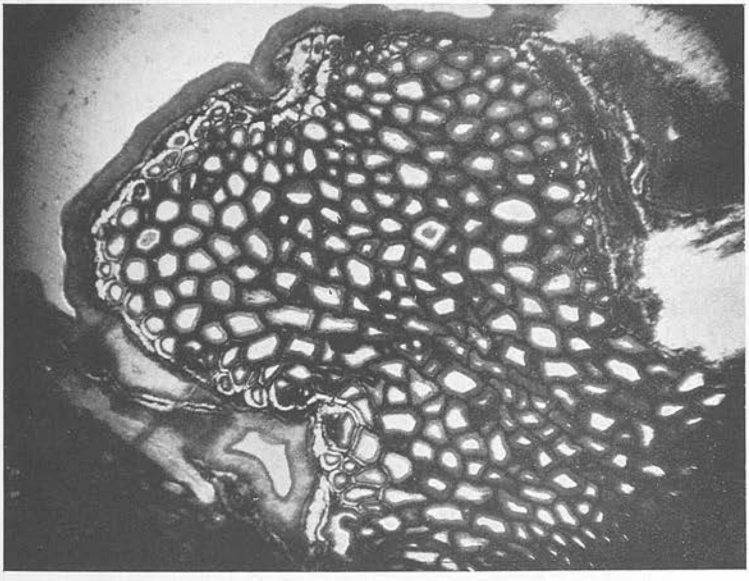

FIG. 2.

(β) Sometimes made up of portions containing no plant remains, suddenly alternating with portions mainly composed of petrified plant tissues.

(γ) Devoid of marine or freshwater organisms.

(δ) Often brecciated, and never occur as nodules but either as large cuboidal blocks, rough angular fragments, or isolated pieces of petrified plant débris.

The explanation I offer is that in the vicinity of the volcanic crater, of the presence of which there is abundant evidence, there were probably small pools fed by thermal waters from underlying volcanic sources. (The extraordinary volcanic activity is indeed the most striking feature of this region.) Into these pools plant débris would be from time to time drifted, and the water, highly charged with mineral matter in solution, would gradually water-log these plants. As the water percolated upwards through limestones it usually contained much lime in solution, but in some cases the material has been silica. The accumulation of the deposits from these springs would form small lenticles of calcarous or siliceous material, parts of which would contain plants while other parts would be composed of purely mineral matter. The next volcanic outburst would destroy these deposits, tearing them into pieces, and depositing the fragments among the other volcanic ejectamenta in tuffs and agglomerates. There would thus be both large masses and small pieces scattered here and there through the tuff. Where a few pieces were associated together they were sometimes recemented into a breccia by either silica or calcite.

At the same time many pieces of plant tissue lying near the area of deposition of the tufa would be petrified but not enclosed in any of the tufaceous matrix. Such pieces would naturally be included in the volcanic agglomerate without any matrix surrounding them, so that their occurrence does not in any way invalidate the theory of thermal springs.

It may be objected that the siliceous masses may have been originally calcareous and subsequently replaced by silica, but preparations show that the silica was obviously first laid down round the cell walls and then grew into the cell lumen. Indeed the silica has been laid down in two distinct forms—the first of the nature of chalcedony and the internal space with crystalline quartz. Had there been subsequent silicification the centres of replacement would have been scattered and would not have coincided with the original centres which started from the cell walls. In other words secondary replacement would have given a concentric spherical replacement irrespective of the position of the cellular structure, whereas in this case the centres of deposition are ranged along the cell walls. This is shown exceedingly well in Pl. XXXII. Fig. 2—a few cells from the stele of a petiole of Zygopteris Duplex. The thermal spring theory satisfactorily explains all the phenomena while none of the other theories so far given does so.

Since this paper was read an additional observation of great interest has been made. I have discovered a large mass of calc tufa with the normal coralloidal structure, enclosed in the volcanic tuff at Pettycur House. It is in this same tuff that the specimens of plants were found (text figure, D). This proves the presence of springs depositing calcareous material during Carboniferous times, and indicates the possibility of plants becoming petrified in the manner I have indicated above.

I am indebted to the Carnegie Trustees for a grant to defray the expenses of the illustrations in this paper.

EXPLANATION OF PLATES (PHOTOGRAPHS FROM UNTOUCHED NEGATIVES).

PLATE XXXI.

FIG. 1. General view, locality at Pettycur. Positions A and D indicate where blocks were got *in situ*.

FIG. 2. Nearer view of block at A.

PLATE XXXII.

FIG. 1. Mass of brecciated limestone, the fragments re-cemented partly by calcite and partly by silica. × $\frac{1}{3}$.

FIG. 2. Petiole trace of Zygopteris Duplex, showing double deposition of silica. × 30.

When we come to examine the plants obtained from the Pettycur Limestone we find that the list is not a long one. Only twenty-six species have been recorded, but these are distributed over most of the main groups into which we may divide the Lower Palaeozoic vegetation, Equisetales, Sphenophyllales, Lycopodiales, Filices and Pteridospermeae being all represented. As forming part of the oldest known flora (Devono-Carboniferous), these plants have acquired considerable botanical value and this is enhanced by the fact that many of them are primitive. Representatives of the same groups in the Coal Measure flora show a much higher organisation.

In my work, however, I have been able to demonstrate that in addition to these primitive types there are others which in many ways may be taken as intermediate between such lowly organised forms and the higher types found in the Coal Measures. For instance Heterangium Grievii, Williamson, is a very simple type but Heterangium Arberi sp. nov. shows some points of similarity with Sutcliffia insignis, Scott, which is one of the simplest of the Coal Measure Medulloseae. Again I have shown that Diplolabis romeri has a very simple stem stele and that Metaclepsydropsis duplex has a type of stele which approximates to that of Ankyropteris (Rachiopteris) corrugata. Yet another example may be quoted, Lepidodendron pettycurense has a solid primary wood, while Lepidophloios Scotii has a mixed pith in its primary cylinder, though sometimes a specimen may have a solid xylem in one part and a mixed pith in the xylem further up or down the stem. This occurrence of intermediate /

intermediate types is increasing the interest and importance of the Pettycur flora.

Although I have obtained specimens of all the Pettycur plants I have not yet been able to study them all carefully. In the meantime I app~~lied~~end a list of the species so far recorded as belonging to this flora, and have placed an asterisk opposite the species to which I have been able to add anything of interest. For completeness short accounts of each species are given.

Fossil Flora of the Pettycur Limestone.

Equisetales...............		Calamites (Protocalamites) pettycurens Scott.
Sphenophyllales............	*	Sphenophyllum insigne, Williamson.
		Cheirostrobus pettycurensis, Scott.
Lycopodiales...............	*	Lepidodendron Veltheimianum, Sternb.
		Lepidodendron brevifolium, Williamson.
		Lepidodendron pettycurense, Kidston.
	*	Lepidophloios Scottii, Gordon.
	*	Lepidostrobus Veltheimianus, Sternb.
		Lepidostrobus mazocarpon, Benson.
	*	Lepidostrobus cylindricus, sp. nov.
		Lepidocarpon wildianum, Scott.
		Stigmaria ficoides. Brongniart.
Filices....................	*	Botryopteris antiqua, Kidston.
	*	Dineuron ellipticum, Kidston.
	*	Metaclepsydropsis duplex (Williamson).
	*	Diplolabis romeri, (Solms.)
		Stauropteris burntislandica P. Bertran
		Bensonites fusiformis, R. Scott.
		Fern sporangia.
Pteridospermeae............	*	Heterangium Grievii, Williamson.
	*	Heterangium Arberi sp. nov.
	*	Heterangium sp. nov.
		Sphaerostoma ovale, (Williamson).
	*	Physostoma sp. nov., Gordon.
		Amyelon sp.

Calamites /

Calamites pettycurensis, Scott. 1908.

The anatomy of this species, the only member of the Equisetales occurring at Pettycur, has not yet been thoroughly investigated. Only stems are known and these are as a rule much crushed, the wood wedges often being completely separated from one another. In the more perfect specimens the centre of the stem contains a cavity in which, no doubt, the pith occurred. This cavity is generally of considerable size and the pith was probably fistular. The numerous wood wedges are arranged round the pith cavity and these consist of both primary and secondary xylem. In each wedge there is a "carinal" canal produced by the disintegration of the protoxylem groups.

The primary wood, however, is not centrifugal as is usual in the Calamites. It is partly centrifugal, it is true, but the greater part is centripetal and lies on the side of the "carinal" canal nearest to the pith cavity. The remainder of the primary wood is in the normal position - on the side of the carinal canal remote from the pith. In other words the carinal canal does not lie on the inner side of the primary wood but is completely surrounded by that tissue. The secondary wood is in the usual position abutting on the external portion of the primary wood, and does not form a very thick zone.

It was the peculiar distribution of the primary wood that led Dr. Lotsy to suggest the name Protocalamites for this genus. Dr Scott, however has only used this name provisionally.

Sphenophyllum /

Sphenophyllum insigne, Williamson. 1874.

The plant described under this name has several peculiarities which make it easy to distinguish. The xylem is triangular in form and round this primary cylinder the secondary wood is developed. The secondary wood often attains a considerable thickness and then the diameter of the wood ~~is~~ may be as much as 1 cm. The protoxylem elements were probably situated at the apices of the equilateral triangle formed by the primary wood and the elements of the centripetally developed primary wood get larger and larger as we pass from these protoxylem groups towards the centre of the triangle. At the protoxylem points there appears to have been considerable breaking down of the tissue and there is generally a canal produced there. This canal is on the inner side of each wedge of secondary wood. The secondary wood is produced in three wedges opposite the three protoxylem groups, but there the elements are much smaller than those of what we may call the interfascicular xylem which is produced along the sides of the triangular primary wood. In the secondary xylem in this species true medullary rays may be observed and not the complicated system of parenchymatous strands which characterise the other species of Sphenophyllum. The presence of a solid primary wood centripetally developed, and the medullary rays in the secondary wood led many observers to consider *S. insigne* a root of some higher plant and not the stem of one of the lower plants. The discovery of cortex and leaves, however, has completely confirmed Williamson's determination of the /

the species as a stem. I have recently succeeded in obtaining the root of this plant but the only specimen which shows the attachment has quite a considerable development of secondary wood. This obscures the appearance of the primary root trace. Meanwhile a photograph of the root while still in the cortex of the stem is given. Pl. B. fig. 6.

<u>Cheirostrobus</u> <u>pettycurensis</u>. Scott. 1897.

The peduncle of this cone was described by Williamson in 1872 as the axis of a Lepidostrobus but the cone itself was not described until 1897 when Dr. Scott published his paper. It was not until then that the real importance of the genus from an evolutionary stand-point was recognised. The structure of the cone is highly complex. In the centre of the axis is a stele whose xylem has 12 prominent angles. It has thus the appearance of a fluted column. The points of the angles consist of small cells - the protoxylem groups and the larger celled metaxylem contains in its more central portion numerous parenchymatous cells. The protoxylem groups are occasionally not peripheral but are sunk in the metaxylem. In the pedicel there is a certain amount of secondary wood round this axis and the presence of secondary wood has also been demonstrated in the axis of the cone itself.

The sporophylls are arranged in verticels and the bundles which supply them have a peculiar distribution. They take their departure from the sharp angles of the stele and when they enter the outer cortex of the axis a division into three takes place in a /

a horizontal plane. Of these three the median one is the largest. The median trace next divides into two in a vertical plane and then the upper of these last formed traces divides into three in a horizontal plane. By the time the trace has left the cortex of the axis these three divisions have taken place so that 3 bundles are placed vertically above the other three. The sporophyll itself divides into six segments and one bundle passes into each segment. The three lower bundles supply sterile bracts and the three upper the fertile segments or bracts. The bundles supplying the sterile portions ~~portions~~ divide once again into two near the extremities of the bracts. The two portions of the sterile bract pass vertically up through several internodes, interlocking with similar vertical ends from the verticels above and below, and thus bind the whole cone together and protect the sporangia borne by the fertile segments.

The bundle in the fertile segment also divides but this division is into four, these branches pass to the corners of the peltate end of the bract and supply the four sporangia borne at these corners. The whole cone is extraordinarily complex - the most complex Cryptogamic fructification - but it combines characters which are met with in several genera so that it is both complex and synthetic.

Nothing is known of the vegetative parts of this genus unless Pseudobornia be accepted as such. This, however, has not yet been conclusively proved. Although I have been searching for such vegetative /

vegetative bodies nothing has yet been discovered which could possibly be the vegetative shoot of this cone. Sphenophyllum insigne is probably too small to bear such large cones unless the cones took a long time to develop and were thus mature only after the axis had become strengthened by a strong development of secondary wood. Only three cones are known, but I have succeeded in obtaining another cone which, however, does not exhibit any peculiarites.

Lycopodiales, Lepidodendron Veltheimianum; Lepidostrobus Veltheimianus; Lepidodendron brevifolium.

I take these three together for reasons which will be made clear as we go on.

When Williamson, in 1872, published his account of Lepidodendron brevifolium he included under that name stems with a considerable amount of secondary wood and a large fistular pith, together with small specimens which had a very small axial cylinder. The small examples were clothed with their leaf-bases but the large ones had either no cortex and leaf-bases or else they were imperfectly preserved. In one or two cases, however, leaf bases were present but not in sufficient number to really prove the identity of the large and the small specimens. In the same paper he referred a lepidostrobus to this same genus.

Dr. Kidston, after an examination of the megaspores of the Carboniferous rocks, has come to the conclusion that those, which are present in this heterosporous lepidostrobus mentioned above, cannot be distinguished from the megaspores of Lepidostrobus Veltheimianus. /

Veltheimianus. Among my specimens there is one which Dr. Kidston has referred to L. Veltheimianum from an examination of the weathered surface. Unfortunately on cutting this specimen after its determination it was found that the plant had been all weathered away and only the imprint left on the surface. This specimen is figured in Pl. A. fig. 9 and proves that L. Veltheimianum did occur at Pettycur. From all this evidence it is clear that L. brevifolium is probably a bad species.

The large specimens of this lepidodendron possessed a large pith cavity which was probably fistular in life. Round the pith cavity is the centripetally developed primary wood with peripheral protoxylem groups, which, however, are not very prominent. Surrounding the whole primary xylem is a broad zone of secondary xylem.

One of the small twigs is represented in transverse section in Pl. A. fig. 6. At X the primary wood with its pith cavity is very distinct. The tissues external to the xylem are not generally preserved but in a few cases a delicate parenchyma may be seen. Between this parenchyma and the woody axis there was no doubt tissue which functioned as phloem. The outer cortex surrounds all the other tissues and it consists of a thick-walled parenchyma. The leaf-bases abut on the outer cortex and to these leaf bases the laminae were attached. In fig. 7 of the same plate two buds are shown in longitudinal section. They exhibit admirably the imbricating of the leaves.

In /

In fig. 10 the ligule of this species is figured. It is cut longitudinally and lies in a pit formed between the outer cortex of the stem and the leaf base. There is no long ligular canal such as is present in *Lepidophloios Scottii* from the same locality. If this species is really *Lepidodendron Veltheimianum* then there must have been continued growth of the cells of the outer cortex on the inner side of the ligule pit so as to throw the leaf base into a more or less horizontal position and the opening of the ligule pit further out on the leaf base. This continued growth has been demonstrated by Kidston in the case of *Lepidophloios scoticus* Kidston.

On the back of the lanceolate leaves of this species I have been able to demonstrate the presence of numerous stomata but they do not differ markedly from those of recent plants.

Before passing from this plant it may be well to state that one of my specimens which has certain of the characteristics of *L. brevifolium* as figured by Williamson is probably a *Lepidophloios* since the leaf bases overlap and the ligule pit appears to terminate in a long canal so that Williamson may have included more than one species under his name. The specimen however has not yet been worked up, so it is premature to say anything further on this point at present.

Lepidodendron pettycurense. Kidston 1907.

In a note to the Royal Society of Edinburgh Dr. Kidston referred two stems to this new species. At that time these were the /

the only two examples of this very interesting and important plant; since that date, however, a few other examples have been obtained and in particular one exceedingly large specimen which I obtained from the tuff at Pettycur House. From the general similarity and from the place where this specimen was obtained I conclude that it is part of the same stem which Mr E. B. Bailey of H. M. Geological Survey, had collected some time before. He told me that part was still left in the cliff but he could not remember exactly where it had been obtained from. As these further specimens may add to our knowledge of the species Dr. Kidston has very kindly handed over the original types to me for examination with a view to redescribe the species and amplify his paper.

The great interest in the species is the solid primary wood the presence of which renders the plant most important phyllogenetically. The protoxylem elements are ranged round the periphery of the primary cylinder but there is no corona. The whole primary zone is surrounded by a thick zone of secondary wood. In the large specimen referred to above the primary wood is a little over $\frac{1}{8}$" diameter while the whole specimen is 1 7/8" diameter and all outside the primary cylinder is secondary wood, no cortex or leaf basees being present. The solid character of the primary wood ~~places~~ renders this species ~~in~~ the most primitive ~~group~~ division yet recorded. The other two species which have solid axes are are L. rhodumneuse Renault from the Culm, and L. saalfeldeuse Solms, from the Devonian.

When we compare this type with the other Lepidodendroid remains /

remains from the same locality a series whose stems show a gradation from a solid to a medullated type can be established. L. pettycurense represents the first stage, then comes Lepidophloios Scottii, Gordon, which may have a solid primary wood but which usually has a mixed pith and finally L. Veltheimianum with a well marked medulla. Lepidophloios Scottii can easily be distinguished from L. pettycurense, even if the wood is solid, by the presence of the corona. It is also found that further along the stem in such a specimen of L. Scottii the pith always makes its appearance.

As will be seen further on in this thesis similar series may be made out among other genera; and it is this presence of primitive and intermediate types such as L. pettycurense and Lepidophloios Scottii which lends the special interest to the whole flora of the Pettycur Limestone.

Lepidostrobus Veltheimianus. As mentioned above Williamson was the first to describe this cone. He referred it to Lepidodendron brevifolium but Kidston has demonstrated that it is identical with Lepidostrobus Veltheimianus. The structure of the axis and the chief anatomical characters of this species are described in a later paper on Lepidostrobus cylindricus.

One important characteristic however is the heterospory exhibited by this species. In the apical region all the sporangia contain microspores which are very small and ~~present~~ occur in great numbers. The basal sporangia contain the megaspores and generally there are a considerable number in each sporangia - from eight to sixteen. The sporangia are sometimes arranged practically in whorls. The whorls are not perfect and perhaps it is better to say that there is a suggestion of a verticellate arrangement. In the megaspores there are sometimes traces of prothallial tissue and in the following short papers this tissue is discussed.

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ON LEPIDOPHLOIOS SCOTTII (A NEW SPECIES FROM THE CALCIFEROUS SANDSTONE SERIES AT PETTYCUR, FIFE).

BY

WM. T. GORDON, M.A., B.Sc.

[With Three Plates.]

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XIX.—On Lepidophloios Scottii (a new species from the Calciferous Sandstone series at Pettycur, Fife). By Wm. T. Gordon, M.A., B.Sc., Carnegie Research Scholar in Geology, Edinburgh University. *Communicated by* Professor Geikie, D.C.L., LL.D., F.R.S., etc. (With Three Plates.)

(MS. received April 3, 1908. Read February 17, 1908. Issued separately November 23, 1908.)

As Carnegie Research Scholar in Geology under Professor James Geikie, D.C.L., LL.D., F.R.S., at Edinburgh University, I have entered upon a systematic examination of fossil plants from Pettycur, Fife. Though many plants have been described from this locality, nothing systematic, as far as I know, has ever before been attempted. The main objects of this research are to endeavour to connect the various strobili obtained at the locality in question with the stems on which they were borne; to describe any new species met with, and to give some account of the mode of occurrence of the material in which the plants are enclosed. Some of these objects have already been attained, but others will require further study to decide.

The material at my disposal was handed over to the University by Dr John S. Flett, H.M. Geological Survey, and has been further added to by my own collection.

The fossil to be described in the present paper occurred in a block lying loose on the shore at Pettycur. In my preliminary note I mentioned that the same fossil had been collected by Dr D. H. Scott, F.R.S., on 4th December 1899, and that that specimen seemed to have been on the outside of a block, and partially weathered away. In it the middle cortex—a tissue almost completely decayed in my specimens—is well preserved. From the general look also of the material from which it came, I conclude that my specimens were derived from quite a different block of the limestone. I have seen other specimens in Dr Kidston's collection, and Mr D. M. S. Watson, B.Sc., tells me that there are specimens in Manchester Museum which may belong to this species; the fossil, therefore, is apparently not a rare one. Dr Scott's specimen does not show the complete circumference of the stem, but it must have been 25 mm. or thereby in diameter, with a central xylem cylinder of 4 mm. Unfortunately, the longitudinal sections cut from this stem are considerably out of the vertical, and do not show some very important points connected with the xylem.

The material in my own collection was all obtained from one block measuring roughly 2 × 1 × 1 ft. This block split along two planes, one across and one parallel to the plane in which the stems were lying. Five stems were exposed longitudinally, and were clothed in parts with leaf-bases. Part of one of these stems and the whole of a sixth were in the third piece of the block, and from them complete tranverse sections were cut.

The whole block had a rudely bedded appearance, while the partial decay of the xylem and central cortex in one stem, and the subsequent penetration of the specimen by stigmarian rootlets (fig. 8, *a*), point to conditions of deposit similar to those present in a swamp. In thickness the seven stems examined varied from 1 inch to $1\frac{1}{2}$ inch, and the total length represented a little over 3 feet of the plant. There can be no doubt that all the stems were of the same species, as each had similar leaf-bases. The other tissues were typical of many of the Lepidodendreæ, and were therefore of no specific importance; in the case of one stem the stele had rotted away. It is not likely, however, that they all formed portions of one individual, the variation in diameter being too great for that. The region of greatest weakness in the fossil was along the inner margin of the periderm, and along this region the stems easily split; hence, as none of the specimens showed a surface view of the leaf-bases, their external form has been constructed from radial and transverse sections.

Owing to incomplete fossilization, or rather to too complete mineralisation of the tissue towards one end, the cortex was there replaced by a layer of coal from which all structure had disappeared, and the stem was useless for making sections. Most of the sections have therefore been prepared from the upper parts of the stems. I have examined nearly 180 sections of this fossil; of these 16 are from the Scott collection, Nos. 960 to 976 inclusive, and were prepared by Mr LOMAX; the rest are of my own making. The large number of my slides is due to the fact that they were cut to show certain structures, sometimes only obtained after several unsuccessful attempts. The new species described in this paper is founded on the slides mentioned in the Scott and my own collections.

The genus *Lepidophloios*, to which this plant belongs, has often been recorded from the Calciferous Sandstone series, but no example from the limestone blocks at Pettycur, showing structure, has yet been described. *Lepidophloios Scoticus*, however, was included in a list from this locality by Dr ROBERT KIDSTON, F.R.S., and Mr D. M. S. WATSON, B.Sc., has also referred to one from Burntisland.

As already mentioned in my preliminary note, I propose to call this new stem *Lepidophloios Scottii*, in honour of Dr D. H. SCOTT, F.R.S., who had collected the plant and described it in MS. some years ago. I am glad of this opportunity of showing my appreciation of Dr SCOTT's kindness in handing over to me all his material. This paper was at first intended to be a joint one with Dr SCOTT, but circumstances have led to its publication by myself earlier than was anticipated. Dr SCOTT has also acted as consultant in all matters of doubt in regard both to the present paper and to my research in general. I also desire to express my thanks to Professor JAMES GEIKIE, LL.D., D.C.L., F.R.S.; Professor I. BAYLEY BALFOUR, F.R.S.; Dr ROBERT KIDSTON, F.R.S.; and Dr HORNE, H.M. Geological Survey, for encouragement and advice in my work; to Mr ROBERT CAMPBELL, M.A., B.Sc., for aid in various matters connected with my research; and to Mr A. G. STENHOUSE, F.G.S., for assistance with the illustrative photomicrographs.

General Structure.

The plant of which the fragments formed parts must have been fairly tall, for, in these stems, there is no change in the various tissues throughout their length. There are slight differences between the individual pieces, chiefly as regards the amount of periderm developed.

No single section shows all the tissues in organic continuity, while some tissues, notably the phloem, are hardly to be distinguished in any section. Taken conjointly, figs. 1 and 8 give a fairly good idea of the transverse appearance, all the parts, from central xylem to the leaf-bases, being organically connected. The xylem at first sight appears solid, but careful examination reveals the presence of short, thin-walled cells distributed near the centre of the xylem, either in groups or occupying the whole of the centre (see *p*, figs. 2, 2A, and 4 respectively). Scattered through this parenchyma as detached strings of cells, or more often between the short-celled parenchyma and the long tracheides of the primary wood, are short, reticulately thickened tracheides with flat ends. In fig. 2, *t′*, the ends are shown, and in fig. 5, *t′*, these cells are cut longitudinally. These tracheides vary greatly in length, being sometimes broader than long, and occasionally they attain a length of from three to four times their width. In *Lepidophloios Scottii* the pith shows a transitionary condition between those lycopods with solid xylem and those with a true medulla. The scattered tracheides in the pith have departed less in their character from those of the primary wood than is the case in *Lepidodendron vasculare* (Binney, sp.).

The primary wood is composed of scalariformly thickened, centripetally developed tracheides (fig. 5, *t*). No secondary wood has been observed in any of the specimens, but other secondary tissue has been developed in successive zones, so that the stems are not of only one season's growth. The protoxylem is peripheral, occurring as blunt points round the woody axis. The leaf-traces have a mesarch xylem and rise abruptly at first, but, after crossing the middle cortex, they bend out horizontally into the leaf-bases (fig. 4, *l.t.*).

Owing to imperfect preservation, the phloem is distinguished with some difficulty, but a zone of partially disintegrated tissue surrounding the xylem probably represents it (fig. 1, *ph.*). Outside the phloem zone is a layer of cells tangentially elongated, probably marking the outside limit of the inner cortex. The middle cortex is well preserved only in Dr Scott's specimen (fig. 1, *m.c*), and in one of my stems near the end, and consists of thin-walled parenchyma. There is no trace of secondary tissue in this zone. The outer cortex is separated from this middle belt by a layer of tangentially elongated cells, two or three rows deep, with thin walls, which passes gradually into the thicker-walled outer cortex. The outer cortex consists of three zones, the inner being parenchymatous, the middle prosenchymatous, and the outer parenchymatous. The elements of these zones are more or less radially arranged, but the outer zone passes into a more irregular parenchyma on which the leaf-bases abut.

While there is no distinct abscission layer in the leaf-base, it breaks away at this parenchyma, which is therefore not present in stems denuded of their leaf-bases.

HISTOLOGY.

In describing the various tissues from the centre outwards, the pith naturally comes first. The stems examined are all of approximately the same diameter, and yet the pith varies greatly in amount. One stem, with primary xylem of 3·3 mm. diameter, has only a few pith cells in patches (fig. 2, *p*); another, with xylem 4·3 mm. diameter, has a pith 2·5 mm. diameter; while yet another, with xylem 3·4 mm. diameter, has a pith 1·6 mm. diameter. But even in the same specimen the pith varies greatly; the example referred to above as showing only a few pith cells in one part (fig. 2), had, in another part (about 10 cm. further down), a pith of 2 mm. diameter, and 5 cm. further up from where the section (fig. 2) was cut, the pith was 1·4 mm. diameter. In certain sections from other individuals there does not seem to be any pith at all. The pith, then, is very variable both in extent and in occurrence; its elements are slightly elongated vertically, and are arranged in vertical rows, the ends of each element being flattened horizontally. Secondary oblique walls also occur in places. The walls of these elements are thin and soft, and do not show any secondary thickening. In fig. 2*a*, *p*—the cell with no secondary thickening, but being bounded by what is the central lamella in the tracheides—is a pith cell.

Scattered through this soft parenchyma are rows of short tracheides; they occur in greater abundance towards the periphery, but are of no greater diameter than the other parenchyma cells of that tissue. These tracheides seem to form an irregular layer between the primary wood and the soft pith. They are thickened in an irregularly scalariform manner, but in some the thickenings have a tendency to assume a reticulate arrangement, whose structure is very similar to those figured by BRONGNIART in the description of the *Sigillaria* which he in error referred to *S. elegans*.

Occasionally also long tracheides occur isolated in the pith, and are easily distinguished from the others by their length and the scalariform thickenings on their walls. The isolated and the short tracheides are somewhat similar to those found in *Lepidodendron vasculare* (BINNEY, sp.) and in *Lepidodendron Hickii* (WATSON).

The zone of primary wood surrounding the pith is seldom broken even when branches are given off. In one branch, however, a row of short tracheides passes out with the xylem, thus indicating a break in the wood ring, while in another case of branching, the soft pith has actually grown out of the gap thus formed in the xylem zone (fig. 6, *p*). Both these examples are in cases of unequal dichotomy. The pith cells average in dimensions ·18 × ·09 × ·09 mm.

From the measurements given of the diameter of the xylem cylinder and that of the pith, it will be seen that the primary wood is in places comparatively small in amount. In a specimen 35 mm. diameter the xylem and pith are together 4·3 mm., and of that the xylem forms an outer ring 9 mm. thick (about 7 or 8 tracheides). Another stem with a small pith has a wood ring 13 to 14 tracheides thick and a total xylem cylinder of 3·3 mm. diameter. Generaly speaking, the innermost tracheides are larger than those round the periphery, but this is not invariable, as small tracheides fill in the spaces between the larger ones, even in the innermost elements of the wood. The largest tracheides had a mean diameter of ·16 mm.; the smaller ones of ·07 mm. In length these tracheides vary greatly, as is shown in cases where pointed ends can be clearly seen—indicating proximity at least to the actual terminations. One of these tracheides was 5·5 mm. in length, while another was nearly 8 mm. The middle lamella can be distinctly seen in these elements both in transverse and in longitudinal sections (fig. 2, *l*, and fig. 2*a*, *l*).

The peripheral layers consist of smaller and more uniform tracheides forming a continuous ring round the whole cylinder. The contour of the wood is fairly smooth, as the protoxylem points are rounded and flat. These protoxylem teeth consist of from 9 to 10 tracheides, and the spaces between are each occupied by a leaf-trace bundle. The elements of the protoxylem are about ·02 mm. diameter, and are scalariformly thickened. In no section examined can any trace of a truly spiral protoxylem element be seen. In certain sections the branching of the xylem cylinder is well shown and will be referred to later.

External to the primary wood there is in most sections a thick band of almost completely decomposed tissue, but in one specimen this tissue is fairly well preserved. A longitudinal section shows three rows of slightly elongated parenchyma abutting on the wood, and this is probably the xylem sheath. Immediately outside this sheath there is a zone of large-celled tissue showing signs of rupture in itself; physiologically this tissue probably represents the phloem, and, wherever a branch is given off, a band of the same tissue occurs on the under side, and gradually surrounds the branch bundle. The leaf-traces do not give much help in describing this tissue, for in them the phloem representatives cannot be distinguished from the ordinary parenchyma round the bundle, except that their cells are filled with dark-coloured material. On the whole, the preservation of the tissue in the phloem region is not sufficiently good to allow of any detailed description.

Outside the phloem is a zone of parenchyma in which all the cells appear similar except the outermost layers, which are elongated tangentially. The preservation here is also very poor.

Succeeding this tissue is the middle cortex, completely preserved in one specimen only (fig. 1, *m.c.*); in others merely isolated patches appear, generally surrounding the outgoing leaf-trace. This tissue consists of thin-walled parenchyma with no definite arrangement of its cells. There is no evidence of meristematic condition in any of these cells, but in certain places they are filled with dark brown substance. It is not clear in the middle cortex how these patches of cells with dark contents are arranged, but in the outer cortex it can be seen that they occupy a definite position, and probably they occupied a definite position also in the middle cortex. The whole zone of middle cortex in a stem 25 mm. diameter is a ring 2·3 mm. in thickness, and shows no trace of secondary growth. In none of the specimens examined can any secondary growth be seen in this middle cortex.

External to the middle cortex comes a belt, two to three cells broad, of tangentially elongated elements with thin walls; these are the inner cells of the outer cortex. These innermost cells are no larger than those of the middle cortex, but they gradually give place to larger cells with thicker walls. The tissue in this region and all the more external parts is in most cases well preserved. The outer cortex can be divided into three zones, of which the inner is composed of parenchymatous elements in no definite arrangement. Here again, however, patches of tissue filled with dark brown contents may be observed. They are seen here to occur in places well removed from the outgoing vascular bundles and also from the outer and inner edges of the parenchyma. It would seem, therefore, either that the cells secreted a resinous substance, or that they acted as storage tissue and that the brown substance represents the stored food. The inner zone stops just where the radial arrangement of the outer cortex begins, *i.e.* five or six cells in from the periderm. The brown patches are therefore confined to the area where there is no secondary growth. Beyond this, in young branches and in older ones which have no periderm, the leaf-bases would be found; in all the specimens examined, however, some secondary cortex existed. Sometimes very little appears, but in other cases there is a succession of periderm layers, denoting some sort of periodic rest and active growth (fig. 8, *pd.*).

The secondary cortex is formed by the rapid division of a belt of cells, near the outside of the primitive outer cortex. The resulting tissue is arranged in radial rows, and is more regularly arranged in vertical rows than the surrounding cortical parenchyma. Passing further out they become much elongated vertically, and in this species are filled with dark material. I cannot see any trace of secretory passages in this species, though they have been observed in others.

The dark belt is succeeded externally by long clear cells, which in turn give place to another dark zone like the last. In my specimens I cannot trace more than two of such zones, but their presence seems to indicate some sort of periodic rest. Outside the last dark peridermic ring, the cells are still radially arranged and vertically elongated, while some rows are at the same time tangentially elongated. The last two or three layers of this tissue become parenchymatous, and on this third cortical zone the leaf-bases abut. There is no distinct abscission layer, but, when the leaf-bases are absent, they have torn away this parenchyma, thus exposing the elongated elements of the secondary cortex on the denuded stem. The leaf-bases persisted even after the upper portion of the leaves had decayed, and on the shape of these leaf-bases specific characters are more safely founded than on other parts of the vegetative tissue.

Dr Kidston has shown in *Lepidophloios* that these leaf-bases pointed upwards on young twigs, and outwards and even downwards on older ones, thus indicating that these leaf-bases continued their growth after the foliage had decayed, and that the growth was longer continued on the upper side. In all the specimens of *Lepidophloios Scottii* the leaf-bases hang downwards, and seem to have reached the limit of their growth (fig. 3).

The leaf-trace bundles, which run from the stem through the leaf-bases to the leaves, arise from the outer surface of the stele. Their xylem is derived from the protoxylem of the stele, and though their direct passage into the protoxylem cannot be traced accurately, it can be inferred. These xylem strands of the leaf-traces contain more tracheides than each individual blunt protoxylem tooth, and are situated between two adjacent protoxylems; they are probably the result of the anastomosing of parts of the protoxylem teeth between which they occur. The number of tracheides to each leaf-trace varies from 15 to 25, and the whole xylem strand is elongated tangentially with the smaller elements in the centre, *i.e.* the xylem is mesarch. The bundle has rather a steep course at first, but passes out almost horizontally through the outer cortex. By examining successive sections it is found that the xylem does not change in shape, and, even in the leaf-base, the trace retains the same form. Before passing into the periderm, however, the xylem becomes augmented by transfusion tissue, which appears to be added chiefly on the lower side of the xylem.

The phloem has mostly disappeared from the traces except in the regions of the outer cortex and the leaf-bases. In the periderm zone it is seen at its best, though even there it cannot be distinguished with certainty. It consists of slightly elongated, soft-walled tissue, but the state of preservation does not warrant further description. Passing out from the periderm, the bundle is accompanied by a parichnos strand, while round it in the leaf-base are spiral cells of the mesophyll, similar to those described in WILLIAMSON's XIX Memoir, and representing transfusion tissue. The leaf-trace passes out of the leaf-base a little below the centre of the leaf-scar, and beyond that cannot be followed, as the foliage has all decayed in the specimens examined.

The leaf-base is of considerable size, measuring 6 × 6 × 3 mm., and is composed of large-celled parenchyma. It is elongated horizontally, as the measurements indicate, and is rhomboidal in section (fig. 9). The leaf-scar is about 1·7 mm. high (figs. 10 and 14, *l.s.*), and considerably broader, though the exact width of the scar has not been fully ascertained. The leaf-base assumes its greatest width about halfway between the leaf-scar and its attachment to the stem, tapering slightly in both directions. The amount of tapering is not great, but is quite distinct. Near the leaf-scar, and especially round the vascular bundle where it emerges on the scar, the large-celled parenchyma of the leaf-base gives place to a smaller-celled and more closely packed parenchyma (figs. 10 and 14).

Within the leaf-base is the ligule pit, a bottle-shaped cavity, much elongated, and lined by a layer of pallisade-like cells. This pit is placed immediately above the vascular bundle of the leaf-base, and, while long cells fill in the space between the bundle and the base of the ligule pit, no tracheides were observed among them. The ligule arises from the base of this pit. It is tongue-shaped, and consists of uniform small-celled parenchyma. It does not quite fill the pit (figs. 10 and 14, *lg.*).

The top of the ligule pit communicates with the exterior by a short, straight canal, surrounded in places, especially near its base, by the same pallisade tissue which lines the ligule pit. This canal (fig. 10, *lg. c.*) opens far back from the leaf-scar into the space between the leaf-base and the next overlying one. In this way the opening is protected from injury and is not exposed on the outside of the plant. In all the other examples of *Lepidophloios* I have seen this canal opens near the leaf-scar and on the exposed portion of the leaf-base. The canal is oval in section, being broader than high, and the opening at the top is triangular, with the base of the triangle towards the axis of the stem.

As mentioned before, a strand of parichnos underlies the leaf-trace for the greater part of its length in the outer cortex and leaf-base. This strand is of very loosely packed, thin-walled cells; it divides into two in the leaf-base, and, rising to the level of the bundle, these two branches pass out at the leaf-scar, one on each side of the bundle. As the tissue of the parichnos is well preserved, I have been able to follow its course by both longitudinal and transverse sections. In the inner part of the periderm *no parichnos can be distinguished*, nor in any case has it been seen further in than the periderm. Fig. 11 shows the bundle *v.b.*, and on the *upper* side there is parenchyma. This section is cut near a branch, so that the traces can be seen both in the periderm and in the inner part of the outer cortex. Those in the periderm have the parichnos on the opposite side of the trace from that of fig. 11. The parenchyma above this trace belongs to the middle cortex. Passing into the periderm the parenchyma above the bundle gets less, but, a little way in, a distinct elongated portion below the bundle becomes visible (fig. 12, 2 *par.*), and this I take to be the true parichnos. As the exterior is approached this tissue increases in amount, until, just outside the periderm, it occupies the lower two-thirds of the leaf-trace (fig. 12, 1 *par.* and 3 *par.*; fig. 13, *par.*). The parichnos then communicates with the inside of the stem through the parenchymatous bundle sheath and not directly.

On entering the leaf-base the parichnos is still long and narrow, but quickly shortens and broadens into the typical kidney-shaped strand. Fig. 12 shows three leaf-traces; of these, two (Nos. 1 and 3) are near the outside of the periderm and just going to pass into the leaf-base, the third (No. 2) is further into the stem; the increase in the parichnos is well seen in these three traces.

In the leaf-base this strand can be traced quite a long distance before it forks (fig. 14, *par.*); the forking takes place just beyond a plane drawn through the opening of the ligule canal and parallel to the main axis. Sections which show any portion of either ligule or ligule canal invariably also show a single parichnos strand. Such a long stretch of unbranched parichnos is unusual. Fig. 9 shows a leaf-base beyond the region where the single strand is got, so the parichnos is represented by two masses of tissue, one on each side of the leaf-trace (fig. 9, *par.*, *par.*).

This tissue does not seem to have had any communication with the exterior other than on the leaf-scar. The examination of a large number of leaf-bases cut in all directions has failed to show any such connection either directly or by pits, as in the Lepidodendrons; indeed, the parichnos is much the same distance from the exterior at all parts of its course in the leaf-base, until it emerges on the leaf-scar.

Fig. 14 shows a radial section of a leaf-base, with parichnos strand (*par.*), leaf-scar (*l.s.*), ligule pit and ligule (*lg*). The section just misses the ligule canal, which was probably slightly bent to one side in this case, as all other radial sections show the canal as well. The point where the leaf-base ceases to be keeled and becomes round is well shown in this figure, as also in fig. 10, *c.d.*, while in fig. 7 the difference in transverse section is well marked. Fig. 7 is part of a section cut sloping outwards, so that the difference might be seen; in the lower part of the figure the leaf-bases are keeled; in the upper part they are rounded. As the lower part is nearer the stem than the upper, the leaf-bases are keeled near the stem and rounded near the leaf-scar.

The leaf-scar is slightly hollow, due probably to contraction of the tissue after the foliage had rotted away, and the leaf-trace shows as a low papilla in this hollow, about one-third of the height of the scar from the bottom.

The branching in all the cases examined was of unequal dichotomy, but apparently of two types. In most cases the wood ring is not broken, only the outer elements passing off to form the branch; but in fig. 6 the ring is ruptured, and the pith cells are seen growing out through the gap. This last type is also seen in transverse section in specimens in my own and in Dr KIDSTON'S collections. The branches, however, are all alike devoid of a pith, and are representative of the "halonial" type of branch.*

In my specimens the branches project very slightly beyond the covering of leaf-bases, where they are broken over, and they seem to have been quincuncially arranged. In one series of longitudinal sections 1 inch long, there are four of these branches, so that they are set somewhat closely together; they are not in vertical rows. In all cases they are sharply broken off outside the leaf-bases, and they taper quickly to this truncation. The leaf-bases do not form rosettes round these tubercles, as is characteristic of *Lepidophloios Scoticus* (KIDSTON).

This new species has points in common with other species. The occurrence, for example, of short tracheides in and round the pith suggests comparison with *Lepidodendron vasculare* (BINNEY, sp.) and *L. Hickii* (WATSON), but the leaf-bases in these species at once differentiate them from *Lepidophloios*. The only species with which more careful comparison is necessary is *Lepidophloios Scoticus* (KIDSTON), and *Lepidodendron Pettycurense* (KIDSTON). The latter was described from the woody axis only, and the complete absence of any pith in that species is sufficient to distinguish it from *Lepidophloios Scottii*. *Lepidophloios Scoticus* is very common through the whole Calciferous Sandstone series in carbonised impressions, and, from the similarity of leaf-base, *L. Scottii* might easily be mistaken for *L. Scoticus*. Comparison is therefore very

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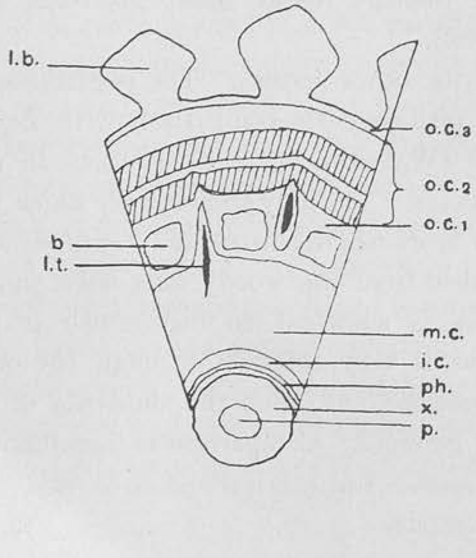
* Mr LOMAX, who prepared the sections of Dr SCOTT'S specimen, referred to it as a halonia-like stem.

necessary, and I have based my comparison on the author's description. It was described from impressions, so that the specific characters depend on the leaf-bases. (Only halonial branches can be compared, as my stems are all in that condition.) In *L. Scoticus* there is a bending back of the leaf-bases round the halonial tubercules into a rosette, and the leaf-bases themselves are smooth, rounded, elongated; in *L. Scottii*, no rosettes have been observed at the base of the cone stalks, and the leaf-bases are smooth, keeled, elongated. Towards the scar the keel disappears, and from that point to the scar the leaf-base is rounded, getting flatter and flatter as the scar is approached. On the under surface of the leaf-base the ridge is more prominent than in *L. Scoticus.*

SUMMARY.

Lepidophloios Scottii occurs in the Pettycur limestone in the Calciferous Sandstone series of Fife. The species is named in honour of Dr D. H. SCOTT, F.R.S., and is founded on sections 960 to 976 in the Scott collection and about 180 sections in the Gordon collection. It is a true *Lepidophloios*, having all the characters of that genus. The stem is typical of the *Lepidodendreæ*, is in this case "halonial," and is clothed with leaf-bases. The leaf-trace is collateral, the xylem mesarch, and a parichnos strand occurs beneath the bundle. The cone branches have no pith, are typically halonial, and are quincuncially arranged. The main stem has a pith with short tracheides and sometimes long tracheides scattered in it. The specific characters derived from the leaf-bases, and irrespective of those derived from the structure of the stele, are as follows:—

1. The leaf-base is keeled for three-quarters of its length, and then slopes suddenly down to the leaf-scar with an unkeeled, concave surface.
2. The ligule canal is short, straight, and has its orifice covered by the overlying leaf-bases.
3. There is a pallisade-like layer round the ligule pit.
4. The parichnos only forks a short distance below the leaf-scar.



$o.c._1$; $o.c._2$; $o.c._3$ = three layers of outer cortex ; $o.c._2$ is the secondary tissue (periderm).
m.c. = middle cortex.
i.c. = inner cortex.
ph. = phloem (physiological).
x. = xylem.
p. = pith.
l.t. = leaf-trace.
l.b. = leaf-base.
b. = section of reticulum of cells with dark-brown contents.

BIBLIOGRAPHY.

KIDSTON, R. (1893), "On *Lepidophloios*, and on the British Species of that Genus," *Trans. Roy. Soc. Edin.*, vol. xxxvii. pt. 3.

SCOTT, D. H. (1900), *Studies in Fossil Botany*, London, 1900.

„ (1906), "The Present Position of Palæozoic Botany," *Progressus Rei Botanicæ*, 1907.

WATSON, D. M. S. (1907), "On a Confusion of two Species (*Lepidodendron Harcourtii*, Witham, and *L. Hickii*, sp. nov.) under *Lepidodendron Harcourtii*, Witham, in Williamson's XIX. Memoir; with a description of *L. Hickii*, sp. nov."

WILLIAMSON, W. C., "On the Organisation of the Fossil Plants of the Coal Measures," *Phil. Trans.*, part ii. (1872); part iii. (1872); part xix. (1893).

EXPLANATION OF PLATES.

Figs. 1–14. Photomicrographs by A. G. Stenhouse, F.G.S., and the author.

Fig. 2*a*. Camera Lucida drawing by the author.

Fig. 1. Transverse section of *Lepidophloios Scottii*. *x* = xylem; *ph.* = phloem; *m.c.* = middle cortex; *o.c.* = outer cortex; *pd.* = periderm; *br.* = branch. Scott Collection 965. × 5.

Fig. 2. Tranverse section of central xylem cylinder. *p* = pith; *l* = central lamella; *t′* = end of short tracheide. Gordon Collection 176. × 36.

Fig. 2*a*. Enlarged drawing of tracheides to show central lamella (*l*).

Fig. 3. Longitudinal section of stem. *x* = xylem; *m.c.* = middle cortex; *o.c.* = outer cortex; *pd.* = periderm. Gordon Collection 173. × 2.

Fig. 4. Longitudinal section of xylem cylinder. *l.t.* = leaf-trace bundle; *t* = tracheides of xylem (scalariformly thickened); *p* = pith. Gordon Collection 228. × 14.

Fig. 5. Longitudinal section of xylem. *t* = tracheide (scalariformly thickened); *t′* = short tracheide (reticulately thickened). Gordon Collection 223. × 36.

Fig. 6. Longitudinal section through a branch. *x* = xylem of main stele; *x′* = xylem of branch; *p* = pith cells growing out through gap. Gordon Collection 228. × 36.

Fig. 7. Transverse section of leaf-bases, showing keeled and unkeeled region of leaf-bases, but sloping out from the stem. Gordon Collection 216. × 2.

Fig. 8. Transverse section of stem with leaf-bases attached. *a* = stigmarian rootlet; *o.c.* = outer cortex; *pd.* 1 and *pd.* 2 = layers of periderm; *l.b.* = leaf-base. Gordon Collection 152. × 3.

Fig. 9. Transverse section of leaf-base. *v.b.* = vascular bundle; *par.* = parichnos. Gordon Collection 215. × 12.

Fig 10. Longitudinal radial section of leaf-base. *l.s.* = leaf-scar; *c.d.* = concave depression; *lg.c.* = ligular canal; *lg.p.* = ligular pit. Gordon Collection 223. × 12.

Fig. 11. Transverse section of leaf-trace bundle in inner part of outer cortex. *m.c.* = middle cortex coming out with the bundle; *v.b.* = vascular bundle. Gordon Collection 196. × 36.

Fig. 12. Transverse sections of leaf-trace bundles in the periderm. *par.* = parichnos. Gordon Collection 194. × 12.

Fig. 13. Part of fig 12. *x* = xylem; *b.s.* = bundle sheath; *par.* = parichnos. × 48.

Fig. 14. Longitudinal radial section of leaf-base. *l.s.* = leaf-scar; *lg.* = ligule; *par.* = parichnos; *c.d.* = concave depression. Gordon Collection 173. × 12.

MR WM. T. GORDON on *Lepidophloios Scottii*.—PLATE I.

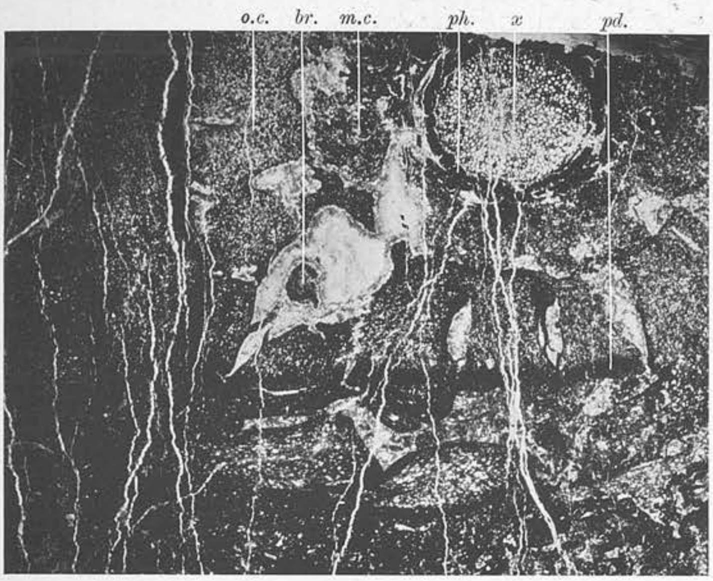


FIG. 1.

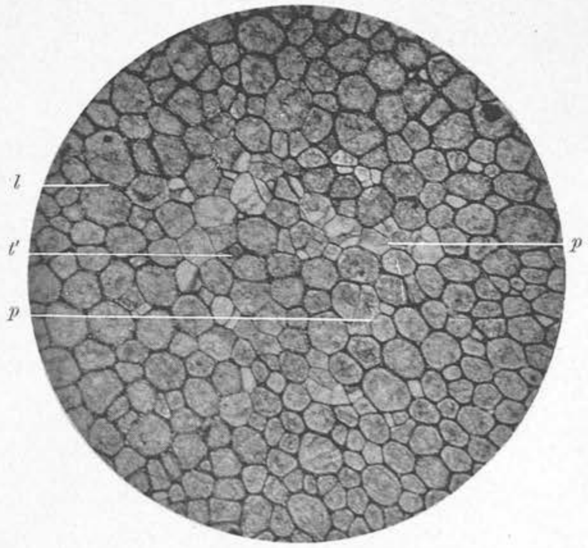


FIG. 2.

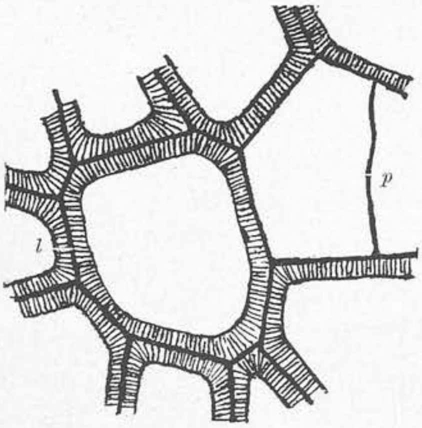
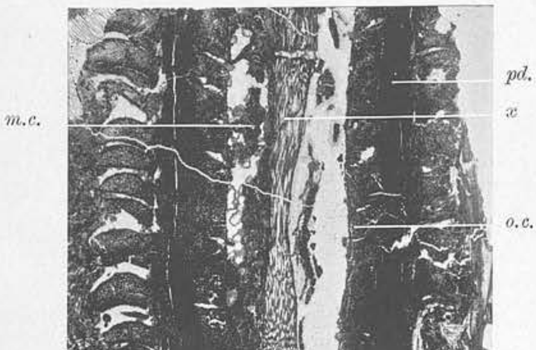


FIG. 2A.



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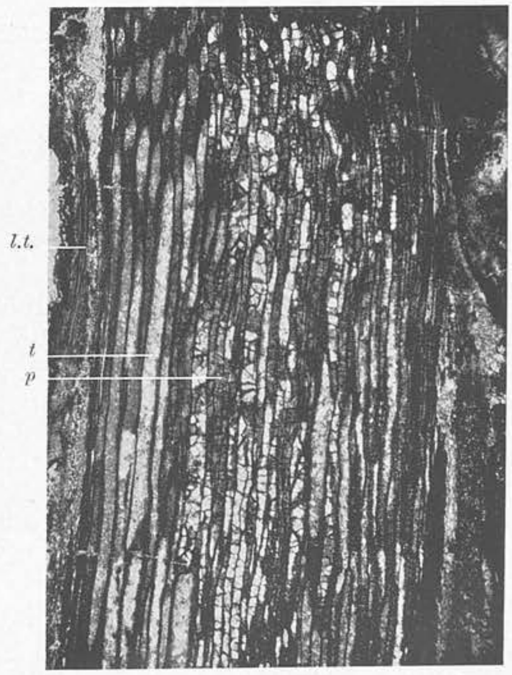

FIG. 4.

MR WM. T. GORDON on *Lepidophloios Scottii.*—PLATE II.

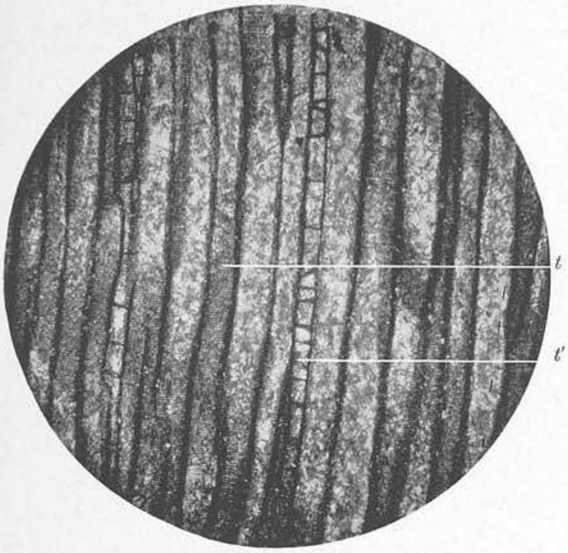

FIG. 5.

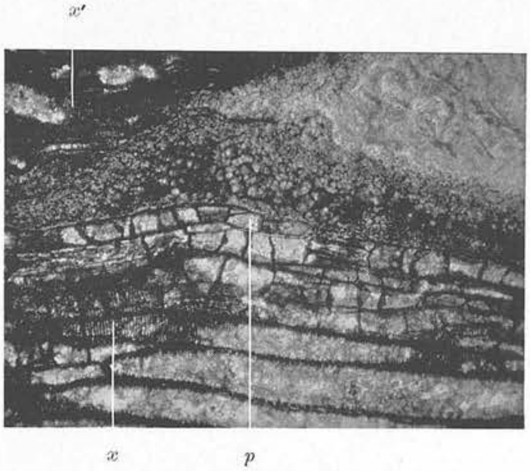

FIG. 6.

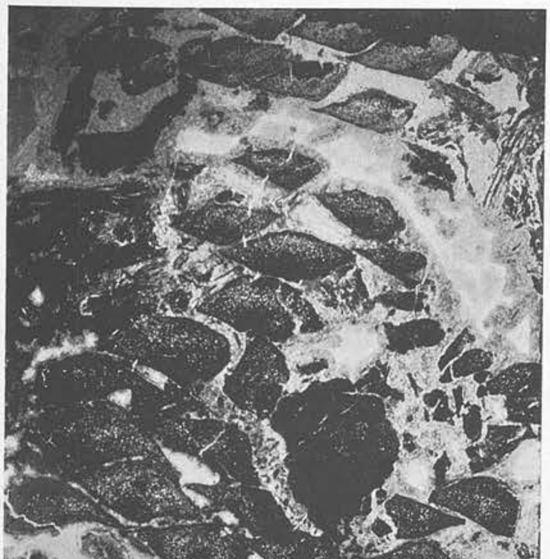

FIG. 7.

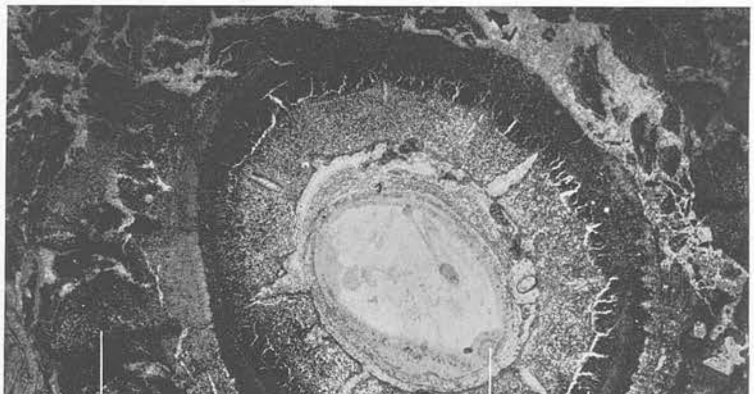

FIG. 8.

Mr Wm. T. Gordon on *Lepidophloios Scottii.*—Plate III.

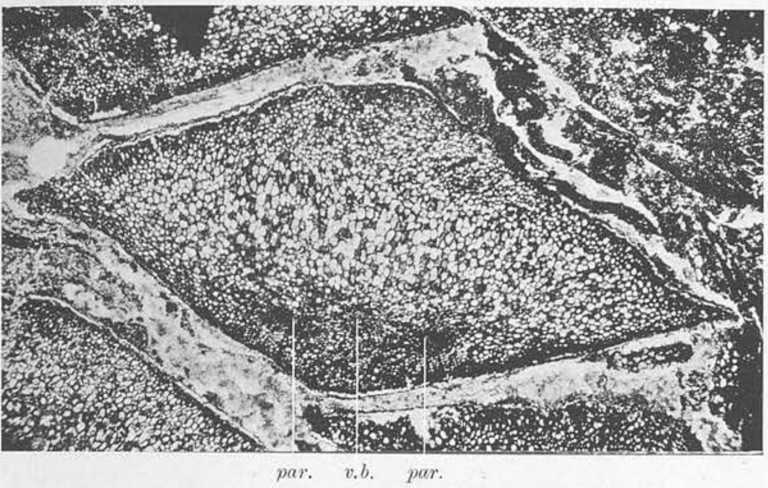

Fig. 9.

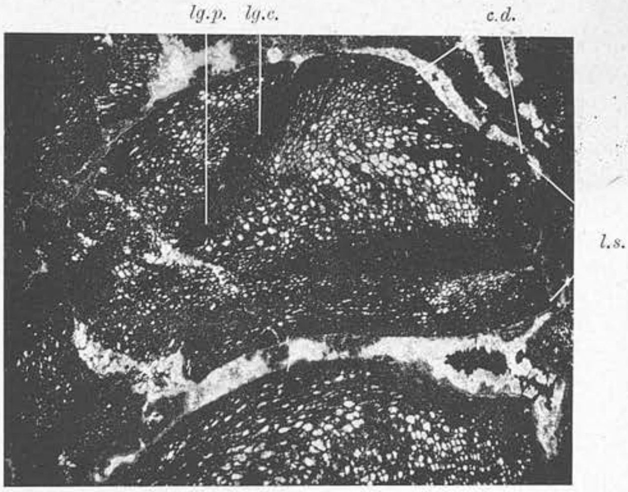

Fig. 10.

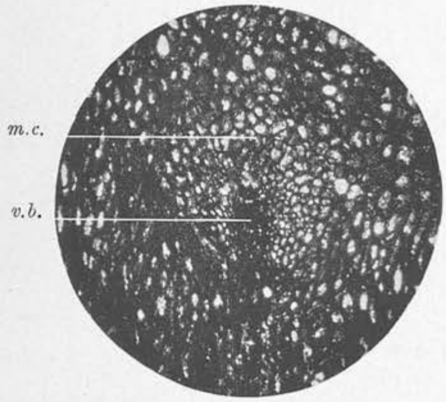

Fig. 11.

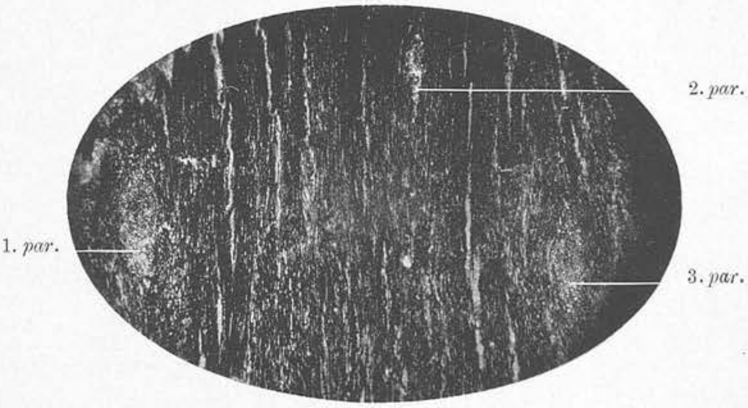

Fig. 12.

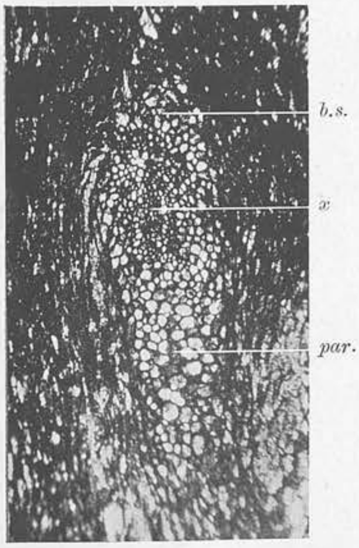

Fig. 13.

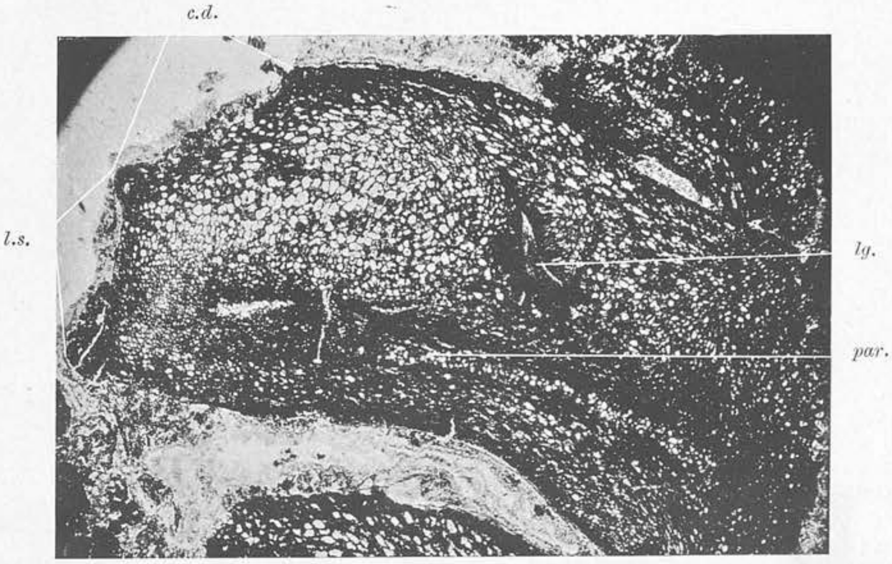

Fig. 14.

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19. *On Lepidophloios Scottii (a new species from the Calciferous Sandstone series at Pettycur, Fife).* By Wm. T. Gordon, M.A., B.Sc., Carnegie Research Scholar in Geology, Edinburgh University. *Communicated by* Professor Geikie, D.C.L., LL.D., F.R.S., etc. (With Three Plates.) Price: to Public, 1*s*. 9*d*.; to Fellows, 1*s*. 4*d*. (*Issued November* 23, 1908.)

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WM. T. GORDON, M.A., B.Sc.

ON THE PROTHALLUS OF LEPIDODENDRON VELTHEIMIANUM

Trans. Bot. Soc. Edin., xxiii. (1908)

ON THE PROTHALLUS OF LEPIDODENDRON VELTHEIMIANUM.

By WM. T. GORDON, M.A., B.Sc. (*Carnegie Research Scholar in Geology, Edinburgh University*). Communicated by the Secretary. (Plate VII.)

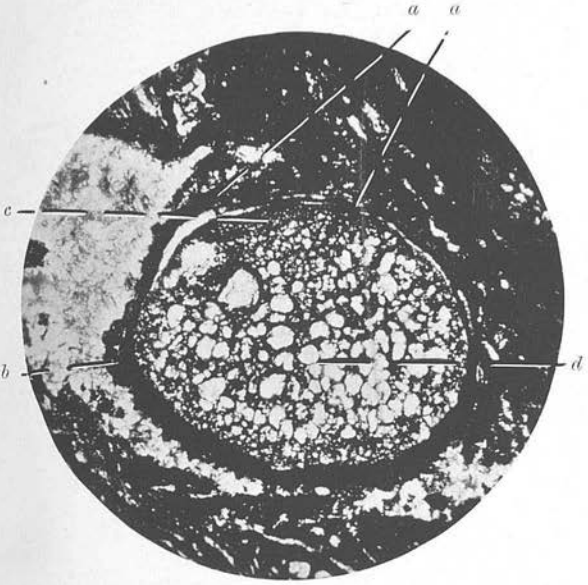
In the Carboniferous Epoch the lycopod alliance formed one of the dominant groups of plants, and contained not merely small forms with a habit similar to the modern representatives of the group, but also large arborescent forms. With such great differences in the vegetative parts we should expect corresponding differences in the reproductive strobili which these plants produced. In *Lepidocarpon*, *Miadesmia* and *Spencerites* we see such specialisation in a marked degree, the seed-like form of the first two showing adaptation to drier conditions than lycopods now grow in. Others show a closer approach to *Selaginella* in the organisation of their strobili, though they are still far removed from that genus. In general the sexual processes are the last to be altered by changing conditions, so the gametophyte stage ought to show affinities with modern forms rather than the sporophyte stage. Unfortunately few gametophytes are ever obtained, and so this method of discussing affinities is limited. When, however, the prothallus develops within a spore wall, either permanently or until fertilisation takes place, there is a better chance for its preservation, and in *Lepidodendron Veltheimianum* we get an example of such preservation.

In the Burntisland limestone blocks, strobili of a lycopodiaceous nature occur in fair abundance, but so far none have been met with in actual tissue connection with stems. Professor Williamson referred these strobili to the *Lepidodendron* common in the same blocks (viz. *Lepidodendron Veltheimianum*) on the ground of their association (Williamson, 1872). Messrs. Kidston and Binnie, after research on megaspores occurring in the Carboniferous strata, have come to the same conclusion. The probabilities are, then, that these strobili were the fructifications of *Lepidodendron Veltheimianum*, and as this prothallus is in a megaspore identical with those occurring in the heterosporous strobili mentioned above, I have referred it to that species. The strobili bear microsporangia in the apical part and megasporangia towards the base. The megaspores have a thick reddish-brown coat covered by knobbed spines, while three ear-like lobes of the spore wall can be seen at the apex of the spore. In the specimen figured there are two of the processes referred to, and at these two places the wall shows a certain amount of splitting, so that the protuberances are at least partly due to rupturing of the spore coat to expose the archegonia Most of these megaspores (which occur in great abundance throughout the blocks) have no tissue inside them, and, when we consider how delicate prothalloid tissue is, this is not surprising. Sometimes, however, they are filled with scattered or broken-up cells, and occasionally with a continuous cellular tissue. In the last case it is justifiable to consider it as a prothallus.

In the specimen figured the plane of section is almost radial longitudinal. It passes through the area enclosed by the three lobes, and which is presumably the apex of the megaspore, and there we should expect to see archegonia if they were present. While I cannot definitely say this is the case, there is at least a cap of small-celled tissue comparable with the archegonial tissue of *Selaginella*. Probably the specimen was not quite mature, for there is no distinct gap in the spore wall at the ear-like lobes, and this immaturity may explain the absence of archegonia. The rest of the prothalloid tissue is of larger-celled parenchyma, the line of demarcation being quite distinct though not constituting a diaphragm. This small-celled archegonial tissue at the apex of a larger-celled prothallus is essentially similar in *Selaginella*, while the splitting of the spore coat along three directions is also shown in that genus. Hence the occurrence of similar tissue in similar position in the megaspore of *Lepidodendron Veltheimianum* leads to the conclusion that the prothallus in that species was similar to that in *Selaginella*. As other Carboniferous *Lepidodendra* had probably a similar development, we may safely say that the gametophyte generation in some *Lepidodendra* was similar to that of *Selaginella*.

EXPLANATION OF PLATE VII.

Figure of megaspore containing prothallus. ×48. Gordon collection, No. 158. *a*, *a*, ear-like lobes of spore wall; *b*, cluster of knobbed spines all curled up together; *c*, small-celled archegonial tissue; *d*, large-celled prothalloid tissue on the apex of which *c* is situated.



Megaspore of *Lepidodendron Veltheimianum.*

WM. T. GORDON.

arises from the base of this pit. It is tongue-shaped, and consists of uniform small-celled parenchyma. It does not quite fill the pit (figs. 10 and 14, *lg.*).

The top of the ligule pit communicates with the exterior by a short, straight canal, surrounded in places, especially near its base, by the same pallisade tissue which lines the ligule pit. This canal (fig. 10, *lg. c.*) opens far back from the leaf-scar into the space between the leaf-base and the next overlying one. In this way the opening is protected from injury and is not exposed on the outside of the plant. In all the other examples of *Lepidophloios* I have seen this canal opens near the leaf-scar and on the exposed portion of the leaf-base. The canal is oval in section, being broader than high, and the opening at the top is triangular, with the base of the triangle towards the axis of the stem.

As mentioned before, a strand of parichnos underlies the leaf-trace for the greater part of its length in the outer cortex and leaf-base. This strand is of very loosely packed, thin-walled cells; it divides into two in the leaf-base, and, rising to the level of the bundle, these two branches pass out at the leaf-scar, one on each side of the bundle. As the tissue of the parichnos is well preserved, I have been able to follow its course by both longitudinal and transverse sections. In the inner part of the periderm *no parichnos can be distinguished,* nor in any case has it been seen further in than the periderm. Fig. 11 shows the bundle *v.b.*, and on the *upper* side there is parenchyma. This section is cut near a branch, so that the traces can be seen both in the periderm and in the inner part of the outer cortex. Those in the periderm have the parichnos on the opposite side of the trace from that of fig. 11. The parenchyma above this trace belongs to the middle cortex. Passing into the periderm the parenchyma above the bundle gets less, but, a little way in, a distinct elongated portion below the bundle becomes visible (fig. 12, 2 *par.*), and this I take to be the true parichnos. As the exterior is approached this tissue increases in amount, until, just outside the periderm, it occupies the lower two-thirds of the leaf-trace (fig. 12, 1 *par.* and 3 *par.*; fig. 13, *par.*). The parichnos then communicates with the inside of the stem through the parenchymatous bundle sheath and not directly.

On entering the leaf-base the parichnos is still long and narrow, but quickly shortens and broadens into the typical kidney-shaped strand. Fig. 12 shows three leaf-traces; of these, two (Nos. 1 and 3) are near the outside of the periderm and just going to pass into the leaf-base, the third (No. 2) is further into the stem; the increase in the parichnos is well seen in these three traces.

In the leaf-base this strand can be traced quite a long distance before it forks (fig. 14, *par.*); the forking takes place just beyond a plane drawn through the opening of the ligule canal and parallel to the main axis. Sections which show any portion of either ligule or ligule canal invariably also show a single parichnos strand. Such a long stretch of unbranched parichnos is unusual. Fig. 9 shows a leaf-base beyond the region where the single strand is got, so the parichnos is represented by two masses of tissue, one on each side of the leaf-trace (fig. 9, *par.*, *par.*).

This tissue does not seem to have had any communication with the exterior other than on the leaf-scar. The examination of a large number of leaf-bases cut in all directions has failed to show any such connection either directly or by pits, as in the Lepidodendrons; indeed, the parichnos is much the same distance from the exterior at all parts of its course in the leaf-base, until it emerges on the leaf-scar.

Fig. 14 shows a radial section of a leaf-base, with parichnos strand (*par.*), leaf-scar (*l.s.*), ligule pit and ligule (*lg*). The section just misses the ligule canal, which was probably slightly bent to one side in this case, as all other radial sections show the canal as well. The point where the leaf-base ceases to be keeled and becomes round is well shown in this figure, as also in fig. 10, *c.d.*, while in fig. 7 the difference in transverse section is well marked. Fig. 7 is part of a section cut sloping outwards, so that the difference might be seen; in the lower part of the figure the leaf-bases are keeled; in the upper part they are rounded. As the lower part is nearer the stem than the upper, the leaf-bases are keeled near the stem and rounded near the leaf-scar.

The leaf-scar is slightly hollow, due probably to contraction of the tissue after the foliage had rotted away, and the leaf-trace shows as a low papilla in this hollow, about one-third of the height of the scar from the bottom.

The branching in all the cases examined was of unequal dichotomy, but apparently of two types. In most cases the wood ring is not broken, only the outer elements passing off to form the branch; but in fig. 6 the ring is ruptured, and the pith cells are seen growing out through the gap. This last type is also seen in transverse section in specimens in my own and in Dr KIDSTON's collections. The branches, however, are all alike devoid of a pith, and are representative of the "halonial" type of branch.*

In my specimens the branches project very slightly beyond the covering of leaf-bases, where they are broken over, and they seem to have been quincuncially arranged. In one series of longitudinal sections 1 inch long, there are four of these branches, so that they are set somewhat closely together; they are not in vertical rows. In all cases they are sharply broken off outside the leaf-bases, and they taper quickly to this truncation. The leaf-bases do not form rosettes round these tubercles, as is characteristic of *Lepidophloios Scoticus* (KIDSTON).

This new species has points in common with other species. The occurrence, for example, of short tracheides in and round the pith suggests comparison with *Lepidodendron vasculare* (BINNEY, sp.) and *L. Hickii* (WATSON), but the leaf-bases in these species at once differentiate them from *Lepidophloios*. The only species with which more careful comparison is necessary is *Lepidophloios Scoticus* (KIDSTON), and *Lepidodendron Pettycurense* (KIDSTON). The latter was described from the woody axis only, and the complete absence of any pith in that species is sufficient to distinguish it from *Lepidophloios Scottii*. *Lepidophloios Scoticus* is very common through the whole Calciferous Sandstone series in carbonised impressions, and, from the similarity of leaf-base, *L. Scottii* might easily be mistaken for *L. Scoticus*. Comparison is therefore very

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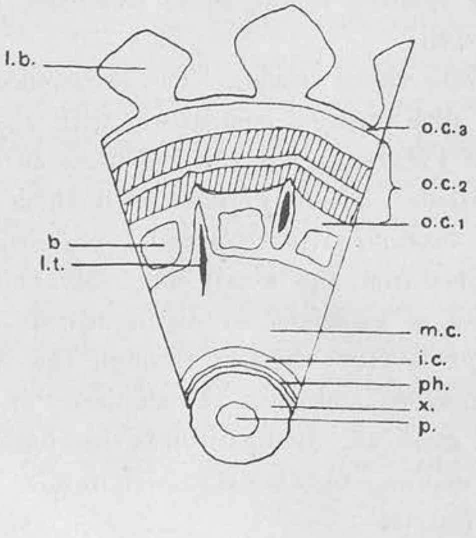
* Mr LOMAX, who prepared the sections of Dr SCOTT's specimen, referred to it as a halonia-like stem.

necessary, and I have based my comparison on the author's description. It was described from impressions, so that the specific characters depend on the leaf-bases. (Only halonial branches can be compared, as my stems are all in that condition.) In *L. Scoticus* there is a bending back of the leaf-bases round the halonial tubercules into a rosette, and the leaf-bases themselves are smooth, rounded, elongated; in *L. Scottii*, no rosettes have been observed at the base of the cone stalks, and the leaf-bases are smooth, keeled, elongated. Towards the scar the keel disappears, and from that point to the scar the leaf-base is rounded, getting flatter and flatter as the scar is approached. On the under surface of the leaf-base the ridge is more prominent than in *L. Scoticus.*

SUMMARY.

Lepidophloios Scottii occurs in the Pettycur limestone in the Calciferous Sandstone series of Fife. The species is named in honour of Dr D. H. SCOTT, F.R.S., and is founded on sections 960 to 976 in the Scott collection and about 180 sections in the Gordon collection. It is a true *Lepidophloios*, having all the characters of that genus. The stem is typical of the *Lepidodendreæ*, is in this case "halonial," and is clothed with leaf-bases. The leaf-trace is collateral, the xylem mesarch, and a parichnos strand occurs beneath the bundle. The cone branches have no pith, are typically halonial, and are quincuncially arranged. The main stem has a pith with short tracheides and sometimes long tracheides scattered in it. The specific characters derived from the leaf-bases, and irrespective of those derived from the structure of the stele, are as follows:—

1. The leaf-base is keeled for three-quarters of its length, and then slopes suddenly down to the leaf-scar with an unkeeled, concave surface.
2. The ligule canal is short, straight, and has its orifice covered by the overlying leaf-bases.
3. There is a pallisade-like layer round the ligule pit.
4. The parichnos only forks a short distance below the leaf-scar.



$o.c._1$; $o.c._2$; $o.c._3$ = three layers of outer cortex ; $o.c._2$ is the secondary tissue (periderm).
m.c. = middle cortex.
i.c. = inner cortex.
ph. = phloem (physiological).
x. = xylem.
p. = pith.
l.t. = leaf-trace.
l.b. = leaf-base.
b. = section of reticulum of cells with dark-brown contents.

BIBLIOGRAPHY.

KIDSTON, R. (1893), "On *Lepidophloios*, and on the British Species of that Genus," *Trans. Roy. Soc. Edin.*, vol. xxxvii. pt. 3.

SCOTT, D. H. (1900), *Studies in Fossil Botany*, London, 1900.

" (1906), "The Present Position of Palæozoic Botany," *Progressus Rei Botanicæ*, 1907.

WATSON, D. M. S. (1907), "On a Confusion of two Species (*Lepidodendron Harcourtii*, Witham, and *L. Hickii*, sp. nov.) under *Lepidodendron Harcourtii*, Witham, in Williamson's XIX. Memoir; with a description of *L. Hickii*, sp. nov."

WILLIAMSON, W. C., "On the Organisation of the Fossil Plants of the Coal Measures," *Phil. Trans.*, part ii. (1872); part iii. (1872); part xix. (1893).

EXPLANATION OF PLATES.

Figs. 1–14. Photomicrographs by A. G. Stenhouse, F.G.S., and the author.

Fig. 2*a*. Camera Lucida drawing by the author.

Fig. 1. Transverse section of *Lepidophloios Scottii*. *x* = xylem; *ph.* = phloem; *m.c.* = middle cortex; *o.c.* = outer cortex; *pd.* = periderm; *br.* = branch. Scott Collection 965. × 5.

Fig. 2. Tranverse section of central xylem cylinder. *p* = pith; *l* = central lamella; *t′* = end of short tracheide. Gordon Collection 176. × 36.

Fig. 2*a*. Enlarged drawing of tracheides to show central lamella (*l*).

Fig. 3. Longitudinal section of stem. *x* = xylem; *m.c.* = middle cortex; *o.c.* = outer cortex; *pd.* = periderm. Gordon Collection 173. × 2.

Fig. 4. Longitudinal section of xylem cylinder. *l.t.* = leaf-trace bundle; *t* = tracheides of xylem (scalariformly thickened); *p* = pith. Gordon Collection 228. × 14.

Fig. 5. Longitudinal section of xylem. *t* = tracheide (scalariformly thickened); *t′* = short tracheide (reticulately thickened). Gordon Collection 223. × 36.

Fig. 6. Longitudinal section through a branch. *x* = xylem of main stele; *x′* = xylem of branch; *p* = pith cells growing out through gap. Gordon Collection 228. × 36.

Fig. 7. Transverse section of leaf-bases, showing keeled and unkeeled region of leaf-bases, but sloping out from the stem. Gordon Collection 216. × 2.

Fig. 8. Transverse section of stem with leaf-bases attached. *a* = stigmarian rootlet; *o.c.* = outer cortex; *pd.* 1 and *pd.* 2 = layers of periderm; *l.b.* = leaf-base. Gordon Collection 152. × 3.

Fig. 9. Transverse section of leaf-base. *v.b.* = vascular bundle; *par.* = parichnos. Gordon Collection 215. × 12.

Fig 10. Longitudinal radial section of leaf-base. *l.s.* = leaf-scar; *c.d.* = concave depression; *lg.c.* = ligular canal; *lg.p.* = ligular pit. Gordon Collection 223. × 12.

Fig. 11. Transverse section of leaf-trace bundle in inner part of outer cortex. *m.c.* = middle cortex coming out with the bundle; *v.b.* = vascular bundle. Gordon Collection 196. × 36.

Fig. 12. Transverse sections of leaf-trace bundles in the periderm. *par.* = parichnos. Gordon Collection 194. × 12.

Fig. 13. Part of fig 12. *x* = xylem; *b.s.* = bundle sheath; *par.* = parichnos. × 48.

Fig. 14. Longitudinal radial section of leaf-base. *l.s.* = leaf-scar; *lg.* = ligule; *par.* = parichnos; *c.d.* = concave depression. Gordon Collection 173. × 12.

Mr Wm. T. Gordon on *Lepidophloios Scottii*.—Plate I.

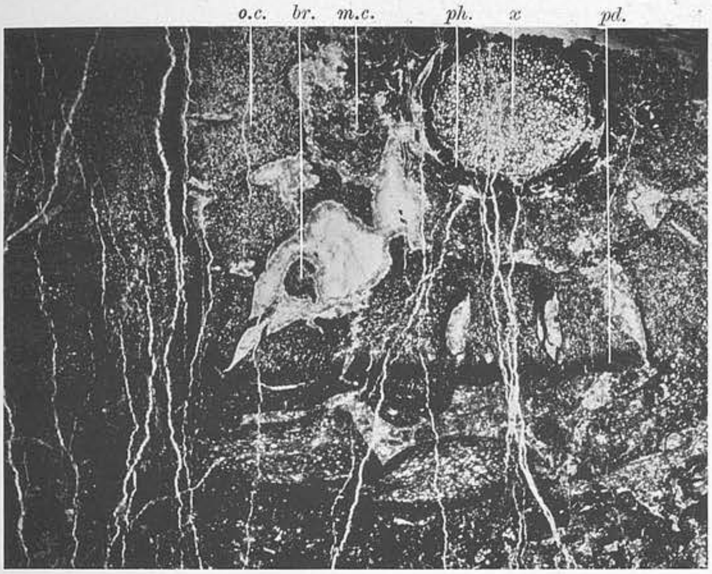


Fig. 1.

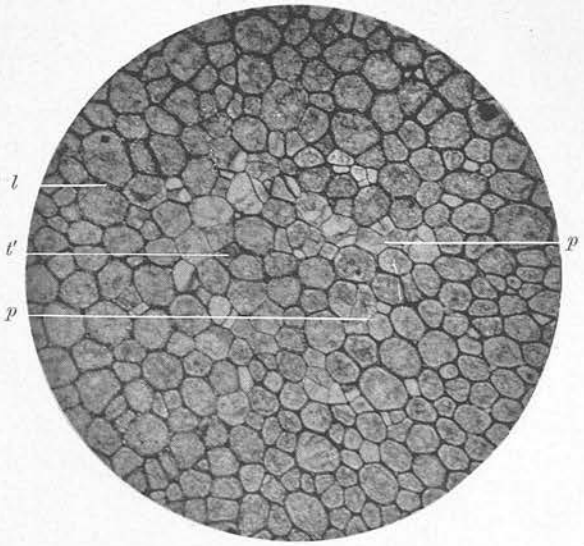


Fig. 2.

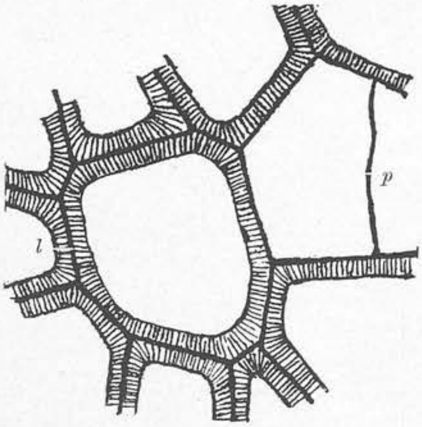
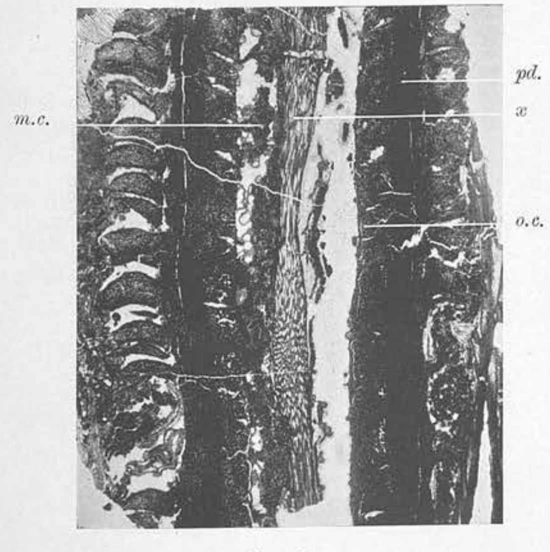


Fig. 2a.



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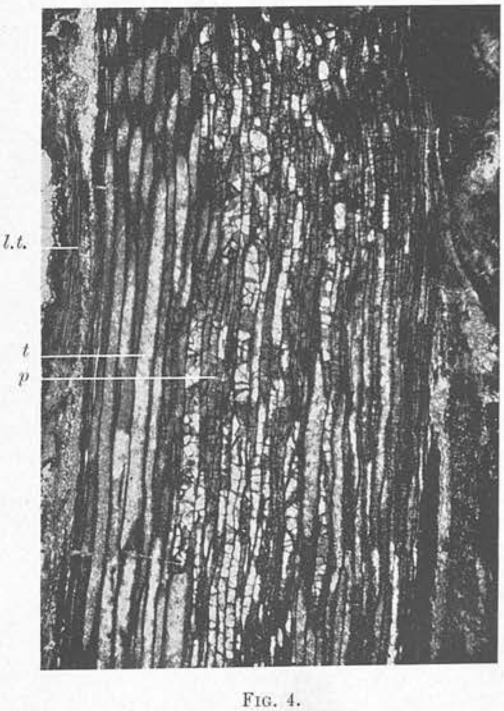


Fig. 4.

MR WM. T. GORDON on *Lepidophloios Scottii*.—PLATE II.

FIG. 5.

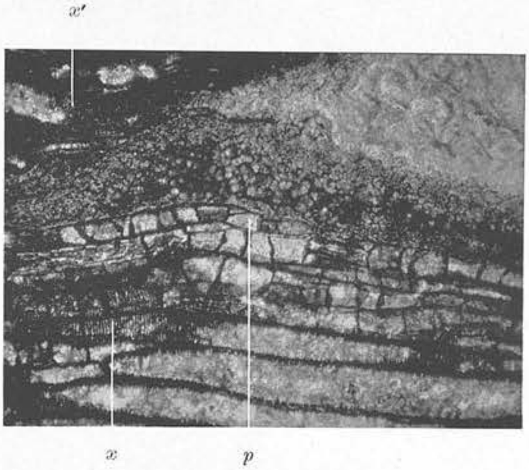
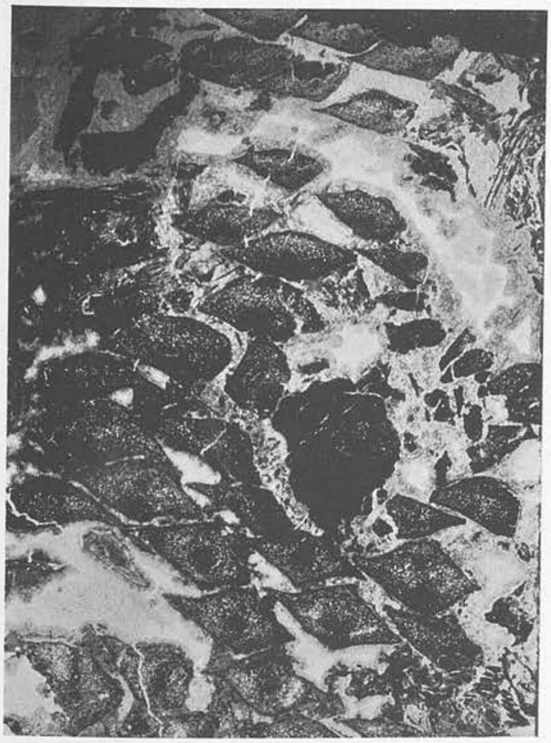


FIG. 6.



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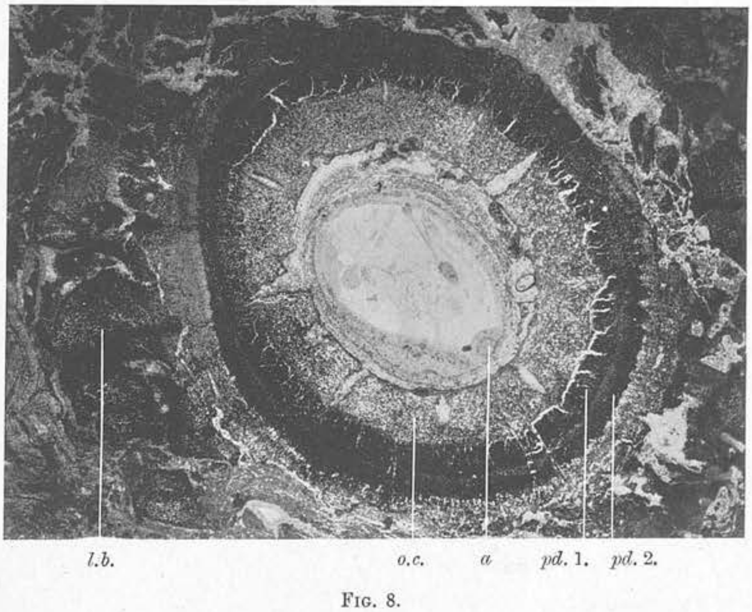


FIG. 8.

MR WM. T. GORDON on *Lepidophloios Scottii*.—PLATE III.

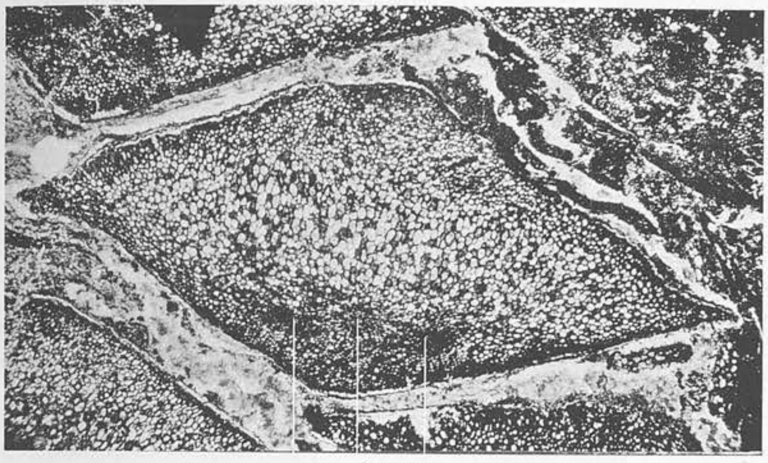


FIG. 9.

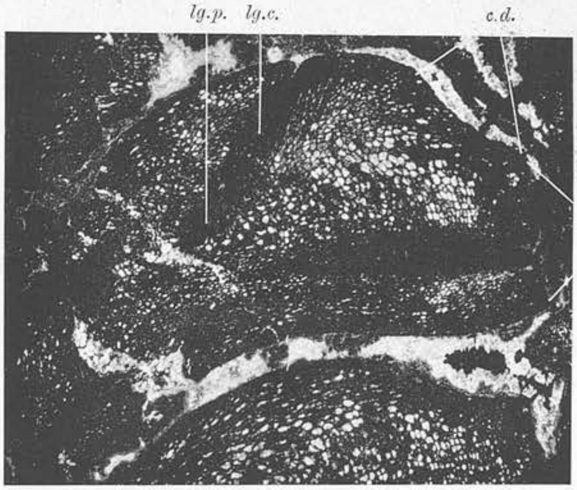
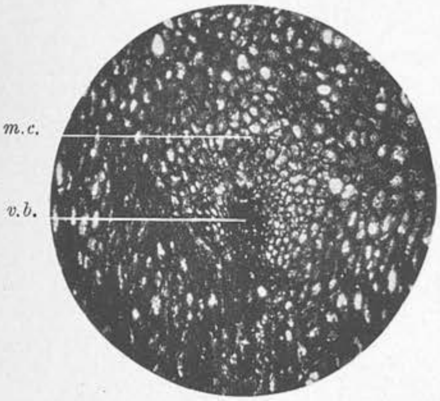


FIG. 10.



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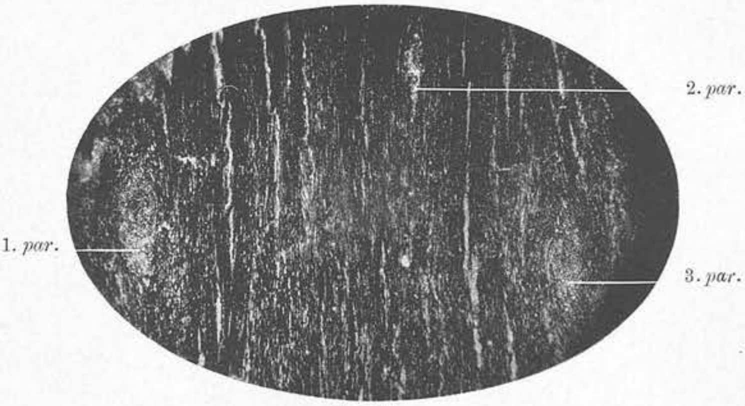

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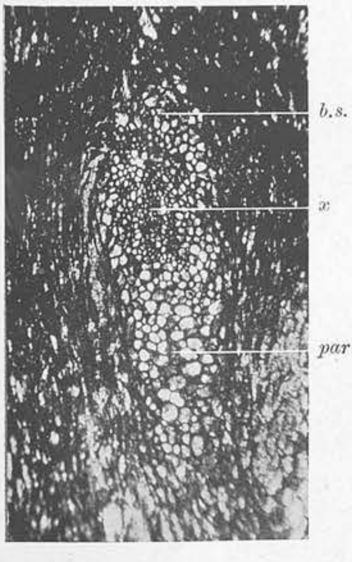

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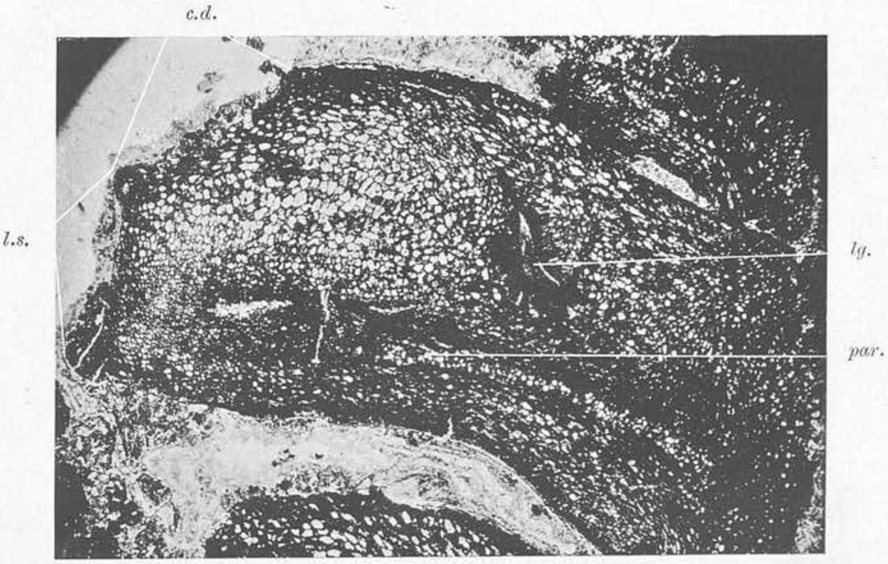

FIG. 14.

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VOLUME XLVI. PART III.

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19. *On Lepidophloios Scottii (a new species from the Calciferous Sandstone series at Pettycur, Fife).* By Wm. T. Gordon, M.A., B.Sc., Carnegie Research Scholar in Geology, Edinburgh University. *Communicated by* Professor Geikie, D.C.L., LL.D., F.R.S., etc. (With Three Plates.) Price: to Public, 1*s.* 9*d.*; to Fellows, 1*s.* 4*d.* (*Issued November* 23, 1908.)

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WM. T. GORDON, M.A., B.Sc.

ON THE PROTHALLUS OF LEPIDODENDRON VELTHEIMIANUM

Trans. Bot. Soc. Edin., xxiii. (1908)

ON THE PROTHALLUS OF LEPIDODENDRON VELTHEIMIANUM.

By WM. T. GORDON, M.A., B.Sc. (*Carnegie Research Scholar in Geology, Edinburgh University*). Communicated by the Secretary. (Plate VII.)

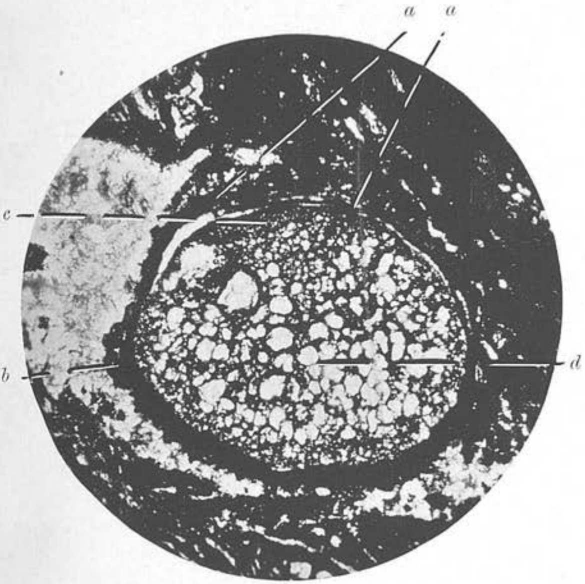
In the Carboniferous Epoch the lycopod alliance formed one of the dominant groups of plants, and contained not merely small forms with a habit similar to the modern representatives of the group, but also large arborescent forms. With such great differences in the vegetative parts we should expect corresponding differences in the reproductive strobili which these plants produced. In *Lepidocarpon*, *Miadesmia* and *Spencerites* we see such specialisation in a marked degree, the seed-like form of the first two showing adaptation to drier conditions than lycopods now grow in. Others show a closer approach to *Selaginella* in the organisation of their strobili, though they are still far removed from that genus. In general the sexual processes are the last to be altered by changing conditions, so the gametophyte stage ought to show affinities with modern forms rather than the sporophyte stage. Unfortunately few gametophytes are ever obtained, and so this method of discussing affinities is limited. When, however, the prothallus develops within a spore wall, either permanently or until fertilisation takes place, there is a better chance for its preservation, and in *Lepidodendron Veltheimianum* we get an example of such preservation.

In the Burntisland limestone blocks, strobili of a lycopodiaceous nature occur in fair abundance, but so far none have been met with in actual tissue connection with stems. Professor Williamson referred these strobili to the *Lepidodendron* common in the same blocks (viz. *Lepidodendron Veltheimianum*) on the ground of their association (Williamson, 1872). Messrs. Kidston and Binnie, after research on megaspores occurring in the Carboniferous strata, have come to the same conclusion. The probabilities are, then, that these strobili were the fructifications of *Lepidodendron Veltheimianum*, and as this prothallus is in a megaspore identical with those occurring in the heterosporous strobili mentioned above, I have referred it to that species. The strobili bear microsporangia in the apical part and megasporangia towards the base. The megaspores have a thick reddish-brown coat covered by knobbed spines, while three ear-like lobes of the spore wall can be seen at the apex of the spore. In the specimen figured there are two of the processes referred to, and at these two places the wall shows a certain amount of splitting, so that the protuberances are at least partly due to rupturing of the spore coat to expose the archegonia Most of these megaspores (which occur in great abundance throughout the blocks) have no tissue inside them, and, when we consider how delicate prothalloid tissue is, this is not surprising. Sometimes, however, they are filled with scattered or broken-up cells, and occasionally with a continuous cellular tissue. In the last case it is justifiable to consider it as a prothallus.

In the specimen figured the plane of section is almost radial longitudinal. It passes through the area enclosed by the three lobes, and which is presumably the apex of the megaspore, and there we should expect to see archegonia if they were present. While I cannot definitely say this is the case, there is at least a cap of small-celled tissue comparable with the archegonial tissue of *Selaginella*. Probably the specimen was not quite mature, for there is no distinct gap in the spore wall at the ear-like lobes, and this immaturity may explain the absence of archegonia. The rest of the prothalloid tissue is of larger-celled parenchyma, the line of demarcation being quite distinct though not constituting a diaphragm. This small-celled archegonial tissue at the apex of a larger-celled prothallus is essentially similar in *Selaginella*, while the splitting of the spore coat along three directions is also shown in that genus. Hence the occurrence of similar tissue in similar position in the megaspore of *Lepidodendron Veltheimianum* leads to the conclusion that the prothallus in that species was similar to that in *Selaginella*. As other Carboniferous *Lepidodendra* had probably a similar development, we may safely say that the gametophyte generation in some *Lepidodendra* was similar to that of *Selaginella*.

EXPLANATION OF PLATE VII.

Figure of megaspore containing prothallus. × 48. Gordon collection, No. 158. *a*, *a*, ear-like lobes of spore wall; *b*, cluster of knobbed spines all curled up together; *c*, small-celled archegonial tissue; *d*, large-celled prothalloid tissue on the apex of which *c* is situated.



Megaspore of *Lepidodendron Veltheimianum.*

Wm. T. Gordon.

GORDON

PROTHALLUS OF LEPIDODENDRON VELTHEIMIANUM

[Annals of Botany, Vol. XXIV, No. XCVI, October, 1910.]

NOTE ON THE PROTHALLUS OF LEPIDODENDRON VELTHEIMIANUM.—As the prothalli of Palaeozoic Lycopodineae are not as a rule well preserved, we know exceedingly little about the gametophyte generation of the members of this group. In the case, however, of the megaspores of *Lepidodendron Veltheimianum*, which occur in abundance in the Pettycur Limestone, the prothallus is never shed from the spore and occasionally its tissue is more or less perfectly preserved. In 1908[1] I drew attention to a specimen of this megaspore which was almost completely preserved, and in the same year Dr. Scott figured another example.[2] The prothallus in my specimen showed a certain amount of differentiation into a cap of small-celled parenchyma at the apex of a larger-celled tissue. This cap was situated below the three ear-like projections of the spore coat which characterize this megaspore. As the spore coat did not show any trace of rupture (although the lines of rupture were indicated) I concluded that the specimen was immature. There were no traces of archegonia present in this example.

The megaspore figured by Dr. Scott also shows traces of this differentiation, the smaller-celled parenchyma occurring where the spore wall is ruptured; but part of the prothallus seems to have been extruded from the spore.

Recently I have obtained a specimen which, though less perfectly preserved than either of the above, throws considerable light on the development of the archegonia. The spore coat in this example also is ruptured (the splitting probably occurring between two adjacent ear-like projections), and below this gap there is a very distinct archegonium. The only cells of the prothallus which are preserved are round the archegonium, and they are similar in size to the cells of the cap in the examples mentioned above. In the accompanying figures, for which I am indebted to Mrs. Scott, this archegonium is exceedingly well shown. Fig. 1 *a* represents the whole spore with the external surface coated by knobbed hairs and the prothallus inside the spore coat. On the surface of this prothallus (which is shown more highly magnified in Fig. 1 *b*) a distinct papilla is seen. This papilla consists of the neck cells of the archegonium (*n. c.*) and immediately below the neck there is a dark mass (*A*) which probably represents the *central cell.* Separating the lower neck cells on the one side from those on the other is a narrow dark mass which in life would be the *neck canal cell* (*n. c. c.*).

As far then as we can judge from this specimen, the development of the archegonium in *Lepidodendron Veltheimianum* was essentially similar to that in *Selaginella*. The archegonium mother-cell appears to have been one of the superficial prothallial cells which has divided into an upper and a lower cell, as in *Selaginella*. By the division of the upper cell into four and the subsequent division of each of these into three, the twelve neck cells have been produced. The whole neck consists of three tiers of four cells and there is no indication that it was ever bent over. On the right-hand side of Fig. 1 *a* there appear to be four neck cells in one row, but this is due no doubt to the wall between the two adjacent cells being oblique. The lower cell then appears to have divided into two, the upper forcing its way between the lower neck cells and

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[1] Trans. Bot. Soc., Edinburgh, vol. xxiii, 1908.

[2] Scott, Studies in Fossil Botany, 2nd ed., Part I, p. 188, Fig. 77, London, 1908.

forming the *neck canal cell* (*n. c. c.*) of the archegonium, while the lower forms the *central cell.* The whole archegonium seems to have been almost ripe, but it had not yet opened.

Fig. 1.a.
(×100)

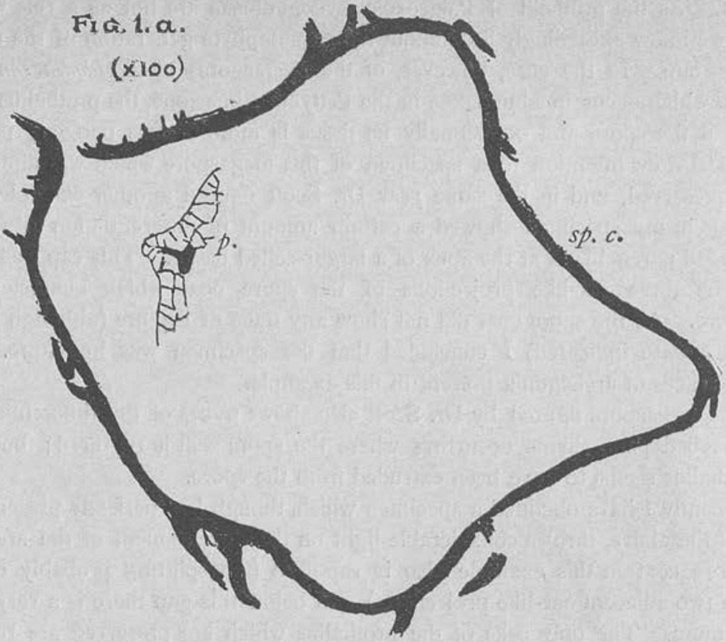

Fig. 1.b.
(×275)

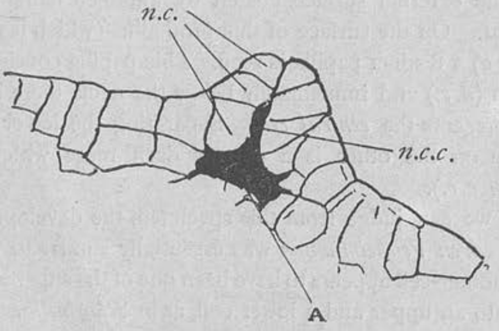

FIG. 1 *a.* Megaspore of *L. Veltheimianum* with prothallus. *sp. c.* = spore coat; *p.* = prothallus. Slide G. C. 1215. × 100.
FIG. 1 *b.* Prothallus of Fig. 1 *a.* *A* = central cell; *n.c.* = neck cells; *n.c.c.* = neck canal cell. ×275.
From drawings by Mrs. D. H. Scott.

The discovery of the archegonium in *Lepidodendron Veltheimianum* still further accentuates the similarity between the gametophyte generation of this plant (and probably of other species) and that of the living *Selaginella.*

W. T. GORDON.

ON THE STRUCTURE AND AFFINITIES OF LEPIDOSTROBUS CYLINDRICUS NOV. SP. FROM PETTYCUR, FIFE.

Introduction.

In the rocks of the Carboniferous Epoch the Lycopodiales are well represented by stems, leaves and reproductive members. These latter parts are generally borne in strobili, though Pinakodendron,[1] the new and undescribed genus of Dr. Kidston's, seems to differ from the other members of the alliance in that its sporangia are not aggregated into strobili.

In certain beds of Carboniferous age the cones are much more common than the vegetative shoots and sometimes the spores are so numerous that they have given rise to a spore coal. The strobili, when preserved as impressions, are very much alike in outward appearance and it is almost impossible to distinguish between the various species. A few such cones have been found attached to their parent stems, but as a rule they are not in continuity with any vegetative shoot.

Great numbers of detached cones occur in the Burdiehouse Limestone at Burdiehouse, Midlothian, though very few stems are found in association with them. The horizon of this limestone is a well marked one, and, in a similar cyprid limestone at Burntisland, Fife, the same cones occur accompanied by numerous stems of <u>Lepidophloios</u> /

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[1] Bower F. O. Origin of a land Flora. p. 305.

Lepidophloios Scoticus Kidston. Many of the specimens at the latter locality are still attached to small twigs. The Burdiehouse limestone lies about the middle of the upper portion of the Scottish Calciferous Sandstone Series (which corresponds to the English Lower Carboniferous Series) and the well-known petrifactions which occur at Pettycur, Fife, belong to a horizon not many feet above this limestone.

From the Pettycur blocks a few species of Lepidodendron stems have been described, but the cones so common in the same limestone blocks have hitherto all been referred to one species = Lepidostrobus Veltheimianus, Kidston M.S., which is regarded as the strobilus borne by Lepidodendron Veltheimianum, Sternb.

Recently in examining specimens from Pettycur, a new and perfectly distinct strobilus was discovered which I propose to distinguish as Lepidostrobus cylindricus sp. nov. This cone may possibly be the fruit of one of the other lepidodendra already recorded from the same locality, but there is no direct evidence as to which of them, if to any, it belonged. The new species is represented by six specimens, the first of which - specimen A - came to my notice some two years ago, but as the axis was poorly preserved it was laid aside in the hope that other examples with better preserved axes might be discovered. Fortunately these further specimens have now been obtained, four from one block and a fifth from a small isolated portion of the limestone. Of the six cones examined, specimen A was completely cut up, and thin

sections /

sections prepared from the slices; while the other five have been examined to prove their identity with the first, and to obtain preparations illustrating features in the anatomy not clearly shewn in the first series. In all about 90 slides have been prepared and examined.

General Structure.

The complete length of specimen A was estimated at between 17 and 18 cm. The apex is present but the base is much crushed, though probably the whole length of the cone is seen. The diameter of the strobilus is between 2.4 and 2.5 cm., and continues practically undiminished throughout its whole length, except just near the apex. This apex is broad and flat thus giving the cone a cylindrical and not a conical shape. (Plate 1, fig. 4)

A second cone was followed for almost 15 cm. without either base or apex being seen; probably, then, specimen A was not an abnormally large cone and may, for all we know to the contrary, have been exceeded in length by other specimens.

A typical transverse section (Plate 1, fig. 1) shews a lepidostroboid axis for the most part uncrushed. The sporophylls are displaced however, and the sporangia empty and much twisted. The longitudinal section in Plate 1, fig. 3 is radial in the upper portion and tangential below; it thus shews both the axis and sporophylls in longitudinal section in the upper part and the sporophylls in oblique transverse section in the lower part. These two /

two sections serve to indicate that the cone is a typical lepidostrobus.

Histology.

The anatomy of the axis is quite typical of a lepidostrobus. The stele has a well-marked pith with small-celled elements which are several times longer than broad. As a rule this tissue is indifferently preserved, but is shewn in transverse section in Plate 2, fig 11 p. and though partially decayed it is distinct in radial section in Plate 2, fig. 9 p. The ring of primary wood surrounding the pith is .25 mm. thick; the diameter of the whole xylem ring being 1.3 to 1.4 mm. This xylem is composed of typical scalariform tracheides, centripetally developed. On the whole these elements are rather small, and are seen in transverse section in Plate 2, fig. 8,x; and in longitudinal in Plate 2, fig. 9. x. Sometimes the xylem cylinder is uncrushed in places but in other parts of the same specimen it may be flattened or even disintegrated. The outer margin of the wood appears to be crenulated, the teeth being short and rounded. (Plate 2, fig. 8)

These protoxylem teeth which form the crenulations of the primary wood have some of their elements spirally thickened (Plate 2, fig. 13) the others being scalariform tracheides. The thin-walled elements external to the wood are not well preserved.

The leaf trace. Surrounding the stele a large number of leaf /

leaf-traces are seen running out to supply the sporophylls. As a rule they are somewhat displaced and their origin is not quite clear, though they appear to arise from the protoxylem teeth round the primary wood. After leaving the xylem of the stele, the leaf-trace passes upwards for a considerable distance at a very acute angle, and thus, as is usual in Lepidostrobus, many traces are seen in any transverse section. The smallest elements of the xylem of this trace lie at or near the centre and thus the bundle is mesarch. The trace is collateral but the thin-walled tissues are not as a rule preserved until the outer cortex is reached and often we go some distance along the sporophyll before any of these tin-walled elements can be seen.

The cortex consists of the usual thick-walled parenchyma; the cells are elongated but the preservation is too poor to warrant any further description.

The sporophyll.

The sporophyll arises at right angles to the axis and the length of the pedicel portion is about 8 mm. The distal or laminar portion rises almost at right angles to this pedicel and attains to nearly the same length, viz., 8 mm. (Plate 1, fig.2 Sph.) A transverse section of the pedicel is triangular in form and is composed of thick-walled parenchyma similar to that of the outer cortex, with which it is continuous. (Plate 1, fig. 1, ped) Further out from the axis the pedicel becomes larger and flatter, while its /

its two upper angles elongate into wing-like projections. At the same time a rhombic pad of tissue is developed in the lower portion of the sporangium. (Plate 2, fig. 12 & 14 ~~r.p~~ pad.) The sporangium is here attached to the upper surface of the pedicel and the tissue of the internal pad is continuous with that of the pedicel. This pad of tissue is of the same nature as that in Miss Benson's *Lepidostrobus mazocarpon* and also in *Lepidostrobus Oldhamium*. Having regard to the development of this tissue we may put the lepidostrobi in the following order - *Lepidostrobus Oldhamius*, *Lepidostrobus cylindricus*, *Lepidostrobus mazocarpon*.

In the angle between the pedicel and the upturned lamina there is a ligule situated in a rather deep pit. (Plate 1, fig. 3, lig., Pl. 2, fig. 15 lig.) The pit is really formed by the sporangium wall on the one side and the upturned lamina in which there is a very distinct groove with rectangular cross-section. (Plate 2, fig. 12, lig.p.; lig.) The ligule measures .5 mm. in length and is composed of thin-walled parenchyma. It is long in proportion to its thickness but is .25 mm. broad.

The lamina is leaf-like and as no downward projection of any size can be seen it is apparently not truly peltate. The length of the lamina is almost as great as that of the pedicel. The parenchymatous tissue of the whole sporophyll is fairly uniform; the tissues surrounding the bundle on the other hand have mostly disappeared but occasionally a well-marked sheath of transfusion tissue of spiro-reticulate tracheides is seen to surround the bundle. /

bundle. The bundle then bends abruptly and passes into the upturned lamina and apparently continues nearly to its apex.

The usual large radially elongated sporangium is seated on the upper surface of the pedicel. In all cases however the cones are much crushed and the sporangia broken and displaced except near the apex of the cone. Tangential sections show that the sporangia are attached at most only for 2/3 of their length, the proximal one-third being free from the sporophyll. In Plate 1, fig. 3 the sporophylls are not attached to the sporangia except where they are cut obliquely. Nor is the sporangium attached by the whole breadth of the sporophyll as is clearly seen in Plate 1, fig. 1, sph.

The pad of sterile tissue within the sporangium increases greatly in size towards the distal end of the sporophyll as also does the sporophyll itself and it is this ridge of tissue with the sporangium wall outside it which forms the proximal wall of the ligule pit. (Plate 2, fig. 12 lg.p.)

The sporangium wall consists of one layer of regular prismatic cells which are however much shorter than is usual in Lepidostrobus, indeed they are in this case almost as broad as they are long. The sporangia are filled with small spores when their contents are preserved, and the spores are often still united in tetrads. Isolated spores show triradiate markings. There is no indication of heterospory in this species.

Comparison /

Comparison with other Lower Carboniferous species.

The first cone with which we naturally compare Lepidostrobus cylindricus is Lepidostrobus Veltheimianus occurring in the same beds. It was described originally by Williamson in 1872,[1] and again later in 1893.[2] A description will also be found in Scott's Studies.[3] The general build of the cone as a whole is similar to that of Lepidostrobus cylindricus but there are several striking differences.

As the axial structure of Lepidostrobus Veltheimianus has not yet been fully described it is necessary to make a digression and give some account of that species before comparing it with Lepidostrobus cylindricus. Williamson says in discussing the former species that "the central axis in this specimen is imperfect, its central vascular bundles having partly disappeared; but there remains a thick and well-defined certical layer composed of elongated forms of parenchyma approaching the prosenchymatous type."[4] In discussing the same species Scott says "In general morphology and structure it is essentially similar to Lepidostrobus Oldhamius, but all the parts are on a smaller scale and the slender stele of the /

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1. Williamson. Phil. Trans. Roy. Soc. Organisation of the fossil plants of the Coal Measures. Part III. 1872.

2. ibid. Part XIX. 1893.

3. Scott. Studies in Fossil Plants, Second edition, London, 1908.

4. Williamson, IV Memoir. p. 294.

the axis has but little pith."[1] A more detailed description is however necessary before proceeding to compare the two species.

Anatomy of the Axis of Lepidostrobus Veltheimianus.

A typical transverse section of the axis shows that the xylem consists of a solid mass of small tracheides with scalariform thickenings. (Plate 2, fig. 10) Other specimens however show that there may be some pith present; while occasionally where an empty cavity is seen it is difficult to say whether there has been a pith or not, for plate 1, fig. 7 shows the section following that figured in plate 1, fig. 5, and it is obvious that the cavity must be due to rupturing of the tracheides of the xylem. Even in the same specimen the presence of a pith is not constant.

Where a central cavity exists the xylem ring is only two rows of tracheides deep and the inner elements appear to be larger than those on the periphery. The outer margin of the wood is crenulated, the teeth being comparatively long and pointed, thus giving a stellate appearance to the whole xylem. In plate 1, fig. 7 there are at least 12 of these points, each composed of a few protoxylem elements, spirally thickened. From these protoxylem groups the leaf traces arise directly, and, while still attached to the protoxylem teeth, these traces tend to still further accentuate the stellate appearance of the wood. The thin-walled elements external to the xylem have in nearly all cases entirely decayed. The /

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[1] Scott. Studies in Fossil Plants. Second edition. p. 183.

The leaf traces pass up nearly vertically for some distance but there are comparatively few in any transverse section. Thus the cone is rather more lax than in other lepidostroboid fructifications. The outer cortex is well preserved and consists of rather thick walled parenchyma which forms a stout zone. (Plate 2, fig.10 o.

We are now in a position to compare the axes of Lepidostrobus Veltheimianus and Lepidostrobus cylindricus. It is quite obvious from a comparison of plate 2, fig. 8 and plate 2, fig. 10 that the detailed structure of the stele of Lepidostrobus cylindricus is entirely distinct from that of Lepidostrobus Veltheimianus. The leaf-traces in the former are larger and more numerous than in the latter, while the cortex seems to consist of thinner walled parenchyma and is more liable to be ruptured and decayed. As regards comparison of the distal ends of their respective sporophylls we have yet no sure evidence for it is still unknown in Lepidostrobus Veltheimianus.

Turning now to the sporangium, if, as Williamson states, the sporangia in Lepidostrobus Veltheimianus are attached by nearly their whole length to the pedicel, then we have a marked contrast to Lepidostrobus cylindricus where they are attached only for 2/3 of their length at most. The pad of tissue in Lepidostrobus Veltheimianus is very much smaller than in Lepidostrobus cylindricus and the cells of the sporangium wall are higher than broad and sometimes more than one layer in thickness. (Plate 3, fig. 2) Finally the cone of Lepidostrobus Veltheimianus is heterosporous.

From /

From what has been said it will be seen that Lepidostrobus Veltheimianus is a much smaller and more lax cone than Lepidostrobus cylindricus. The chief differences are shown in the following resume. The specimen of Lepidostrobus Veltheimianus whose axis is shown in plate 2, fig. 10 has a diameter of 12 mm., and this seems to be similar in size to those figured by Williamson and Scott and which have been previously referred to. Taking this therefore as a typical specimen we can tabulate the distinctions as follows:-

	Lepidostrobus Veltheimianus.	Lepidostrobus cylindricus.
Diameter of xylem	.3 to .4 mm.	1.4 mm.
Diameter of axis	1.3 mm.	3.5 mm.
Diameter of cone	12 mm.	19.5 mm.
Leaf traces	few in any transverse section.	Many leaf traces in one transverse section.
Length of cone	4 cm.(Scott "Studies")	18 cm.

The length of the cone of Lepidostrobus Veltheimianus is not however quite settled for I have specimens shewing only megasporangia which are nearly 4 cm. long and others shewing microsporangia only which are also about that length. In any case there are sufficient differences in the actural measurements, apart from the anatomical differences, to separate these two species. In proportion Lepidostrobus Veltheimianus carries more widely separated and therefore much larger sporangia than does Lepidostrobus cylindricus, for in both cases the sporangia are closely adpressed.

We /

We may next compare the new species with Lepidostrobus Brownii (Schimper) which is preserved in silica, and the age and origin of which was for many years unknown. It is now known almost with certainty to have been derived from the Lower Carboniferous Rocks of the Pyrenees. [1] The axis of Lepidostrobus cylindricus agrees in certain respects with that of Lepidostrobus Brownii as given by Bower.[2] A pith is present in both and if anything the xylem ring in Lepidostrobus cylindricus is thicker but the teeth of the corona are shorter. The leaf traces in Lepidostrobus Brownii are more numerous than in Lepidostrobus cylindricus thus indicating a more compact cone, but they have a similar origin in both species. The sporophylls are rather different in appearance. Those of Lepidostrobus Brownii have much stouter laminae and each has a downwardly projecting lobe. The sporangia also are attached by their whole length.

The shape of Zeiller's specimens recently referred to this species is ellipsoidal and judging by the dimensions as given by him, viz., 10.5 cm. long and 5.3 to 6.0 cm. diameter Lepidostrobus cylindricus must have been a much longer, more slender and more lax cone.

With regard to the mere outward shape and number of sporangia (indicated by great or small number of leaf traces in any transverse section) we can place the three species from the Lower Carboniferous /

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[1] Zeiller. Comptes rendus des seances de l'Academie des Sciences CXLVIII, p. 890, 1909.

[2] Bower. Ann. Bot. Vol. 7, p. 329, pl. 16.

Carboniferous in the following order - Lepidostrobus Veltheimianus, Lepidostrobus cylindricus, Lepidostrobus Brownii. The last named is also much nearer the Upper Carboniferous forms than either of the others. With regard to their stelar development this same order also holds for Lepidostrobus Veltheimianus has occasionally a protostele, Lepidostrobus cylindricus has a medullated monostele ~~solenostele~~ with a fairly thick ring of xylem, while Lepidostrobus Brownii has a medullated stele ~~solenostele~~ with a proportionately thinner ring of xylem.

Comparison with Upper Carboniferous species.

The best known example of an Upper Carboniferous cone is Lepidostrobus Oldhamius and here we get an axis agreeing closely with that of Lepidostrobus cylindricus, especially in the shape of the stele and leaf-traces. But while the diameter of the former cone is greater than that of the latter, the diameter of its stele xylem is in general less. The sporangia in Lepidostrobus Oldhamius are attached for almost the whole of their length to the sporophyll, only being free for a distance of 1.5 mm., according to Maslin.[1] They are attached for about 1 cm. In Lepidostrobus cylindricus the attachment is much shorter than this and at most is about .5 cm., or about 2/3 of the length of the sporophyll. Further, in this Upper Carboniferous species there is a downward projection of the lamina at the end of the sporophyll thus forming a peltate lamina.

Another /

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[1] Maslin. Trans. Linn. Soc. Series 2, Vol. 5, p. 361. 1899.

Another Upper Carboniferous cone with which we may compare the new species is Lepidostrobus foliaceous (Maslin). The axis of this cone does not appear to be known but the sporophylls rise at a steep angle. From the characters of the sporophyll both in shape and direction of insertion on the axis, there can be no confusion between Lepidostrobus cylindricus and Lepidostrobus foliaceous.

The recently described Lepidostrobus Bertrandi, Zalessky,[1] may also be compared with Lepidostrobus cylindricus, and it seems desirable to tabulate the measurements of this species to render the comparison clearer. In the same table are inserted the measurements of some of the more important lepidostrobi whose structure is known.

	L.cylind.	L.Velt.	L. Brownii.	L. Oldham.	L.Bertrandi.
ameter of cone	19.5 mm.	12. mm.	53-60 mm.	26-30 mm.	50 mm.
ameter of axis	3.5 mm.	1.3 mm.	11 mm.	3.5-4 mm.	12. 5 mm.
ameter of xylem	1.4 mm.	.3-.4 mm.	-	.7-1 mm.	2. 5mm.
ngth of cone	170-180	Unknown	105	Unknown	Unknown.
ngth of sporophyll	8	5.4	-	11.14	15.20
ape of cone	cylindrical	-	ellipsoidal	-	-

From a comparison of the figures given above it will be seen that the new species described above is very distinct from any of the others.

Conclusions. /

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[1] Zalessky. Vegetaux fossiles du terrain carbonifere du bassin du Donetz. 1908.

Conclusions.

The type of cone known as Lepidostrobus seems to have been one peculiarly adapted to the conditions obtaining in the Carboniferous. Several species are known but they all approximate so closely to the type that it is almost impossible to get criteria which will separate the various species on purely anatomical grounds. Yet characters sufficient to differentiate certain species are always present. Probably the most important character, as far as is known, is the actual size of these cones. The members of each species agree closely among themselves and are distinct from all other species. The cone whose length has been determined most accurately is *Lepidostrobus Brownii*[1]; and *Lepidostrobus cylindricus* is nearly twice as long but its diameter is only about 1/3 that of *Lepidostrobus Brownii*. The lengths of the other species are still doubtful. The general proportions of *Lepidostrobus cylindricus* are very nearly the same as those of certain impressions which are very common in the rocks of Lower Carboniferous age. It is at present impossible, however, to connect these impressions with petrifactions.

Probably the most interesting feature in this new species is the lengthening of the upper corners of the sporophyll to support and slightly embrace the sporangia. In one case of *Lepidostrobus Oldhamius* (Maslin), Dr. Scott has noticed a similar character and has /

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[1] Zeiller. Comptes rendus des seances de l'Academie des Sciences. T. CXLVIII, p. 890. 1909.

has referred to it as a possible male fructification of *Lepidocarpon*.[1] At Pettycur a Lepidocarpon occurs (*Lepidocarpon Wildianum*) and it is possible that *Lepidostrobus cylindricus* may be the male cone of that species. As far as is known the latter is homosporous whereas the other cones from Pettycur *Lepidostrobus Veltheimianus* and *Lepidostrobus mezocarpon* are heterosporous so that *Lepidostrobus cylindricus* is the only cone of the three species recorded from Pettycur which could possibly be related to *Lepidocarpon Wildianum*. In any case, as had been pointed out, the elongated dorsal corners of the sporophyll, which support and more or less invest the lower portion of the sporangium, exhibit what is may be considered a stage on the way to Lepidocarpon. In the male cone, whose function is quickly over, there is no necessity for the protective outgrowths from the sporophyll, which characterise the genus Lepidocarpon, to completely invest the sporangium, and as Lepidostrobus cylindricus may possibly have been such a male cone.

Summary.

A new and distinct lepidostroboid cone from Pettycur, Fife, is described under the name *Lepidostrobus cylindricus*. The name is given on account of the flat apex of the cone and the regularity of the length of the sporophylls throughout the whole strobilus. This gives a distinct cylindrical appearance to the strobilus. The /

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[1] Scott. Phil. Trans. Roy. Soc. B. Vol. 194, p. 312. 1901.

The anatomy does not differ greatly from that of the other Lepidostrobi but it can easily be distinguished from all the others.

The axis of Lepidostrobus Veltheimianus, from the same locality, is figured for the first time and compared with that of Lepidostrobus cylindricus. The latter species is also compared with the other known Lepidostrobi and its possible relation to Lepidocarpon, as the male cone of Lepidocarpon Wildianum Scott, is noted.

Diagnosis.

The cone is of considerable length - 17 to 18 cm. - and is cylindrical, not conical, in shape. The diameter is nearly 2 cm. and so the cone must have been long and thin. The axis is rather large, 3.5 mm. in diameter, and the xylem of the central cylinder is also large in proportion, viz., 1 to 1.4 mm. The sporophylls are set at right angles to the axis and have a spiral arrangement. The traces which supply these sporophylls rise from the central axis and have a steep course in the cortex of the axis so that in any transverse section 20 to 25 traces are shown. The sporangia are seated on the dorsal surface of the sporophylls from whose surface a pad of tissue projects some distance into the sporangia. The attachment of the sporangium is along the distal 2/3 of the sporophyll. The dorsal corners of the sporophyll tend to invest the sporangium for a short distance. The wall of the sporangium consists /

consists of a single layer of cells which are more or less square in section and not rectangular as is usual in Lepidostrobus. There is no downward projection of the lamina of the sporophyll and the ligule is set in a deep ligular chamber which is formed by a trench-like hollow in the lamina on three sides of the ligule, and the sporangium wall on the fourth side.

There are six specimens recorded.

Locality Calciferous Sandstone Series (=Culm) of Pettycur, Fife.

Explanation of Plates.

Plate 1.

Fig. 1. Transverse section of the axis, cutting the axis nearly transversely but owing to distortion the sporophylls are truncated rather obliquely. x = xylem of axis; l.t. = sporophyll traces; sph. = sporophyll; lg = ligule; A - transverse section of axis of Lepidostrobus Veltheimianus; p = pith; ped = pedicel.

Slide G. 281 (2) x 6

Fig. 2. Longitudinal radial section of the cone. x = xylem; p = pith; sph = sporophyll; lg.p. = ligule pit.

Slide G. 263 x 3

Fig. 3. Oblique tangential section. It cuts the axis at the top but is well out from the axis at the bottom. ax = axis; sph = sporophyll; l = lamina; lg.p. = ligule pit; lg = ligule.

Slide G. 262 x 3

Fig. 4. Radial longitudinal section of cone apex. x = xylem of axis; c = cortex; sph = sporophyll; s = spores.

Slide G. 274 x 6

Fig. 5. Longitudinal section of xylem of Lepidostrobus Veltheimianus to show scalariform thickenings.

Slide G. x 68.

Fig. 6. Transverse section of xylem of Lepidostrobus Veltheimianus. Solid wood.

Fig. 7. Transverse section of xylem of Lepidostrobus Veltheimianus, the cavity in the centre is probably due to rupture of the xylem tissue and not to decay of a true pith. The section follows that figured in Plate 2. fig. 10.

Slide G.

Plate 2.

Fig. 8. Transverse section of xylem of axis (specimen 6). x = xylem; prx = protoxylem; p = pith cavity; l.t. = sporophyll trace.

Slide G. 491 42.

Fig. 9. Longitudinal section of xylem from same specimen. x = xylem with scalariform tracheides; p = pith.

Slide G. 494 x 42.

Fig. 10. Transverse section of axis of Lepidostrobus Veltheimianus. x = xylem (solid); prx = protoxylem teeth; l.t. = sporophyll traces; c = cortex.

Slide G. 555 x 35.

Fig. 11. Transverse section of xylem of cone axis. p = pith; x = xylem; l.t. = sporophyll trace.

Slide G. 451 x 30.

Fig. 12. Transverse section of sporophyll, part of Plate 1, fig. 1. sph = sporophyll; pd = pad of tissue in sporangium; sp.w = sporangium wall; lg.p. = ligule pit; lg = ligule.

Slide G. 281c(2) x 42

Fig. 13. Spiral tracheide from the protoxylem.

Slide G. 88.

Fig. 14. Transverse section of sporophyll showing spiro-reticulate mesophyll cells; pad = pad of tissue inside sporangium; ped. sph. = pedicel of sporophyll; sp.w = sporangium wall; s.r. = spiro reticulate elements.

G. 495. x 42.

Fig. 15. Longitudinal section of distal end of sporophyll v.b. = vascular bundle; lam = lamina; sp.w. = sporang wall; pad = pad of tissue inside sporangium; lig.p = ligule pit; lig = ligule.

G. 262. x 42.

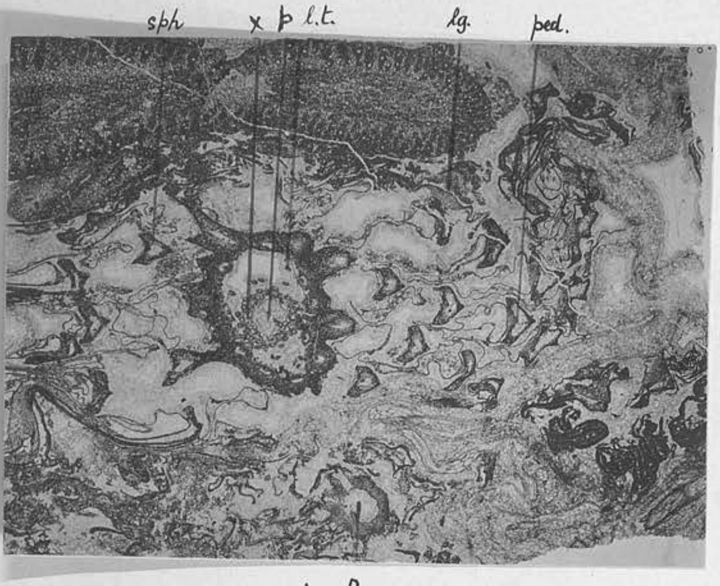
Fig. 16 Camera lucida drawing of cells of sporangium in Lepidostrobus cylindricus. x 350.

Fig. 17 Surface view of cells of sporangium wall of L. cylindricus. x 350

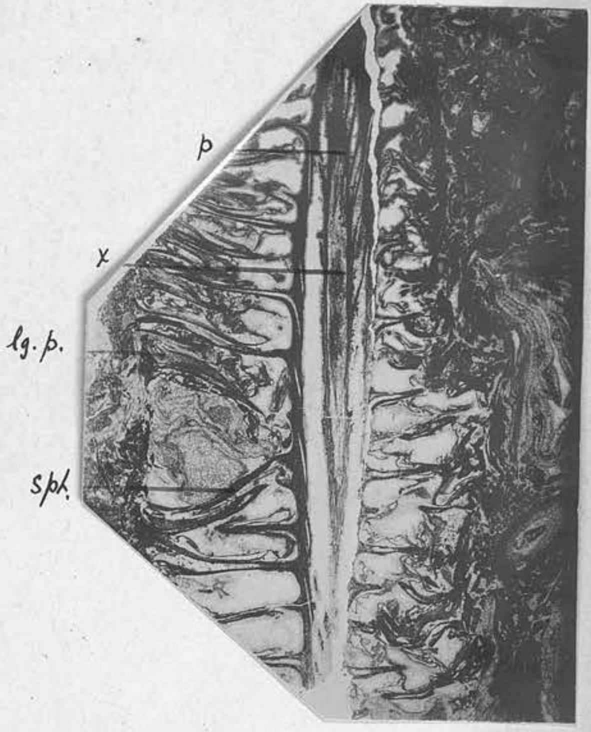
Fig. 18 Camera lucida drawing of cells of sporangium wall in Lepidostrobus Veltheimianus. x 350.

Fig. 19 Surface view of cells of sporangium wall of L. Veltheimianus. x 350

Plate



1. A



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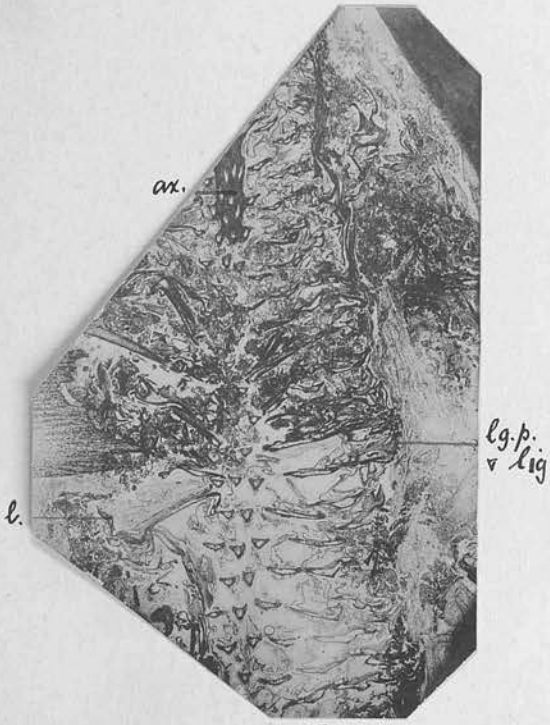

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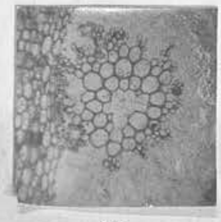
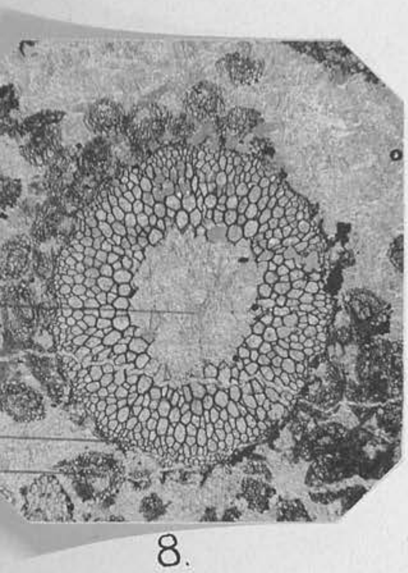


7.

x.
c.
sph.



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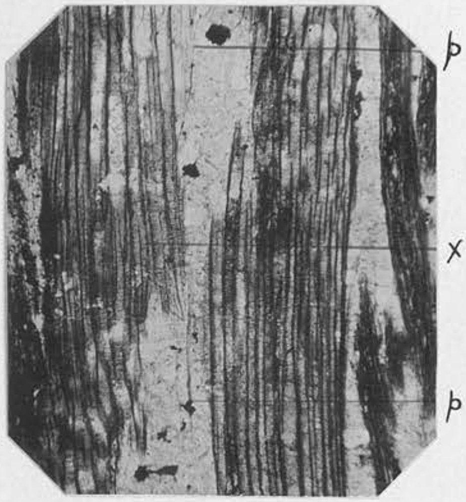

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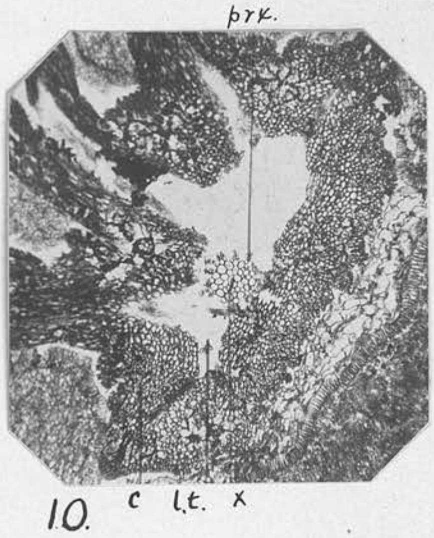

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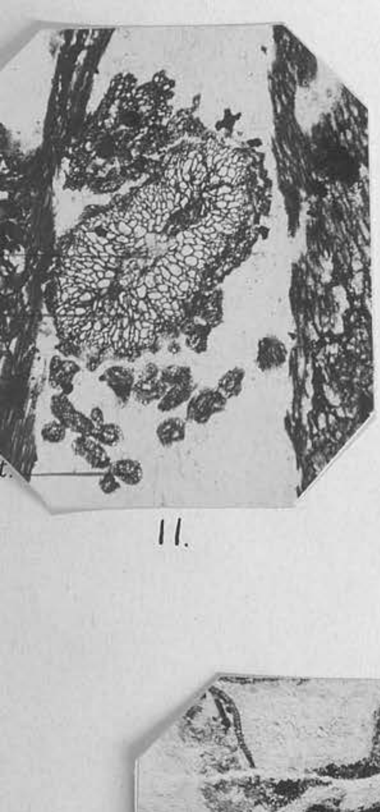

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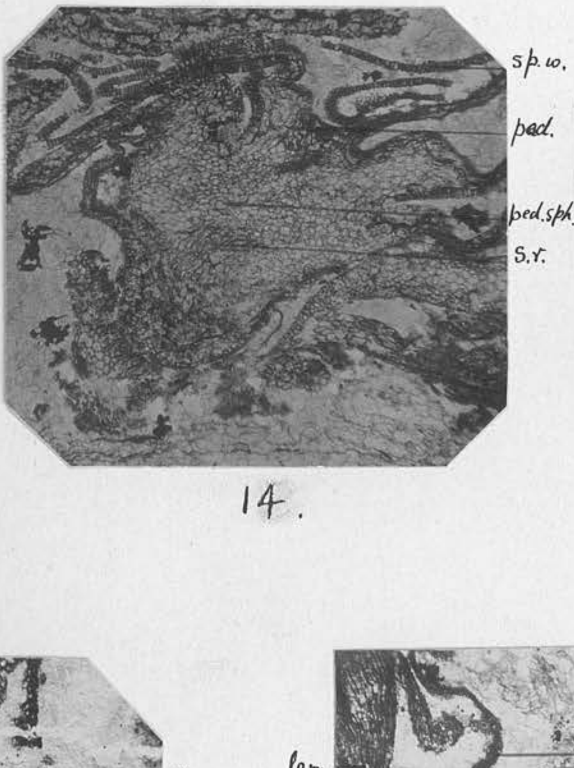

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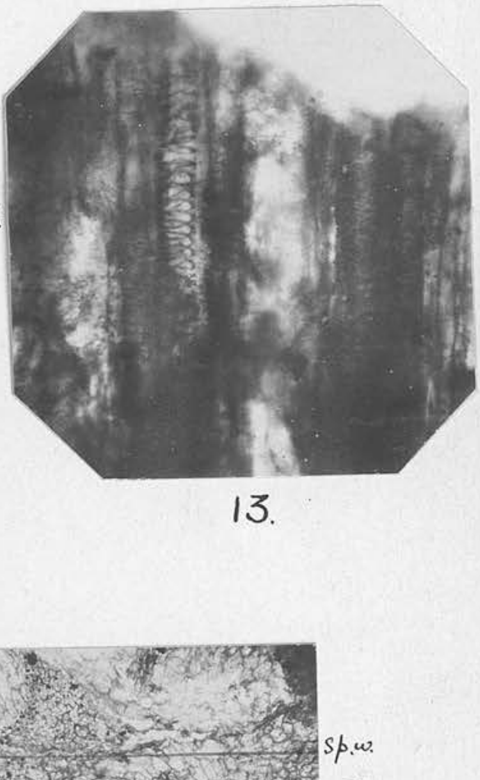

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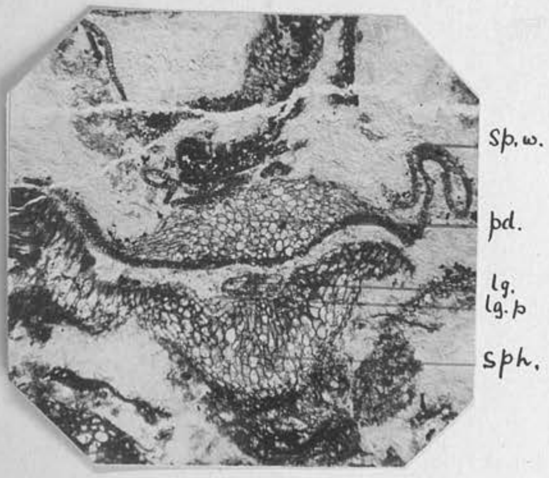

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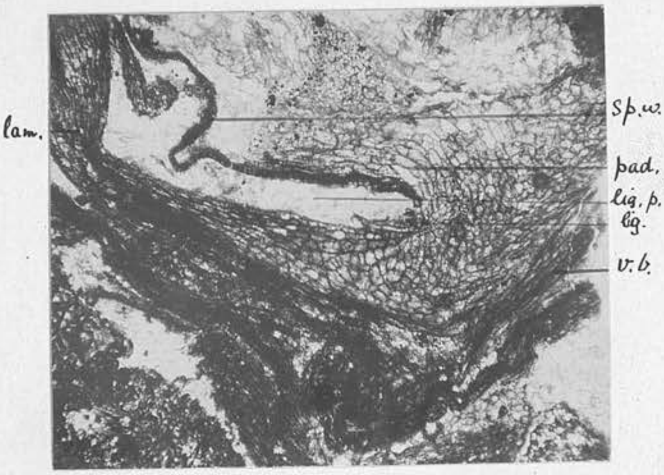

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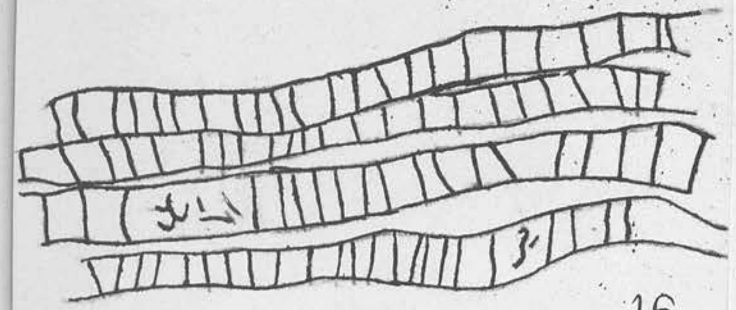
Plate III.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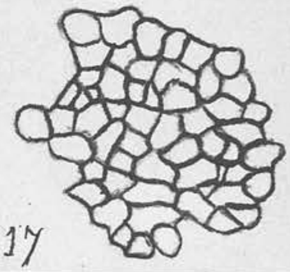
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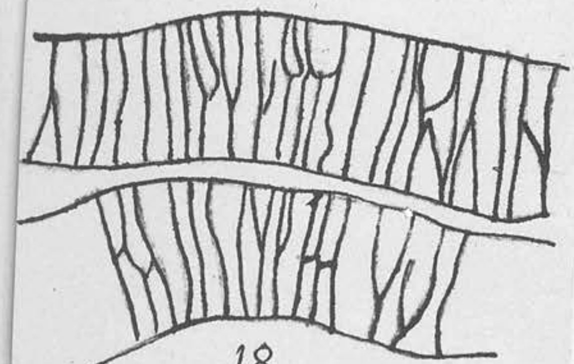
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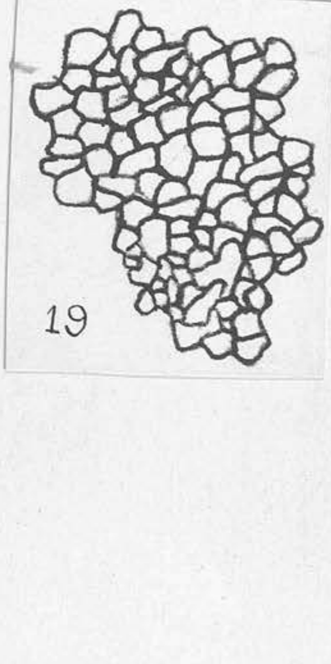
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Lepidostrobus mazocarpon Benson.

This species was created to contain a few detached sporangia which appear to contain sterile tissue inside. The spores occupy a comparatively small area in the sporangia. Both megaspores and microspores occur, so that the cone is heterosporous. Only a few isolated sporangia are known and until further specimens are obtained little more can be said about the species.

Lepidocarpon Wildianum. Scott 1901.

The integumented megasporangia which are fairly common in the Pettycur blocks have been described under this name by Dr. Scott. They were described originally by Williamson as gymnospermous seeds and referred to Cardiocarpon anomalum Carruthers, but the discovery by Wild and Lomax that an allied species from the Coal Measures occurred in strobili similar to Lepidostrobus and the subsequent work of Scott proved that the body was not really a seed but an integumented megasporangium. In the apical portions of the strobilus younger sporophylls showed the gradual development of the integumenting outgrowths from the pedicel of the sporophyll. The axis of the cone, also, was distinctly lycopodiaceous.

The outgrowths from the pedicel enveloped both sides of the sporangium while the distal end was closed in by the laminar portion of the sporophyll. Thus there was a micropylar slit along the top which no doubt functioned in fertilization. The whole sporophyll was shed from the strobilus and probably fertilization took place subsequently on the ground. This genus shows a marked adaption /

adaption to dry conditions and is an instance of an attempt in the lower plants to suit themselves to such conditions.

One specimen of the Pettycur species was found to contain a certain amount of prothallial tissue but this is the only recorded example and there were no traces of archegonia.

Stigmaria ficoides Brongniart. 1822.

The rootlets of this genus are not nearly so common in the Pettycur Limestone as they are in the Coal Balls of the Upper Carboniferous. They are quite common however and are generally much crushed. The large stems also are not rare, and one specimen which I have collected had a xylem cylinder some 5 inches in diameter. A more average size is about 2 inches diameter. The large fistular pith is surrounded by the wedges of wood which appears to be centrifugally developed. There is no marked distinction between primary and secondary wood though the elements nearest the pith are smaller than those further out. There is a gradual increase in size however as we pass outwards so that no hard and fast line can be drawn between the primary and secondary xylem.

Filices

Botryopterideae

Botryopteris antiqua Kidston. 1908.

The plant described by Dr. Kidston under this name is an exceedingly small one and is usually met with by chance. The petioles /

petioles are quite common and probably the small size of the stem accounts for its rarity among the preparations made from the Pettycur material. One comes across a specimen by the merest chance and unless a careful note is kept the chances are that the rest of the specimen may be lost. I have succeeded in obtaining four or five specimens and from one of these a series of 9 sections was prepared. The specimens were beautifully preserved in two cases, and while confirming all Kidston's observations I have been able to fill in one of the lacunae in our knowledge of this species.

Generally only small fragments of the stem are obtained perhaps only $\frac{1}{8}$ inch long and from a consideration of the long series mentioned above I am inclined to believe that the stem was very short and died away rapidly behind. This is confirmed by the great abundance of roots round the stem compared with the rarity of such appendages in other ferm genera from the same blocks.

The xylem of the stem is circular in transverse section, (Pl. A. fig. 1. st.) and consists of rather small elements with scalariform thickenings. Occasionally there are groups of very small elements probably protoxylem embedded in the stem (Pl. A. fig. 3. prx.), but these are the decurrent petiolar protoxylems and are not really cauline. Surrounding the xylem is a zone of decayed tissue but the outer portions of this are sometimes preserved and consist of a rather delicate parenchyma. The inne portion - the phloem - is not preserved however. Many of the cells /

cells of this parenchyma have dark contents and may have been mucilage cells. Pl. A. fig. 2. i.e. Surrounding the whole is the outer cortex with its thick walled cells (Pl. A. figs. 1, 2. & 3. o.c.)

In my specimens the pinna trace departure is exceedingly well shown. At Pl. A. fig. 3 prx. the earliest stage is figured Here there is a sunk protoxylem group and the elements nearer the periphery are seen to be larger than the others. At the lower end of the same figure - prx. - we find a later stage. Here the protoxylem group is distinctly mesarch and the tracheide outside it are very much larger than those of the stem. This petiole trace is still connected with the stem xylem but a slight later stage is shown in Pl. A. fig. 2 where it has become detached. The protoxylem group in this latter figure is still mesarch. Soon, however, the protoxylem group comes to lie on the periphery of its trace in an adaxial position. From the start this group has been excentric and in an adaxial position.

The tracheides of the petiole are much larger than those of the stem and have reticulate thickenings. In one of my specimen which happens to be cut rather obliquely the transition between the reticulate and the scalariform type is shown in the same tracheides. Indeed the explanation is simply that the elements became too small to have reticulate thickenings the scalariform bars giving quite sufficient strength.

One of the mature petioles is seen in Pl. A. fig. 1 pet. The /

The large elements of the trace and its peripheral protoxylem being quite distinct. The root trace is diarch and does not call for further description here.

Zygopterideae

Dineuron ellipticum. Kidston 1908.

The single transverse section on which this species was founded had been over twenty years in Dr. Kidston's Collection. The description was delayed in the hopes that further specimens would be discovered but until 1908 no others were known. Shortly after Kidston's paper was published I succeeded in obtaining several specimens and have now considerably over 50 sections of this interesting plant. Several of these examples I have not been able to work up yet but so far I am able to confirm all Dr. Kidston's observations and to prove that his conclusions with regard to certain points are correct.

My friend Dr. Paul Bertrand has also given considerable attention to an allied species from Autun - D. pteroides, Renault, but with his conclusions I cannot altogether agree. My specimens have elucidated the details of the pinna-trace departure and show that it presents features quite different from what he states though it agrees exactly with the example he has figured.[1]

In size Dr. Kidston's type specimen is about 2.25 mm. diameter and the specimen shown in Pl. B. fig. 5 would probably be about the /

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[1] Etudes sur la froude des Zygopteridies. Lille 1909.

the same if it were uncrushed. The slight crushing, however, does not affect the xylem which is beautifully preserved. The following description is largely based on this - the most perfect example yet discovered. The outer cortex may be divided into two zones an outer sclerotic zone which is only 3 or 4 cells deep (fig. 5 sc. o.c.) and an inner zone of thick-walled parenchyma (o.c.) Inside this cortex there was no doubt in life a delicate parenchymatous inner cortex terminated on the inner side by an endodermis and its associated layers. Of phloem there is no trace but the xylem is beautifully preserved, and it consists of large elements with reticulately thickened walls and small elements with scalariform thickenings. The scalariform tracheides form the protoxylem groups and occur at the ends of the trace in a groove. (Fig. 5 prx.)

Figure 1 Plate B. represents a section from another specimen which shows the insertion of the pinnae on the petiole. These enter the petiole in pairs as in many of the other Zygopterideae. The traces of this particular pair are not well seen in the photograph but are present at pin. tr., and pin. tr.$_2$. In the section below this (fig. 2) the traces are distinctly seen and at a still lower level (fig. 3) the two traces have united to form one. Renault figures a stage similar to this last photograph in his paper on <u>D. pteroides</u>.

In no specimen examined have I seen any aphlebia-traces so that the whole pinna-trace bar of figure 3 is derived from two pinna /

pinna-traces. The bar unites with the end of the petiole-trace much lower down the petiole, indeed the pinna-traces pass out quite suddenly into the pinnae and not nearly so gradually as in the next two genera to be described - *Metaclepsydropsis duplex* (Williamson) and *Diplolabis römeri* (Solms).

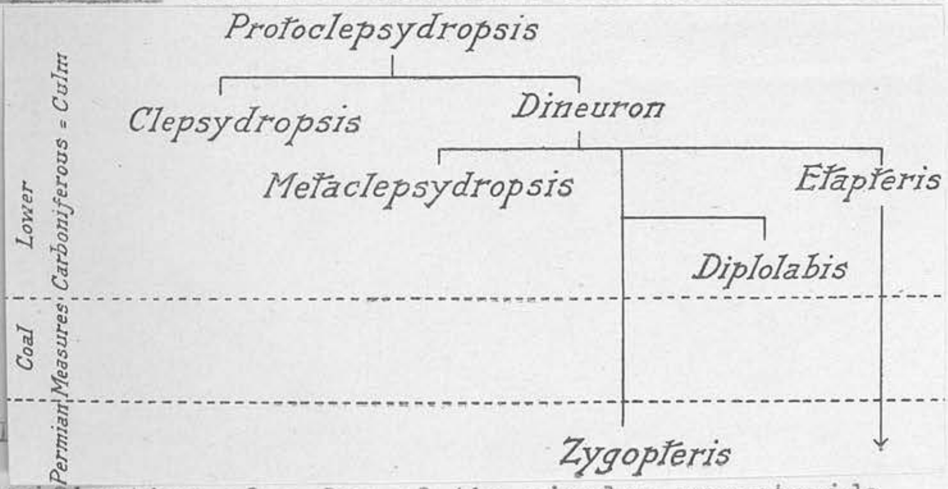
With the junction of the pinna-trace-bar and the petiole-trace an island of parenchyma is cut off from the tissues outside the trace and round this island the protoxylem groups are distributed. Two of these groups belong to the pinna traces higher up and have not yet disappeared on the face of the petiole trace. They are situated in a groove- now very shallow - at prx.', prx.' in figure 4. Other protoxylem elements belonging to the pinna-trace bar just entering are at prx.", prx." Passing downwards the groove on the petiole trace probably disappears and those of the now reduced pinna-trace bar take their place. Finally the island opens again to the exterior and the groove with its two protoxylems is re-established on the end of the petiole trace. (Fig. 4 right hand end of trace.)

So far I have not succeeded in obtaining the stem of this species but in the new material which has just come to light such a stem may occur.

These new observations show that *Dineuron* is really much more closely allied to *Metaclepsydropsis* than has been generally assumed There is absolutely no evidence for the existence of Bertrand's "renflements recepteurs"; nor are the pinna-traces smaller in proportion /

proportion to the size of the petiole trace than in the corresponding traces of Metaclepsydropsis. To put the matter shortly the petiole trace is elliptical in shape and cannot be divided into "apolaire mediane" and "renflements recepteurs". The trace indeed is much simpler than Dr. Bertrand had made out. In this connection it will be interesting to compare Pl. B. fig. 4 with Pl. 2 figs. 23 and 24 of the next paper on M. duplex.

In the light of the discoveries of the early stages in petiolar departure from the stems of Metaclepsydropsis duplex and Diplolabis romeri as recorded later in this thesis, the trace of Dineuron is exceedingly interesting. At certain stages of the petiole trace in each of these genera the petiole would, without hesitation, be referred to Dineuron. On the other hand there is no doubt that Dineuron is a distinct species, but one must admit that it is much more closely allied to Metaclepsydrops and Diplolabis than Dr. Bertrand's classification indicates.



Text figur
Relation of D
to certain other
of the Zygopteri

I published a classification of a few of the simpler zygopterids. This is inserted above (Text figure) and as will be seen later my work on Metaclepsydropsis)

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1. See later in this thesis.

Metaclepsydropsis entirely confirms the view expressed in this table. At the same time the facts now known about Dineuron (though the early stages of petiolar departure are not known) also confirm this classification.

On the Structure and Affinities of Metaclepsy dropsis duplex, (Williamson) by W. T. Gordon, M.A., B.Sc., B.A., Falconer Fellow of Edinburgh University, Lecturer in Palaeontology, Edinburgh University. Communicated by Professor James Geikie, D.C.L., LL.D

Introduction.

While collecting specimens of Diplolabis romeri (Solms) at Pettycur some three years ago, I discovered several blocks of stone containing numerous petrified fragments of another zygopter fern - Metaclepsy dropsis duplex (Williamson. Two of the blocks were found to be parts of one large mass and the petrifactions could be traced from the one block into the other. In size the complete mass must have been about 3 ft. x 2 ft. x 2 ft. The larger portion had to be broken into two before it was possible to remove it. Another block containing similar specimens was obtained later, but the preservation was so poor that the whole of the material was discarded.

The Pettycur plants are usually preserved by an infiltratio of calcareous material, chiefly carbonate of lime, but in these blocks the petrifying material was siliceeous. This silica was present in two forms - chalcedony and crystalline quartz. As a result, hollow stems had the appearance of agates, generally with a crystalline centre. The surfaces had been more or less weathered and the specimens stood out on the surface, their tissu being /

being perfectly visible, and giving an appearance like lace to the surface of the blocks.

As the occurrence of Diplolabis romeri was a new record from a British source, and as the specimens could be more easily examined, (since thin sections are more readily prepared from calcareous than from siliceous material) I decided to finish my work on that genus before proceeding with a systematic investigation of the silicified specimens of Metaclepsydropsis duplex.

On looking over the specimens, however, about a year after they had been collected, I noticed, among the petioles, a fragment of what appeared to be a fern stem. Two sections were prepared from it and the length was ascertained by cutting that par of the block into pieces ½ to ¾" thick. The same stem was followed into another part of the block and its extent in that direction also determined. The total length of this stem fragment was about 8 inches; it was hollow in the centre and throug out its length no petioles or roots were emitted.

When the block was cut up it was found to be so dark that no structure could be observed; in the hope that exposure to th atmosphere would soon weather the surfaces and so render the specimens visible, another part of the block was sawn into piece 3" thick and the slabs placed outside for about 9 months. Silic however, takes a very long time to weather and even after all these months there was no appreciable difference. On experimen ing with hydrofluoric acid I discovered that in a few minutes th surfaces /

surfaces could be etched, and after this treatment the petrifactions were even more clearly seen than when they had been naturally weathered. The alteration also was a mere surface one, and the specimens were not destroyed. So clearly did the specimens appear that the surface could be examined with a fairly high power - a $\frac{1}{4}$" objective - and even the thickenings on the walls of the tracheides could be made out by reflected light. It was thus possible to examine roughly the contents of a piece of material without making any thin sections. In this way much time was saved and suitable examples of stems, petioles and roots detected at once.

As mentioned above the Pettycur plants are usually preserved in calcareous material and the thickenings on the cell walls are generally distinct. I have never, however, seen such perfect preservation as is exhibited in these silicified specimens. Locally in the blocks the petrifying substance has been replaced by iron pyrites, and the tissue can only be seen by reflected light, when it appears like black tracery in the yellow matrix. On the whole the preservation is magnificent. As previously remarked, however, the whole matrix is very dark and so the preparations require to be very thin before they become transparent. With care the sections can easily be reduced to about .025 mm., the homogeneity of the material and its lack of cleavage rendering this easier than in the case where calcite is the petrifying medium. The test used to determine whether the sections were thin enough /

enough, was that employed in the preparation of rock sections, viz. silica (quartz) grey between crossed nicols.

In a previous paper [1] it has been noted that the silica is present in two states, (a) chalcedony, and (b) quartz. The chalcedony appears to have been laid down first and forms a layer round the wall of each element of the tissue. With this layer increasing in thickness the lumen is reduced in size. After the cell lumen is reduced to about one quarter of its original size the whole is filled in by crystalline quartz. All the silica, whether chalcedony or quartz, is almost perfectly transparent, and the strong contrast between the glassy interior of the cell and its dark walls has rendered the preparation of photomicrographs much easier and more effective than in cases where calcite forms the matrix. In this latter case the cleavages interfere with the delicate cell structure and sometimes render it almost impossible to photograph.

In July of last year a more systematic study of the specimens, contained in the fragments of the large block, was begun. Several additional examples of the stem were obtained and their occurrence among so many petioles might have been cited as a proof that stems and petioles belonged to one and the same plant. Such evidence, however, is of very little value and cannot be relied upon, This is especially the case when other genera occur in the same block. As a general rule the Pettycur blocks contain a great number of different genera; indeed practically the whole flora

may /

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[1] Gordon. Trans. Geol. Soc. Edinburgh. Vol ix. pt iv 1909.

may be represented by the specimens in one block. In the siliceous masses on the other hand, there are singularly few genera and at first sight this lends weight to the evidence of association. There is, however, another member of the *Zygopterideae* present - *Stauropteris-burntislandica* P. Bertrand, and therefore the evidence of mere association must be discarded. The other genera present in the block were *Botryopteris antiqua*, Kidston; *Lepidophloios Scottii*, Gordon; *Lepidostrobus cylindricus*, Gordon in M.S.; *Lepidocarpon Wildianum*, Scott; *Bensonites fusiformis* R. Scott, and *Stegmaria ficoides*, Brongn.

The fragments of the petioles of *Metaclepsydropsis duplex* were exceedingly numerous but of no great length. Some were about 8 inches long but many did not exceed 3 inches while some were under 1 inch in length. Most of these petioles were crushed but often there were short lengths which showed no crushing. There were so many specimens that, by choosing the uncrushed portions only, a complete picture of the anatomy of the genus could be obtained. One remarkable feature about the specimens is that very few would be classed as normal petioles of *M. duplex* and yet they would never be referred to any other genus as will be seen later.

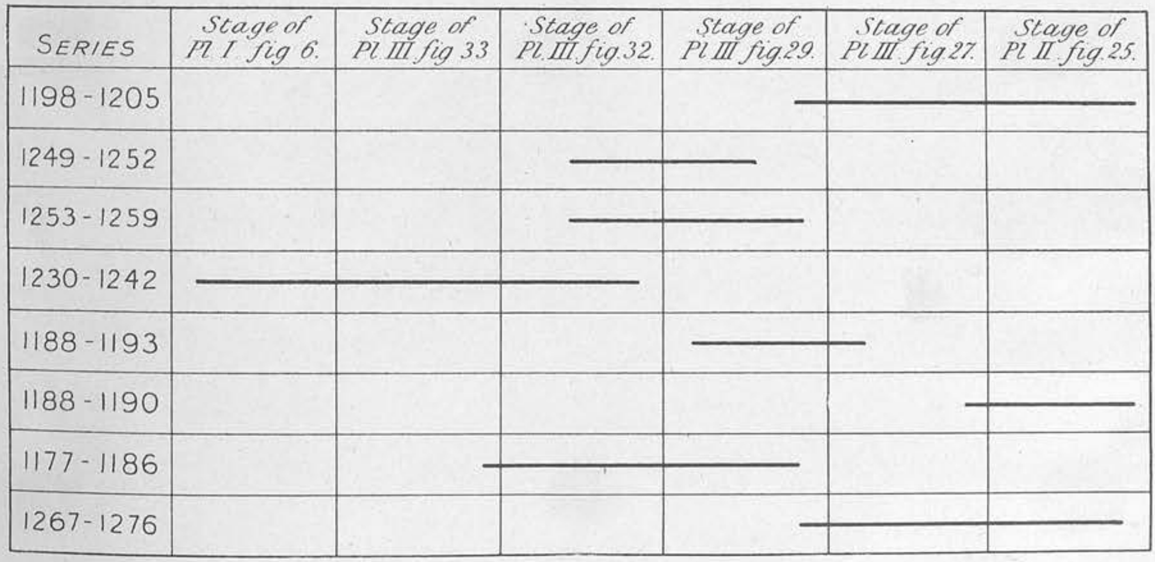
By October 1910 sufficient positive evidence had been obtained to refer the stems found in the block to *M. duplex*. The excellent specimens figured here were not discovered, however, until January 1911. Since then the early stages of petiolar development /

development have been ascertained. The preparations examined number about 200 . I have made most of these myself in order that nothing important might be lost during the process of preparation. As a rule the slides number 12 to 14 per inch of material and they are generally in fairly long series. The series showing the branching of the stem and the departure of the petiole-trace was cut from a piece of stem 3" long. From this piece 39 sections (including two longitudinal sections each ¼" long) were prepared; the sections thus run about 16 to the inch.

Apart from the silicified specimens I have made several series of sections from calcified examples which happened to illustrate points not shown in the case of the siliceous petrifactions. For the sake of completeness, also, I propose to redescribe the species, particularly as previous accounts have been based on a few isolated sections from several distinct individual specimens. All previous work on this genus has been based on petioles whose xylem strand had an hour-glass shape; I hope to show, however, that this type of trace has been developed from a simpler type.

The species was first recorded by Williamson in 1873. His specimens had the hour-glass shaped xylem strand so characteristic of the mature petiole. From 1873 until P. Bertrand's description in 1909 no further work was done on this genus although it was constantly referred to. Kidston and Gwynne Vaughan in Pt. IV. of their memoir On the fossil Osmundaceae refer to Metaclepsydropsis but /

but have discussed its affinities rather than its anatomy. Apart from Kidston no observer seems to have had more than a few isolated sections to deal with. Some years ago, however, Dr. Kidston had a particularly fine series prepared and these he has kindly placed at my disposal. In addition to showing the anatomy so far as it is known, they exhibit the remains of apheblia and the passage of the aphlebia-traces out to these organs. The unique opportunity I have had of studying hundreds of petioles of all sizes has resulted in the elucidation of the petiolar development. The material on which I have been working is practically a felted mass of petrified stems, roots, petioles, pinnae and pinnules of the species. All of them are fragmentary, but, by cutting overlapping series of sections from various individuals, a more or less continuous chain of development has been established. The extent of the overlapping is shown in the following table.



SERIES	Stage of Pl I fig 6.	Stage of Pl III fig 33	Stage of Pl. III fig. 32.	Stage of Pl III fig. 29.	Stage of Pl III fig 27.	Stage of Pl II fig. 25.
1198-1205				—	—	—
1249-1252			—	—		
1253-1259			—	—		
1230-1242	—	—	—			
1188-1193				—	—	
1188-1190					—	—
1177-1186		—	—	—		
1267-1276				—	—	—

General Structure.

In order to obtain a general idea of the organisation of this fern - Metaclepsydropsis duplex, it will be most convenient to follow its tissues from above downwards. By proceeding in this way we shall find that we pass from what is already known to what is unknown. In the first place we shall concentrate our attention on the xylem tissue partly because it is better preserved and more continuous than any other, but chiefly because it changes very considerably as we descend.

In the smallest divisions of the pinnae which we are acquainted with - those of the 3rd order probably - the trace is curved in form with tapering, incurved ends. In the sinus, formed between the hooked ends and the body of the trace, the protoxylem elements may be found. These bundles then are C shaped or horseshoe shaped and they are emitted, alternately on each side, from the ends of a similarly shaped pinna-trace of lower order. At the point of emission the combined trace has four protoxylem groups. Lower down the two inner groups die out and the resulting trace is again C shaped with hooked ends and two protoxylem groups in the sinuses formed by these hooks.

The smallest traces known are distinctly curved with parenchyma in the concavities. In one or two examples, however, the pinna trace of the second order is not open although it gives off open traces of the third order. In this case the emission of the small strand is distinctly of the "extra marginal" type as defined by /

by Davie, and strongly resembles the departure of the secondary pinna-trace from the primary one in the genus <u>Clepsydropsis</u>. Pl. 4 fig. 42 is a good example of this extra-marginal emission.

The occurrence of a "closed" bundle has also been noted in several primary pinnae. This probably only takes place fairly high up the pinna because, as such primary pinnae are followed downwards into the petiole, each pinna-trace becomes like a much flattened C with hooked ends. No pinna-trace has been observed which was "closed" while still passing through the cortex of the petiole (Pl. 4 fig. 41). Apart from these few exceptional examples the pinna-traces of one order join those of a lower order alternately on opposite sides as described above.

When we come to the primary pinnae, however, a change takes place. They do not enter the petiole separately but in pairs and these pinna-pairs enter alternately on each side of the petiole. Two primary pinna-traces, then, enter the cortex of the petiole at the same level and pass downwards to join the petiole-trace. They are placed symmetrically one on each side of the principal plane of the petiole and are thus "mirror images" in this plane of symmetry. A short distance below the point where the two primary pinna-traces enter the cortex of the petiole two pairs of very small traces may be seen to pass into the petiole. These are the aphlebia-traces. These are also "mirror images" /

images" of one another in the principal plane of the petiole. They are situated outside the pinna-traces. A transverse section through a petiole at this level shows 7 traces, the petiole trace, two primary pinna traces and two pairs of aphlebia traces. (Text fig 2 no 3.4 & 5).

Lower down in the petiole the four aphlebia-traces unite to form two, or, if we momentarily change our point of view and follow the aphlebia-traces upwards, the single strands each bifurcate. In Pl. 3 fig. 36 & 38 a section at a still lower level is shown. The aphlebia-traces have almost joined on to the outer ends of the pinna-traces. In Pl. 3 fig. 35 the junction is complete but the 4 protoxylem groups on each combined trace indicate that there has been a fusion of two distinct strands. The two inner protoxylem groups die out downwards and at the level of Pl. 3 fig. 34 each combined-trace has two protoxylem groups, one at each end.

Proceeding still lower, the two combined-traces unite to form the pinna-trace- bar on which there are 4 protoxylem groups. A short distance below this the bar joins on to the hour-glass shaped xylem of the petiole. In Pl. 2 figs. 19 & 18 the bar is shown immediately before and immediately after its union with the petiole strand. (These figures are not, however, from the same specimen). An island of parenchyma thus appears at the end of the petiole-trace (Pl. 2 figs. 18 & 21 is.ø.) and round the periphery of the island there are 6 protoxylem groups. Four of these belong /

belong to the pinna-trace-bar and two to the petiole-trace. These latter lie on the sides of a small bay situated at the end of the hour-glass shaped petiole strand. Still continuing downwards the island becomes gradually smaller and the protoxylem groups of the pinna-trace-bar unite in pairs to form two groups (Pl. 2 fig. 20 prx.) The small bay with its two protoxylem groups also gradually disappears and the island becomes elliptical with a protoxylem group at each apex. Pl. 2 fig. 21 prx.

As we descend still further, the island gradually becomes circular; then it opens to the exterior again and an open bay with two protoxylem groups results. (Pl. 2. figs. 17, 18, 19, 22, 23 and 24. g.) This bay is vertically below the one which was mentioned above and so the mistake has arisen that there was a permanent groove running down the petiole trace on each side. As has been shown above the groove ultimately dies out and is re-formed lower down; indeed it is the last vestige of the wedge of parenchymatous tissue shut in between the entering pinna-trace-bar and the petiole-trace. The disappearance of the groove and a diagrammatic representation of the reduction of the island is represented in Text Figure 3.

So far we have seen that two primary pinna-traces and their "spreads" of pinnae of a higher order have joined the petiole-trace and gradually disappeared into it. A similar sequence is shown at the opposite end of the petiole-trace but the two ends are never in the same phase of pinna-trace emission. Thus four /

four orthostichies of pinna "spreads" are borne by each petiole. Up to this point every stage has been ascertained by reference to numerous series.

In following out the changes in the petiole-trace considerable more difficulty has been met with and the stages figured are not from long series. This was due to the fact that the material consisted of short lengths of petioles; no specimen exceeding 6 inches. In that distance the changes were very slight, so that long, - very long - series would probably be necessary to show the gradual change from one of the stages figured to the next. In spite of this discontinuity the position I take up will be readily accepted for there is sufficient evidence to prove the general problem namely, that there is a gradual disappearance of the "waist" [1] or constriction in the middle of the hour-glass shaped petiole-trace and that this reduction takes place as we descend in the petiole. The second part of the problem is much more difficult to prove than the first but, synchronous with the disappearance of the "waist" of the petiole trace, there is a marked reduction in the size of the whole trace and in the pinna-traces which join it. We know that the petiole trace in other ferns gradually becomes smaller as we descend towards the stem, and that there are reduced pinna-traces towards the base of the petiole. This is exactly what one would naturally expect. It is not surprising then to find a similar state of affairs in Metaclepsydropsis. But apart from the xylem tissue, we find that the outer

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[1] I shall use the word "waist" as it gives the idea of a constriction in the middle of the trace.

cortex loses its sclerotic outer layer as we follow this series. Now, from a study of the stem cortex which has no sclerotic elements, we should naturally expect that the free petiole near its base would have no sclerenchyma in the outer cortex. From this evidence also, we must conclude that the series as figured shows the various stages in a descending order. In other words the proof of the problem lies in the following observations :- the size and shape of the petiole-trace, the development of the pinna-trace bar and pinna-traces, and the sclerotic outer cortex are all gradually reduced as we proceed through the figures shown from Pl. 2 fig. 17 to Pl. 3 fig. 32.

It might be said that this was not conclusive since all the figures do not represent different levels in one and the same specimen; and that there are perhaps several different species mixed up in the series. Such an objection can easily be met, for each stage figured is intermediate between its two neighbouring figures; there is no sudden jump at any point from one type of trace to a totally different one. In fact there is a continuous variation in one direction and this is the only variation that is shown by the specimens.

PL. II. fig. 17 represents a petiole-trace perfectly typical of the species *Metaclepsydropsis duplex*; the waist is very pronounced and the pinna-trace bar is also well marked. The specimen shown in figure 18 is also perfectly typical though rather smaller, but, apart from a few details in the phase of the pinna-trace /

trace departure, the two figures represent specimens which are specifically identical. In figure 19 however, the waist is much less marked than in figures 17 and 18, while figure 20 exhibits a trace with hardly any constriction in the middle. There is still a slightly sinuous appearance in figure 21 but in figs. 22 and 23 this has entirely disappeared. Indeed, had the petiole whose trace is shown in the last mentioned figure been discovered separately, there is no doubt that it would have been referred to another genus, namely, <u>Dineuron</u>. Figure 24 represents another example where the trace is even more like <u>Dineuron</u> than that of figure 23.

The next two figures (25 and 26) are cut rather obliquely and the traces are perhaps not quite so long as they appear but the angle of section is very near 90° so that any reduction in their size on account of the obliquity of section must be very slight. They are from different specimens but represent stages which are practically identical and show the departure of a much reduced pinna-trace bar (~~pt~~.b.) If anything, fig. 26 is further up than 25 and the bar shows clearly that it will divide into two portions. A somewhat similar example cut from the same specimen as fig. 26 is shown in Pl. III. fig. 27 though here the trace is rendered shorter than it really should be by a slight crushing. In Pl. III. fig. 28 the trace is still further reduced but it is clearly identical with that of fig. 27 while that shown in fig. 29 is also similar.

The /

The next three figures are taken from the same specimen and this specimen joins the stem two sections below that figured in fig. 32. Figure 30 is similar to fig. 29 except that both ends of the trace are closed instead of only one end as in the former figure, where the left hand end has an island in the xylem and the right hand end has a bay. Figure 31 shows clearly the two almost circular islands one at each end of the trace and also the stem which the petiole joins at a lower level. Near the junction with the stem the islands disappear and only the small protoxylem elements remain. These protoxylem groups occur in pairs at each end in fig. 31 but in fig. 32, where unfortunately the lower part of the trace is crushed, there only appears to be one group. Two sections lower down this series the petiole-trace joined the stem (figs. 31 and 32. st.) We have thus followed the petiole-trace of M. duplex through all its stages into a stem which presents certain peculiarities but is very simple in structure.

A typical transverse section is shown in Pl. I. fig. 1. Two regions can at once be distinguished, an outer of large tracheides which are seen to be reticulately thickened when viewed in longitudinal section and a central zone composed of a mixture of tracheides and parenchyma. The inner tracheides are long, pointed elements and have reticulate or scalarifom thickenings on their walls but they are smaller in diameter as a rule than those of the outer zone. The stem was long and dichotomously branched. /

branched.

On the whole it had the appearance of a rhizome and evidence in favour of this will be brought forward immediately.

Root traces have been met with on one or two occasions but only one example actually joined the stem xylem. One of these root traces is shown in Pl. 1V. fig. 43. It is large for a root trace and is diarch.

So far merely the xylem tissue has been considered but the cortex is also of some importance for while there is a sclerotic layer in the cortex of the mature petiole there is none in that of the stem or of the lower parts of the petiole. The inner cortex has generally all decayed but small patches sometimes appear in the islands formed between the pinna-trace-bar and the petiole-trace. It has always the appearance of a delicate parenchy-ma.

Numerous groups of ~~synaugia~~ Sporangia, probably synangia, occur scattered through the blocks containing the petioles and stems of M. duplex There are gemerally four sporangia in each group but there is no evidence that these were borne by the pinnules of this plant.

Histology of the Stem.

The stem which has just been referred to M. duplex is of peculiar interest both on account of its simple structure and because it is of considerable phyllogenetic importance. In transverse section it is circular in outline (Pl 1. fig.1.), and about 1.8 mm. in diameter. Two zones may easily be distinguished, the inner consisting of a mixture of parenchyma and tracheidal tissue and the outer being made /

made up entirely of tracheides. Pl. 1 fig. 8 probably gives the best idea of the distribution of the tracheides and parenchyma in traverse section (although a petiole trace is shown connected to the stem the former has not disturbed the more central tissues.). In other examples the tracheides are almost absent and in Pl 4. fig. 44 p. such a specimen is figured. Only one tracheide is present immersed in the centre of a thin-walled parenchyma. The general circular shape of the stem is distorted in this specimen since a petiole-trace is shown connected with the stem. This trace apparently belonged to a petiole which had been torn away, leaving a ragged stump still connected to the stem and so crushing the tissues of the trace, that one protoxylem group is unrecognisable and the whole trace very irregular in outline.

In most specimens, however, the parenchyma has been ruptured and only fragments of the delicate cell-walls remain. As a result the tissue is seen better in transverse than in longitudival section. In one example (Pl 1V. fig. 45) a peculiar condition was discovered. There is no parenchyma present in the stem and there is a distinct radial arrangement of the tracheides. This stem is very much smaller than any of the others and I have only seen it in one preparation.

I am inclined to think that it is an unequal dichotomy of the stem and it will be referred to later. In the meantime the absence of conjunctire parenchyma is worthy of notice.

The tracheides of this zone are generally small in diameter and vary considerably. The largest are only about 45μ to 50μ while the /

the small ones are 30μ and under. Those nearest the periphery are generally the largest and they abut on the inner tracheides of the outer xylem zone which are not much larger than the outer tracheides of the mixed pith. The thickenings on the walls of the inner elements are scalariform in the smallest but reticulate in the largest. In the same tracheide the transition between scalariform and reticulate thickening is often clearly seen (Pl. 1 fig.2.) The largest of these elements have rarely more than 3 rows of pores on each wall.

The outer zone of the stem xylem is four to five cells deep thus constituting a ring of solid wood round the inner zone. The elements of this ring are much larger than those of the inner wood but these of the inner layers are much smaller than the others. The average size is from 100μ to 130μ but near the bifurcation to be noted shortly, some of the elements are as much as 250μ in diameter. Some of these large tracheides may be seen in Pl 1. figs. 4, 5, and 6. At the departure of a petiole-trace larger elements also occur (Pl 1. fig.8). Like those of the inner zone, the outer tracheides are long, pointed, and their walls reticulately thickened but there are 6 to 9 rows of pores on the walls. The pores on the walls of the elements of both zones are about the same size. Groups of small tracheides may occasionally be seen in the outer xylem zone but these are the protoxylem elements of a petiole trace and do not belong to the stem itself.

Outside the xylem there is generally a dark layer which in very thin section is seen to consist of cellular tissue. This tissue

no /

no doubt represents inner cortex and phloem but it seems to have been composed of very delicate elements which are too much crushed to warrant more than a passing notice. The outer cortex, on the other hand, is generally well preserved. It consists of a thick-walled parenchyma but there are no sclerotic layers present. This outer cortex is sometimes produced into ragged protuberances.

To the stem xylem petiole and root-traces are attached but they only occur at considerable distances. In the material examined only three or four of such emissions have been noted and only in one case was a root-trace found joining the stem. In the case of each of these appendages, however, there is sufficient evidence to show that the departure is protostelic ~~1. 2.~~ i.e. the outer xylem ring is never broken, thus exposing the inner zone on the surface of the cylinder.

Branching of the Stem.

In several of the stems examined it was possible to cut long series of sections but the changes were very slight except in the neighbourhood of the emission of a petiole or root-trace. In one specimen, however, just above the point of departure of a petiole-trace, I was fortunate enough to discover both a root-trace emission and a bifurcation of the stem. These three divisions all took place within a length of 1½ inches. In another case just above a petiole trace departure the very small solid stem was discovered, this being probably an unequal dichotomy of the stem, for the ~~other~~ first cited division was a distinct equal dichotomy.

Pl 1. fig. 3 represents the first stage of the bifurcation (the small /

small trace rt, tr. represents a root trace which arches over at this point and the top of the arch is here shown), and the inner zone of mixed pith is distinctly alongated, as is the whole Stem xylem. Roughly speaking the stem xylem is an ellipse. Higher up the stem the mixed pith divides into two large masses connected by a thin neck or in other words becomes figure-of-eight shaped the outer xylem still remaining elliptical. As a result of this the large elements previously noted are found towards the outside of the narrow neck connecting the two masses of the mixed pith Pl 1. figs. 4 and 5. The pith then divides into two separate masses and the outer xylem becomes eight-shaped with large xylem elements in the constriction of the eight (Pl 1. fig. 6) and finally the two parts separate. The division is into two equal parts i.e. it is a dichotomy. During the division there is no appearance of a branch gap i.e. the departure of the branch is protostelic. Hence all departures of petiole, root, and branch have proved to be protostelic. The small solid branch - if it be a branch - is of interest because it is quite similar to a case noted in <u>Diplolable romeri</u> (Solms), where the ~~minor~~ inner wood almost entirely disappeared at a bifurcation of the stem. Such a reduced branch also might be expected to show primitive characteristics and to give some indication of the race from which the plant had sprung. The evidence from this specimen points to an ancestor with a solid stele and this is in harmony with the evidence from a study of the petiole.

Histology of the Petiole.

It is generally admitted, that at the junction of the petiole and the stem, ancestral characters may be expected, so it is very important /

important that the changes in the petiole-trace near the base should be carefully noted. In making a more minute examination of the xylem tissue in this region it will be found more convenient to work up the petiole and not down as in the general description.

The first figure to be noted is Pl 11. fig. 16 which represents a transverse section of the stem in a rather flattened condition. At "A" a short arm of parenchymatous tissue may be seen stretching from the central mixed pith into the outer xylem. Near the end of this radial arm are some rather small elements which constitute one of the protoxylem groups of a petiole-trace. The other protoxylem group is not differentiated until later so that, at this early stage, the difference ~~of~~ in phase of the two ends of the petiole-trace is quite marked. In the next section of the series (Pl 2. fig. 15) the arm "A" is very much longer and the protoxylem group is at the end of the arm furthest from the inner zone of mixed tracheides and parenchyma. There is still no sign of the second protoxylem group. Figure 14, which follows, shows one group of protoxylem elements isolated in the o outer xylem zone, the arm of parenchyma and its accompanying small tracheides having disappeared. On tbe inner margin of the outer wood, a short distance round from where the first medullary arm appeared, a second small sinus containing protoxylem may be seen at "A'". The next section represented by fig. 13 shows the first protoxylem group (Prx. 1) well out in the outer zone and the second group (Prx 2) quite distinct.

In Pl 1. fig. 12 both groups are clearly seen and in the next two sections /

sections (figs. 11 and 10) little change can be noticed. One group has come to lie close to the margin of the stem xylem while the other is at the outer extremity of the arm of parenchyma and small tracheides. When the level of fig. 9 is reached, however, the second arm has disappeared and at that end of the stem xylem there are two sunk protoxylem groups. At the same time the whole end of the stem has a distinct bulge on it. (A closely similar stage is seen in Pl 1. fig 1.) One section higher up (fig. 8) the bulge on the stem is still more pronounced, indeed the petiole-trace has now become a distinct body connected to the stem at C, by a number of very large tracheides. The protoxylem groups are placed at opposite foci of the elliptical trace.

In the section above that shown in fig. 8, the trace has separated from the stem as an elliptical mass (fig. 7). This trace was followed for three sections more but no change was noted, and above that level it had disappeared. The subsequent changes in the petiole-trace will be followed in another series which starts with a much crushed section just about the level shown in Pl 1. fig. 8. Below this level both stem and petiole have rotted away. The first section of this new series which is figured, is shown in Pl 111. fig.32. Here the much distorted petiole-trace is closely adpressed to the stem xylem and only one protoxylem group can be seen. This group is quite similar in position and shape to either of those in Pl 1. fig. 7. A few sections higher up however, each protoxylem group has divided into two (Pl 111. fig. 31 prx) and an island of parenchyma is developed at each end separating the two parts into which each protoxylem group has divided (fig. 31 io.). Fig. 30 represents the highest section /

section in this same series and at the top of the trace there is a mere filament of xylem tissue on the outer margin of the island of parenchyma. A closely similar specimen is represented by Pl. IV. fig. 29a where one end of the trace is open while the filament is just leaving the other end. There has been some slight lateral crushing in this specimen as is indicated by the flattened cortex but it has not affected the trace very much.

In Pl. III. fig. 29, however, a closely similar trace is shown, and there appears to have been no distortion in this case. The right-hand end of the trace is open and shows the bay "g" with the protoxylem elements at each side. The other end is closed and, there also, the two groups of protoxylem are clearly seen. So far no distinct pinna-trace-bar has been detached from the petiole-trace; the filaments, however, no doubt represent very reduced examples of such departures. The trace shown in Pl. III, fig. 28 while practically identical in form with that of fig. 29, is slightly larger, and on the left-hand end the filament of xylem of fig. 29 is represented by a stouter bar. Unfortunately these petioles were only short fragments, generally less than half an inch long, so that the pinna-trace-bars could not be followed very far. In one example, however, from which about 20 sections were prepared two of these bars were followed a short distance but they never, as far as could be seen, passed out into pinnae. Though these figures, then, are taken from different specimens it will be noticed that as the trace increases in size /

size the pinna-trace-bar becomes better and better developed.

Pl. III., fig. 27 represents a cross section of another of these petiole fragments which is exactly similar to that of fig. 28. The one end is open and the other closed by a pinna-trace-bar in exactly the same condition as in the latter figure. In this specimen at a higher level the pinna-trace-bar became detached from the petiole trace and showed some signs of dividing into two. (Pl. II., fig. 26b.) A twisting of the whole petiole-trace at this level gives a much longer appearance than is shown in Pl. III., fig. 27. In the next figure (fig. 25) an exactly similar section is represented. The plane of section in this case is horizontal except at the left-hand side. In this specimen there is also a reduced pinna-trace-bar given off from the petiole-trace and as in the case of fig. 26 the bar shows signs of dividing in the middle to form two traces.

Passing to the trace shown in Pl. II., fig. 24 the first thing to be noticed is that it has suffered no distortion and that it is quite similar to that of fig. 25. In general form it greatly resembles Pl. III., fig. 29 but it is larger and the pinna-trace-bar "b" at the top of the figure is much better developed than in that specimen. The petiole from which the section of fig. 24 was prepared is about 6 inches long and higher up two pinna-traces were noted. They were fairly well developed but did not penetrate the cortex to enter into distinct pinnae. The outer cortex (o.c.) in this figure is also worthy of notice since /

since it contains no sclerotic layer.

A very similar example is shown in Pl. II., fig. 23. This trace is not quite so long as the last but it is much stouter and the bar "b" is rather better developed. Yet this bar also never gives rise to traces which enter into distinct pinnae. In fig. 23 it is practically divided into two but both die out higher up. The outer cortex in this specimen had a distinct sclerotic band towards the periphery. Up to this point all the traces examined would have been referred to <u>Dineuron</u> had they occurred separately and indeed would still be referred to that genus unless the next three stages had been discovered. The first of these transition examples is shown in Pl. II., fig. 22. It is essentially like that of fig. 23 but a flattening is making its appearance on both sides and the pinna-trace-bar is exceedingly well developed. A similar flattening may be noted in Pl. II., fig. 26 but this is due to the obliquity of the plane of section. Pl. II., fig. 21 exhibits another of these transition stages. Here the trace gives some indication of a waist. The pinna-trace-bar is also much more robust than in the last figure. This trace is exactly intermediate, both in size and shape, between the Dineuron-like example of fig. 24 and the normal Metaclepsydropsis trace of figs. 17 and 18.

In the specimen shown in fig. 20 we have the last of the transition types. A distinct waist is shown thus giving the appearance of an hour-glass to the trace. An early stage of pinna-trace /

pinna-trace departure is also demonstrated by this specimen and the bar is quite robust and well developed. Even this specimen would probably be referred to *Metaclepsydropsis duplex* with some misgivings. Fig. 19, however, supplies the last link in the chain and while the trace shown in it would at once be accepted as typical of *Metaclepsydropsis duplex*, there is one peculiarity, the broad waist, which links up the trace of fig. 20 with those of figs. 17 and 18.

While it would be absolutely impossible to pass from the trace of Pl. II., fig. 17 to that of Pl. I., fig. 7 or even that of Pl. II., fig. 24, yet when all the intermediate stages are shown it becomes not only possible but quite simple. The whole development may be summed up thus:- the demands made on the xylem of the petiole by more and more robust pinna-traces have caused the petiole-trace (1) to become larger, and (2) to increase the size of the ends so as to accommodate the much ~~larger~~ stouter pinna-trace-bar. A closely similar conclusion was arrived at in the case of the petiole-trace in *Diplolabis romeri* but instead of the ends of the trace becoming inflated they were drawn out into two long arms at each end.

In Pl. IV., fig. 39 an interesting example is shown. The specimen was very short but it happened to include the portion of the petiole to which the pinnae are attached. These pinnae were seen to be quite normal though small. This has led me to believe /

believe that the specimen must have been a portion near the top of a petiole. In that region we would naturally expect the trace to be smaller and, if the hypothesis be correct that the hour-glass shape was impressed on the petiole-trace in order that it might accommodate more robust pinnae, we would also expect that the petiole-trace near the apex would revert to its elliptical form since the pinnae diminish in size near the top of the frond. The trace in this example is exactly similar to that in Pl. II., fig. 21 except that it is smaller and this latter figure represents a section well down towards the base of the petiole.

Turning now to examine the pinna-trace, we find that one of the earliest obvious stages in its development on the petiole-trace is seen in Pl. III., fig. 38, where, at "g" a round island of parenchyma is seen. At each side of this island there are groups of small elements - the protoxylem. Such a stage, however, is not the earliest that can be seen for the protoxylem groups may be observed before the island is formed, i.e., when there is a <u>groove</u> at the end of the petiole-trace and not an island. (Pl. II., figs. 17, 18, 19, 22, 23, 24, prx$_1^{a}$, prx.$_2^{a}$). They may be distinguished at an even lower level (fig. 21, prx$_1^{c}$ prx$_2^{c}$ or fig. 17 prx$_1^{b}$, prx.$_2^{b}$). Pl. II. fig. 18 is probably just below the level at which the last vestiges of these groups are visible but the bay or groove which results from the island opening /

opening to the outside, is seen shallowing away at C.

A stage beyond that of fig. 38 is shown in Pl. II. fig. 21 at the lower end of the trace. The island of parenchyma which was circular in the former figure is elliptical in the latter and has still two protoxylem groups, one at each end of the major axis of the ellipse. At a still higher level (Pl. III. fig. 38 lower end of trace) the island is much larger, and the protoxylem groups of the pinna-traces vertically above the pair represented by the pinna-trace-bar we are considering, are quite distinct on the inner margin of the island. A somewhat similar example may be seen at the top of the trace in Pl. II. fig. 20. There are at this stage four protoxylem groups arranged round the island. The groups at the ends of the island become spread out on the outer margin and then divide into two. The stage just before the division is shown in the last mentioned figure.

Passing to the top of the trace in Pl. II. fig. 22 it will be noticed that the pinna-trace bar has four protoxylem groups peculiar to itself. These have been derived as indicated above from the original two groups. There are thus six groups round the island which has now attained a larger size. Two closely similar examples are figured in Pl. II. fig. 21 and fig. 18 at the top of the trace in each case. In figs. 17 and 19 the bar has become detached from the petiole trace and gives some indication that it will divide into two equal parts. Pl. III, fig. 34 represents /

represents a still later stage where the division is complete and two curved xylem strands are produced. In the section above, other protoxylem groups make their appearance on the inside of each of the curved xylem strands, but they are near the lower ends of these strands and not in the centre. Two sections above this last one these extra protoxylems are distinct and the arc of xylem is converted into a double arc (Pl. III. fig. 35.) In Pl. III. fig. 36 - about 3 sections above fig. 35 - the small traces are cut off from the larger median bundles. The small bundles pass out to supply aphlebiae and during their passage outwards they each bifurcate. The two branches of each bifurcation pass out at the same level and not, as in Diplolabis romeri, at different levels.

The larger median bundles - destined to supply pinnae - become more curved (Pl. IV., fig. 40) and finally pass out at the same level into the pinnae of which there are two for each pinna-trace-bar. In some cases, however, the incurved ends unite and the arc then becomes a closed ring of xylem (Pl. IV. fig. 41.) Such a closed trace is very interesting and probably indicates an ancestral character. Very few of such annular traces have been discovered and unfortunately they could not be followed far enough to see if they ultimately resumed the open form. In one secondary pinna a similar character was noted and here the emission of the tertiary pinna is exactly comparable with the emission of the /

the secondary pinna from the primary.in <u>Clepsydropsis antiqua</u> as shown by Dr. P. Bertrand.[1] This ~~has~~ may bee~~n~~ called ~~by Davis~~ a variety of ~~the~~ the "extra-marginal" type of emission.

Apart from these abnormal cases the pinna-trace is open and consists of reticulately thickened tracheides with scalariform protoxylem elements in the sinuses formed by the incurved ends. The pinnae of one order are cut off from the ends of the trace of lower order and pass out alternately at each side.

The foliage and fructifications are quite unknown though several groups of sporangia (probably synangia since there are always four sporangia in a group and there is sometimes only one wall between two sporangia) occur in the same sections as contain the petioles and pinnae of this species. In the absence of evidence of continuity, however, it would not be safe to connect the two.

<u>Histology of the root.</u>

The root trace is very similar to that of <u>Diplolabis römeri</u> (Solms); it is barrel shaped and consists of reticulately thickened tracheides. There are two protoxylem groups of scalariform elements situated one at each end of the barrel-shaped trace. In one specimen a rootlet seems to be given off from the main trace but it is very much crushed and one cannot determine whether the smaller rootlets were similar to the large ones. Another specimen curved up at first but ultimately turned and grew in the opposite /

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[1] P. Bertrand. Etudes sur la froude des Zygopteridus.

opposite direction to the departure of a petiole trace lower down. Very few root-traces were discovered and then only the xylem was preserved.

Comparison with other species.

In their memoir on the fossil Osmundoceae, Kidston and Gwynne-Vaughan have divided the Zygopterideae into three great groups, and, although few stems belonging to this family are known, at least one of the recorded specimens belong to each group. Ankyropteris corrugata, (Williamson), A. Brongniarti, (Renault), and probably A. scandeus, (Stenzel) belong to the first group; Diplolabis romeri, (Solms) and Metaclepsydropsis duplex, (Williamson) to the second; and Etapteris di-upsilon (Zygopteris Grayi), (Williamson) to the third. The stele of the stem in all of these species is either circular or roughly stellate in transverse section. When examined in detail, however, there are considerable differences between them.

In comparing the newly discovered stem of Metaclepsydropsis duplex with the others, we shall begin with the simplest known type (it is also the oldest known type) Diplolabis romeri. This latter species is derived from the same locality as M. duplex. In it the stem xylem is circular in transverse section and consists of two kinds of tracheides both of which have reticulate thickenings on their walls. The xylem elements are arranged in two zones, the inner of which contains only short, square-ended tracheides, /

tracheides, while the elements of the outer zone are long and pointed. The inner tracheides are smaller in diameter than those of the outer zone and they are arranged in vertical series as though they had been derived by the septation of long elements. There is no conjunctive parenchyma present in the stele. The stem branched dichotomously and was a rhizome.

The departure of the petiole-trace from the stele is protostelic and the trace is at first elliptical with sunk protoxylem groups one near each focus of the ellipse. In the subsequent development of the petiole-trace long arms are gradually produced and the trace then becomes H or X shaped. Pinnae depart from the petiole in pairs, one pair alternately on each side so that four rows of pinnae are produced on the one petiole. The root-traces also leave the stem xylem in a protostelic manner, they are diarch and barrel-shaped.

As we have seen, the stele of *M. duplex* is also circular in outline and the xylem consists of two kinds of tracheide. Both kinds are long, pointed and reticulately thickened, except the smallest in the inner zone, which have scalariform thickenings on their walls. There is conjunctive parenchyma present, however. The stem branched dichotomously and was a rhizome as in the last species.

The petiole-trace left the stem stele in a protostelic manner as an elliptical mass with two sunk protoxylem groups but its subsequent /

subsequent development is quite different from that of *Diplolabis romeri*. No arms are produced but both ends of the trace become dilatated. In *D. romeri* the island of parenchyma enclosed by the entering pinna-trace-bar is constant in size whereas that in *M. duplex* gradually diminishes until it is exceedingly small, when it opens to the exterior and a small groove is left in the petiole trace instead of the wide V shaped groove between the arms in *D. romeri*.

The pinnae are borne in four orthostichies just as in Diplolabis but occasionally the trace becomes closed as in Clepsydropsis. The roots of M. duplex are also quite similar to those of *D. romeri*. I have gone into considerable detail in this comparison as these two species have many points of similarity and form two important links in the chain of evolution among the *Zygopterideae*.

In comparing *M. duplex* with *Ankyropteris corrugata* a great similarity in the shape of the stele must be noted. Both have two zones of tracheides and there is conjunctive parenchyma in the inner zone in each. But while only a few of the elements in the inner zone in *M. duplex* are scalariform tracheides, all the elements in both zones of *A. corrugata* have that type of thickening. It has also been shown that the arms of parenchyma and tracheidal tissue which radiate out from the inner zone of the stem stele do not persist for any great vertical distance in *M. duplex*. In the case of *A. corrugata*, on the other hand, these arms seem to persist /

persist for a greater vertical distance, so much so, that the outer zone of the stele xylem appears to consist of five groups of tracheides alternating with five parenchymatous arms which project from the inner zone. The largest tracheides in *A. corrugata* appear in the centre of each group and in *M. duplex* the largest are in the central portion of the outer xylem; but if the radiating arms broke up the outer ring as in *A. corrugata* the smaller tracheides would be situated along the sides of the arms and then the large tracheides would occupy a central position in the resulting groups of the outer xylem zone. In both species these radiating arms of parenchyma and tracheides are intimately connected with the petiole-trace departure, and this emission is more distinctly protostelic in character in *M. duplex* than in *A. corrugata.* In the type of branching shown by both species there is a striking similarity, it is a dichotomy in each case and in neither case has any "axillary" branching been recorded. It is also worthy of notice that the Botrychioxylon-like specimen shown in Pl. IV. fig. 45 as paralleled in Williamson's figure of *A. corrugata*.[1] (Pl. 5 fig. 19)

The petiolar development, however, is entirely different in the two species *A. corrugata* having only two rows of pinnae and these, as Kidston and Gwynne-Vaughan point out,[2] being little more /

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[1] Williamson, Phil. Trans. Roy. Soc. Vol 167 1876

[2] Kidston & Gwynne-Vaughan, Trans. Roy. Soc. Edinr. Vol XLVII 1910

more than scale leaves.

The French Permian species *A. Brongniarti* is also very similar to *M. duplex* as far as its stem stele is concerned. In size they are almost identical but in *A. Brongniarti* the radiating arms are exceedingly well developed and the tracheides have all scalariform thickenings on their walls. Very little is known about this species particularly about the petiole-trace, but the petiole referred by Renault to the species is distinctly of the Ankyropteris type. The branching of the stem is of the "axillary" type now shown to be of the nature of an unequal dichotomy.

Compared with *Etapteris di-upsilon* (*Zygopteris Grayi*) the stem of *M. duplex* is very distinct. The stellate structure of the stem xylem in the former species is the result of the rapid emission of petiole-traces, and, when one has departed, the outline becomes rounded at that part of the stem and not stellate. The arms of parenchyma and tracheides radiating from the central zone of the stem xylem are much more prominent here than in *A. corrugata* or *A. Brongniarti*. The type of branching also in this species is an unequal dichotomy. The petiole-trace which is emitted from the stem belongs to the third group as defined by Kidston and Gwynne-Vaughan. This correlation of the petiole known as *Etapteris di-upsilon*, (Williamson) with *Zygopteris Grayi* has only recently been published by Dr. Kidston.[1] The species is /

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[1] Ann. Bot. Vol. XXIV April 1910.

is therefore distinct from *M. duplex* in all its salient features.

Ankyropteris (Zygopteris) *scandeus*, (Stenzel) is another zygopterid fern with a stellate stem stele. It was in this species that the presence of the "axillary" branch was first demonstrated and in some respects it is closely similar to *Etapteris di-upsilon*. The petiole-trace, however, is of the Ankyropteris type. It is thus quite distinct from *M. duplex*.

Quite apart, then, from the appearance of the petiole-trace *M. duplex* may be distinguished from all other species of the Zygopterideae by the structure of the stem. As regards the petiole-trace itself there is no species so far described with which it is likely to be confounded in its mature stages but as has already been shown the early stages of the petiole might quite well be confused with *Dineuron*. It is quite true that no specimen of *Dineuron* has been discovered which has as large a stele as *M. duplex* but it is quite conceivable that some species of *Dineuron* may be discovered with a petiole-trace as large as that of the early stages in the trace of *M. duplex*. None of the early stages of petiolar development in the latter species is comparable with *Clepsydropsis*. In *Diplolabis*, on the other hand, there was a distinct resemblance to that species in the early form of the petiole-trace.

Summary.

In this paper a fern stem is described and the evidence for referring /

referring it to Metaclepsydropsis duplex, (Williamson) is cited. The stem is shown to be a long, dichotomously branched, rhizome from which petioles and roots are only emitted at considerable intervals; indeed, although several inches of ~~the~~ one stem were cut into transverse sections, only one petiole departure was observed. Several pieces of the stem were discovered. Branching of the stem is shown to be of the nature of a dichotomy.

The petiole-trace is followed from the earliest stages of its differentiation from the stem until it departs as a separate trace. From that level it is followed through several series until the normal form of the M. duplex petiole-trace is attained. The Dineuron-like type of the early petiole-trace is recorded.

The pinna-trace departure is next studied and the changes noted from the time the pinna-trace-bar leaves the petiole-trace until the tertiary pinnae are reached. Several cases of abnormal traces are noted in which the xylem forms a closed ring. The resemblance which such abnormal types has with what is the normal form in Clepsydropsis is commented on.

Root-traces are also observed and they are diarch with a barrel-shaped xylem mass.

The cortex is dealt with in general terms as there is nothing of special note in its organisation. In the cortex of the stem and early stages of the petiole, however, there is no sclerenchyma present.

One specimen is recorded which shows secondary thickening but it /

it is probably abnormal. It appears similar to <u>Botrychioxylon</u>. The species is then compared with the members of the Zygopterideae which resemble it.

<u>Metaclepsydropsis</u> <u>duplex</u>, (Williamson).

1874. <u>Rachiopteris</u> <u>duplex</u>, Williamson. Phil. Trans. Roy. Soc. Vol. 164.

1889. <u>Asterochloena</u> (<u>Clepsydropsis</u>) <u>duplex</u>, Stenzel. Die Gattung Tubicaulis.

1896. <u>Clepsydropsis</u> <u>sp</u>., Renault. Bass. honill. et perm. d'Autun et D'Epinac.

1909. <u>Metaclepsydropsis</u> <u>duplex</u>, P. Bertrand, Etudes sur la fronde des Zygopteridees.

<u>Diagnosis</u>.

Stem long, dichotomously branched; xylem of stem circular in transverse section, 2 mm. in diameter, elements in two zones. Inner zone of long, narrow, reticulately or scalariformly thickened tracheides together with some conjunctive parenchyma. Arms of inner zone radiate into outer zone in certain places. Outer xylem of long, broad, reticulate tracheides. Protoxylem groups, of scalariform elements, not cauline but decurrent from the petiole into the stem, disappear at outer margin of inner zone. Cortex without sclerenchyma.

Petiole-trace at first elliptical in transverse section with a sunk protoxylem group near each end. Ends ultimately ~~dilate~~ enlarged and /

and trace becomes hour-glass shaped with sinus at centre of each end. Protoxylem groups two at each end situated on sides of sinus. Tracheides with reticulate thickenings except protoxylem elements which are scalariform. Primary pinnae in four orthostichies; inserted on petiole in pairs. Pinna-traces of third order enter those of second order in marginal or extramarginal manner in two orthostichies. Insertion of secondary pinnae on primary similar to tertiary on secondary. Trace of primary pinnae sometimes closed but open lower down. Last traces to join primary pinna-traces are from aphlebiae. Aphlebia-traces bifurcate during passage through petiole-cortex.

Pinna and aphlebia-traces unite to form pinna-trace-bar which joins petiole-trace. Aphlebia-trace branches pass out at same level.

Root-traces large, barrel-shaped, diarch.

Foliage and Sporangia unknown.

Localities. Calciferous Sandstone Series, (=Culm) Pettycur, Fife. Culm of ~~Autun~~ Régny and Devonian of ~~Falkenberg~~. Saalfeld

Conclusions and General Considerations.

In the light of recent discoveries of stems of Zygopterid and Osmundaceous affinities it is not surprising that the stem of Metaclepsydropsis should be such a simple one. As a matter of fact it is not so simple as that of Diplolabis romeri, (Solms). At the same time it must rank next to Diplolabis in order of complexity for the elements of its axis are chiefly reticulate tracheides /

tracheides and the mixed pith does not play so important a part as in *Ankyropteris corrugata* and the other known zygopterid stems. The radiating arms of parenchyma and tracheides so prominent in *A. corrugata* are also present in *M. duplex* but they are not so well marked. In all cases they are intimately connected with the emission of the petiole-trace and ~~indeed~~ the radial arm shown in Pl. II., fig. 15, a, is shown to be intimately related to one of the protoxylem groups of the trace of Pl. I. fig. 7. Indeed the insertion of the petiole-trace into the stem has probably been the cause of the stellate appearance of the latter in *Etapteris di-upsilon* (*Zygopteris Grayi*). A similar cause may be assigned to the apparent grouping of the xylem into certain areas in *A. corrugata* and *A. Brongniarti*. In other words the departure of the petiole-trace is beginning to have a greater effect on the stem xylem in *M. duplex* than it had in *Diplolabis*, and the series from *Diplolabis* to *Etapteris* (*Zygopteris Grayi*) through Metaclepsydropsis and *Ankyropteris corrugata* and *Brongniarti* foreshadows a type of petiole-trace departure which will no longer be protostelic but cause a gap in the outer xylem ring. In the Zygopterideae the departure seems to have been protostelic in all cases but the Osmundaceae show the change from the one type to the other. *M.* duplex is thus, as far as the axis is concerned, distinctly intermediate between the *Diplolabis* type and that of *Ankyropteris corrugata*. Indeed it holds the same position among the Zygopterideae with four rows of primary pinnae, that *Ankyropteris* /

Ankyropteris corrugata does among those with two orthostichies of such appendages.

Dividing up the Zygopterideae according to this criterion, as Kidston and Gwynne-Vaughan have done, we establish the two stem-series *Diplolabis romeri* - *Metaclepsydropsis duplex* - *Etapteris di-upsilon* (*Zygopteris Grayi*) and *Ankyropteris corrugata* - *Ankyropteris scandeus*. To make the intermediate position of *M. duplex* in the first series quite clear the following table has been inserted :-

	Diplolabis.	*Metaclepsydropsis*.	*Etapteris*.
hape of stem exylem in transverse section.	Circular with inner and outer zones.	Circular with inner and outer zones.	Pentagonal with inner and outer zones.
ype of Stele.	Solid.	With conjunctive parenchyma in central zone.	With conjunctive parenchyma in central zone.
ype of) outer zone.	long, pointed, reticulate.	long, pointed, reticulate.	Long, pointed, scalariform.
cheide) inner zone.	Short, square-ended, reticulate.	long, pointed reticulate or scalariform.	Long, pointed, scalariform.
rms radiating rom inner zone.	Absent.	Slightly developed.	Strongly developed
ype of branching.	Equal dichotomy.	Equal dichotomy.	Unequalled dichotomy, so-called "*axillary*" branch.

It has been shown that the reticulate type of thickening on the walls of tracheides is more primitive than the scalariform type, so that as far as we can judge *M. duplex* occupies a position above /

above Diplolabis in the Zygopterid series and the other criteria at our disposal all point to the same conclusion.

Before passing to a discussion of the systematic position of the petiole I wish to enumerate the reasons for believing that the stem was a rhizome; (1) the xylem of the stem is small compared with that of the petiole, (2) the internodes, if we may call the distance between two petioles by this name, are long, (3) what evidence there is regarding the distribution of adventitious roots seems to indicate that they are irregular in their occurrence, (4) the petiole-trace is at first small and then grows larger, as though it were supported in the lower portion, either by overlying vegetable matter or soil and did not attain its maximum development until it got above the substratum, (5) there is no sclerenchyma in the cortex of the stem or of the lowest part of the petiole, (6) the pinnae are in four orthostichies on the petiole and the latter must therefore have been held erect.

The study of the petiolar development has demonstrated certain points of interest. The term "arm" has been used to characterise the portion of the petiole-trace between the protoxylem groups and the"horizontal-bar" and while such arms do exist in Diplolabis and most other zygopterid petioles they do not occur in Metaclepsydropsis duplex. The increasing size of the island of parenchyma at the emergence of a pinna-trace-bar from the petiole no doubt gives the petiole-trace at certain levels the appearance of having such arms, Pl. II., fig. 18, but this stage is not constant /

constant. As has been already pointed out the ends of the trace in M. duplex have become dilatated instead of being produced into arms. This has permitted the insertion on the petiole of more robust pinnae. In Dineuron we find a petiole-trace quite similar to that of the early stages in M. duplex. In no case, however, have petioles of the former genus been discovered, which had dilatated ends.

Etapteris on the other hand appears to be a case where the dilatations have increased so much that they have become quite arm-like. The origin of the arms in this case is quite different from that of the arms in Diplolabis. Here they are mere swellings similar to those on the outer ends of the arms in Diplolabis and on the ends of the trace in M. duplex. Dr. P. Bertrand has pointed this out in his memoir on the Zygopterid petiole-trace and has also shown how the pinna-traces arise from the petiole-trace. As Dr. Bertrand has also pointed out there is some slight trace of arms comparable with those in Diplolabis.

In order to decide whether arms are present on the petiole-trace or not, it is necessary to examine a section immediately above the level of a pinna-trace bar departure. In the case of Diplolabis very distinct arms may be seen with the protoxylem groups at the ends and the same applies to Etapteris, but Metaclepsydropsis and Dineuron do not exhibit such arms, the ends of the trace have grooves in them and in these grooves lie the protoxylem elements. The grooves of Metaclepsydropsis and Dineuron are therefore equivalent to the wide bay in Diplolabis, Zygopteris and /

and Etapteris. In all cases the development of new pinna-traces is essentially similar, small tongues of xylem elements are developed round each protoxylem group and these grow towards one another until they meet and form a xylem bar across the end of the trace. The bay or the groove now ~~forms~~ becomes an island of parenchyma.

In *Diplolabis* the xylem bar is well developed and the size of the island is constant, as is also the case in *Zygopteris*. In *Etapteris* the tongues of xylem do not meet but break away and unite after being detached; this is rather a specialised type of pinna-trace departure. *Dineuron* and *Metaclepsydropsis*, however, exhibit quite a different type. The small groove is bridged across much more quickly than in *Diplolabis* and *Zygopteris* but subsequent growth causes the island to become larger and larger until it reaches a maximum at the level of the departure of the pinna-trace-bar. In *Dineuron*, it is true, the island does not reach the proportionate dimensions that it does in *Metaclepsydropsis* but the increase is distinct and I believe that these two genera must be grouped together.

Such a grouping would necessitate a division into two groups of Kidston and Gwynne-Vaughans' first subdivision of the Zygopterideae with quadriseriate pinnae. In the first group would be included all forms with well-marked arms and the bay between them always constant in size;

Diplolabis romeri (Solms)

Zygopteris /

Zygopteris primaria Cotta.

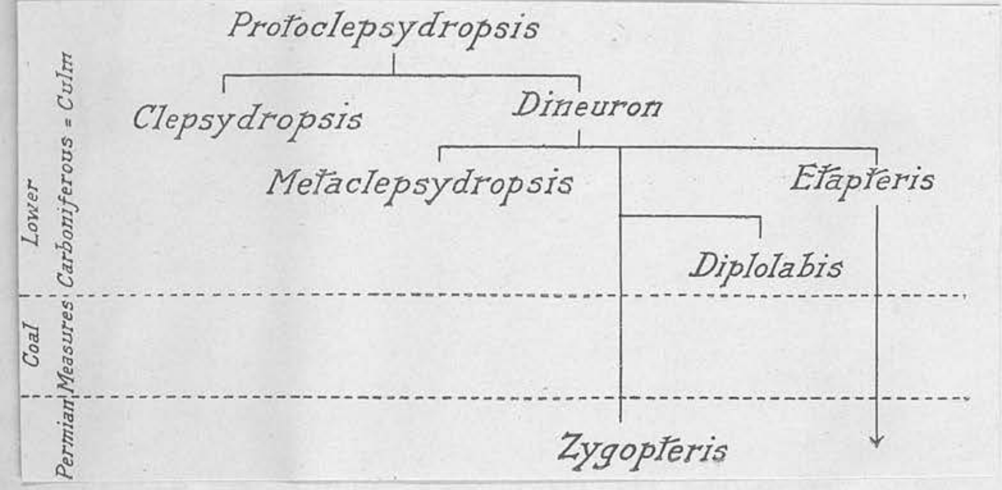
The second group would include forms where distinct arms are not developed and where consequently the bay is reduced to a mere groove. The island of parenchyma formed by the bridging of this groove becomes gradually larger until a maximum is reached just before the departure of the pinna-trace-bar;

Dineuron ellipticum, Kidston, & D. pteroides, Renault
Metaclepsydropsis duplex, (Williamson).

This subdivision, however, is based entirely on the mature form of the petiole trace. In members of each division (Diplolabis and M. duplex) it has been shown that in early stages of petiolar development the traces are distinctly similar in appearance to that of Dineuron.

In a recent paper on Diplolabis romeri I drew attention to an hypothetical type of petiole-trace (Protoclepsydropsis) from which some other Zygopterid traces might be derived, and, in a tabular form, I indicated what I believed to be the relationship of these Zygopterid petioles to one another. The table is inserted below, and in it M. duplex has been placed in close relation to Dineuron, in fact it has been considered one of the forms directly derived from a Dineuron ancestry. Zygopteris and Diplolabis have been grouped as a second derived form and Etapteris as the third. It is exceedingly interesting to find that the discovery /

discovery of the stem and early stages of the petiole-trace of M. duplex has entirely confirmed the view set forth in that table.



Of course all this grouping has been based on the hypothesis that the forms of the trace at low levels in the petiole (i.e. at early stages of development) are comparable with ancestral forms. This is also the basis of the work of Kidston and Gwynne-Vaughan on the fossil Osmundaceae and of Sinnott's studies on recent ferns. The hypothesis seems reasonable and when applied to Diplolabis and Metaclepsydropsis (two forms closely allied on other grounds) the results lead to the same conclusion, and show that evolution was parallel in these two genera.

As far as the relationships between the Osmundaceae and Zygopterideae are concerned the stem of M. duplex occupies an important position. In the medullation of the zygopterid stele the series taken was Diplolabis, Ankyropteris corrugata, Etapteris di-upsilon (Z. Grayi). Now this is open to criticism, for the first /

first and last have quadriseriate pinnae and petiole-traces with two planes of symmetry while the central type has biseriate pinnae and one plane of symmetry in the petiole-trace. If we substitute *M. duplex* for *Ankyropteris* we strengthen the position from two points of view for (1) we get a series of forms which are similar in all respects and (2) we may construct a parallel series in the zygopterideae with biseriate pinnae and one plane of symmetry thus :- *Ankyropteris corrugata*-*A. scandens*. To complete the series in this second main division of the Zygopteride we only want a form with a solid stem stele similar to *Diplolabis*. *Clepsydropsis* may supply this form for the stems referred to that genus by Dr. Paul Bertrand are not above suspicion. *Clepsydropsis* petioles have *not* been traced into these stems and until this is done the Cladoxylons cannot be accepted as the stems of *Clepsydropsis*.

Meanwhile the general trend of evolution as shown in the Zygopterideae is parallel to that demonstrated by Kidston and Gwynne-Vaughan in the *Osmundaceae* namely from a simple to a more complex type i.e. both groups show an ascending series as we pass upwards in the geological series.

In concluding this paper I desire to express my thanks to Dr. Kidston, Dr. Scott and Miss Benson with whom I have been in constant communication during my work on the genus described here. I have also benefited greatly by a study of Dr. Paul Bertrand's memoir /

memoir on the Zygopteridean frond and, although I cannot agree with all his conclusions, this pioneer work has been of great service to me.

EXPLANATION OF PLATES.

PLATE I.

METACLEPSYDROPSIS DUPLEX.

Fig. 1. Transverse section of stem. x_1 = outer xylem; p = pith with tracheides; prx_1, prx_2 = protoxylem groups.

Slide 1126 x

Fig. 2. Longitudinal section of stem. x_1 = outer xylem; x_2 = inner xylem.

Slide 1128 x

Fig. 3. Dictotomy of the stem, stage 1. x_1 = outer xylem; x_2 = inner xylem; rt. tr. = root trace.

Slide 1120 x 18

Fig. 4. Dictotomy of stem, stage 2. lettering as in last figure.

Slide 1121 x 18

Fig. 5. Dictotomy of stem, section above fig. 4. x_1 = outer xylem; x_2, x_2 = inner xylem.

Slide 1122 x 18

Fig. 6. Dictotomy of stem just before the branches separate. Lettering as before.

Slide 1123 x 18

Fig. 7. Insertion of petiole-trace in stem. Petiole trace detached prx_1, prx_2 = protoxylem groups; x_1 and x_2 as before.

Slide 1110 x 18

Fig. 8. Insertion of petiole-trace in stem. Petiole-trace attached . x_1 = outer zone of xylem; x_2 = inner zone; prx_1, prx_2 = protoxylem J = large xylem elements.

Slide 1109 x 18

Fig. 9. Stage below that of fig. 8. prx_1, prx_2 = protoxylem groups

Slide 1108 x 18

Fig. 10. Section further in than fig. 9. prx_1, prx_2 = protoxylem groups as before.

Slide 1107 x 18

Fig. 11. Below fig. 10. a^1 = radial arm from inner xylem zone; prx_1, prx_2 = protoxylem groups.

Slide 1106 x 18

Fig. 12. Stage preceding that of fig. 11. Lettering as before.

Slide 1105 x 18.

PLATE 12.

METACLEPSYDROPSIS DUPLEX.

Fig. 13. Insertion of petiole trace in stem. Stage below Pl. I. fig. 12. prx_1, prx_2 = protoxylem group; a^1 = arm of parenchyma and tracheides radiating from inner xylem zone.

Slide 1104 x 18.

Fig. /

Fig. 14. Section following that of fig. 13. Prx_1 = first protoxylem group; a^1 = sinus which is really the beginning of another radial arm similar to that of fig. 16.

Slide 1103 x 18.

Fig. 15. Section below that shown in fig. 14. prx_1 = first protoxylem group of petiole trace; a = radial arm of parenchyma and tracheides.

Slide 1102 x 18.

Fig. 16. Section below that shown in fig. 15. prx_1 = protoxylem group; a = arm of tracheides and parenchyma radiating from inner zone of stem axis.

Slide 1101 x 18.

Fig. 17. Transverse section of mature petiole-trace showing hourglass shape. w = waist; b = pinna-trace bar; g = groove; prx = protoxylem groups; end - endodermis.

Slide 1146 x 17.

Fig. 18. Transverse section of mature petiole-trace showing a large island of parenchyma at one end and an open groove at the other. w = waist; b = pinna-trace bar; g = groove; prx = protoxylem group; is = island of parenchyma; c = shallow depression - the last bestage of the groove.

Slide 1155 x 17.

Fig /

Fig. 19. Section similar to fig. 18. Pinna-trace bar just detached from petiole-trace. Waist not as well marked as in last two figures.

Slide 1151 x 17.

Fig. 20. Example of a petiole-trace with "waist" still less marked than in fig. 19. At the top an early stage in the development of the pinna-trace bar is shown.

Slide 1167 x 17.

Fig. 21. Transverse section of petiole-trace in which the "waist" is scarcely developed at all. A pinna-trace bar is shown attached to the petiole-trace at the top of the figure. Prx^{b}_{1}, prx^{b}_{2}, prx^{c}_{1}, prx^{c}_{2} = protoxylem groups on petiole-trace; prx_1, prx_2, prx_3, prx_4 = protoxylem groups on pinna-trace bar; is = island of parenchyma; b = pinna-trace bar.

Slide 1171 x 17.

Fig. 22. Section of a petiole-trace from which all indication of a "waist" has vanished. Lettering as in other figures.

Slide 1152 x 17.

Fig. 23. In the petiole-trace of this figure a further reduction to an elliptical trace is clearly seen. The pinna-trace bar (b) is a much reduced one and the pinna-traces do not pass beyond the cortex of the petiole. i.e. they are reduced.

Slide x

Fig. 24. Transverse section of petiole-trace showing distinct elliptical form of trace. Pinna-traces in this case also are reduced. The outer cortex (o.c.) has no sclerotic layer.

Slide 1194 x 18.

Fig. 25. Rather oblique transverse section of a reduced petiole-trace. Pinna-trace bar (b) does not divide into two pinna traces.

Slide 1189 x

Fig. 26. Another oblique transverse section of petiole-trace. Pinna-trace bar shows a double curve but it does not divide into two to supply two pinnae.

Slide 1204 x 15.

PLATE 3.

METACLEPSYDROPSIS DUPLEX.

Fig. 27. Transverse section of petiole-trace. Fig. 26 shows this same petiole-trace at a higher level.

Slide 1199 x 15.

Fig. 28. Transverse section of petiole-trace similar to that of Fig. 27.

Slide 1184 x

Fig. 29. Transverse section of another closely similar petiole-trace

Slide 1189 x 17

Fig. 30. Furthest out section of a series showing the connection between petiole-trace and stem xylem.

Slide 1242 x 15·5

Fig. 31. Section below that shown in fig. 30. The interval between is about ¼ inch. prx, prx = protoxylem groups; is. = island of parenchyma; st. = xylem of stem.

Slide 1240 x 15·5

Fig. 32. Section some distance below that of fig. 31. Petiole-trace crushed against stem. Two sections below this the two unite but are very much crushed at that level.

Slide 1233 x 15·5

Fig. 33. Transverse section of petiole-trace closely similar to that shown in fig. 31. This is inserted to show the great similarity, at this level, of the traces of <u>Metaclepsydropsis</u> and <u>Dineuron</u>.

Slide 1180 x

Fig. 34. Transverse section of petiole showing the division of the pinna-trace bar into two equal xylem arcs.

Slide 1248 x 8·3

Fig. 35. Transverse section above that of fig. 34. (There are three other sections between these two). The xylem arcs of the last figure are each dividing into two traces, a large one and a small one.

Slide 1244 x 8·3

Fig. 36. Section above that of fig. 35. There are now five traces in the petiole. The petiole-trace itself, two large xylem arcs - the pinna-traces, and two small arcs - the aphlebia-traces.

Slide 1243 x 8·3

Fig. 37. Transverse section of petiole to show the arrangement of the tissues. The sclerotic outer zone of the cortex is very distinct. The petiole-trace is shown more highly magnified in Pl. II., fig. 21.

Slide 1171 x 8·3

Fig. 38. Petiole-trace of fig. 36 more highly magnified. g = groove; prx = protoxylem groups at the sides of the groove.

Slide 1243 x 19.

PLATE 4.

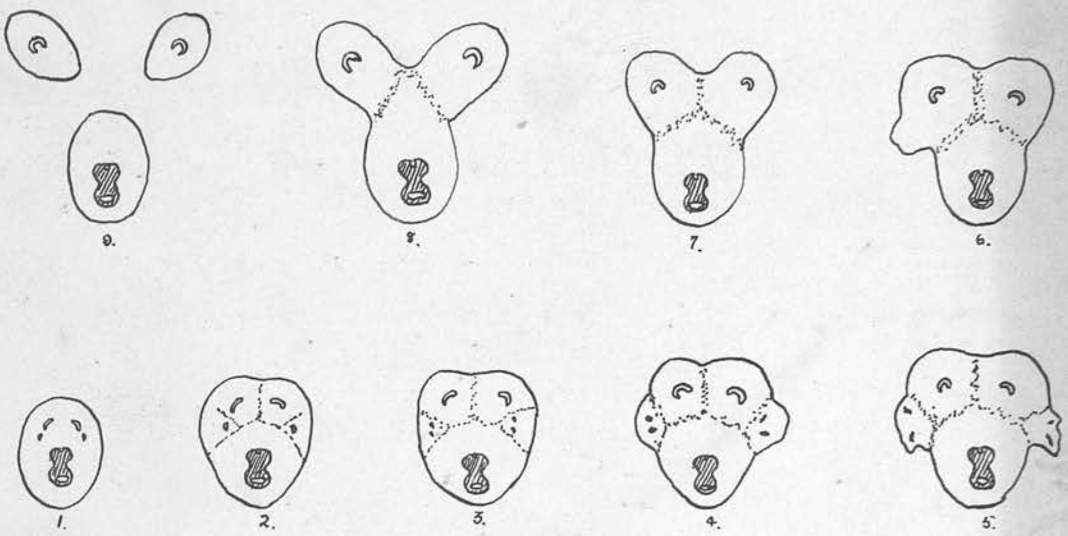
METACLEPSYDROPSIS DUPLEX.

Fig. 39. Transverse section of petiole-trace at a high level in the petiole.

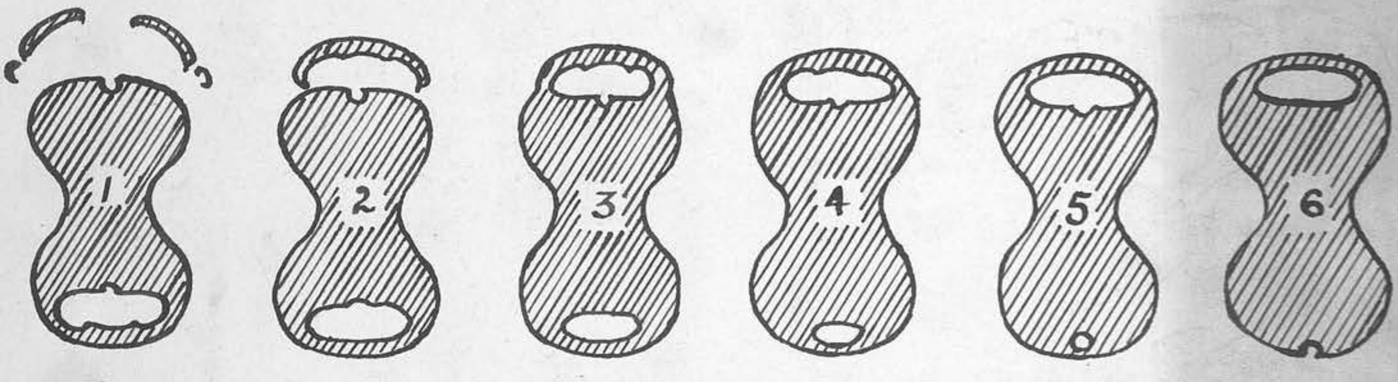
Slide 1140 x 17.

Fig. 40. Transverse section of normal pinna-trace. The shape is like a horse-shoe with open ends.

Slide 1261 x

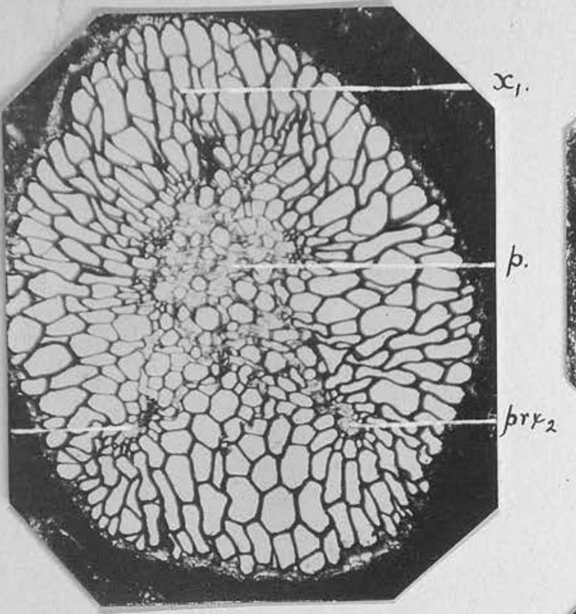


Text figure 2. M. duplex. Transverse sections of petiole showing pinna departure. After sections 1310 - 1318 Kidston Coll.
Natural size.



Text figure 3. Formation and gradual reduction of islands of parenchyma in the petiole-trace.

Plate I.



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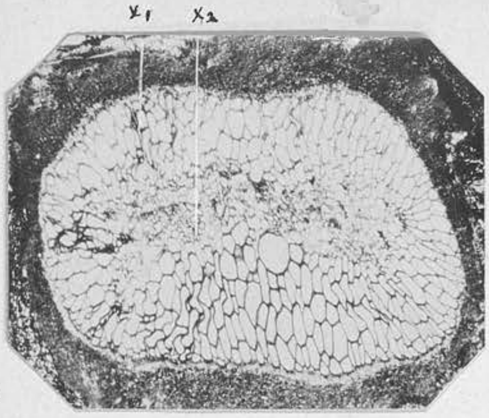

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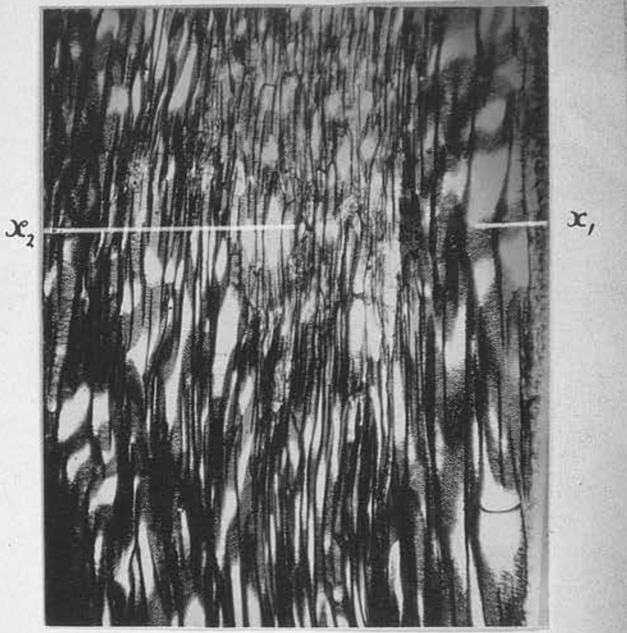

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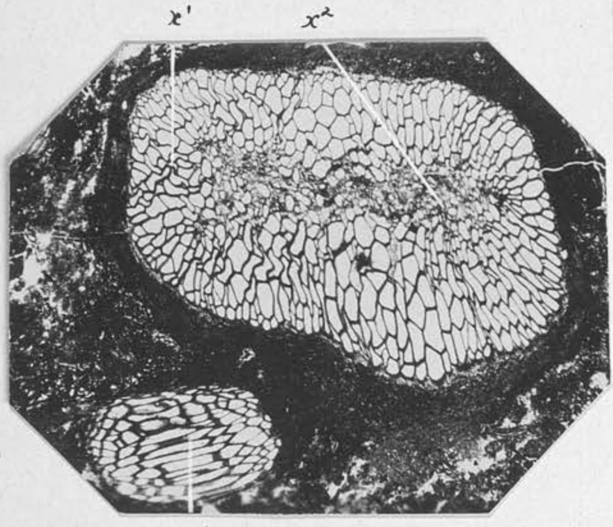

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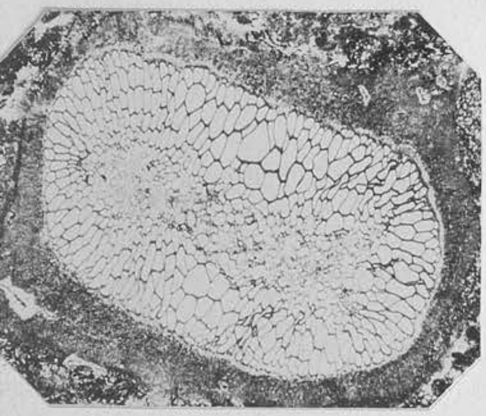

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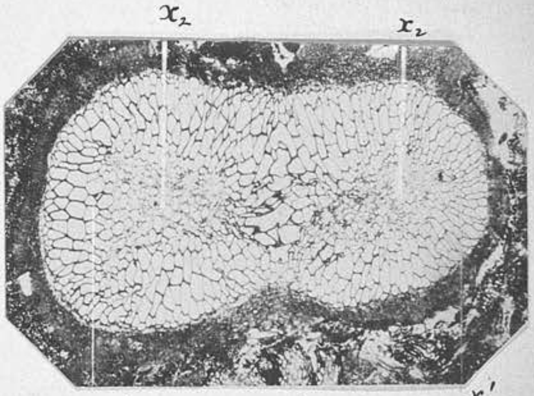

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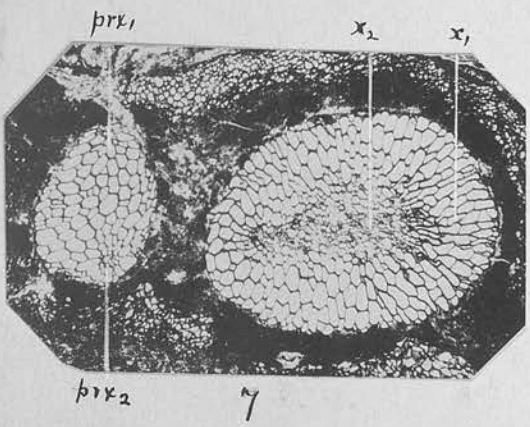

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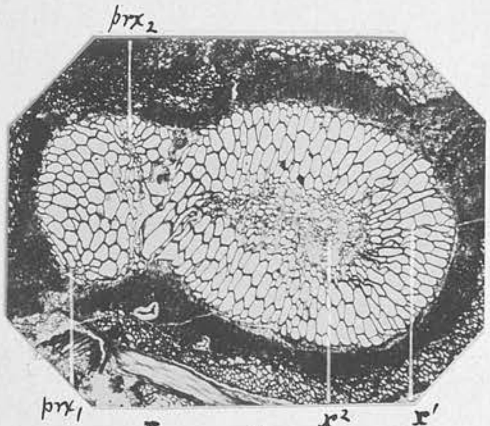

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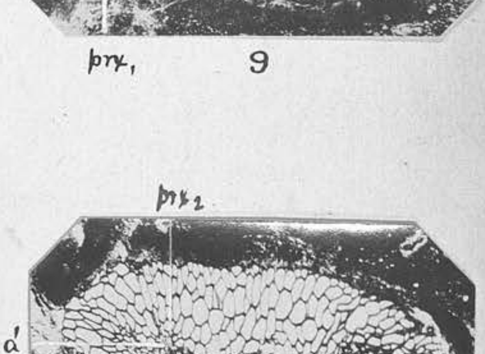

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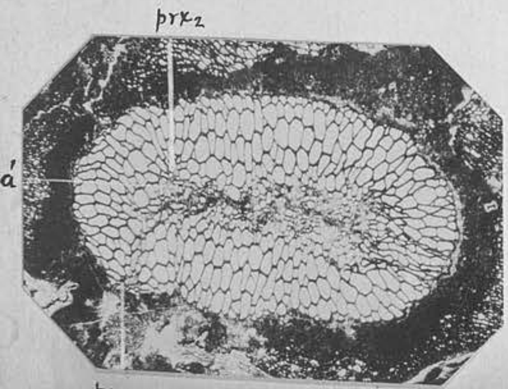

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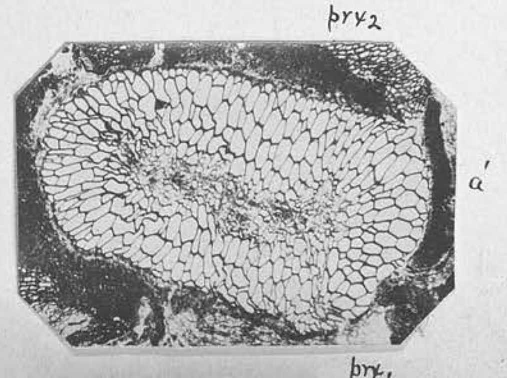

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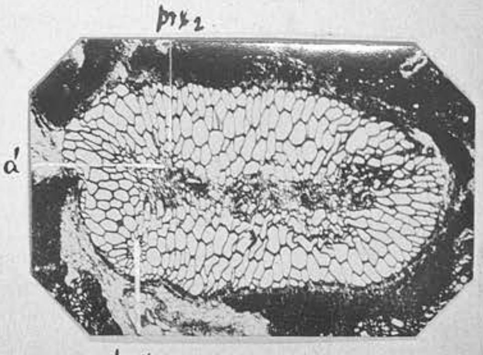

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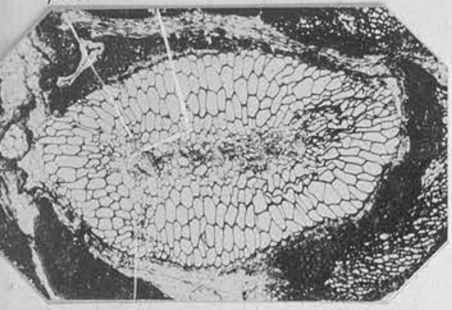

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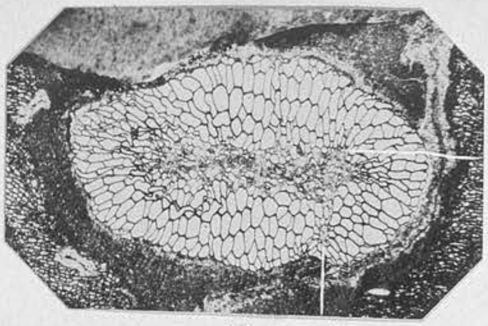

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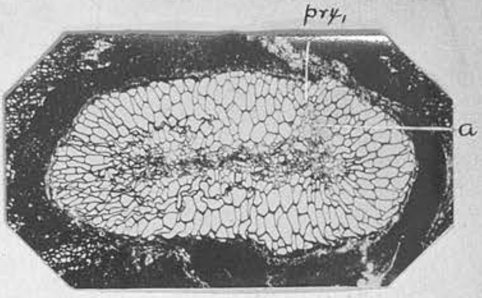

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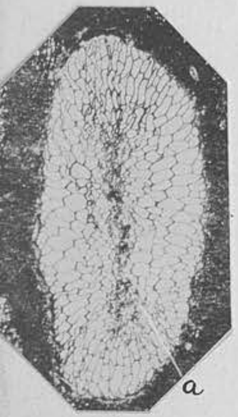

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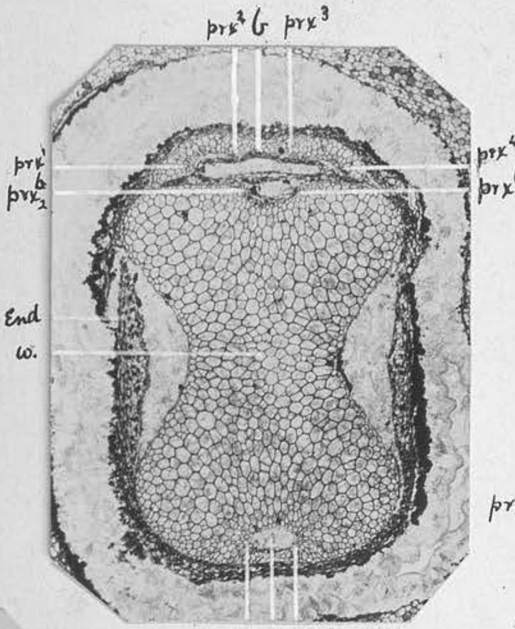

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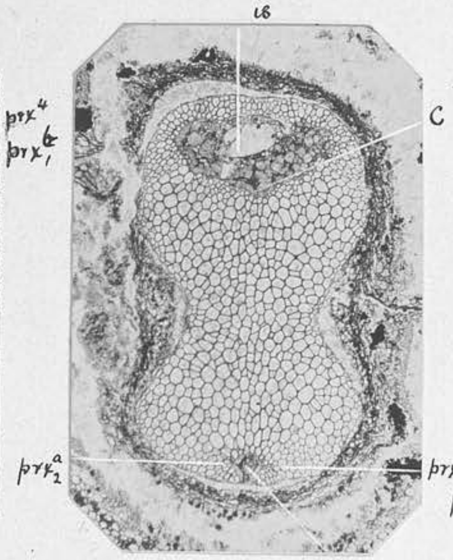

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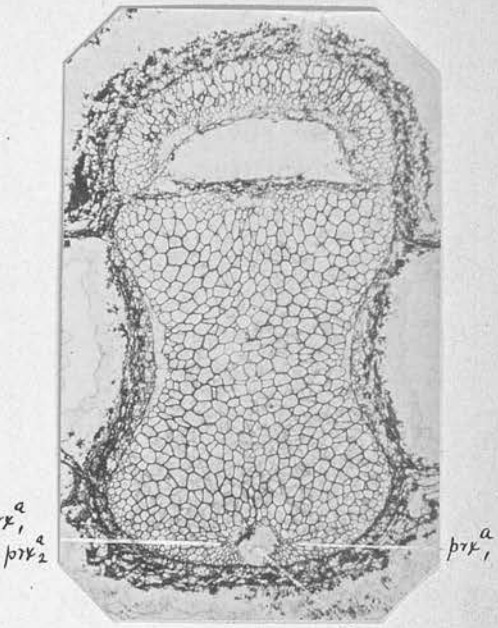

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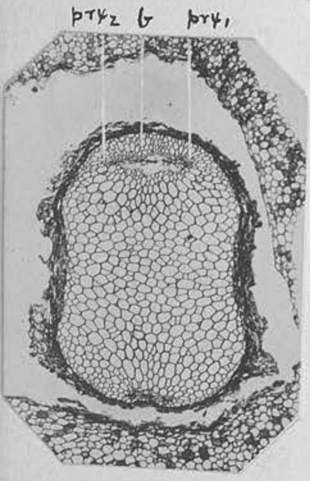

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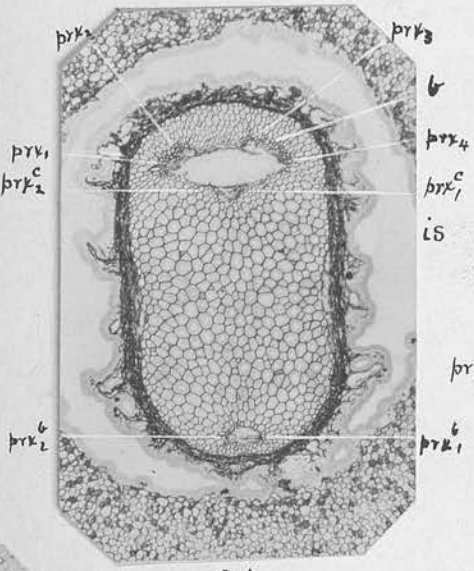

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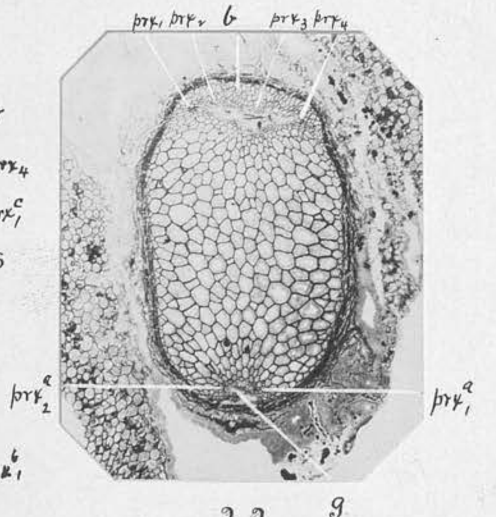

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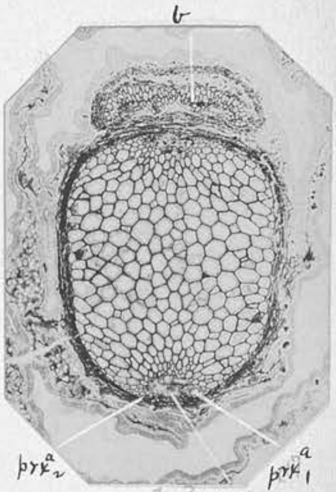

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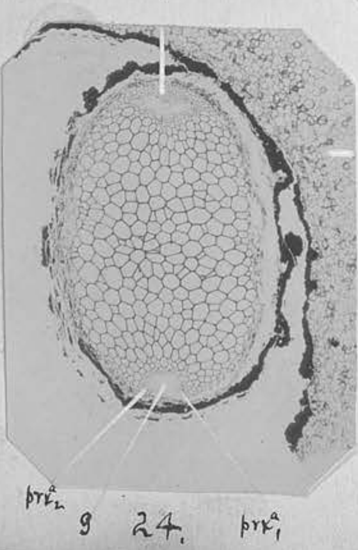

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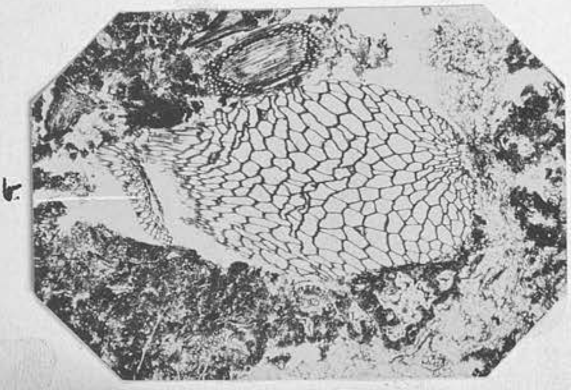

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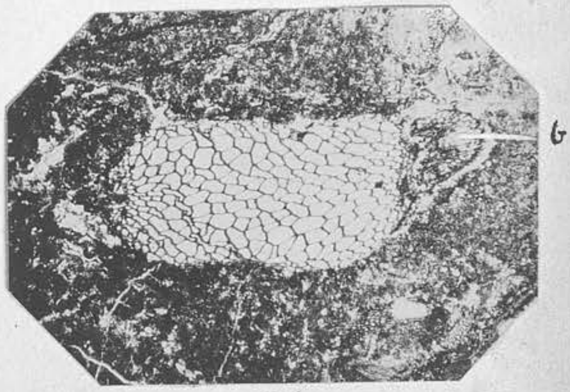

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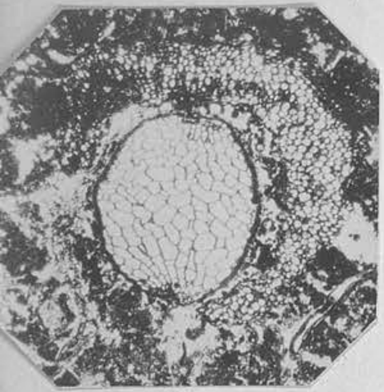

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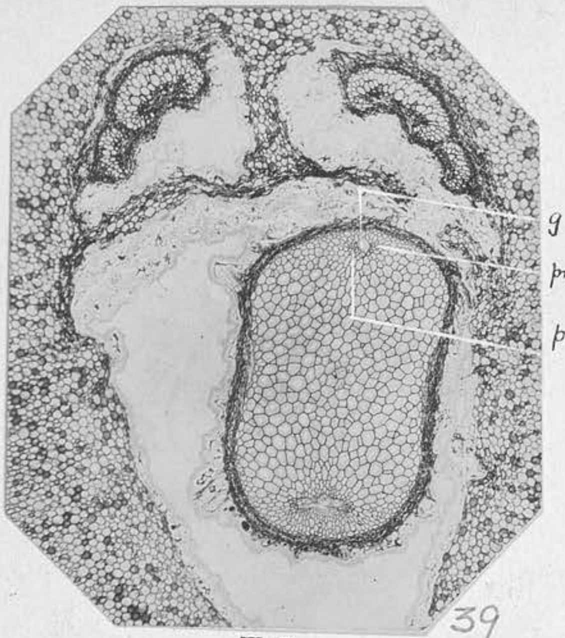

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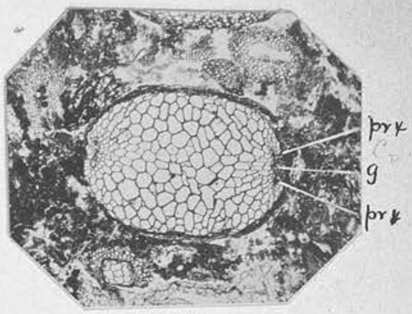

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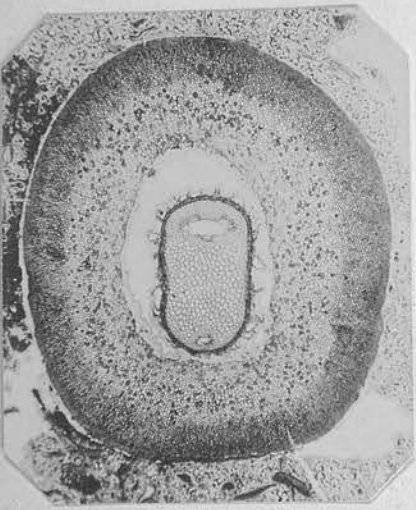

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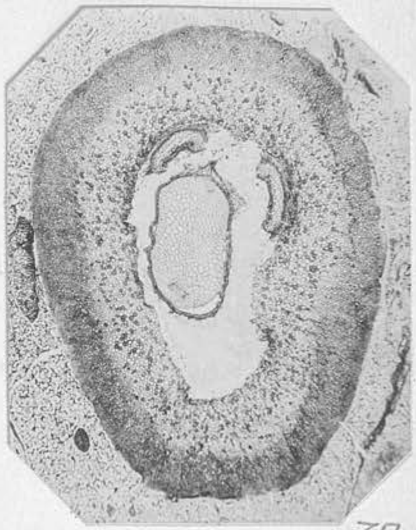

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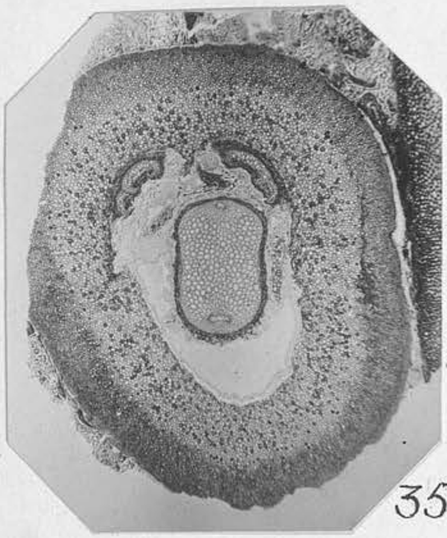

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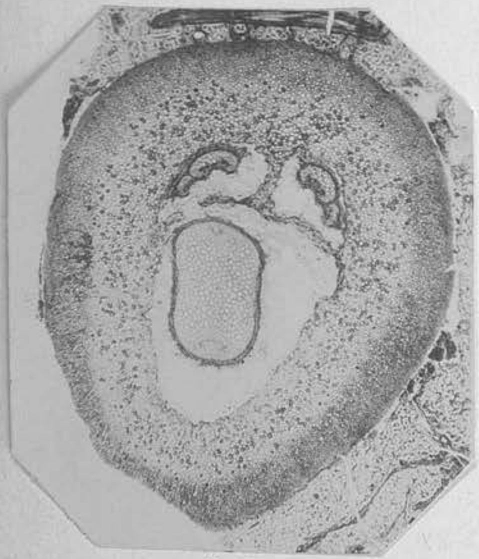

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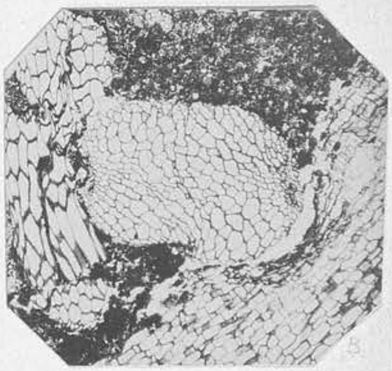

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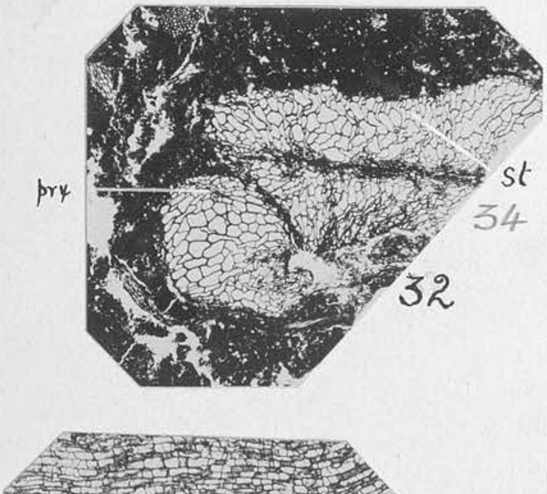

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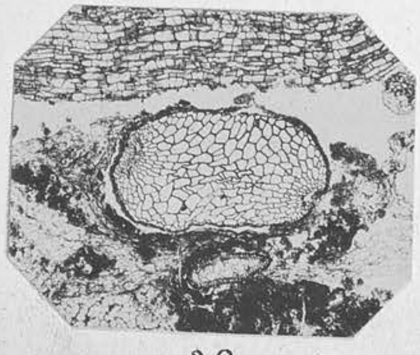

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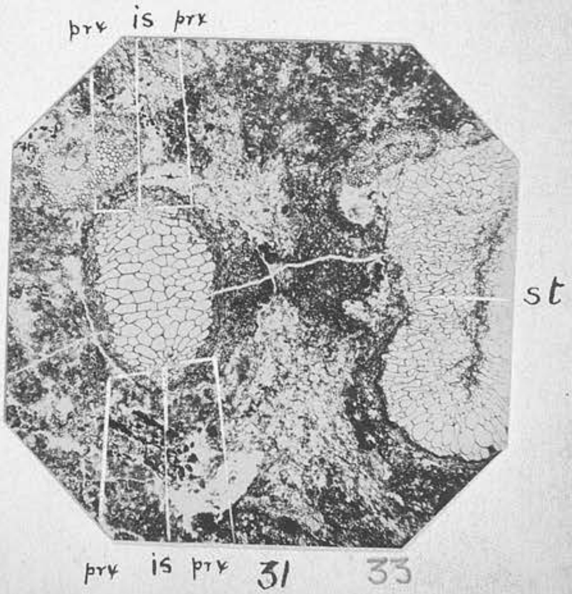

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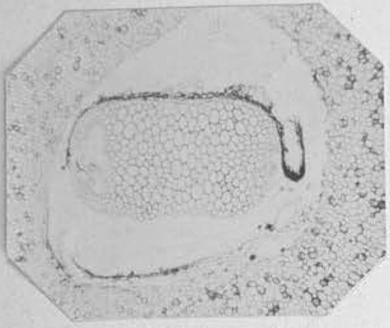
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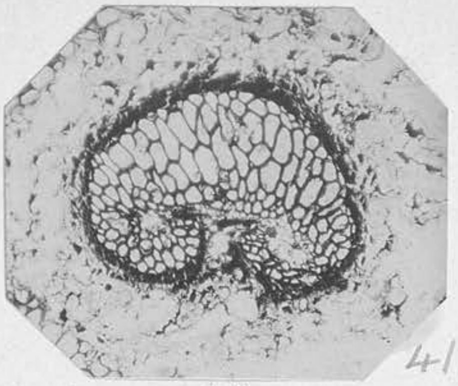
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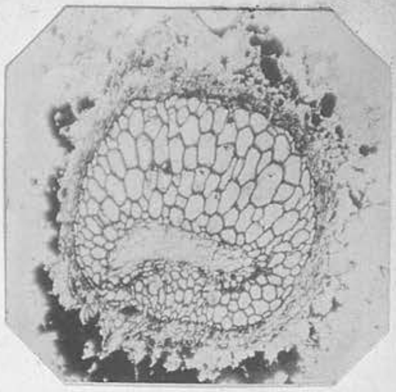
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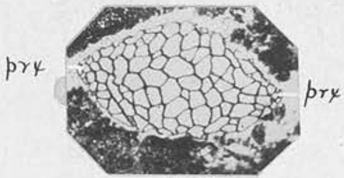

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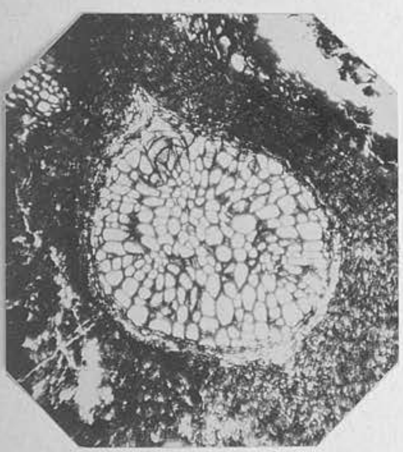
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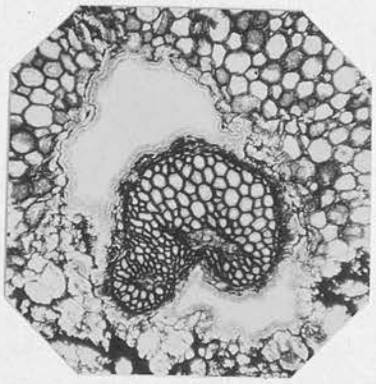
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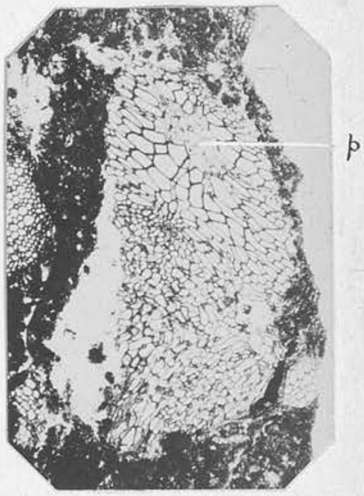

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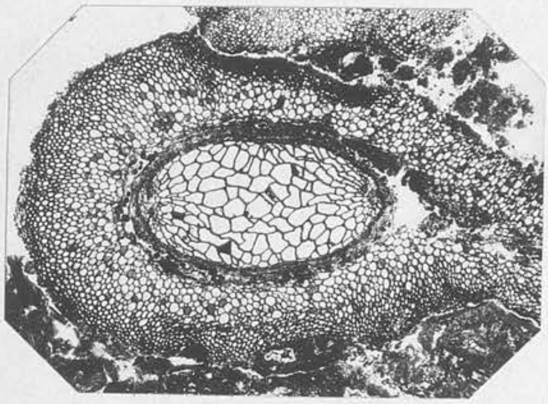
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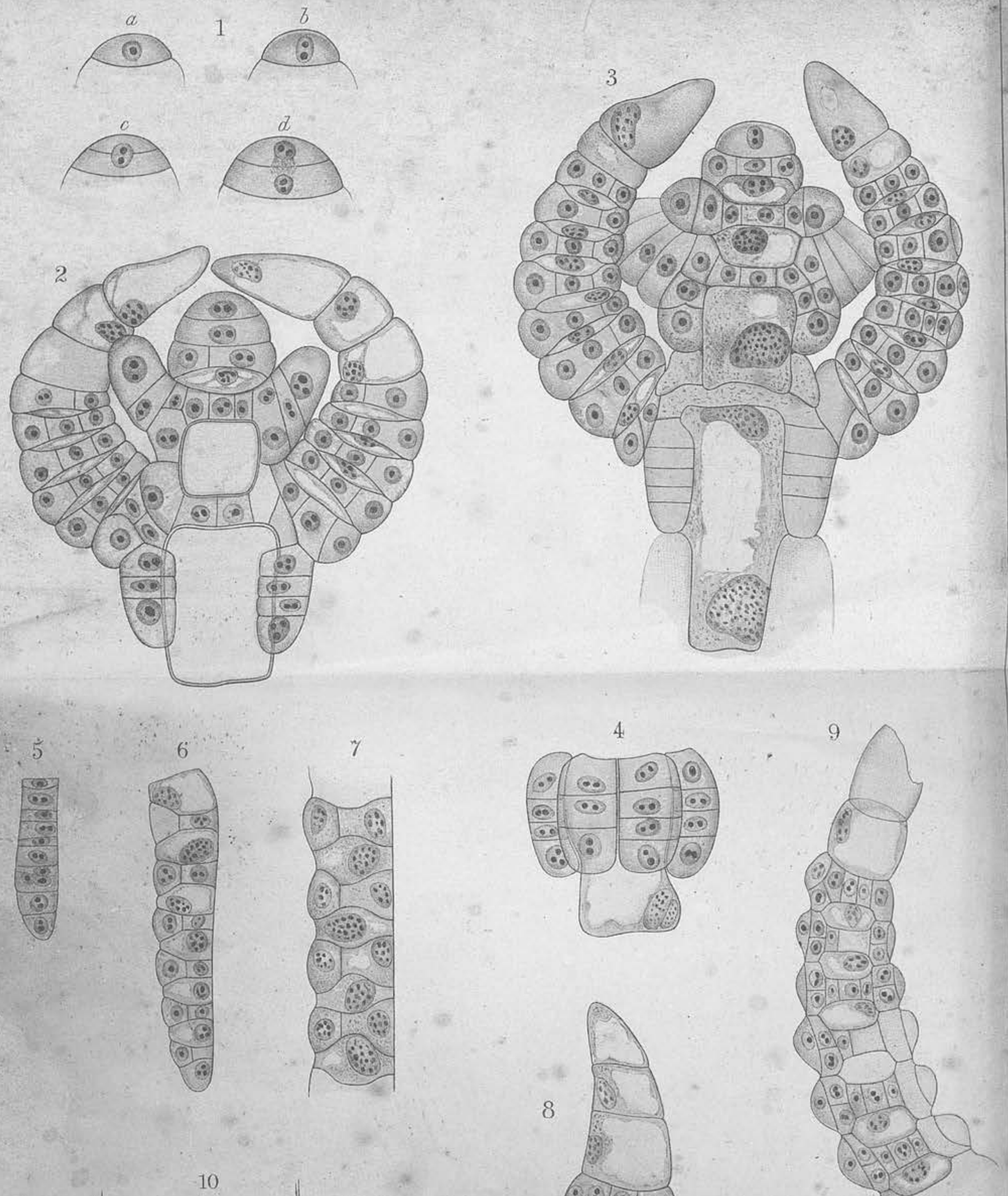

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TRANSACTIONS

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ROYAL SOCIETY OF EDINBURGH.

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ON THE STRUCTURE AND AFFINITIES OF DIPLOLABIS RÖMERI (SOLMS).

BY

W. T. GORDON, M.A., B.Sc., B.A.

[With Four Plates.]

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XXIV.—On the Structure and Affinities of Diplolabis römeri (Solms). By W. T. Gordon, M.A., B.Sc., B.A., Falconer Fellow of Edinburgh University, Lecturer in Palæontology, Edinburgh University. *Communicated by* Professor JAMES GEIKIE, D.C.L., LL.D., etc. (With Four Plates.)

(MS. received November 4, 1910. Read December 20, 1909. Issued separately February 4, 1911.)

CONTENTS.

INTRODUCTION.

Probably the commonest type of foliage among the impressions of Carboniferous plants is one which simulates that of our living ferns. These palæozoic fronds were originally believed to belong to the true ferns, but recently some of them have been taken from this group and included in the Pteridospermeæ. There remain, however, a large number of fronds the true affinities of which are yet doubtful. Thus, though there are still a considerable number of species which belong to the ferns, the number of doubtful examples and of those now definitely known to be pteridospermous far exceeds the number of those attributed to the Filices. Indeed, we cannot now consider the latter group to have been dominant during the Carboniferous epoch.

What is true of the carbonised impressions is equally true of the petrifactions. In the petrified specimens, however, it is rather easier to determine which are likely to belong to the fern group and which are not. It was among these petrified examples, indeed, that the first indications of the Pteridospermeæ (Cycadofilices) were detected, and it was also from petrified specimens that the seed habit among fern-like plants was demonstrated.

There are several well-marked genera among the ferns[*] of Carboniferous times, and recently a great deal of attention has been devoted to this group. Mr ARBER (1) has instituted the group of the *Primofilices* to contain the ancient palæozoic ferns such as the Botryopterideæ and Zygopterideæ. Dr SCOTT, Professor BOWER, and others have discussed the relation of palæozoic ferns to recent forms, showing how they may be classified, and that that classification is in harmony with the geological evidence.

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[*] The Botryopterideæ, though very different from modern ferns, are generally classed with the Filicales. Under that name (Botryopterideæ), two very distinct orders are placed, viz.:—Botryopteris and Zygopteris. The differences between these, however, seem too great to allow of their inclusion in the same order. In what follows I use the terms Botryopterideæ and Zygopterideæ as representing orders which are as distinct from one another as, say, that of the Osmundaceæ is from either of them.

Dr Kidston and Professor Gwynne-Vaughan have worked out a scheme of evolution among the Osmundaceæ founded upon the hypothesis that the original representatives of that order had solid woody axes, and this is receiving much support from a comparison with other groups. The specimen described below has also a very distinct bearing on this question.

All the above-mentioned recent research has been from an evolutionary and taxonomic standpoint, with the intention of clearing up many of the difficulties continually met with in studying a flora which is at best fragmentary.

The classification of palæozoic ferns has been attempted from two standpoints. M. Paul Bertrand (2), who has just published an exhaustive treatise on the *Zygopterideæ*, has taken the form of the petiole-trace as his basis of classification, and has demonstrated five distinct series among the members of that order. He does not, however, lay much stress on the anatomy of the stem. As few zygopterid stems are known at present, this classification founded on the petiolar structure is quite a feasible one. As our knowledge of the stems of this order increases, modifications may have to be made in his scheme.

In their work on the fossil *Osmundaceæ*, Dr Kidston and Professor Gwynne-Vaughan (6) have called attention, on the other hand, to the nature of the stem structure. They show that the stems of the older members of that order exhibit characters which may be regarded as primitive, such as the absence of any pith in the centre of the stele and the protostelic departure of the leaf traces. The fossil *Osmundaceæ* can thus be arranged in an ascending series, and their occurrence in geological time corresponds with their position in this series. A parallel development can be demonstrated among the *Lepidodendreæ*. In the zygopterid alliance, however, no such series has been established; but, as these authors remark,* "if the zygopterid line of descent is at all close to the Osmundaceous, we must be prepared for the existence of a *Zygopteris* with a solid xylem like that of *Thamnopteris*, the central elements consisting entirely of short tracheæ without any parenchyma. Such a discovery, in fact, we hopefully anticipate."

In this paper it is proposed to describe a zygopterid stem which satisfies the requirements of the above prediction. Some specimens of a portion of the petiole belonging to this fern have been recorded previously, but these fragments have not been sufficiently long to give an adequate idea of the complete structure even of the petiole itself. Of course, specimens of fossil plants showing all their various members in organic continuity are of the rarest occurrence, but I have been fortunate enough in this case to obtain specimens exhibiting stems, petioles, and roots in actual connection with one another.

Zygopterid stems and petioles have been obtained from several different horizons, but the specimens described here were derived from the lowest of the great Carboniferous subdivisions—the Calciferous Sandstone Series (Culm)—to which the rocks at Pettycur belong. The petrifactions occurring at Pettycur are either found lying loose

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* K. and G.-V., *Trans. Roy. Soc.*, Edinburgh, vol. xlvi. pt. iii., pp. 663, 664.

on the shore, or, as has been demonstrated,* embedded in the overhanging cliffs. Some of my specimens were obtained from loose blocks, while others occurred *in situ* in the agglomerate which forms the cliff near Pettycur House. I have collected two large blocks (one being about 1 ft. 6 ins. × 1 ft. × 1 ft., and the other 1 ft. × 9 ins. × 6 ins.), and a small rounded fragment about 6 ins. diameter, containing petrified specimens of this plant. I have further been able to obtain numerous detached petioles and pinnæ of the fern from the agglomerate at Pettycur House. All these specimens, with the exception of one of the first-mentioned blocks, were obtained *in situ* in the cliff. The plant petrifactions were more or less continuous in the blocks, and thus it was possible to prepare long series of sections illustrating the structure of the various members of the plant. These sections were cut approximately at equal distances from each other, the interval between the sections being from $\frac{1}{10}$ in. to $\frac{1}{12}$ in., though in some cases it did not exceed $\frac{1}{16}$ in. In general, the changes in the specimen from section to section are not rapid. The slides examined, which number about 250, were prepared either by myself or by Mr F. PHILLIPS of the Sedgwick Museum, Cambridge, under my supervision. From one petiole 55 slides were prepared *in series*, but even that number was not sufficient to illustrate completely all the stages in the change of form of the petiole-trace. The various series which were prepared overlap so much, however, that there is no doubt of the stages described below, each series serving to check the others. The extent of the overlapping is indicated in text-fig. 1.

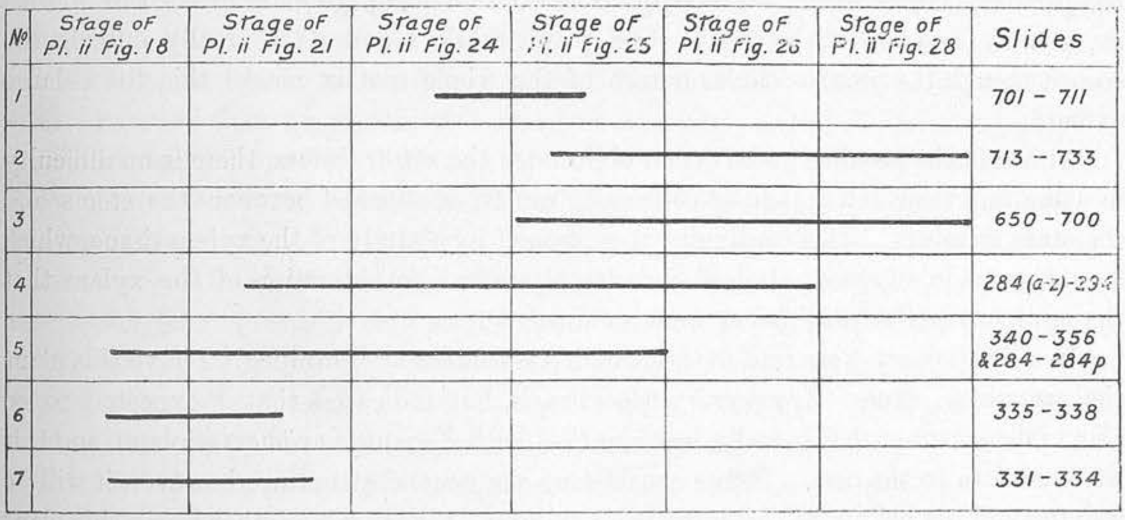

FIG. 1.—Diagram illustrating the amount of the overlapping in the various series of sections cut from the petiole-trace of *Diplolabis römeri*.

The mode of preservation of most of the specimens is somewhat peculiar. The xylem elements are generally clearly preserved, but the thin-walled tissues of the cortex are not as a rule well petrified. Even in the xylem elements the crystallisation of the calcite has often distorted the walls. In the softer cortical tissues, the spherules of calcite

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* GORDON, *Trans. Geol. Soc.*, Edinburgh, vol. ix. pt. iv., 1909.

growing from the centres of crystallisation have so distorted the cells that the latter have become completely disintegrated. When the small spherules had grown out so as to touch each other, the carbonaceous matter from the ruptured cortical tissue was imprisoned between them, and thus a pseudo-cellular structure was produced. Each individual spherule resembles a cell, but careful examination shows that the outlines are not really cell walls. This has occurred throughout the whole block, so that, at first sight, the entire mass appears to be a continuous cellular tissue with various xylem-strands traversing it. Closer examination, however, reveals the true nature of the pseudo-cellular structure, and shows that the various strands really belong to separate and distinct plant fragments. Plate I. fig. 11, illustrates this structure exceedingly well. At first sight, the strands *st.*, *pet. tr.*, *rt. tr.*, *z* and *z'* are all apparently set in a continuous parenchymatous tissue, but a comparison with Pl. I. fig. 10 shows that the strands *st.*, *pet. tr.*, and *rt. tr.*, belong to one plant, while *z* and *z'* are really outside the cortex, though the pseudo-cellular nature of the whole matrix masks this to a large extent.

Although the peculiar preservation obliterates the softer tissues, there is no difficulty in delimiting their extent, and so continuity can be established between the stems and the other members. This continuity is confirmed by a study of the xylem tissue, which is continuous in all cases. Indeed, it is largely from a consideration of the xylem that the results to be described below were obtained.

In a Preliminary Note read to the British Association at Winnipeg,* I gave this plant the provisional name—*Zygopteris pettycurensis*, but indicated that I expected to be able to demonstrate that it really was identical with *Zygopteris römeri* (Solms), and this has proved to be the case. Before considering the general structure, however, it will be well to recall the history of this interesting species. Like many another fossil, this plant has had a checquered history. In 1892 COUNT SOLMS-LAUBACH (11) gave the name *Zygopteris römeri* to detached petioles with peculiar traces. These specimens were obtained by SOLMS and HERR VOLGEL from the Devonian of Falkenberg. Similar petioles were discovered in the Lower Carboniferous rocks of Esnost in France and called *Diplolabis esnostensis* by RENAULT (8) in 1896. In 1908, M. PELOURDE (7) described a partially disintegrated specimen from Esnost under *Flicheia esnostensis*. This new genus and species is identical with some of my specimens which can be traced into the normal petiole-strand of *Diplolabis römeri*. The five strands are derived by the arms of the trace breaking away from the horizontal bar. An example of a rotted trace comparable with those figured by this author is reproduced in Pl. IV. fig. 46. M. PAUL BERTRAND (2), in 1909, recognised that RENAULT's specimens were identical with those of SOLMS, and has therefore reverted to the original specific name *römeri*, while retaining RENAULT's genus *Diplolabis*. This course I have also followed here.

The specimens from Pettycur are much more complete than those previously obtained elsewhere, and my work on them has convinced me that we are dealing with a

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* *Report Brit. Assn.*, Winnipeg, Section K, 1909.

very primitive type of stem and a petiole-trace which might be placed in several different form-genera according to the relative position in the petiole of the section under consideration. These Pettycur specimens are the first examples of this species recorded from a British source, and are interesting both from a botanical standpoint and on account of their geological age, since this species helps to link up more closely the flora of the Calciferous Sandstone Period in Scotland with that recorded from the Culm and the Devonian on the Continent.

GENERAL STRUCTURE.

The structure of the stem is exceedingly simple. It consists of a fair-sized stele (the xylem being 3 to 5 mm. in diameter), surrounded by a cortical zone whose tissues are not as a rule preserved, though its limits are indicated. A typical transverse section of the stem-xylem is shown in Pl. I. fig. 1; and in Pl. I. fig. 9, *o.c.*, the cortex is delimited by the lighter-coloured area surrounding the stele. The outer cortical zone is rather darker than the matrix containing the specimen, and so the outer boundary of the cortex is quite distinct, Pl. I. figs. 9 to 11, *o.c.* In some specimens the dark outer layers of the outer cortex are preserved, but the cells do not appear to have been sclerotic.

The xylem, however, is usually well preserved, or at least sufficiently so to be traced continuously through the block. Occasionally even the xylem has become partially decayed or disintegrated during petrifaction. As seen in Pl. I. fig. 1, the xylem of the stem is circular in transverse section, and consists of an outer and an inner zone x and x' respectively. The elements of the outer zone, which show a strong suggestion of radial arrangement, are long, pointed tracheides without any admixture of parenchyma. The inner tracheides are short, square-ended, and reticulately thickened; they are very distinct in Pl. I. fig. 7. The two kinds of wood can easily be distinguished, even in transverse section, for the elements of the inner wood are rather smaller in diameter than these of the outer xylem. They are not radially arranged, and the walls appear to have been more delicate, since these are often much distorted even in cases where no distortion is visible in the outer xylem (Pl. I. fig. 1). In longitudinal section the distinction is exceedingly obvious (Pl. I. fig. 5, x and x'). There is no secondary wood.

Diplolabis römeri, in possessing a solid stele with two kinds of xylem elements, closely resembles the Permian osmundaceous stem, *Zalesskya gracilis* (Eichwald), or more nearly *Thamnopteris schlechtendalii* (Eichwald). Both of these stems have been shown by KIDSTON and GWYNNE-VAUGHAN (6) to possess an inner and an outer xylem. In habit, however, *D. römeri* differs from these osmundaceous specimens, for its stem was long and often branched, while appendages were given off only at long intervals and not in a close spiral. Indeed, the whole appearance of the stem of this plant strongly suggests that it was a rhizome. Numerous petioles of *Diplolabis römeri* occur associated with the stems described above, and in some cases such petioles can be traced into the stem. In the normal petiole the trace is **X**-shaped, or the two sides of the **X** may be separated by a horizontal bar of xylem **)—(**, or the trace may become quite

H-shaped by the two arms on each side leaving the horizontal bar at 90° (Pl. IV. fig. 42). At intervals pinnæ depart from these petioles, and, except in a few details, the departure of the pinna-traces from the petiole-trace is exactly as RENAULT has stated. His material was not complete enough, however, to show these details. In the Pettycur specimens I find that, shortly after the departing pinna-trace-bar* (Pl. IV. fig. 42 *b*) has left the petiole-trace (and while still in the cortex of the petiole), it divides up into several traces. The division is probably into two and then into four. Of these four traces, the two extreme are smaller than the two mean. The large median strands soon become C-shaped and pass out into the pinnæ. Pl. IV. fig. 42 shows the xylem-bar departing from the petiole-trace, while Pl. IV. figs. 43, 44, 45, 47, and 48, *pin. tr.* show the pinna-trace at different levels.

The smaller traces on the extremes of the pair of pinna-traces become gutter-shaped or even rounded, and no doubt supplied aphlebiæ. They divide into two in passing through the cortex of the petiole, thus producing four traces which leave the petiole in pairs, one of each pair being derived from each of the original aphlebia-traces. These aphlebia-traces do not enter the pinnæ, but emerge at their bases. No such aphlebia-traces appear at the base of the petioles, but they are found at every normal pinna departure (Pl. IV. figs. 43, 44, and 45, *aph. tr.*). Similar bundles have been recorded by WILLIAMSON (15) as departing at a similar level in the petiole of *Metaclepsydropsis duplex*. He called them "ternary bundles," *i.e.* secondary pinnæ. They are, however, specialised pinnæ, and, by their cortex remaining fixed to that of the petiole and of the pinna for a considerable distance, they would serve both to support the heavy pinnæ to some extent, and to prevent these latter from snapping away from the petiole if the plant were subjected to any strain.

As the two pinna-traces pass slowly out through the cortex of the petiole they diverge, and so, when the pinnæ themselves are free from the petiole, there is an angle of more than 90° between them. This angle increases as they pass out. At the same time, the angle between the plane containing the two pinnæ and the vertical plane † of the petiole is a small one. The open side of the pinna-trace always faces the petiole; and the whole array of secondary pinnæ belonging to each primary pinna, *i.e.* each "spread" of secondary pinnæ, lies in a plane facing obliquely upwards towards the main rachis.

The pair of pinnæ immediately succeeding are on the opposite side of the petiole; the next pair are inserted vertically above the first pair, and so on. There are thus four orthostichies of primary pinnæ, and therefore of secondary pinna-spreads, but the small angle between the plane of the two departing pinnæ and the vertical plane of the petiole, coupled with the large angle between the pair of pinnæ, causes the whole frond to assume a more or less bilateral character (text-fig. 2). It is not bilateral in the sense that all the primary pinnæ face in one direction, for those on one side of the

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* It is convenient to have a special name for the arc of xylem formed by the fusion of the two entering pinna-traces. The pinna-trace-bar (the name explains itself) has been used for this xylem arc.

† See A. G. TANSLEY (14).

petiole face towards those on the other, *i.e.* the petiole rachis is analogous to the stem of living ferns, since the pinnæ face the petiole in the same way that the fronds of modern ferns face the stem.

Each pinna-trace is at first bow-shaped, but the ends gradually turn inwards until they almost meet, thus giving a **C**-shaped trace. An intermediate stage between the bow-shaped and the **C**-shaped trace is shown in Pl. IV. fig. 47. In its subsequent divisions the pinna-trace gives off small bundles from its free ends alternately on each side. These, in turn, continue to divide in a similar manner. The ultimate branchings of the pinnæ, the foliage, and the sporangia of this interesting fern are unknown, though Renault referred certain synangia to *D. römeri* on the grounds of association. Mere association cannot, however, be taken as a criterion of any relationship between plant members which are discovered detached.

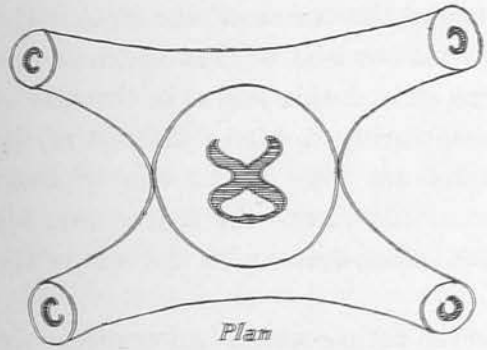

Fig. 2a.

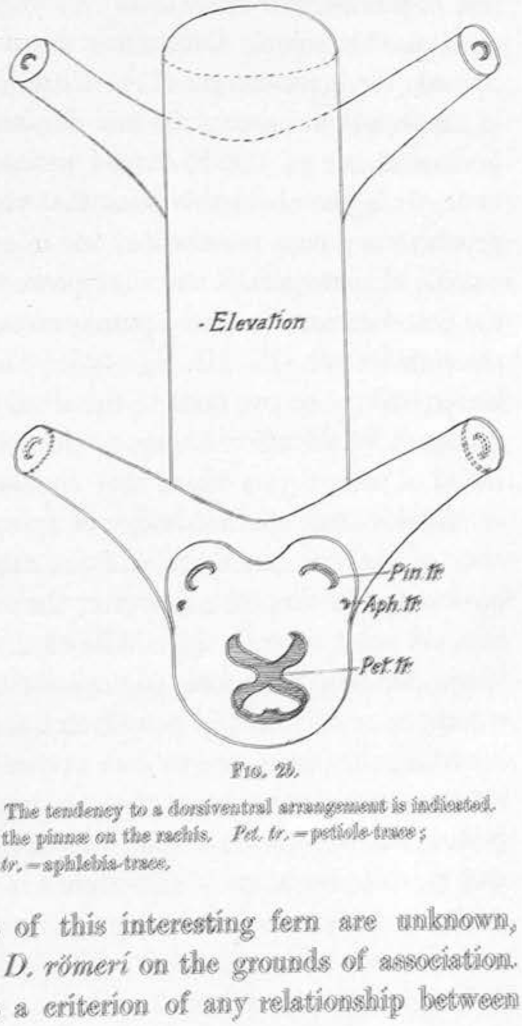

Fig. 2b.

Fig. 2a.—Plan of the pinnæ on the rachis of *Diplolabis römeri*. The tendency to a dorsiventral arrangement is indicated.
Fig. 2b.—Elevation showing the vertical arrangement of the pinnæ on the rachis. *Pet. tr.* = petiole-trace; *pin. tr.* = pinna-trace; *aph. tr.* = aphlebia-trace.

Turning now to follow this petiole into the stem, we find that at a lower level of the petiole the parts corresponding to the vertical lines of the **H** bend outwards until the angle made by each of those four arms and the horizontal bar of the **H** becomes over 150° (Pl. II. fig. 27).

Each of these arms has a protoxylem group near its apex on the inner side (Pl. II. fig. 27, *prx.*). At this point the strands of a pair of reduced pinnæ join together, and the single bow-shaped strand thus formed then joins on to the **)—(**-shaped petiole-strand, bridging over the space between the two arms on one side of the petiole-trace and enclosing an island of parenchyma between the entering pinna-traces and the two arms. The island then becomes smaller in size and the xylem-bar divides in the centre, one half disappearing gradually into each arm. The diminishing size of the arms in proportion to the horizontal bar is very marked at this stage (Pl. II. fig. 26). Another pair of traces of reduced pinnæ enter at a still lower level, and again a bridge is formed, but the island now enclosed is very small indeed compared with that enclosed by the pair of pinna-traces immediately above. The petiole is still free from the cortex of the stem at this point. Continuing downwards, this second bridge is seen to bend in towards the inner margin of the island (Pl. III. fig. 40), which thus becomes reniform in shape, and ultimately the middle part of the xylem bridge fuses with the end of the horizontal bar of the **H**-shaped petiole-trace, cutting the island of parenchyma into two. It is just about this point that the petiole enters the cortex of the stem. The protoxylem groups are situated one in each parenchymatous island. The xylem on the outside of these islands now disappears into the arms on each side just as in the case of the first-mentioned reduced pinna-traces, but, in disappearing, it leaves the end of the trace tridentate (Pl. III. fig. 34). The three arms are very short: two of them correspond to the two arms of the trace higher up, and the third—the central arm—is produced by the union of part of the entering reduced pinna-traces with the base of the island of parenchyma which they enclose.

At this stage another bridge of xylem joins into the petiole-strand and connects the ends of the two outer arms of the tridentate end; thus a reniform island is again produced. In this case, however, the two extremities of the island are on the inner side, *i.e.* point towards the middle of the petiole-trace, whereas, in the former reniform island, the two extremities pointed out from the trace. At least one protoxylem group enters the trace with this new strand, and so there appear to be three protoxylem groups bordering the island, one at each extremity and the third in a median position at the apex of the island (Pl. III. fig. 31, $prx._1$, $prx._2$, $prx._3$). Further down, the two inner protoxylems fuse, and thus the tongue-like central arm of the trace disappears. In this way an elliptical island is substituted in place of the reniform one. The trace meanwhile has become rather shorter and more dumb-bell shaped. The island of parenchyma soon dies out, and we are left with a double protoxylem group sunk in the xylem at each end of the dumb-bell shaped trace (Pl. II. fig. 21). The trace now becomes shorter and more rounded, while the double protoxylem groups unite in pairs. This takes place at each end of the trace, and so we have now one sunk protoxylem group at each end of an elliptical xylem. Immediately below this level the trace joins on to the stem without any gap being formed in the outer xylem zone of the latter. The petiole-trace gradually disappears into the stem, but the petiolar protoxylems can be followed down into it for a considerable distance before they disappear (Pl. II. figs. 21–16, and Pl. I. figs. 15 and 14).

HISTOLOGY OF THE STEM.

The stem-xylem is of great interest, since it consists of tracheides without any admixture of parenchyma. Further, the thickenings on the walls of all the elements are porose or reticulate, a type which recent work has shown to be the most primitive of all. These reticulate thickenings can be distinctly seen in Pl. I. figs. 5 and 6. The inner zone of the wood, which is composed of short elements, appears to have offered less resistance to crushing strains than the outer zone, and, as a result, its tracheides have generally suffered considerable distortion during petrifaction (Pl. I. fig. 7). These inner xylem elements vary considerably in size; some are two or three times as broad as they are long, while others are much longer than broad; the diameter varies from 100 μ to 120 μ. Where vertical rows of these short elements occur, there is a suggestion that they may possibly have arisen by the septation of long tracheides. No trace of xylem-parenchyma can be detected intermixed with these tracheidal elements, and hence we must conclude that the plant possessed a solid xylem axis, *i.e. the axis was a protostele.* The importance of this will be seen later, when the systematic position of the species is discussed.

Towards the outer boundary of the inner xylem narrow scalariform elements may occasionally occur. These are shown in longitudinal section in Pl. I. fig. 8, where the thickenings are clearly scalariform. Such groups constitute the protoxylem, though probably they are petiolar protoxylems which are decurrent into the stem for a considerable distance, and not truly cauline.

The elements of the outer xylem zone are greater in diameter than those of the inner zone, and they consist of elongated, reticulate tracheides with a mean diameter of 160 μ. Towards the periphery the elements tend to become slightly smaller. Sometimes groups of small elements can be detected, as in Pl. I. fig. 15, *prx.*; these are the protoxylems of a petiole-trace which is being differentiated from the stem, and which will become detached higher up the stem. As mentioned above, these protoxylem groups die out as they pass downwards into the stem, but only after they have reached the boundary between the outer and inner xylem zones. Owing to the pseudo-cellular structure previously referred to, the tissues outside the stem-xylem are almost entirely disintegrated. There is no trace of phloëm or of inner cortex that would warrant more than a passing notice, but small patches of the outer cortex are undoubtedly preserved. This outer cortex has no special features. It consists of a thick-walled parenchyma, but it contains no sclerotic layers.

From the stem there depart, at intervals, petioles and roots. The distance between the points of emission of any two petiole-traces is considerable. In no case, however, is the outer xylem-ring of the stem ruptured by such emissions, so that the inner xylem takes no part in the formation of the leaf-trace, *i.e.* these organs leave the stem in a protostelic manner. The roots are quite irregular in their distribution, as can be observed in Pl. I. figs. 9, 10, and 11, where photographs of three successive sections are shown. These sections were cut rather thicker than usual, and they are about $\frac{1}{8}$ in. apart. In the first (fig. 9) a root (*rt.*) is passing towards the upper part of the figure from the left-hand lower corner: in the second (fig. 10) another is observed about to depart from the centre of the right-hand side (immediately below the petiole in the drawing, but really above the departing petiole-trace); while in the third (fig. 11), the root shown in the last figure is seen detached though still in the cortex of the stem, and another root is seen going towards the lower left-hand corner. This irregular distribution of the roots will be referred to again when we discuss the question whether the stem was a rhizome or an erect aerial shoot.

Branching of the Stem.

Several stems were examined, and in some cases they continued for a considerable distance. In one case, continuous serial sections were cut for nearly seven inches without reaching either end of the specimen. In the case of other stems occurring in the same block a considerable length could be followed, but the preservation was very bad. In these last examples, gaps occurred in the xylem-tissue, and in places it had all decayed away, though the same stem could be again recognised a few sections further on. In the parts of the stem which were continuous, branchings were sometimes met with, and in all cases the branching was dichotomous. Even at these bifurcations the outer xylem-ring remains unbroken, so that every departure from the stem, whether of root, petiole, or branch, is protostelic. In Plate I. figs. 1 to 4, the various stages of the branching are figured. The first figure shows an almost circular cross-section of the stem-xylem, with no sign of an approaching bifurcation. In the next section the xylem becomes elliptical in shape and much larger. The inner zone increases in size along with the outer, and forms an ellipse concentric with that formed by the outer zone. In the following section (fig. 3), the inner xylem has become contracted in the centre and thus assumed a dumb-bell shape, while the outer xylem remains elliptical. At the next stage the outer xylem also becomes dumb-bell shaped, and the inner xylem divides through the middle into two groups (fig. 4). The outer xylem of the stem is here 8-shaped with the inner xylem in the loops of the 8. With the outer xylem dividing through the middle, two equal branch strands are produced. It is interesting to note that the inner xylem never, on any occasion, abutted directly on the periphery of the stele. It will be seen that this branching is distinctly *protostelic*, and also that it is a true dichotomy. In one case examined, the inner xylem showed a tendency to diminish in size just before the bifurcation, and in one of the branches of this particular dichotomy there is an almost entire absence of inner xylem for a short distance above the point of bifurcation. In no case, however, is there any branch gap.

HISTOLOGY OF THE PETIOLE.

A typical transverse section of the xylem of a petiole is figured in Pl. IV. fig. 42. This may be taken as the normal Diplolabis petiole-trace as described by RENAULT.*

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* "Bass. houill. et perm. d'Autun et d'Épinac," pp. 17 and 18, *Gîtes minéraux*, 1896.

This xylem consists of a short rectangular central portion—the horizontal bar of the H—,* and four arms, one arising from each angle. These arms are thinnest where they join on to the horizontal bar of xylem, and they become considerably broader near their free ends. At their extremities, however, each arm tapers sharply and ends in an acute claw-like portion which is bent almost at right angles to the arm. The smallest elements are found in the sinus formed between the arm and the claw-like end. These claw-like ends are the beginnings of a pair of pinna-traces. They are not present just after the pinna-trace-bar (such as *b*, Pl. IV. fig. 42) has departed from the petiole-stele. At the departure of the pinna-trace-bar the ends of the arms are blunt (Pl. II. fig. 29, and Pl. IV. fig. 42). In the latter figure—fig. 42—the blunt ends are indicated at *a*, *a*, but the bar *b* is only completely detached from the arms two sections higher up the petiole. The arms face one another in pairs, and so each end of the trace resembles a pair of engineers' calipers, more or less closed, according as the pinna-traces are completely developed or not. In the figure referred to above (fig. 42), the space between one pair of arms is completely bridged over by the pinna-trace-bar (*b*), which at a later stage breaks away and divides to supply a pair of pinnæ. The pair of arms on the opposite side of the trace are also developing xylem which will ultimately form a complete bridge between the arms. In its turn, this bridge will leave the petiole-trace and give rise to the next pair of pinna-traces. This side of the petiole-trace shows remarkably well that each arm contributes equally to form the bridge (fig. 42, *c*, *c*). In Pl. II. fig. 29, another specimen is shown where there are no bridges between the arms, but the main trace is exactly similar to that of Pl. IV. fig. 42. This figure (29) represents a section at the outer end of a series (No. 3, text-fig. 1) which we shall follow in towards the stem. It is therefore a very important illustration, since the whole interpretation of the specific character of this plant depends on the identity of the petiole of fig. 42 with that of fig. 29. In another series, similar to No. 3, text-fig. 1 (viz. No. 2, text-fig. 1) the last stage shown is just slightly beyond that figured in fig. 29. The chief difference in this series is that a pair of reduced pinnæ are represented by their traces only. These traces are very small, but can easily be distinguished. They can be followed into the petiole-trace; indeed, fig. 28 (from Series 2) is the section where the last appearance of these reduced pinnæ can be detected. The two left-hand arms in that figure are connected by a bar of xylem elements, though it can only be followed in the photograph for a short distance from the upper left-hand arm. The bar is merely a thread one cell deep, but it is complete.

Returning now to fig. 29 and passing down the petiole, the first change to be noted is that the arms diminish in breadth near their outer ends, and remain either equally broad until they taper at their extremities (Pl. II. fig. 28, *d* and 27); or they diminish gradually throughout their length, and then suddenly taper as before at the ends (Pl. II. fig. 26).

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* The horizontal bar is equivalent to the "apolaire médiane" of Bertrand. (Vide *Études sur la fronde des Zygoptéridées.*)

Each arm in Pl. II. fig. 28 is shorter in proportion to the length of the horizontal bar than is the case in fig. 29. Further in towards the stem (Pl. II. fig. 27) the four arms bend towards one another in pairs, and on the right-hand side at p_1 and p_2, two traces belonging to another pair of reduced pinnæ can be distinguished. These two traces are connected together by a thin line of crushed cells, and there is also a connection between the two ends of the double trace and the tapering ends of the adjacent arms. Thus we have in fig. 27 an island of parenchyma formed similar to that in Pl. IV. fig. 42, between the bar *b* and the two arms. In this case, however, the bar is poorly developed, and probably supplied a very reduced pair of pinnæ; the island is not so broad as that in fig. 42.

We have now seen two pairs of reduced pinna-traces entering the petiole, and the only difference between them lies in this, that the lower pair is more rudimentary than the upper. For, in the upper pair, the traces were followed in through the cortex until they joined together, and the united trace became fused on to two adjacent arms. In the lower pair, however, there was no actual fission of the two traces, though the xylem was aggregated into two large groups which were connected to the arms and to one another by a thin filament of xylem cells. Both pairs of reduced traces failed to reach the exterior; they disappeared in the outer cortex. Still continuing downwards, the lower combined pinna-trace disappears gradually into the arms, thus leaving them open. Below this level the arms are still closer than they were before (Pl. II. fig. 26), and they are still shorter in proportion to the length of the horizontal bar, which now constitutes the bulk of the trace. The trace has still, however, a typical zygopterid form, having four arms with a protoxylem group lying at the extremity of each. Still going lower down the petiole, we find the arms are again bridged over by what is probably the xylem-bar of a still lower pair of reduced pinna-traces (Pl. II. fig. 25, *b*). In this case, however, there is no evidence that the connecting bridge of the xylem was ever aggregated into two groups, but it remains as a thin strand one cell deep between the arms. Since the arms have become shorter, as indicated above, the island of parenchyma between the two arms and the connecting xylem bridge is very small.

Before proceeding further, we had better recapitulate the results derived from following the petiole-trace downwards. The arms of the petiole-trace have been reduced in length compared with the horizontal bar, they have arched over towards each other in two pairs, and they have lost the dilatations at their extremities. Three pairs of reduced pinna-traces have been met with, and each pair is more rudimentary than the pair immediately above. We have now reached the stage represented in Pl. II. fig. 25.

Continuing inwards, the bridge shown in fig. 25, *b* bends in at its centre towards the end of the horizontal bar (which now constitutes almost the whole of the petiole-trace). Thus the island formed by the bridge and the two small arms becomes reniform in shape (Plate III. fig. 40). The two ends of the island *c*, *c* point outwards from the petiole-trace. The central portion of the xylem bridge then unites across the centre of the island with the horizontal bar, and thus two small islands are produced (Plate III. figs. 39, 38, and 37, *is.*, *is.*, and Plate II. fig. 24) with a protoxylem group on the inner side of each. The xylem on the outer edge of the two islands now thins out and gradually disappears into the two very short arms (Plate III. figs. 36 and 35), thus leaving the end of the trace open, with a prominence in the middle (fig. 34). The tridentate appearance is still more clearly seen in fig. 33. The petiole now enters the cortex of the stem.

Immediately below the stage in the last figure, yet another bridge appears between the two arms (Plate III. fig. 32, *d*). In some of the slides examined, this bridge seemed to give rise to a root-trace, but it was always cut longitudinally, and could never be followed very far out. Whatever the trace belonged to, petiole or root, the bridge again connects the two arms, but it does not fuse with the central pillar of the tridentate end of the petiole-trace (Plate III. fig. 32). The persistence of the prominence causes the island to be reniform and it is concave outwards.

Thereafter the reniform island becomes elliptical in shape (Plate III. fig. 30). This has obviously been derived from the other by the disappearance of the xylem separating the protoxylem groups. It is therefore permissible to conclude that the pillar was originally derived from the division of a protoxylem group, and the subsequent separation of the two parts by xylem-tissue. In the elliptical island only two protoxylem groups occur, one derived from the last trace which joined the petiole, and one from the fused petiole protoxylems. Thus the two protoxylem groups lie in a line parallel to the long axis of the petiole-trace. Up to this point the protoxylems at each end of the trace lay in lines perpendicular to that axis. The island of parenchyma now completely disappears, and the petiole-trace takes the form represented in Plate II. fig. 22, where two groups of protoxylem elements $prx._1$ and $prx._2$ are found at each end of the trace. At the level of this figure the petiole-trace is rather dumb-bell shaped, but, at a lower level, it becomes more rounded in outline, Pl. II. fig. 21. The double protoxylem groups are still, however, very distinct. These double groups eventually fuse into one as in Pl. II. fig. 20, $prx._1$ and $prx._2$. A similar succession can be traced in Plate I. figs. 11, 10, and 9. (The petiole-trace of fig. 11 is shown more highly magnified in Pl. II. fig. 21.) In fig. 10 the trace is elliptical, and has also two double protoxylem groups, one at each end. These double protoxylem groups are closer together than the corresponding groups in fig. 11. In fig. 9, only one protoxylem group is seen at each end, and it is derived from the double group of the petiole of fig. 10.

In Pl. II. fig. 20 the stem is also shown, and, in the section below, the petiole and the stem are fused together. Plate II. fig. 19 represents the second section below fig. 20, and there the petiole-trace is firmly fused to the stem-xylem. We have thus followed the *Diplolabis* petiole of Pl. II. fig. 29 into the stem of Pl. I. fig. 1.

The lowest trace which departs from the petiole is quite close to the point where the latter joins the stem, and among other ferns, *e.g.* the Osmundaceæ, this is exactly where numerous roots occur. This trace, therefore, may quite well be a root.

One point which must be noticed here is that the two ends of the petiole-trace *never show the same stages simultaneously.* The difference in development of the departing traces at opposite sides of the petiole increases as we ascend. At the level of Pl. II. fig. 23, the difference in phase of the traces at the two ends is not great. The ends of this trace are shown more highly magnified in Pl. III. figs. 33 and 41. From a comparison of fig. 41, showing one end of the trace, with fig. 36, showing the other end at a higher level, it will be seen that they are in the same phase. Between these two sections two others were prepared, so that the difference in phase between the two ends of fig. 24 corresponds to about four sections, or $\frac{1}{3}$ in. to $\frac{1}{4}$ in. Near the union of the petiole with the stem the difference in phase is much less. In Pl. I. fig. 10, *pet. tr.*, the only dissimilarity is that one end of the trace has become free from the stem before the other. This difference is always exhibited until the xylem of the petiole has become completely merged in that of the stem, as is shown in Pl. II. figs. 19, 18, and 17, where the top part of the trace is distinctly more merged in the stem than the lower end. In fig. 18 the petiole-trace as a whole is becoming completely incorporated into the stem-xylem, and in fig. 17 the fusion is still more perfect. The petiole-trace has now lost its identity except for the protoxylem groups which are still very distinct ($prx._1$ and $prx._2$).

The stage before fig. 17 is seen in Pl. II. fig. 16, where again the protoxylem groups are distinct ($prx._1$ and $prx._2$). The elongated shape of the whole stem-xylem, the truncated outline at one end, and the two distinct protoxylem groups are the only indications of petiolar departure that can be seen. Pl. I. figs. 15 and 14, represent still earlier stages in the departure of the petiole-trace, and the protoxylem groups are coming to lie almost on the periphery of the internal xylem. At the earliest stages observed, the stem-xylem is slightly elliptical, with two adjacent protoxylem groups lying at the border of the inner xylem. This fact that the petiole is decurrent into the stem for such a long distance makes it impossible to say whether the stem had protoxylem groups peculiar to itself or whether the only protoxylem groups present belong to the petiole-traces.

Among the Botryopterideæ we meet with this same difficulty. Another interesting fact is that, as in the Botryopterideæ, the tracheides of the petiole of *Diplolabis römeri* are larger than those of the stem. The average diameter of a stem tracheide is 160 μ for the outer xylem and 100 μ to 120 μ for the inner xylem. The average for the petiole-trace is 200 μ. This difference in size of the tracheides of stem and petiole is very marked in *Botryopteris antiqua* Kidston.

As mentioned above, the stages of the petiolar departure were examined in more than one series, but no one series gave a complete sequence of these stages. There is, however, a great amount of overlapping (see text-fig. 1), and it has been possible to give an estimate of the distance between the departure of the petiole-trace from the stem, and its assumption of the typical *Diplolabis* form. This distance is between

6·5 ins. and 7 ins. In order to show clearly the early stages of the petiole-trace figured in Pl. II. figs. 21 to 24, and Pl. III. figs. 30 to 34, I have inserted text-fig. 3, where only the petiole-trace outline, the protoxylem groups, and the islands of parenchyma are indicated.

We shall now return to Pl. IV. fig. 42 and examine the departure of the pinnæ from the normal petiole-trace. In that figure two distinct stages of pinna-trace departure are seen. On the left-hand side, the two claw-like projections from the arms are very distinct, whereas, after the departure of a pair of pinna-traces, the extremities of the arms become exactly like those on the left-hand side of Pl. II. fig. 29, with blunt ends, though short claws soon appear as on the right-hand side of that figure.

Since the ends of the arms are enlarged equally in fig. 42, the arms apparently take an equal share in the formation of the pinna-traces. On the right-hand side of fig. 42 the claw-like processes have united in the centre. At *a*, *a* the line of abscission along which the bar of xylem *b* will break away from the arms of the petiole-trace is very distinct. Along the bar itself groups of small cells are easily seen; these are the protoxylem strands, and they are arranged in a perfectly symmetrical manner with regard to each other and to the horizontal plane of symmetry of the trace. When the bar becomes detached from the petiole-trace it breaks up into two and then into four strands. The two inner (Pl. IV. fig. 43, *pin. tr.*), which are much larger than the two outer (*aph. tr.*, *aph. tr.*), are destined to supply the pinnæ. These four strands continue in the petiole cortex for a considerable distance before they diverge into the various organs they supply. In the specimen figured in Pl. I. fig. 12, the traces supplying the two pinnæ can be recognised quite distinctly at the lower end of the specimen, as is proved by sections cut from that end. This means that they continue to travel upwards in the petiole as distinct, separate strands, without showing any change in form, for nearly three inches before they pass out into the pinnæ. In shape the two larger traces resemble that shown in Pl. IV. fig. 47, though at first they are rather flatter (Pl. IV. fig. 43, *pet. tr.*). Higher up they become still more curved (Pl. IV. fig. 44), and finally, in the pinna, form almost a complete ring. Where the secondary pinna-traces are given off from the primary pinnæ, the ring becomes more horseshoe-shaped (Pl. IV. fig. 48).

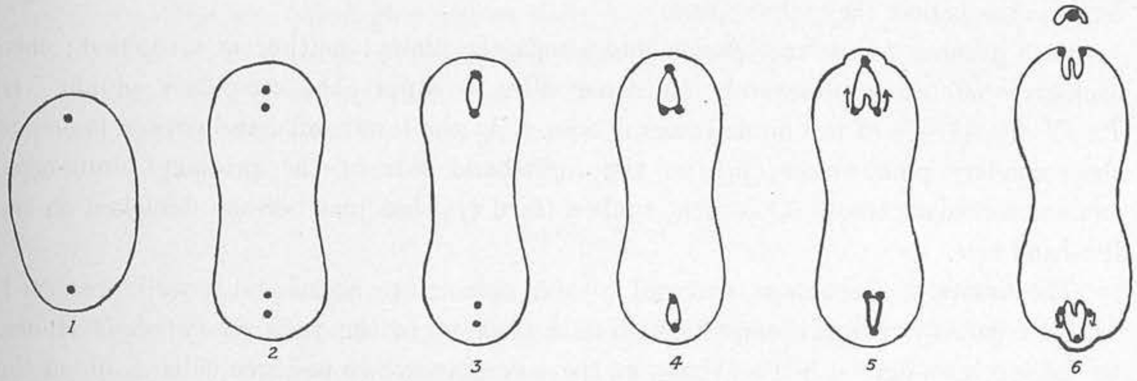

FIG. 3. —Outline drawings of the early stages of the petiole-trace. The protoxylem groups are shown as black dots. The arrows indicate the path of these protoxylem groups as they come to lie at the ends of the short arms.

In Pl. IV. fig. 44 the pinna-traces are cut very obliquely, but it is obvious that they would be almost circular in outline had they been cut transversely. In fig. 45 of the same plate, the section above fig. 44 is shown. The pinna-trace on the right-hand side is cut almost longitudinally as it is passing into the pinna. The trace on the left-hand side has already passed out. These traces really pass out on the same level, but this section is not perfectly transverse.

The smaller pair of bundles, derived by division of the same bar as gave rise to the pinna-traces, are also seen in figs. 44 and 45. In fig. 44 they have each bifurcated (*aph. tr.*). One branch of each bifurcation passes rapidly through the cortex of the petiole to the outside, while the other branches continue for some distance further in the petiole and then they also bend suddenly outwards. The presence of large aphlebiæ in this position supports or buttresses the departing pinnæ, which are each almost as large as the petiole they sprang from.

Each primary pinna-trace passes into a separate pinna; neither is atrophied; then each gives off traces, alternately on either side, to supply the secondary pinnæ. In Pl. IV. fig. 48 one of the pinna-traces is seen. At the lower left-hand corner is one of the secondary pinna-traces (p_1), on the right-hand side of the primary pinna-trace another secondary trace (p_2) is seen, while a third (p_3) has just become detached on the left-hand side.

The tissues of the petiole, external to the xylem, are occasionally well preserved. This is especially true of the specimens found isolated in the tuffs at Pettycur House. In the specimen figured in Pl. IV. fig. 46 there is a layer, two to three cells deep, on the inner side of the arms, which consists of very delicate tissue of small elements. Probably it is due to the xylem of the arms offering some protection to this tissue against decay that it is preserved at all. In the island of parenchyma enclosed by the arms of the petiole-trace we also find the inner cortex to some extent preserved. Outside the layer of delicate tissue referred to, there is a zone of decayed tissue probably representing the phloëm and other stelar tissues. Outside this, patches of cellular tissue are occasionally preserved; these patches consist of delicate parenchyma and are the remains of the inner cortex. One patch is shown in Pl. IV. fig. 46, *i.c.* This inner cortex probably extended all round the petiole stele, filling in the clear space usually seen between the petiole-trace and the outer cortex. The outer cortex forms a stout zone surrounding the more internal tissues, and may be divided into two parts, an inner and an outer. The inner consists of typical thick-walled parenchyma, and the outer consists of sclerotic cells. The sclerotic outer cortex is figured in Pl. IV. fig. 50, and the inner portion of it can be distinctly seen in Pl. IV. fig. 46, and also fig. 43.

HISTOLOGY OF THE ROOT.

The examination of the root has proved less satisfactory. It is small in diameter compared with the stem (Pl. I. fig. 4, *rt. tr.*), but very large for a root. Usually great numbers of these roots are seen detached and scattered all through the block, but one or two examples have been found in continuity with the stem. A typical transverse section is shown in Pl. IV. fig. 49; it consists of an elliptical mass of xylem with a protoxylem group at each end. Like the xylem of the stem and petiole, that of the root consists of scalariform and reticulate tracheides, the former occurring in the protoxylem groups. As has been pointed out, when considering the histology of the stem, these roots appear to rise irregularly and not in definite rows.

Root-like bodies were also noted as occurring near the base of the petioles. Unfortunately, the sections showing these somewhat peculiar traces in this position pass through the petiole transversely, and therefore through these traces longitudinally. They did not extend for any distance, and so all that can be stated with confidence at present is that they were certainly not normal pinna-traces. On the other hand, they may not have been roots, but bundles supplying outgrowths of the petiole base just as similar bundles pass out higher up at the pinna-trace departures to supply aphlebiæ. Further evidence, however, is necessary, and this evidence may be supplied in the future when well-petrified specimens of the stem are discovered. The locality at Pettycur House may possibly yield such examples.

SUMMARY.

The stem of *Diplolabis römeri* is circular in transverse section, and consists of xylem without any conjunctive parenchyma. The xylem is aggregated into an inner zone of short tracheides and an outer zone of long tracheides. The internodes are long and the stem is frequently branched.

The petiole-trace is at first elliptical, with two sunk protoxylem groups, but it rapidly elongates until it resembles that of *Clepsydropsis* in shape. Further up the petiole, the trace is similar to that of *Zygopteris*; but, still higher up, it assumes the form of the normal *Diplolabis* petiole-trace.

The root-traces are barrel-shaped, or elliptical, with a peripheral protoxylem group at each end, *i.e.* they are diarch.

The cortex is not generally well preserved except in the petiole. Two regions may be distinguished in this tissue, an inner and an outer. The outer zone in the petiole is sclerotic towards the periphery. In the stem cortex, however, there is no evidence of sclerenchyma.

Diplolabis, B. Renault, 1896.

The characters of the genus are those of its only species, *D. römeri*.

Diplolabis römeri (*Solms*).

1892. *Zygopteris römeri*, Solms, "Ueber d. in d. Kalks. d. Kulm v. Glätzisch-Falkenberg in S. erhalt. Strukturb. Pflanzenreste," *Botan. Zeitung*, vol. l., 1892.

1896. *Diplolabis esnostensis*, B. Renault, "Bass. houil. et perm. d'Autun et d'Épinac" (fig. 11 *à* 14, pp. 17 *et* 18).

1896. *Rachiopteris esnostensis*, B. Renault, "Bass. houil. et perm. d'Autun et d'Épinac" (pl. xxx. fig. 5 *à* 8).
1896. *Diplolabis forensis*, B. Renault, "Bass. houil. et perm. d'Autun et d'Épinac" (fig. 6 *à* 10, pp. 14 *et* 15).
1908. *Flicheia esnostensis*, F. Pelourde, "Observations sur un nouveau type de Petiole fossile le Flicheia esnostensis, nov. gen., n. sp.," *Mémoires de la Société d'Histoire naturelle d'Autun*, xxi.
1909. *Zygopteris pettycurensis*, Gordon, *Report British Association*, Winnipeg, 1910.

Localities. Devonian of Falkenberg, Culm of Autun, and Calciferous Sandstone of Pettycur, Fife.

DIAGNOSIS.

Stem long, frequently branched, the xylem strand consisting of two kinds of tracheides. Inner tracheides short, square-ended, reticulately thickened and arranged more or less in vertical rows. Outer tracheides long, pointed, reticulately thickened, rather larger than the inner tracheides. No xylem parenchyma present. Xylem strand circular in transverse section and from 3 to 5 mm. in diameter. Inner xylem 1·5 to 3 mm. diameter. Protoxylem groups of scalariform tracheides probably belong to the decurrent petioles and not to the stem itself. They are seen either between the inner and outer xylem, or passing through the outer xylem. Cortex of stem without sclerenchyma. Root-traces very large, barrel-shaped, diarch.

Petiole-trace at first elliptical but gradually becoming **H** or **X**-shaped; the arms inclined at a high angle to the cross-bar of the **H**. Protoxylem groups, of scalariform tracheides, situated one near the apex of each arm, in a sinus. Tracheides of petiole-trace reticulately thickened. Ends of the arms dilated. Pinnæ in four orthostichies. Pinna-traces inserted on the arms of the petiole-trace in pairs. Each pair unites to form a bar of xylem before it joins the arms. Two small aphlebia-traces, one on each side, join the pair of pinna-traces. The four fused strands constitute an arc or bar of xylem which closes over the ends of the two arms. The bar encloses with the two arms a large triangular island of parenchyma. Trace of the pinna horseshoe-shaped, and not unlike that of *Metaclepsydropsis duplex*. Secondary pinna-traces tend to assume the same shape as the primary ones.

Aphlebia-traces branch once, one branch passing out at a higher level than the other. Sporangia and foliage unknown.

CONCLUSIONS AND GENERAL CONSIDERATIONS.

From the characteristic form ultimately assumed by the petiole-traces which arise from the stem described above, there can be no doubt that the stem is that of a *Diplolabis*. The petiole to which this generic name was applied has now been recorded from three localities, from the Devonian rocks of Falkenberg, from the Culm measures of Autun, and from the Calciferous Sandstone Series of Pettycur, Fife. Among the specimens from these localities no characters can be found sufficiently distinct to discriminate the petioles specifically. Even *D. forensis* (Renault) cannot be distinguished from *D. römeri*, or at least, although the original specimens appeared different, there are no characters which might not easily occur among different individuals of the same species. The only difference between *D. forensis* and *D. römeri* is apparently the greater length of the horizontal bar of the trace as compared with the length of the arms, and its consequent relatively thinner appearance. This is exactly the sequence shown in *Diplolabis römeri* in the *same* petiole, as we trace it upwards. Indeed, Pl. II. fig. 28, would be called *D. forensis*, and fig. 29 *D. römeri*. I therefore propose to include *D. forensis* under the name *D. römeri*.

I have already mentioned that *D. römeri* had a creeping rhizome, and the evidence on which the assertion is made may be briefly stated here. The grounds for this are (1) the internodes are very long; (2) the stem frequently branches; (3) the xylem of the stem is about 4 mm. diameter while that of the petiole is 6 mm., *i.e.* the petioles are very heavy in proportion to the stem; (4) the pinnæ are arranged in four orthostichies, and the petiole must therefore have been held erect; (5) the roots are given off irregularly and in all directions; (6) there is no evidence of any sclerenchyma in the stem. Taken together, these afford sufficient evidence in support of the contention that the stem was a creeping rhizome, the petioles being held erect as in *Pteris aquilina*.

The elements of the stem-xylem are reticulate tracheides and there is no conjunctive parenchyma. The xylem, however, consists of two zones, the inner of short elements and the outer of long elements. The stem is therefore a good example of a protostele. The elements are all reticulate, and therefore belong to the most primitive type known; but, since there are two distinct types of tracheide in the stem, the latter cannot be considered the most primitive possible protostele. In more primitive stems we would expect to find only one type of reticulate tracheide, namely, the long type, and, in that the tracheides of the inner xylem of *D. römeri* are usually arranged in vertical rows, this more primitive stem is distinctly indicated. It appears as if the short tracheides were derived from long ones, by the latter becoming segmented. The stem-xylem of *D. römeri*, therefore, probably represents a stage in the development, first, of a stele with a mixed pith, and finally of a medullated monostele.

The discovery of a solid zygopterid stem similar to that of the osmundaceous plant *Thamnopteris*—*i.e.* with two types of wood and no xylem-parenchyma—has been foretold by KIDSTON and GWYNNE-VAUGHAN. The stem of *D. römeri* exactly suits this prophecy, and its discovery is a striking testimony to the high probability of the truth of a theory which they have recently elaborated. We would naturally expect to find the most primitive types among the oldest rocks, and the stem of *D. römeri* also bears out this expectation. The plant has been recorded in Devonian and Calciferous Sandstone (Culm) rocks, all of which contain a more ancient type of flora than that of the Permo-Carboniferous series. All the other zygopterid stems belong to higher horizons and are less primitive. Among the Zygopterideæ, the stems of *Ankyropteris corrugata* (Williamson) and *A. Brongniarti* (Renault) show the strongest superficial resemblance to *D. römeri*, but their tracheides are scalariformly thickened, and both possess a parenchymatous pith with a system of internal tracheides. The other known zygopterid stems are still more complicated and distinct. Thus, among the known Zygopterideæ the stem of *D. römeri* is the most primitive in its anatomy, and it is also among the earliest known zygopterids in time.

The position of this genus in the zygopterid alliance is exactly paralleled by that of *Thamnopteris schlechtendalii* (Eichwald) among the Osmundaceæ. In this latter species a solid protostelic stem-xylem is also present, but again it is not the most primitive stele conceivable on theoretical grounds. The internal short tracheides are reticulately thickened, but the outer long elements have multiseriate pits on their walls. Probably more primitive examples of the Osmundaceæ possessed porose or reticulate tracheides.

We have seen that the shape of the trace at different levels in the petiole is very distinct. If sections cut near the base of the petiole were compared with sections cut higher up, they would be classed in different genera according to current nomenclature. Of course, it is just at the base of the petiole that we would expect ancestral characters to be preserved, and this, I think, is what actually occurs. The trace at first is elliptical, with a sunk protoxylem group at each end, but without any islands of parenchyma. In one specimen examined, this elliptical shape is retained even after the islands of parenchyma do appear, and then the trace bears a strong resemblance to that of *Dineuron*. In all the other examples, however, the trace has become dumb-bell shaped before the islands are present. At this stage (Pl. II. fig. 22) the trace resembles to a great extent that of *Clepsydropsis antiqua*. The single elliptical specimen, on the other hand, is distinctly similar in form to *Dineuron*.

Returning to the normal *Clepsydropsis* stage we find that, at the first departure from the petiole-trace, viz. the trace of the root-like body (or, it may be, very reduced pinna-trace-bar), a constriction forms across the island of parenchyma. On this trace departing from the petiole-trace the end remains open, whereas in *Clepsydropsis* the constriction becomes complete and the departing trace is a closed ring, while the end of the trace is also closed. Further along the petiole, in *D. römeri*, the short arms (Pl. II. fig. 24, and Pl. III. fig. 33), which are formed by the first departing trace leaving the end of the petiole-trace open, become larger and longer until a stage closely resembling that of the normal petiole-trace in *Zygopteris primaria* results. Still passing upwards in the petiole, the arms of the trace become more and more prominent, and the horizontal bar less so, until the normal *Diplolabis* type is attained. In this one petiole, therefore, the trace at different levels is exactly similar to the characteristic petiole-trace in three of the more primitive members of the Zygopterideæ (if we regard simplicity of the xylem of the petiole as synonymous with primitiveness). There are thus the *Clepsydropsis*, the *Dineuron*, and the *Zygopteris* stages. When the stems of any of these three genera are discovered, we shall expect to find that their stem is at least as simple in structure as that of *D. römeri*, and probably more so.

In brief, the changes in the petiole-trace of *Diplolabis*, as we ascend in the petiole, may be stated as follows:—The arms of the **H** or **X** become more and more important in comparison with the horizontal bar the higher we go, until a constant stage is reached. This constant stage we may regard as the normal *Diplolabis* petiole-trace. Thus we cannot regard the *Zygopteris primaria* trace as derived from that of *Diplolabis*, but we must consider the *Diplolabis* trace as having been evolved through a *Zygopteris primaria* stage. It is also clear that the *Zygopteris primaria* stage must come somewhere between the *Clepsydropsis* stage with the arms non-existent, and the *Diplolabis* stage with the arms dominant.

As far as we can judge from the sequence shown in the petiole-trace of *Diplolabis römeri*, the earliest zygopterid petiole-trace must have been elliptical, with two sunk protoxylem groups—one at each end. A petiole with such a trace is, of course, entirely hypothetical; but, if the early stages of the petiole-trace of *Diplolabis* are of any phylogenetic value, such a type must certainly have existed at some previous time. This type we may call the *Protoclepsydropsis* petiole. The stem of this type would have been solid, as in *Diplolabis*, but probably all the tracheides would be of one type. The traces which would depart from such a stem must of necessity have done so in a protostelic manner. If the petioles were given off at infrequent intervals, the general shape of the xylem would be circular in transverse section, *i.e.* similar in outline to that of *D. römeri*. But if, on the other hand, the internodes were short, then a stellate form would be impressed on the xylem, since more than one trace would be shown connected with the stem in any transverse section. M. PAUL BERTRAND has derived the Zygopterideæ from a different type, also hypothetical—the *Eoclepsydropsis*—with a stellate stem-xylem. This stem, however, has a pith, and the islands of parenchyma are shown decurrent into the pith of the stem.* The stem of *Diplolabis* throws some further light on this question, and the *Protoclepsydropsis*, as defined above, seems to be more in accordance with the known facts than the *Eoclepsydropsis*. Further, the *Protoclepsydropsis* comes much nearer to the type from which the Osmundaceæ appear to have been derived, but this will be considered shortly. The relationships of the Zygopterideæ immediately connected with *Diplolabis* may be expressed in the table of text-fig. 4.

From the hypothetical type, *Protoclepsydropsis*, the other zygopterid stems have been derived by the formation of a pith. As has been lately pointed out, the increase in diameter of the stem-xylem probably causes the central tracheides to become functionless as far as water conduction is concerned, though they probably serve as storage tissue. With this change of function the shortening of the tracheides may be correlated. *D. römeri* exhibits this type of stem-xylem. A still further extending of the idea shows how the *Ankyropteris corrugata* type would be evolved from the *Diplolabis*. The tracheides would never be differentiated as such, *i.e.* the cells would remain parenchymatous.

Our conceptions of palæozoic fern genera are gradually becoming clearer, and the work of BERTRAND, KIDSTON and GWYNNE-VAUGHAN, ARBER, TANSLEY, and others have

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* *Études sur la fronde des Zygoptéridées*, p. 261.

indicated that a strong family likeness exists between the *Osmundaceæ*, *Zygopterideæ*, and *Botryopterideæ*. The discovery of the stem of *Diplolabis* has still further strengthened this general position, as it indicates that evolution in the zygopterid stem-xylem was along the same lines as that shown in the *Osmundaceæ*.

In their petiolar structure the *Botryopterideæ* seem to stand much nearer the *Osmundaceæ* than are the *Zygopterideæ*. In *Botryopteris antiqua* Kidston, for example, I find that the petiole-trace has *a single sunk protoxylem group* which lies adaxially in the trace and soon comes to lie adaxially on the periphery of the trace. In its subsequent divisions the trace gives off primary pinnæ in two orthostichies. This is quite similar to the osmundaceous trace, which in general has a sunk protoxylem group on the adaxial side. Gradually the trace opens up on the adaxial side as we ascend until it becomes horseshoe-shaped; the protoxylem strand has meanwhile divided into several branches, all lying on the inside of the horseshoe-shaped trace. Here, again, there are two orthostichies of primary pinnæ.

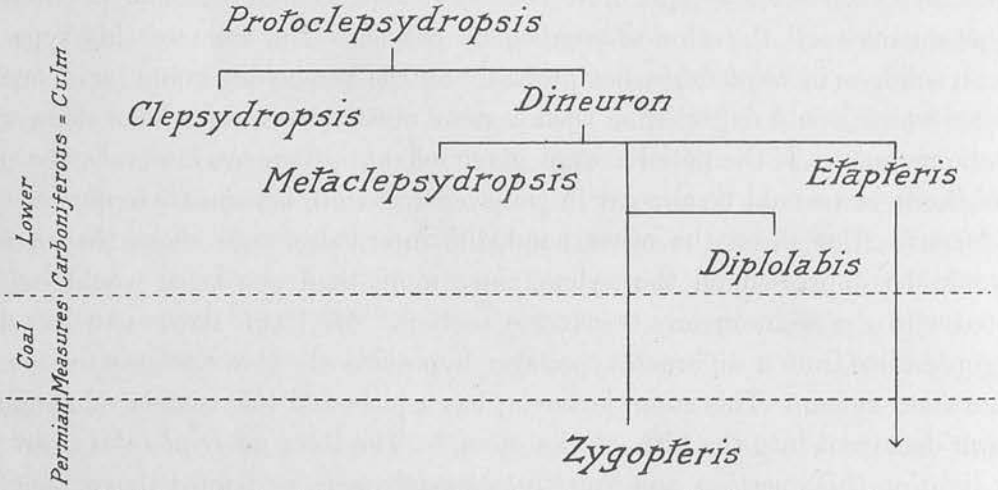

FIG. 4.—Table illustrating the relation of *Diplolabis* to the other Zygopterideæ in which two pinna-traces are derived from a single pinna-trace-bar.

The *Zygopterideæ*, on the other hand, have *two* sunk protoxylem groups in the petiole-trace, and *two* or *four* orthostichies of primary pinnæ. In the cases where there are four orthostichies, the arrangement of the pinnæ on the rachis would not appear to have been very successful, for the pair on one side must necessarily shade the pair on the other side, if the petiole were held flat; if the petiole were held erect, as was the case in *D. römeri*, the higher pinnæ would shade the lower.

The discovery of KIDSTON and GWYNNE-VAUGHAN, that several traces in their specimen of *Thamnopteris schlechtendalii* possessed two protoxylem groups, is exceedingly interesting as connecting the osmundaceous leaf-trace with the zygopterid type of trace. Thus *Thamnopteris schlechtendalii* seems to indicate an ancestral relationship with the *Zygopterideæ*.

In stem structure the *Botryopterideæ* are certainly more primitive than either of the other two groups—the *Zygopterideæ* and the *Osmundaceæ*, though the petiolar structure is not more primitive than that shown in the *Osmundaceæ*. On the whole, the *Botryopterideæ* seems much nearer the osmundaceous type than are the *Zygopterideæ*. Indeed, the *Zygopterideæ* seem to form a side branch from the main line of fern descent, which did not survive into the Mesozoic period. The *Osmundaceæ*, on the other hand, seem to have been a late branch, which was better suited to the conditions prevailing in Mesozoic and Tertiary times, and therefore they have persisted until to-day.

In conclusion, I desire to express my thanks to the many friends who have given me assistance in my work. I am especially indebted to Mr ARBER, under whose supervision I have carried on my research. The Master and Fellows of Emmanuel College, Cambridge, have supplied me with the machinery necessary for the preparation of sections, and Professor T. M'KENNY HUGHES has given me every facility in his laboratory at the Sedgwick Museum, Cambridge. I have also to thank Professor JAMES GEIKIE for similar facilities in Edinburgh University and for communicating this paper. Finally, I am greatly indebted to Dr KIDSTON, Professor GWYNNE-VAUGHAN, and Dr SCOTT for many valuable suggestions and the advice they have given me in this research during the past two years.

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BIBLIOGRAPHY.

(1) ARBER, E. A. N. "On the Past History of Ferns," *Ann. Bot.*, vol. xx., July 1906.

(2) BERTRAND, P., *Études sur la fronde des Zygoptéridées*, Lille, 1909.

(3) BOWER, F. O., *On the Origin of a Land Flora*, London, 1908.

(4) CORDA, *Beiträge zur Flora der Vorwelt*, 1845.

(5) COTTA, B., *Die Dendrolithen*, 1832.

(6) KIDSTON, R., and GWYNNE-VAUGHAN, D. T., "On the fossil Osmundaceæ," Parts i. to iii., *Trans. Roy. Soc. Edin.*, vol. xlv., pt. iii., p. 759, 1907; vol. xlvi., pt. ii., p. 213, 1908; vol. xlvi., pt. iii., p. 651, 1909.

—— —— "On the Origin of the adaxially curved Leaf-trace in the Filicales," *Proc. Roy. Soc. Edin.*, vol. xxviii., pt. iv.

(7) PELOURDE, F., "Le *Flicheia esnostensis*, nov. gen., n. sp.," *Mémoires de la Société d'Histoire naturelle d'Autun*, xxi., 1908.

—— "Recherches comparatives sur la structure des fougères fossiles et vivantes," *Ann. des Sciences naturelles* (neuvième série), p. 115, 1909.

(8) RENAULT, B., "Étude sur quelques végétaux silicifiés d'Autun," *Ann. des Sciences naturelles*, ii. série, Botanique, xii., 1869.

—— "Bassin houiller et permien d'Autun et d'Épinac: *Flore Fossile*," fascicule iv., 1896, *Gîtes minéraux de la France.*

(9) RICHTER u. UNGER, "Beitrag zur Palæontologie des Thüringer Waldes," *Denkschr. d. k. k. Akademie zu Wien*, Math. naturw. Cl., Band xi., 1856.

(10) SCOTT, D. H., *Studies in Fossil Botany*, 2nd edit., vol. i., 1908.

(11) SOLMS-LAUBACH, H. Graf zu, "Ueber d. in d. Kalks. d. Kulm v. Glätzisch-Falkenberg in S. erhalt. Strukturb. Pflanzenreste," *Botan. Zeitung*, vol. l., 1892.

(12) STENZEL, G., "Die Gattung Tubicaulis Cotta," *Mitth. aus dem Kgl. min. geol. Museum in Dresden*, Heft 8, 1889.

(13) STOPES, Miss M. C., "A New Fern from the Coal Measures: *Tubicaulis Sutcliffii*, sp. nov.," *Mem. and Proc. Manchester Lit. and Phil. Soc.*, vol. l., pt. iii., 1906.

(14) TANSLEY, A. G., "Lectures on the Evolution of the Filicinean Vascular System," *New Phytologist*, 1907.

(15) WILLIAMSON, W. C., "On the Organisation of the Fossil Plants of the Coal Measures," *Phil. Trans. Roy. Soc.*, 1874.

EXPLANATION OF PLATES.

(Figures are all from untouched negatives.)

PLATE I.

Diplolabis römeri.

Fig. 1. Transverse section of stem-xylem. *x.* = outer xylem; *x.*^{1} = inner xylem. × 12. (Slide 742.)

Fig. 2. Transverse section of stem near a dichotomy. *x.* = outer xylem; *x.*^{1} = inner xylem. × 12. (Slide 735.)

Fig. 3. Section following that of fig. 2. *x.* = outer xylem; *x.*^{1} = inner xylem. × 12. (Slide 736.)

Fig. 4. Section following fig. 3. *x.* = outer xylem; *x.*^{1} = inner xylem; *rt. tr.* = root-trace (compare relative size of root and stem). × 10. (Slide 737.)

Fig. 5. Longitudinal section of stem-xylem. *x.* = outer xylem; *x.*^{1} = inner xylem. × 10. (Slide 806.)

Fig. 6. Longitudinal section of outer xylem showing reticulate fitting of tracheides. × 30 (Slide 806.)

Fig. 7. Longitudinal section of inner tracheides, showing the short tracheides with reticulate thickenings. × 48. (Slide 807.)

Fig. 8. Longitudinal section of protoxylem elements with scalariform thickenings. × 130. (Slide 338.)

Fig. 9. Oblique transverse section of stem-xylem near a dichotomy. One arm of the branch is cut transversely (*st.*$_2$), the other is cut obliquely (*st.*$_1$). A petiole and a root are also shown passing out. *st.*$_1$ *st.*$_2$ = the two branches of the dichotomy; *pet. tr.* = petiole-trace; *rt. tr.* = root-trace; *o. c.* = outer cortex. × 3·2. (Slide 338.)

Fig. 10. Section following that shown in fig. 9. *st.* = stem-xylem; *pet. tr.* = petiole-trace; *rt. tr.* = root-trace; *o. c.* = outer cortex; *z.* = root-trace lying outside the stem-cortex; *z.*^{1} = petiole-trace external to outer cortex. × 3·2. (Slide 337.)

Fig. 11. Section after fig. 10. Lettering similar to that of fig. 10. *rt. tr.* = root-trace of fig. 10 after the xylem has become detached from that of the stem; *rt. tr.*^{1} = root-trace, leaving the stem at a higher level than the former. × 3·2. (Slide 336.)

Fig. 12. Specimen of petiole with pinnæ departing from it. Elevation. *pet.* = petiole; *pin.* = pinna. $\times \frac{5}{6}$.

Fig. 13. Same specimen as fig. 12. Plan. *pet.* = petiole; *pin.* = pinna. $\times \frac{4}{3}$.

Fig. 14. Transverse section of stem showing an early stage of petiole departure. *x.* = outer xylem; *x.*^{1} = inner xylem; *prx.*, *prx.* = petiolar protoxylems. × 10. (Slide 771.)

Fig. 15. Transverse section of stem following that of fig. 14. *x.* = outer xylem; *x.*^{1} = inner xylem; *prx.*, *prx.* = petiolar protoxylems. × 10. (Slide 772.)

PLATE II.

Diplolabis römeri.

Fig. 16. Transverse section of stem and petiole following fig. 15. *x.* = outer xylem; *x.*^{1} = inner xylem; *prx.*, *prx.* = protoxylem. × 10. (Slide 773.)

Fig. 17. Transverse section above fig. 16. *x.* = outer xylem; *x.*^{1} = inner xylem; *prx.*, *prx.* = protoxylem. × 10. (Slide 775.)

Fig. 18. Petiolar departure, later stage than fig. 17. Petiole-trace distinct. *x.* = outer xylem; *x.*^{1} = inner xylem; *prx.*, *prx.* = protoxylem. × 11·6. (Slide 740.)

Fig. 19. Petiolar departure, stage beyond fig. 18. *x.*, *x.*,^{1} and *prx.* as before. × 11·6. (Slide 741.)

Fig. 20. Petiolar departure, petiole-trace free from stem-xylem. *x.*, $x.,^1$ and *prx.*, as before. × 11·6. (Slide 742.)

Fig. 21. Petiole-trace—transverse section—while still in cortex of stem. Each protoxylem has divided into two. $prx._1$, $prx._1{}^1$, $prx._2$, $prx._2{}^1$ = protoxylems. × 7·5. (Slide 336.)

Fig. 22. Transverse section of petiole-trace similar to that of fig. 21, but slightly further out. It is still, however, in the stem-cortex. Lettering as before. × 10. (Slide 285.)

Fig. 23. Transverse section of petiole-trace beyond fig. 22. *t.* = tongue of xylem; *is.*, *is.* = island of parenchyma; *d.* = departing trace (root?). × 10. (Slide 343.)

Fig. 24. Section following fig. 23. *t.* = tongue of xylem; *is.*, *is.* = island of parenchyma. × 11. (Slide 344.)

Fig. 25. Stage after fig. 24. *b.* = xylem-bar (the united traces of two reduced pinnæ); *is.*, *is.* = islands of parenchyma, one large one at top and two small ones at lower end. × 11. (Slide 348.)

Fig. 26. Stage following fig. 25. *prx.* = protoxylems. Arms are now distinct. × 10. (Slide 284E.)

Fig. 27. Stage beyond that of fig. 26. *prx.* = protoxylem; $p._1$, $p._2$ = united traces of a pair of reduced pinnæ; the traces are connected together by a thread of xylem. × 7. (Slide 719.)

Fig. 28. Stage above fig. 27. Trace similar to that of *Diplolabis forensis* Renault. *prx.* = protoxylem. × 7. (Slide 726.)

Fig. 29. Stage following that of fig. 28. This is the normal *Diplolabis römeri* trace. *prx.* = protoxylem. × 7. (Slide 699.)

PLATE III.

Diplolabis römeri.

Series of photomicrographs illustrating the changes in the petiole-trace.

Fig. 30. One end of a transverse section of peliole-trace above stage of Pl. II. fig. 22. *is.* = island of parenchyma. × 25. (Slide 341.)

Fig. 31. Section above fig. 30, same end of trace. *t.* = tongue of xylem; *prx.* = protoxylem. × 25. (Slide 342.)

Fig. 32. Next section above fig. 31. *t.* = tongue of xylem; *d.* = departing trace (root?). × 25. (Slide 343.)

Fig. 33. Section above fig. 32. Note tridentate end of trace. × 22. (Slide 344.)

Fig. 34. Following fig. 33. Arms closing over to unite with xylem tongue. × 25. (Slide 345.)

Fig. 35. Section following fig. 34. Arms united with tongue of xylem. Two islands. × 25. (Slide 346.)

Fig. 36. Stage after fig. 35. The two islands of parenchyma are very distinct. × 25. (Slide 347.)

Fig. 37. Trace beyond stage of fig. 36. *is.*, *is.* = the two islands of parenchyma. × 25. (Slide 348.)

Fig. 38. Section above that shown in fig. 37. *is.*, *is.* = islands of parenchyma. × 25. (Slide 349.)

Fig. 39. Stage after fig. 38. *is.*, *is.* = islands of parenchyma. × 25. (Slide 350.)

Fig. 40. Two sections above fig. 39. The two islands have united into one. *c*, *c* = two ends of reniform island of parenchyma. × 25. (Slide 352.)

Fig. 41. Trace of fig. 33, other end of trace, to illustrate the difference in phase of the two ends of the same trace. × 22. (Slide 344.)

PLATE IV.

Diplolabis römeri.

Fig. 42. Transverse section of normal *Diplolabis römeri* petiole-trace. *a.*, *a.* = lines of abscission of pinna-trace-bar; *b* = pinna-trace-bar; *c*, *c* = claw-like ends developed from the arms. They ultimately join and form the next pinna-trace-bar. × 14. (Slide 793.)

Fig. 43. Transverse section of petiole showing the division of the pinna-trace-bar. *pin. tr.* = pinna-trace; *aph. tr.* = aphlebia-trace; *o. c.* = outer cortex. × 2·4. (Slide 789.)

Fig. 44. Transverse section of petiole showing bifurcation of aphlebia-trace. *pin. tr.* = pinna-trace; *aph. tr.* = aphlebia-trace (four of them). × 2·2. (Slide 796.)

Fig. 45. Transverse section of petiole above fig. 44. The pinna-trace on the right-hand side is cut almost longitudinally; that on the left-hand side has already passed out through the cortex. The two traces pass out together, but the section is not quite level. One part of each aphlebia pair has also passed out through the cortex. *pin. tr.* = pinna-trace; *aph. tr.* = aphlebia-trace. × 2·2. (Slide 797.)

Fig. 46. Transverse section of petiole-trace showing relation of *Flicheia esnostensis* to *Diplolabis römeri*. *a* = *Flicheia* trace; *b* = half of the normal *Diplolabis* trace; *i. c.* = inner cortex; *o. c.* = outer cortex. × 10. (Slide 800.)

Fig. 47. Transverse section of pinna-trace immediately after the pinna is free from the stem. × 10. (Slide 809.)

Fig. 48. Transverse section of pinna-trace dividing to give the secondary pinna-traces. Stage beyond fig. 47. *pin. tr.* = pinna-trace; $p._1$, $p._2$, $p._3$ = secondary pinna-traces. × 10. (Slide 324.)

Fig. 49. Transverse section of root-trace. *prx.* = protoxylem. × 36. (Slide 791.)

Fig. 50. Part of outer zone of outer cortex in petiole showing sclerenchymatous tissue. This is from lower end of petiole shown in Pl. I. figs. 12 and 13. × 43. (Slide 811.)

Fig. 51. Longitudinal section of petiole-trace showing reticulately thickened tracheides. × 30. (Slide 812.)

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W. T. Gordon: Structure and Affinities of Diplolabis Römeri (Solms)—Plate I.

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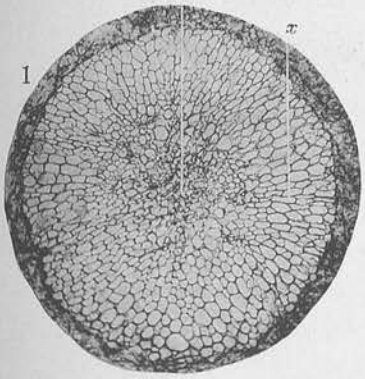

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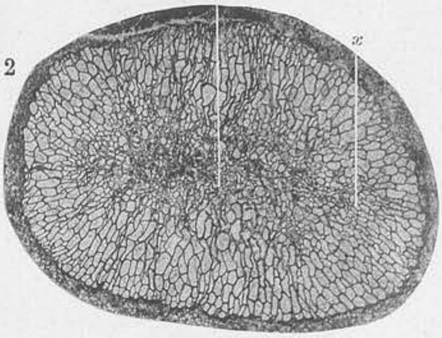

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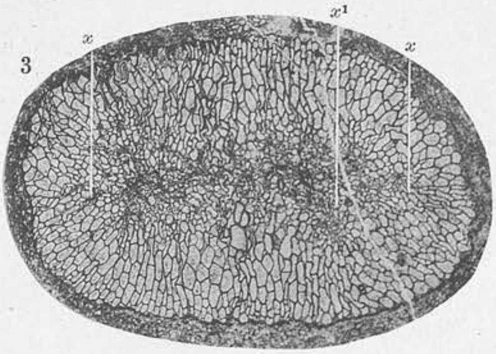

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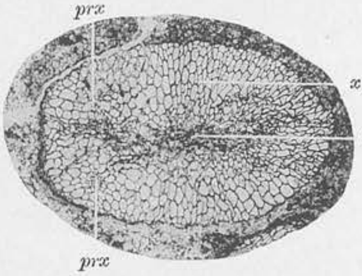

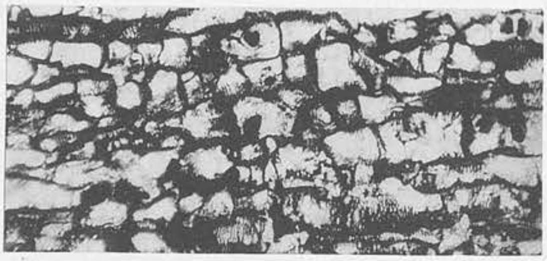

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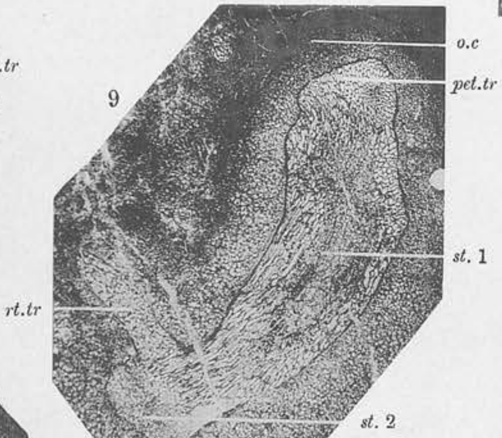

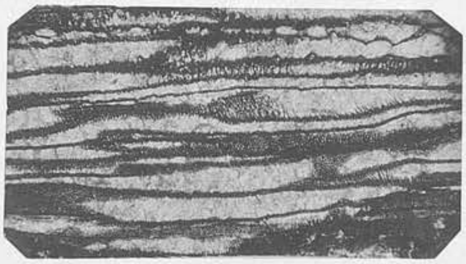

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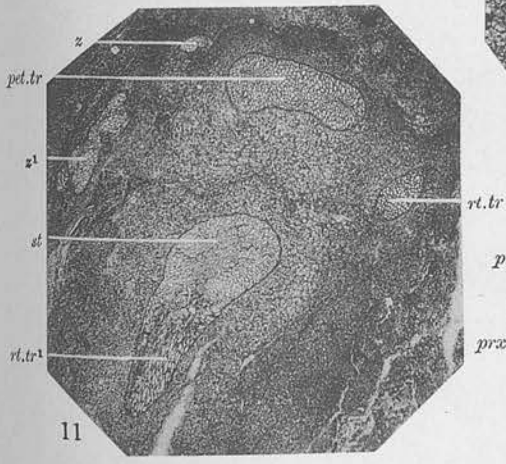

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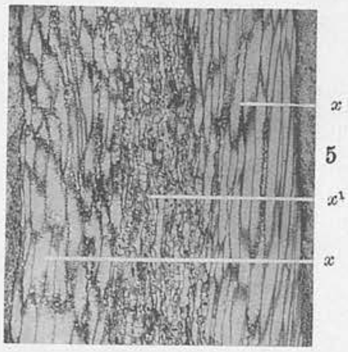

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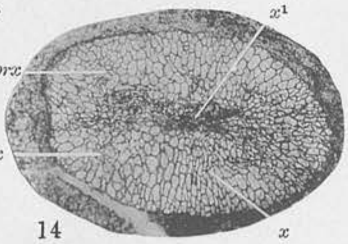

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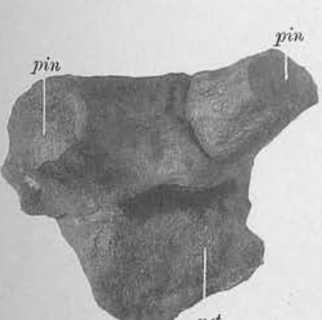

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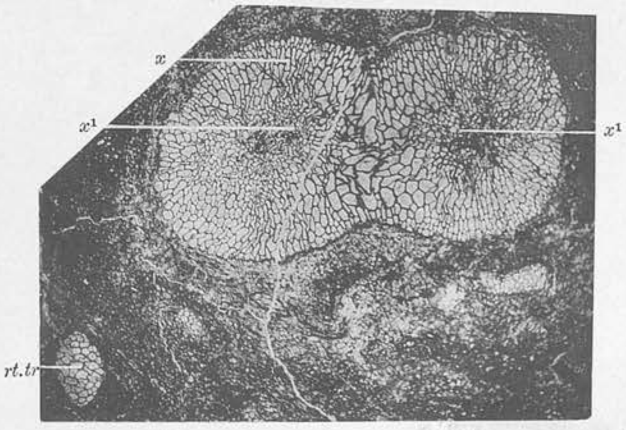

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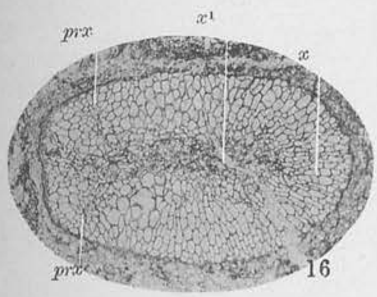
W. T. GORDON: STRUCTURE AND AFFINITIES OF DIPLOLABIS RÖMERI (SOLMS)—PLATE II.



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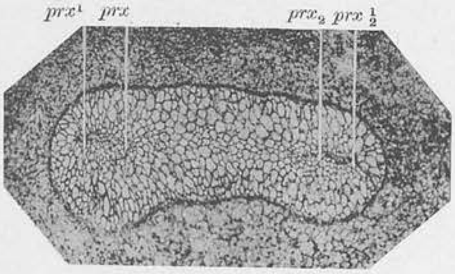

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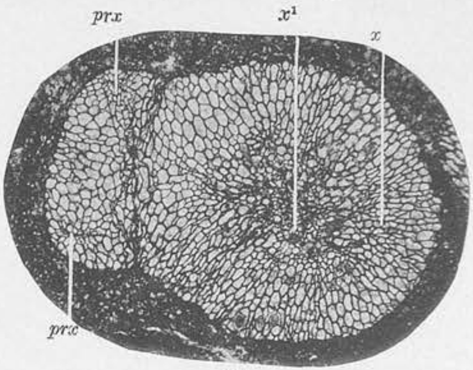

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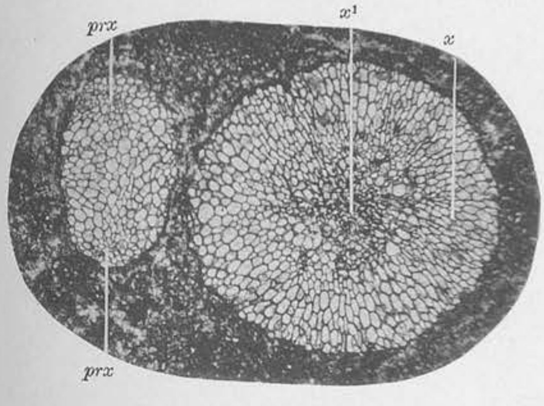

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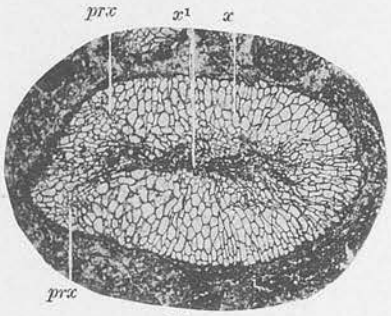

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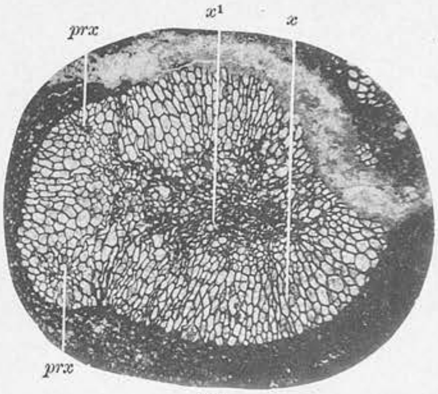

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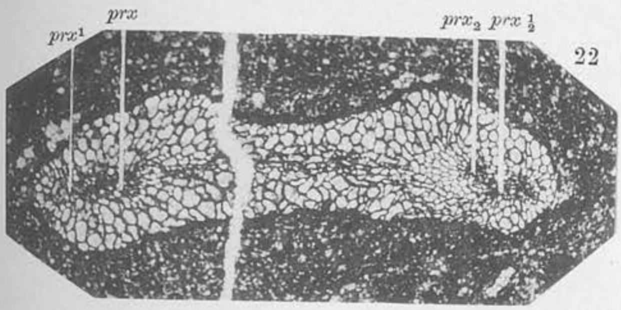

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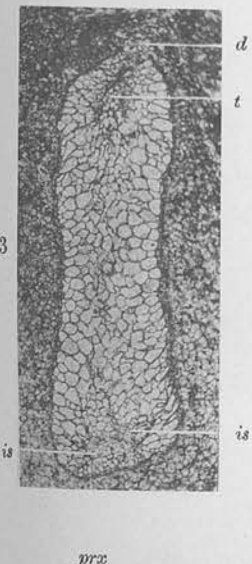

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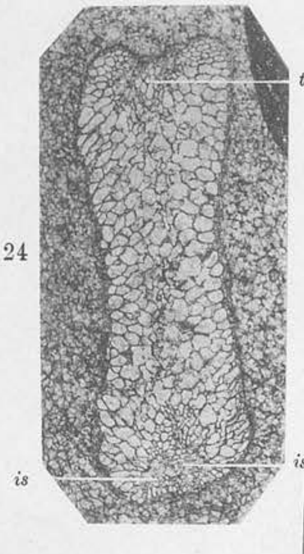

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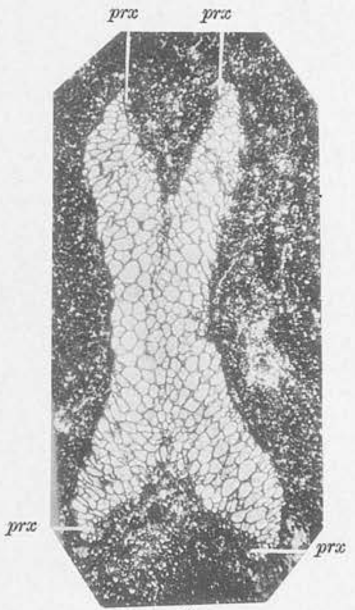

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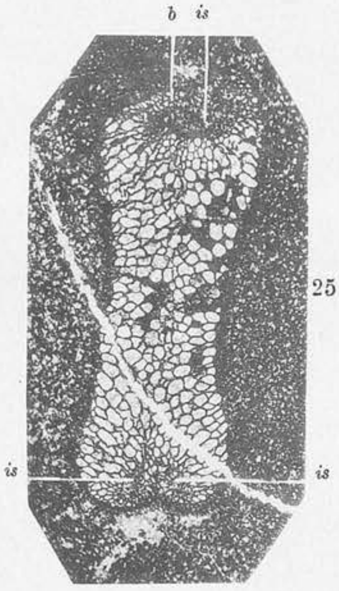

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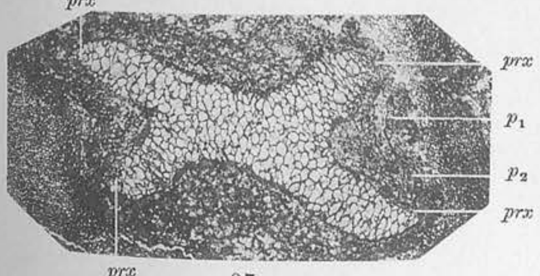

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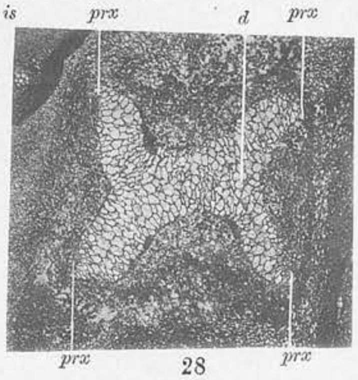

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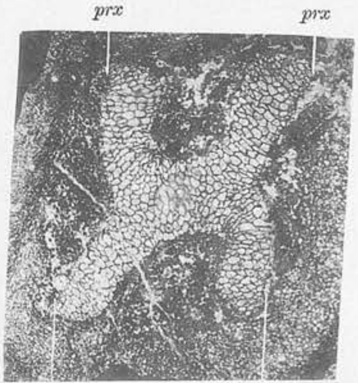

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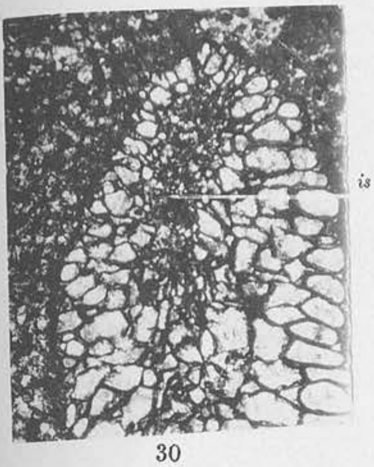
W. T. GORDON: STRUCTURE AND AFFINITIES OF DIPLOLABIS RÖMERI (SOLMS)—PLATE III.



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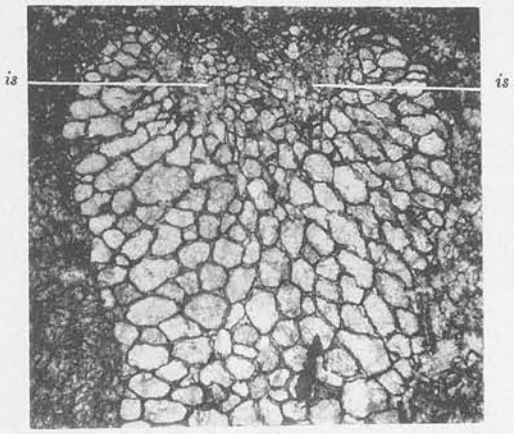

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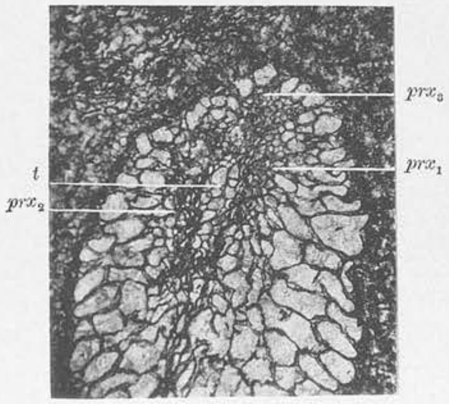

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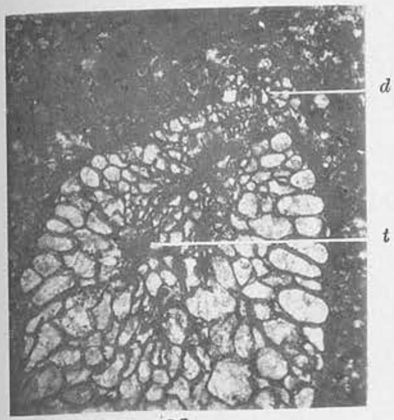

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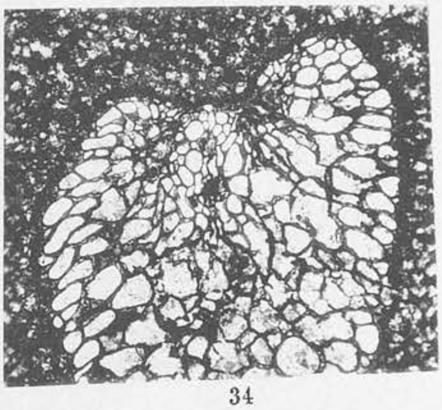

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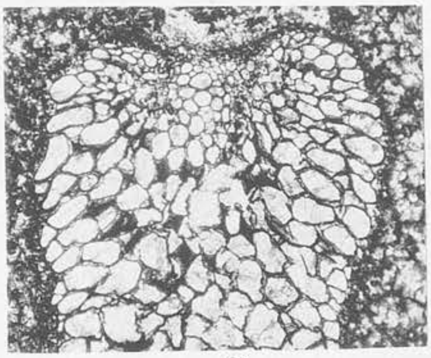

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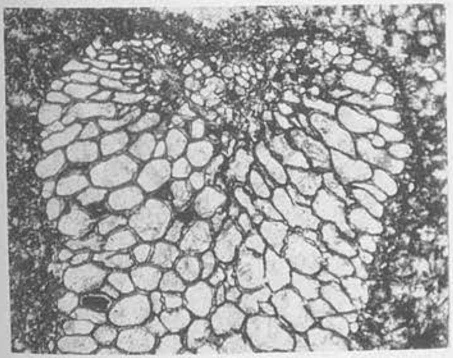

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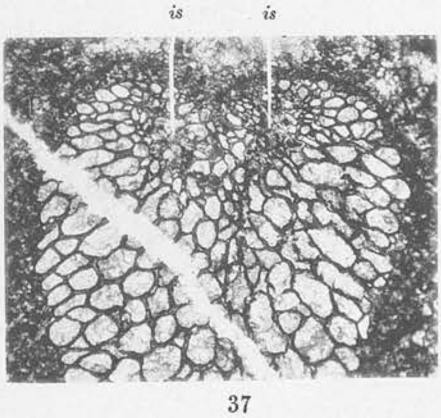

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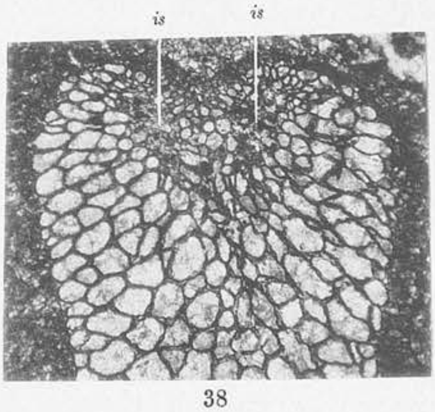

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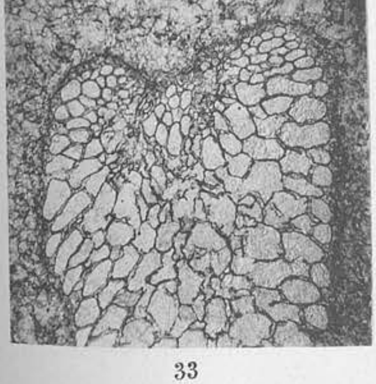

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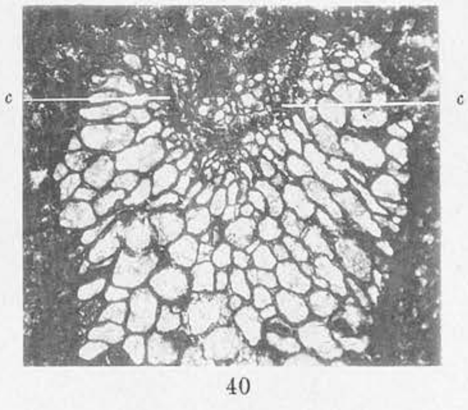

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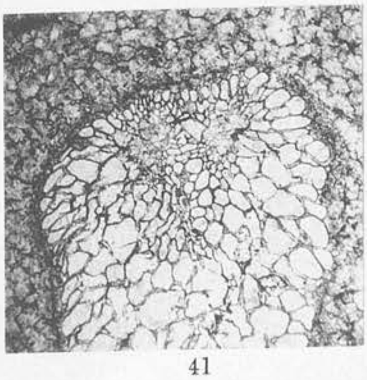

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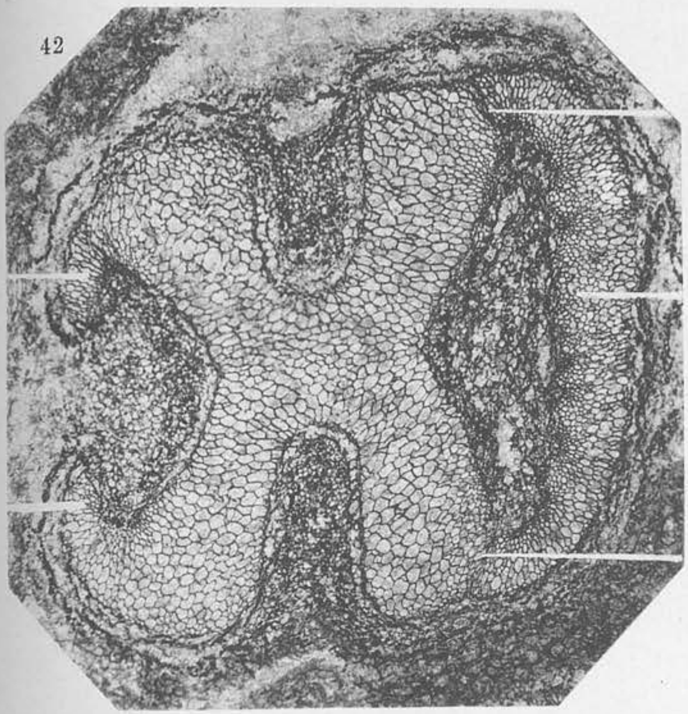
W. T. GORDON: STRUCTURE AND AFFINITIES OF DIPLOLABIS RÖMERI (SOLMS)—PLATE IV.



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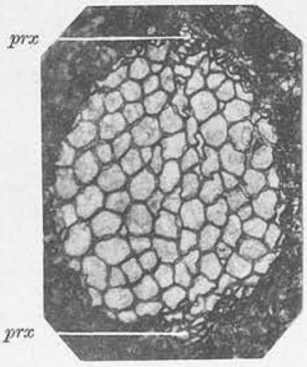

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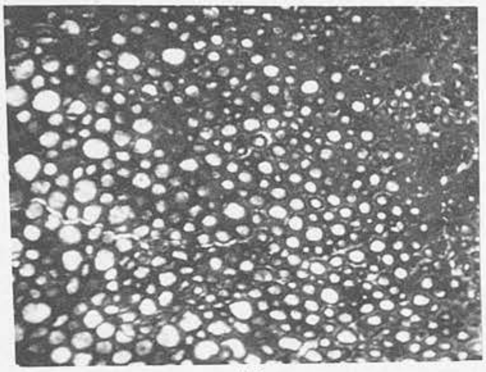

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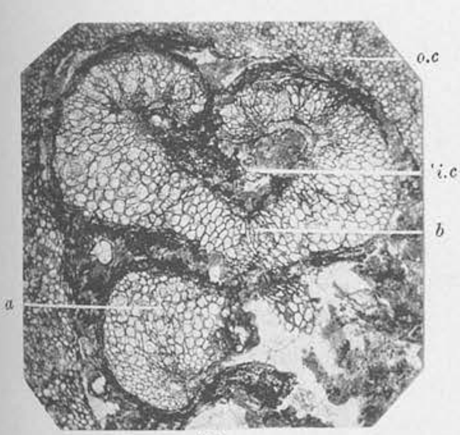

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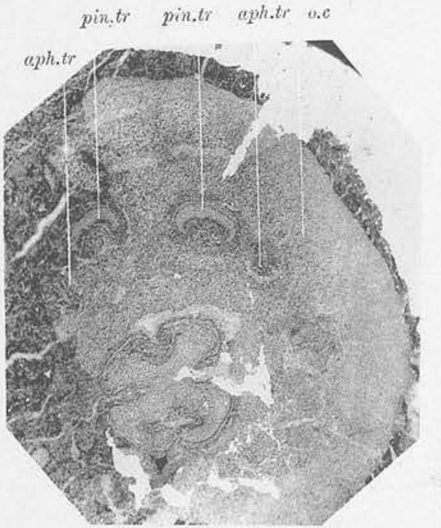

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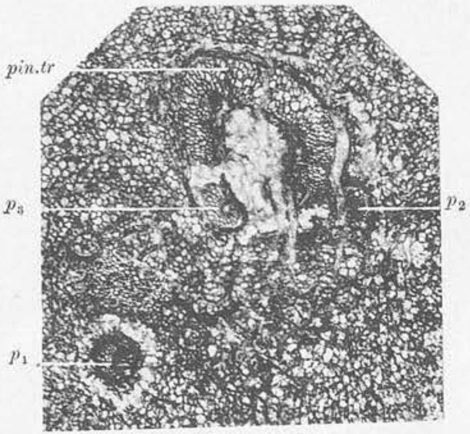

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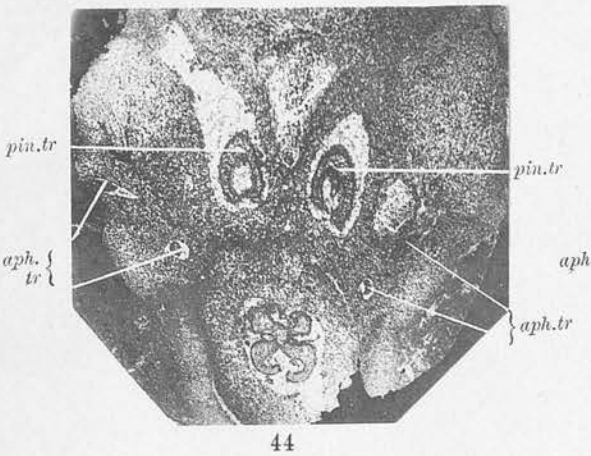

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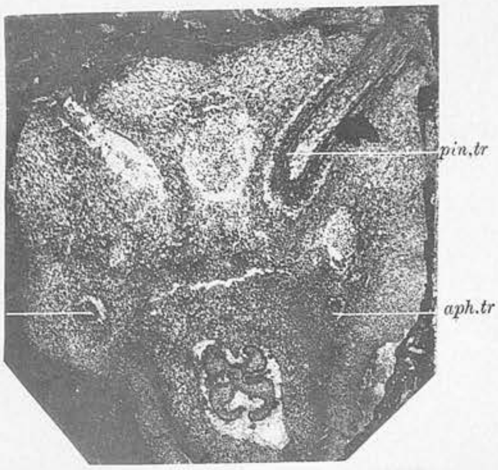

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,, Part 4.	0 7 6	0 5 8
XXXI.	4 4 0	3 3 0
XXXII. Part 1.	1 0 0	0 16 0
,, Part 2.	0 18 0	0 13 6
,, Part 3.	2 10 0	1 17 6
,, Part 4.	0 5 0	0 4 0
XXXIII. Part 1.	1 1 0	0 16 0
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XXXIV.	2 2 0	1 11 0
XXXV.*Part 1.	2 2 0	1 11 0
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XXXVI. Part 1.	1 1 0	0 16 0
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XXXVII. Part 1.	1 14 6	1 5 6
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XXXVIII. Part 1.	2 0 0	1 10 0
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,, Part 3.	2 5 0	1 13 6
XLII.	2 2 0	1 11 0
XLIII.	2 2 0	1 11 0
XLIV. Part 1.	1 18 6	1 9 0
,, Part 2.	1 1 0	0 15 9
XLV. Part 1.	1 9 0	1 2 0
,, Part 2.	1 7 0	1 0 0
,, Part 3.	1 13 9	1 5 3
,, Part 4.	0 4 6	0 3 6
XLVI. Part 1.	1 1 10	0 16 6
,, Part 2.	1 5 8	0 19 4
,, Part 3.	1 7 3	1 0 11
XLVII. Part 1.	0 19 9	0 15 0
,, Part 2.	1 3 0	0 17 4
,, Part 3.	1 0 10	0 15 8

* Vol. XXXV., and those which follow, may be had in Numbers, each Number containing a complete Paper.

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TRANSACTIONS

OF THE

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Stauropteris burntislandica. P. Bertrand 1907.

When Williamson first recorded this species he referred it to S. Oldhamia the Coal Measure Species, but in 1907 it was elevated to the position of a distinct species by Bertrand. The differences between the two are very slight and it is just possible that we may have to revert to the old name in spite of the difference of stratigraphical position between the two plants.

All the specimens recorded are fragments of petioles and pinnae, though strictly speaking petioles and pinnae should not be used and petioles of various orders would be better since there is little difference between one trace and the branches it gives off. As a rule the petiole trace is in the form of a cross with one sunk protoxylem group near the outer end of each arm. This is not an invariable rule, however, because I find in one of my specimens that one of the arms has become detached from the other three and that there is parenchyma between the single arm and the rest of the trace. Such an example recalls strongly the specimen of S. Oldhamia figured by Tansley[1], as one of the strongest specific differences between S. burntislandica and S. Oldhamia was that the trace in the former never divided into pieces. It is on this specimen, therefore, that the doubt expressed above about the correctness of Bertrand's diagnosis, is founded.

One interesting point about the petiole is that it bifurcated.

In /

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[1] Tansley A. G. "Lectures on the Filicinean Vascular System" New Phytologist Reprint No. 2. 1908.

In Pl. B. fig. 7 an example of such a division is shown. The trace here has eight protoxylem groups and, no doubt, four of these belong to each branch. I have not yet followed this example until the bifurcation was completed but there seems no doubt that it did so. Surrounding the xylem of the trace is a zone of delicate parenchyma with two or four groups of large cells which are probably the phloem (Pl. A. fig. 8 ph.). Outside the delicate tissue of this zone is a layer of thick walled parenchyma and about half way through the layer the cell walls are at their thickest. Towards the exterior they get thinner walled again but whether they form an aerenchyma is doubtful. A well marked epidermis of palisade-like cells is present in the best preserved specimens (Pl. ~~B~~A. fig. 8 ep.). No sporangia have ever been shown to belong to this plant though some associated sporangia have been referred to it.

Always associated with these petioles, also, there occur peculiar bodies described by Mrs Scott under the name *Bensonites fusiformis*. These are elongated oval masses of delicate parenchyma with some signs of vascular tissue in the centre while at the top there is a cavity containing usually one but sometimes two spore-like bodies. Their constant association with *S. burntislandica* led Mrs Scott to suppose that they were the fructifications of this species but absolute continuity must be insisted upon and proved before this can be accepted without hesitation. /

hesitation. *Bensonites fusiformis* therefore is at present a rather mysterious organism and indeed may be the prothallus of some other species.

PRELIMINARY PAPER

ON TWO NEW SPECIES OF HETERANGIUM FROM PETTYCUR, FIFE.

The Calciferous Sandstone of Pettycur has, so far, yielded only one species of Heterangium - H.Grievii - but this plant is exceedingly common. Certain points in the anatomy of that species at once distinguish it from the Upper Carboniferous members of the genus and the specimens to be described below can also be separated from it with great ease.

One of these new Heterangium species is at present represented by a single stem from Pettycur and another from Berwick, but several stems of the second occurred in one small block of the Pettycur material. To the former I propose to give the name Heterangium Arberi in honour of Mr. Arber but the second species I do not propose to differentiate specifically meanwhile.

Heterangium Arberi sp.nov.

General Structure.

As mentioned above in addition to the stem from Pettycur, which forms the type of this species, Dr. R. Kidston has collected a stem probably identical at Whitadder Water near Edrom Church, Berwickshire. The Pettycur specimen is beautifully petrified, whereas the structure of the Berwickshire one is not so well preserved. The anatomy will therefore be described from the former specimen.

Unfortunately this example occurred near the surface of a block /

block and was only about 5 to 5½ inches in length. The stem which was probably 1.6 to 1.8 cm. in diameter is shown in Plate 1 fig. 1. Where the petiole base joins the stem there is an enormous development of buttressing tissue between the sclerenchyma of the stem and that of the petiole, and so the stem often appears very much larger than it really is. The leaf base also was decurrent into the stem for a considerable distance below the point where the petiole trace enters the stem and this also causes the latter to be irregular in outline. The axis itself is about .7 cm. in diameter and is not much crushed in general. At some point or other every tissue of the stem is well preserved and thus it is possible to obtain a fairly complete knowledge of its anatomy. The axis is nearly always well shown but sometimes the ring of the cortex is not continuous especially the portion opposite a departing petiole trace.

The wood of the axis consists of a primary cylinder and a secondary zone (plate 1, fig.2); the primary wood is composed of anastomosing groups of tracheides as is typically the case in Heterangium but the groups are considerably larger than those of Heterangium Grievii and there are fewer of them. The conjunctive parenchyma is much better developed than in Heterangium Grievii and presents another peculiarity in that it contains numerous secretory sacs similar to those found in the pith of Lyginodendron and in the primary wood of the Medulloseae, especially Sutcliffia insignis, Scott.

The /

The ring of secondary wood is continuous round the periphery of the primary wood and each group of primary xylem is bounded externally by a wedge of secondary wood. The principal medullary rays thus pass out between adjacent peripheral xylem groups of the primary cylinder. In the wedges themselves the rows of tracheides are separated by the secondary medullary rays. Sometimes a ray occurs between every two rows of tracheides but usually there are several rows of tracheides between the rays.

The phloem tissue is well preserved in places. It consists of long elements with thin walls and light brown contents. No definite sieve plates can be detected in longitudinal section. In the phloem region and especially opposite the primary medullary rays, secretory sacs may occasionally be seen.

The inner cortex which abuts on the phloem consists of thin walled parenchyma associated with long secretory sacs which have no distinct epithelium. The whole of this inner cortex appears to be largely composed of mucilage cells. Towards the periphery of this zone the cells become tangentially elongated and form a distinct layer between the thin walled inner cortex and the thick walled outer cortex.

In the outer cortex three regions may be distinguished, an inner parenchymatous zone; a hypodermal zone of sclerotic nests in a smaller celled parenchyma; and an outer parenchyma. The more internal region consists of large celled thick walled parenchyma and frequently contains elongated secretory sacs. (Pl.1. fig. 8 and /

and Pl. 11. figs. 9 & 10) The elements which adjoin the hypodermal zone however have become elongated tangentially or radially. There is no change however in the vertical direction. The great extension of these cells has apparently caused them to divide in some cases; and cross walls appear in a few of them dividing the cell into two. (Pl. II, fig. 9,a) This inner region of the outer cortex contains neither secretory sacs nor secretory cells. The hypodermal layers of the outer cortex consist of a reticulum of sclerenchymatous elements, the interspaces of which reticulum are filled in by a small-celled parenchyma.(Pl. II, fig. 9, 22, o.c The sclerotic nests of cells contain long elements which have extremely thick walls and small lumens. Large and long secretory sacs are very numerous in the sclerotic outer cortex and these are sometimes surrounded by the sclerotic nests or they are partly bounded by the parenchyma of the cortex. The great length of these sacs and the general appearance of their contents would lead to the supposition that they are the result of cell fusion. No epithelium can be distinguished lining these sacs and what Dr. Scott says of <u>Sutcliffia</u> is equally applicable to Heterangium Arberi, viz. "Secretory organs probably of the nature of gum canals, though no clear evidence of an epithelium has been obtained, are frequent in the cortex, especially in association with the fibrous strands."

The sclerotic hypoderm is usually the outermost tissue seen though occasionally parenchymatous tissue is present on its exterior. /

exterior. (Pl. 1, fig. 8, Z_3 o.c.)

The Petiole.

The petiolar trace departs from the central axis in an exceptional and highly interesting manner. Several of the anastomosing bundles of tracheides of the primary xylem become closely associated at one part of the periphery, and join together into one xylem group which possesses a sinuous outline. As the trace passes outwards the secondary wood disappears (plate I, fig. 6). To some extent the trace now assumes a more circular appearance, though the sinuous outline may still be traced. In the specimen examined I have not been able to follow any trace between this stage and the stage at which the petioles become free. The sections showing the petiolar continuity with the stem are very obliquely cut and we must therefore turn to similar detached petioles. The identity of the detached petioles is very obvious on account of the characteristic appearance of the cortical tissues. In these associated petioles the trace is concentric with a very markedly crenulate margin. No roots, foliage, or fructifications are known.

Histology.

The protoxylem elements are confined to the peripheral groups of xylem tissue, and these elements are in all cases exarch (plate I, fig. 5 prx.) and not mesarch as in Heterangium. These elements have scalariform or sub-spiral thickenings. The secondary wood attained /

attained a considerable thickness all round the central stele. The secondary zone is from 18 to 20 cells deep and just below the periphery at A the cells become rather smaller than those either on the outside or the inside, and thus this region simulates in appearance the autumn wood in recent plants.

The tracheides of both primary and secondary wood have multiseriate pits on their walls. Pl. I, fig. 4. The elements of the primary wood are much larger than those of Heterangium Grievii and each group also contains a greater number of tracheides. The conjunctive parenchyma is also much better developed than in that species. Thus the primary wood contains fewer though larger groups of xylem elements than does that of Heterangium Grievii.

Interspersed with the conjunctive parenchyma are numerous secretory cells and also long secretory sacs. The principal medullary rays are broad, and so, as a rule, are the secondary ones. The primary rays broaden out when they become free from the wood.

The phloem is on occasion well preserved but no sieve plates can be detected on the cell walls. The whole of the tissue in this region resembles elongated parenchyma.

The cells of the inner cortex are exceedingly peculiar. The whole tissue consists of very thin-walled elements and has the appearance of being mucilage tissue. This tissue consists of normal parenchymatous cells with dark brown contents. In addition there are numerous long secretory sacs interspersed in this tissue

On /

On account of its soft nature the inner cortex is only preserved in patches in the stem but in the petioles it is often quite distinct. Owing to the delicate nature of the inner cortex, the petioles are invariably crushed, so that they assume an elongated elliptical form. The outer cortex is very interesting on account of its hypodermal sclerenchyma and its secretory sacs. Just after a leaf trace has departed from the stem a gap appears in the sclerotic hypoderma opposite to it; and the cortical parenchyma of the petiole is seen in continuity with the inner zone of the outer cortex of the stem. In transverse sections of the stem passing through this region the sclerotic part seems to have bent in towards the xylem in two claw-like curves. The breadth of the parenchymatous cortex of the decurrent leaf base is very considerable in this region as can be seen both in longitudinal and in transverse sections. When the petiole trace becomes free the sclerenchyma closes in until the ring is again complete.

The secretory sacs in this sclerotic region are very interesting particularly on account of their great length. Similar sacs without epithelium are described as probably of the nature of gum-canals by Dr. Scott in the case of Sutcliffia. It is just possible that a lining of epithelium was originally present.

It is to be hoped that other examples of this interesting plant will be discovered in order that a clear knowledge may be had of the course of the petioles in particular.

Heterangium /

Heterangium Arberi sp. nov.

Diagnosis.

Stem with a single axis consisting of multiseriately pitted tracheides and conjunctive tissue. Protoxylem groups peripheral i,e, exarch; and secondary wood developed round the whole axis. A distinct phloem occurs in the normal position. Leaf bases long and decurrent. Leaf traces of a peculiar sinuate form. Strand in the free petiole more or less concentric, but the xylem is crenulated. Inner cortex of the stem and petiole contains numerous gum-canals. The outer cortex resembles that of the Medulloseae and particularly that of Sutcliffia in that it contains gum-canals or secretory sacs without epithelium but of great length and size.

Affinities.

While provisionally classing this new species in the genus Heterangium there seems to be considerable room for doubt whether this is its proper systematic position. The axis is distinctly like a typical Heterangium and differs chiefly in the occurrence of secretory sacs and the exarch character of the protoxylem. The inner cortex has no sclerotic discs as in Heterangium Grievii and the outer cortex is exactly similar to that of Sutcliffia except that it has no accessory bundles. The Medulloseae have several steles or rather possess a dictyostele which is generally of considerable size. It would seem reasonable to suppose that this dictyostelic condition was originally derived by the dividing up of /

of a monostele and among the more ancient specimens we would expect monostely and not dictyostely. In Sutcliffia from the Lower Coal Measures an approximation to this condition is seen but still the dictyostely is distinct. In that case, as in all the other Medulloseae, the primary wood is essentially like Heterangium except that it is exarch.

Heterangium Arberi comes from a still lower horizon than that from which Sutcliffia is derived and in certain directions shows a greater advance towards the Medulloseae than any other species of Heterangium hitherto described. At the same time the petiolar trace shows features which distinguish it from all the species of Heterangium and Medullosa at present known. These very features however might also be expected to appear in a primitive member of the Medulloseae and it appears to me that this new species combines more characters typical of Heterangium and of the Medulloseae than any other plant hitherto described.

Since this paper was written I have discovered another specimen among the Pettycur petrifactions. So far it has confirmed the observations recorded here and one example of an adventitious root has been found. It is hoped that further study will reveal other points of interest.

Heterangium nov. sp.

This new species of Heterangium was discovered in a small fragment of the Pettycur Limestone near Pettycur Harbour. In the /

the block, which was about 6" diameter there were 9 stems. A typical transverse section is shown in Pl. II fig. 14 and the most striking features it presents are the absence of conjunctive parenchyma in the primary wood, the great development of secondary wood, and the Lyginodendron-like sclerotic outer cortex. That the primary wood is solid is not quite proved but it certainly contains very little parenchyma, if any. The diameter of the primary wood is also exceedingly small and measures from 1.4 mm. to 1.5 mm. The small size of the primary wood is constant in all the specimens examined, as is also the strong development of the secondary xylem. The protoxylem elements appear to be slightly sunk in the wood of the primary axis, i.e. they are mesarch, though the centrifugal wood beyond the protoxylem elements consists of tracheides which are not much larger than those of the protoxylem.

Leaf traces occur in all the transverse sections but their number is small compared with the number usually shewn in a transverse section of H. Grievii. In this new species the number never exceeds 3 or 4. These traces are also peculiar in that they occasionally have secondary xylem at their bases on the abaxial side. They travel upwards for a long distance and then pass out through the cortex to supply the petioles.

The middle cortex is a very narrow zone and is usually quite decayed. Where present, however, it does not exhibit the sclerot plates so characteristic of H. Grievii. The outer cortex consists of /

of thick-walled parenchyma and contains bars of sclerotic fibres similar to those in H. Grievii. These bars continue down into the stem for a long distance before they anastomose with any neighbouring bar and so a reticulum of sclerotic tissue with long narrow meshes is produced. This is quite similar to what occurs in H. Grievii. In Pl. 11, figs. 11 & 12 photographs of the sclerotic outer cortex of Heterangium sp. and of H. Grievii respectively are shown, while in figs. 14 & 13 the stems of these species are also photographed. These figures are of the same dimensions among themselves, i.e. the stems are of the same dimensions, and the cortex, though more highly magnified than the stem, is magnified the same number of diameters in both cases. These figures show the differences between the two species.

The roots of this new species are also shown in attachment with the stem; they have the typical Amyelon organisation and usually have a considerable amount of secondary wood developed round them.

The small diameter of the primary wood and the small number of petiole-traces seen in any transverse section seem to indicate that this species had a scrambling habit. It does not seem to have branched very often as no such bifurcation has so far been met with.

Heterangium n. sp.

The following preliminary diagnosis may be given:- Stems with /

with small primary wood and conjunctive parenchyma, in consequence, small in amount, if any is present at all. Secondary xylem well developed. Protoxylem groups mesarch. Petiole trace double as in H. Grievii, but usually with secondary wood near its base. Middle cortex small in amount and contains no sclerotic plates. Outer cortex consists of a meshwork of sclerotic tissue with its interstitial spaces parenchymatous.

Roots of the Amyelon type.

Explanation of Plates.

(Prints from untouched negatives by the author.)

Plate 1.

Fig. 1. Heterangium Arberi transverse section of stem, x = primary wood; x, = secondary wood; i.c. = inner cortex; p. o.c. = parenchymatous outer cortex; sc.o.c. = sclerotic outer cortex.

A 16 x 4.

Fig. 2. H. Arberi transverse section of xylem. x_1; x_2; i.c.; o.c. as before.

A 16 x 7.

Fig. 3. H. Arberi longitudinal radial section. x_1; x_2; o.c.; as before.

984 x 9.

Fig. 4. H. Arberi longitudinal section in part. x_1; x_2; as before; ph = phloem; m.r. = medullosy ray.

984 x 23.

Fig. 5. Two xylem wedges to show exarch wood. x_1; x_2; m.r.; as before, prx = protoxylem; A.A. = zone of smaller celled secondary xylem comparable with Autumn wood.

100 3 x 23.

Fig. 6. Petiole trace departing from stem. x_1; x_2; as before. pet. tr - petiole trace.

994 x 9.

Fig. /

Fig. 7. Transverse section of small petiole. Note bundle (v.b.) which is broken up accidentally into 3 portions.

Fig. 9. Transverse section of part of outer cortex. o.c. = parenchyma of outer cortex; Sc.n. = sclerotic nests; s.s. = secretory sacs; o.c. z_3 = outermost zone of cortex.

100 3 x 30.

Plate II.

Fig. 9. Longitudinal section of outer cortex. Z. o.c. = inner zone of outer cortex; Z_2 o.c. = outer zone of outer cortex; a.a. = cross walls on distended parenchyma cells; Sc.n. = sclerotic nest.

984 x 30.

Fig. 10. Longitudinal section of outer zone of outer cortex; s.s. = secretory sac; Sc.n. = sclerotic nest.

984 x 30.

Fig. 11. Heterangium sp. transverse section of outer sclerotic cortex. sc.b. sclerotic bar; p. o.c. = parenchymatous outer cortex.

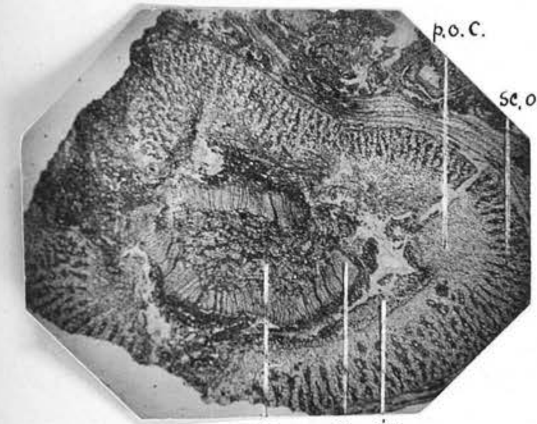
A x 30.

Fig. 12. Heterangium Grievii sclerotic cortex. Sc.b. & p. o.c. as before.

573 x 30.

Fig. 13. Transverse section of Heterangium Grievii; x_1; x_2; o.c. as /

Plate. I.



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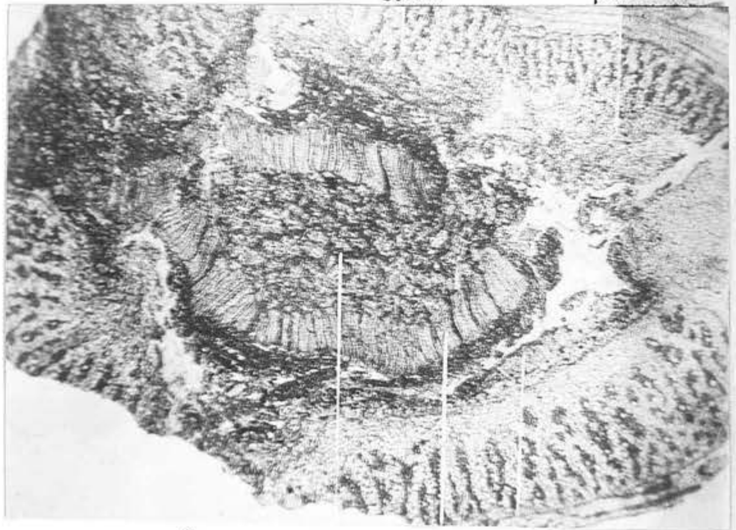

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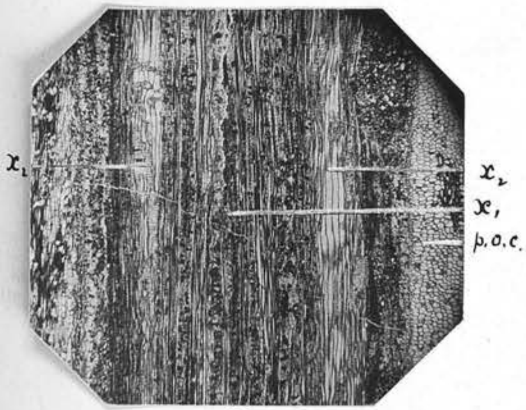

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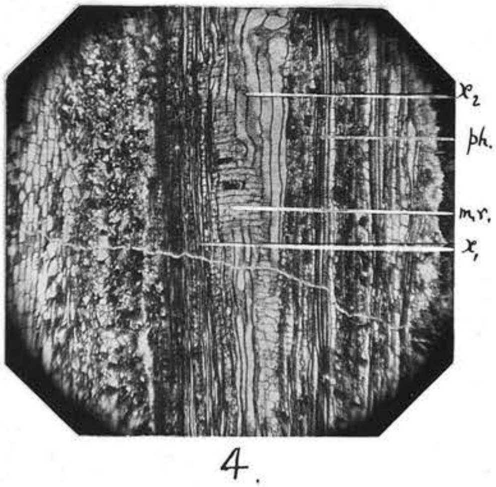

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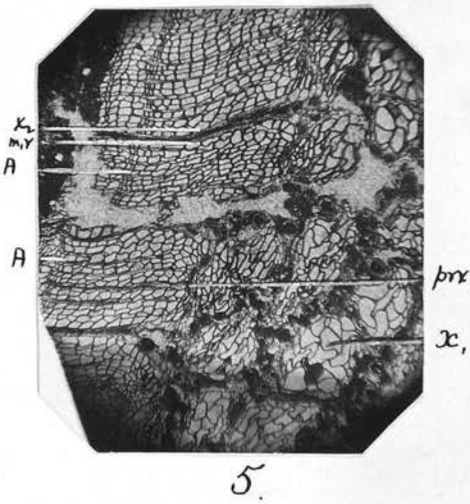

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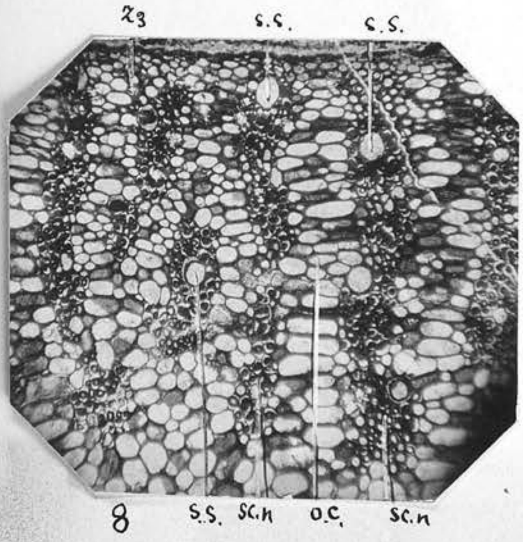

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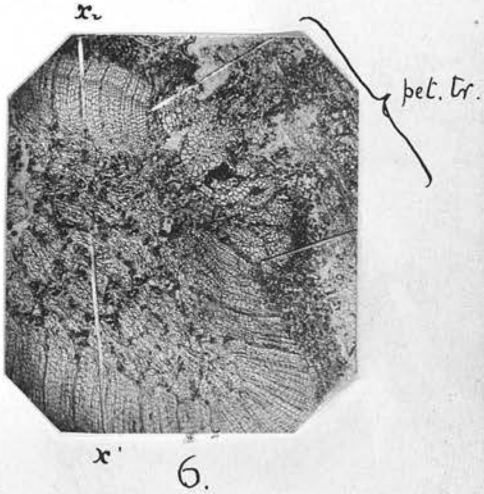

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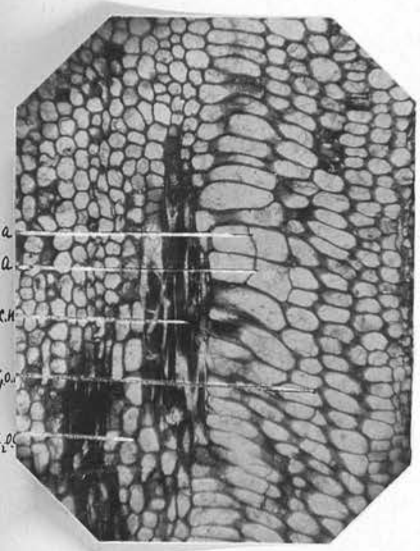
Plate 2.



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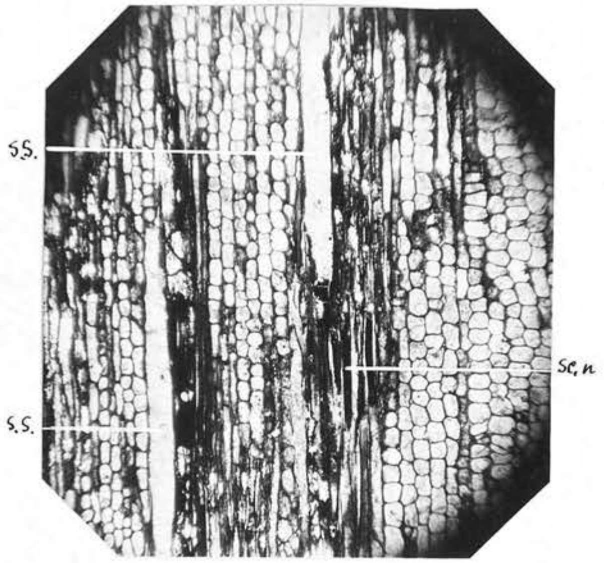

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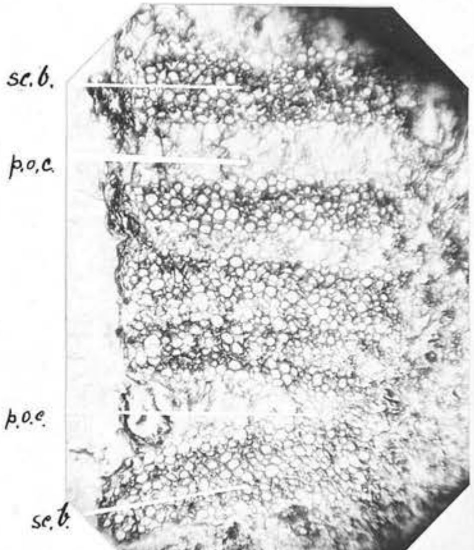

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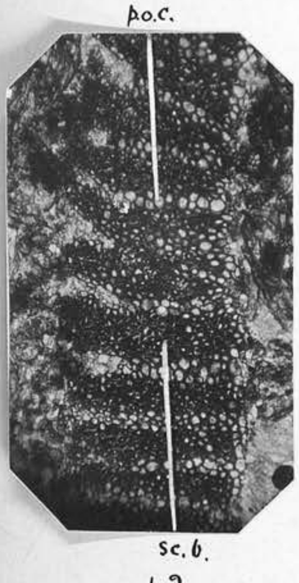

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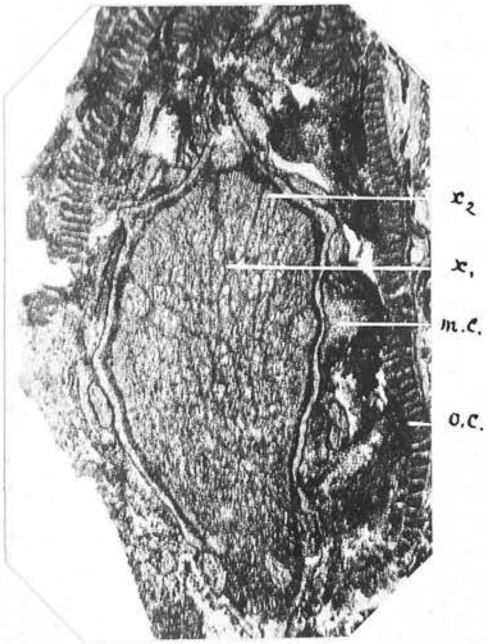

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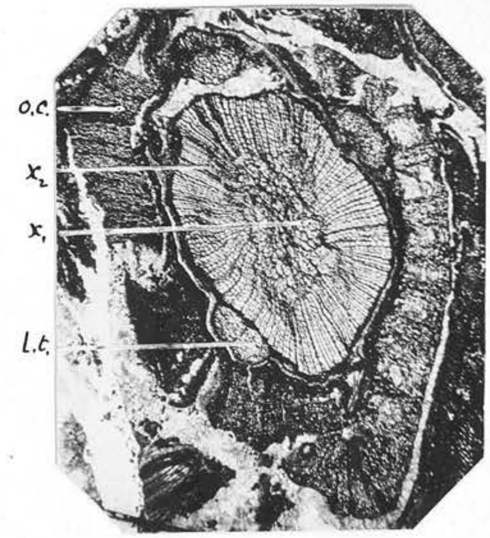

14.

Heterangium Grievii. Williamson 1872.

This, the most ancient known example of the genus, was described originally by Williamson under the name Dictyoxylon Grievii but shortly afterwards he referred it the genus Heterangium. Specimens are exceedingly common at Pettycur and they are generally well preserved though usually crushed.

The axis is composed of a great number of small, anastomosing groups of tracheides set in a ground tissue of parenchyma. These tracheides have multiseriate pits on their walls except the protoxylem elements which have spiral thickenings. These protoxylem groups are arranged round the periphery of the metaxylem but slightly below the surface, i.e. they are sunk and mesarch. A zone of secondary xylem sometimes surrounds the primary cylinder but it is often very irregular in its development and distribution. In some cases such secondary wood only occurs where adventitious roots join the stem. Such roots were discovered by Miss Benson and myself, about the same time, and we shall describe them in a joint-paper. They are either triarch or diarch and we have never found any without secondary xylem. The peculiar aggregation of secondary wood round the point of emission of the root traces is very interesting.

External to the woody axis there is a zone of phloem and delicate parenchyma but it is not usually preserved. Surrounding the phloem there is a layer 5 or 6 cells deep of thin walled mucilaginous /

mucilaginous tissue. There are no ducts present and the tissue is specially abundant where the root-traces are passing out. It is generally well preserved in the roots themselves.

The inner cortex, which is outside the mucilaginous zone, also consists of thin walled parenchyma but it contains vertical rows of sclerotic discs. These do not pass continuously right round the stem but there are generally several vertical series of such discs in each stem. Special transverse and longitudinal sections pass between the series of discs but such sections are very rare.

The outer cortex is very narrow. It is made up of alternate areas of thin walled parenchyma and sclerotic fibres. In longitudinal section the fibres are seen to be elongated and the groups anastomose. There is thus a reticulum of fibrous elements in the outer cortex. The meshes of this reticulum are very long and narrow.

Turning now to the petiole traces, we find that they are emitted in rapid succession but that they travel up through more than one internode so that 10 or more traces may be seen in one transverse section. The petiole bases also are decurrent for long distances into the stem. The trace is concentric and has a constriction in the middle which is often very deep so that there is the appearance of a double bundle. There are never, however, two separate masses of xylem in the petiole bundle.

Though no foliage has ever been recorded in continuity with the /

the petioles of H. Grievii, there is good reason to refer Sphenopteris elegans to this species. The small sclerotic discs which stand out so markedly on a weathered surface of H. Grievii are also distinctly visible on the carbonised impressions of S. elegans. As such discs are unknown in any other species there is every reason to accept this correlation of foliage and stem.

Sphaerostoma ovale (Williamson) 1876.

Williamson made two species to contain what were afterwards shown to be differently orientated sections of one species. These were Conostoma ovale and Conostoma oblonga. Professor Oliver and Mr Salisbury have just published a memoir on Conostoma and have shown that the Pettycur specimens do not belong to the Conostoma group. Miss Benson has given the name Sphaerostoma to the Pettycur seed but no description has yet been published.

In one small part of a block I discovered quite a nest of these seeds but unfortunately there was no indication of the plant which bore them. There were probably between 60 and 70 of these seeds in the one small piece but the preparations are not all completed yet. In the case of one example great care was taken to obtain a perfectly radial section and Pl. A. fig. 4 represents this specimen. At the chalazal end a single vascular bundle enters the seed but this divides up into from 7 to 9 strands, which radiate out and keeping parallel to the outer coat of the seed end close together round the micropyle.

The /

The outer coat or testa is poorly preserved and the whole layer looks like one continuous mass without cellular structure. At the micropyle however, the preservation is better and the testa is seen to consist in that region of radially elongated cells. They get longer near the top of the micropylar orifice and so the opening appears to be on the top of a broad dome-like papilla.Entering the micropylc we reach the sinus between the free epidermis of the nucellus and the inner layer of the integument (testa), (Pl. A. fig. 4.s.). Immediately below the micropyle in the opening into the pollen chamber (Pl. A. fig. 4 p.c.) the wall of which is the epidermal layer of the nucellus. The lower part of the pollen chamber is produced upwards as a cone of delicate tissue and completely plugs up the opening of the pollen chamber. It seems to have been a mechanical arrangement for allowing pollen in only under certain conditions. Apart from this truncated conical plug the nucellar tissue is not preserved.

This seed has been referred to <u>Heterangium</u> <u>Grievii</u> on the grounds of association but we now know two other Heterangia from Pettycur and one other seed so that this correlation cannot be accepted.

[Extracted from the *Proceedings of the Cambridge Philosophical Society*
Vol. XV. Pt. V.]

On a new species of Physostoma from the Lower Carboniferous Rocks of Pettycur (Fife).

By W. T. GORDON, M.A., B.Sc., Falconer Fellow of Edinburgh University, and Advanced Student Exhibi-ioner of Emmanuel College. (Communicated by Mr E. A. Newell Arber.)

[*Read* 7 February 1910.]

Among the rarer petrifactions of plant-remains occurring in he Calciferous Sandstone Rocks at Pettycur are seed-like bodies f various kinds. Perhaps the commonest example is *Lepido-arpon wildianum*, Scott*, while occasionally the pteridospermous ructification—*Conostoma ovale*, Williamson†, is also met with. Under the name *Conostoma intermedia*‡ Williamson also placed what are probably elongated specimens of *C. ovale*. These two eed bodies are very distinct, for *Conostoma* has a funnel-like micropyle, whereas *Lepidocarpon* has no true micropyle. The megaspore in the latter was exposed to the exterior by means of a slit-like aperture between two enveloping outgrowths from the sporophyll.

Last year Prof. Oliver§ published his work on *Physostoma elegans*, and showed that in that genus the apex of the seed consisted of closely adpressed, free, tentacular processes; the micropyle was thus capable of great enlargement.

In the same paper he refers to *C. ovale* as being probably the seed of *Heterangium grievii*, Williamson. The only evidence however is association. Recently, while examining a new species of Heterangium from Pettycur, I discovered several specimens of *C. ovale*, and among them what appears to be a new and distinct seed. The specimen had been cut through in an oblique tangential direction, but by careful preparation I was able to get one of the sections more nearly radial. One section is through the micropylar orifice and the other passes through the chalaza.

GENERAL STRUCTURE.

The seed is radially symmetrical and is considerably larger than *C. ovale*. The following table gives the dimensions of the new seed and those of *C. ovale*.

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* Scott, *Phil. Trans. Roy. Soc.* B. Vol. CXCIV. 1901, p. 291.

† Williamson, *Ibid.* Vol. CLXVII. 1877, p. 243.

‡ *Ibid.* p. 246.

§ Oliver, *Ann. Bot.* Vol. XXIII. 1909, p. 73.

	New Seed (*Physostoma*)	*Conostoma ovale*	
Length	3·8 mm.	3·2 mm.	Average of 5 radial sections
Breadth	3·3 mm.	2·1 mm.	

The length of the new seed is probably greater than indicated, since both sections are oblique, and 4 mm. would probably not be an excessive estimate of the true length. The breadth is also considerable, and indeed the almost globular shape of the seed is striking. The base is rather flat and the micropyle is not prominent.

The seed at the apex shows a number of tentacular processes and the outer surface is studded with small peg-like hairs. The occurrence of these characters warrants its inclusion in the genus Physostoma as lately defined by Oliver.

All the Pettycur seeds I have examined are poorly petrified, and this new one is no exception. The description must therefore be meagre.

The nucellus is capped by the pollen chamber but there is no dome-like projection of the nucellar apex into the cavity of the pollen chamber. Indeed, in that region the seed is quite like Conostoma and not Physostoma. Outside the membrane of the nucellus the tissues are all decayed; only the vascular bundles remain. Near the chalaza however and in one of the apical processes a slight amount of delicate parenchymatous tissue can be observed, but it is too fragmentary to warrant detailed description.

The outer layers of the integument have all decayed into a structureless dark zone about ·2 mm. thick. There are no ribs on the outside of the seed, but the whole periphery is covered with small dark dots. These lie in a zone concentric with the seed and about ·1 mm. outside. Near the micropyle these dots are seen to occupy the ends of short finger-like cells which clothe the seed externally. They are quite similar to the peg-cells of Lagenostoma and may be equivalent to the hairs on *Physostoma elegans*. In this new specimen the hairs are equal in length all over the surface. In outline the hairs are short and have rounded ends.

The most interesting part of the seed, however, is the micropylar end. There we find a pollen chamber in the usual position at the apex of the nucellus. The orifice of this chamber is not visible owing to the obliquity of the section and it is uncertain whether there was a funnel-shaped aperture as in *Physostoma* *elegans* or a depressed aperture as in *Conostoma ovale.* The micropyle which lies immediately over the opening of the pollen chamber is also cut tangentially and in the most radial section is clearly bounded by three separate tentacle-like processes.

The chalazal end is also interesting from the fact that the bundles enter the seed independently as in Physostoma.

This new species of Physostoma, which is more ancient than *P. elegans* recently described by Professor Oliver, combines with its Physostoma characters, others which are typical of the genus Lagenostoma. The tentacular processes at the apex suggest affinities with Lagenostoma in that they are less divergent than in Physostoma (i.e. they clasp the pollen chamber more tightly), and thus the seed has the whole apex flattened as in Lagenostoma. On the other hand the structure of the pollen chamber, so far as is known, is quite unlike that of Lagenostoma. The seed may however eventually require to be placed in a new genus.

In conclusion I have to thank my supervisor Mr Arber for his kindly criticism and advice.

Amyelon sp. The root described under this name is one of very doubtful affinities. It resembles to some extent the root of Sphenophyllum Pl. B. fig. 6 rt., but it also resembles the supposed roots of Heterangium Arberi. The primary wood is very small but there is a remarkable development of secondary xylem. Very little is known, however, about the relationship of this root-body. Pl. B. fig. 8 represents a transverse section of this root.

Traquairia Carruthers 1872.

Several specimens referable to this genus have been discovered. In his memoir of 1879 Williamson assigns Traquairia to the Lycopodiales and not to the Radiolaria as Carruthers did. Mrs Scott has recently read a paper on this genus but it has not yet been published. In the meantime the affinities are doubtful. The structure is very simple; the body is a small spherical organism with muricated spiny outgrowths from the investing wall. Inside in some cases small cells have been found.

EXPLANATION OF PLATES.

Photographs from untouched negatives.

PLATE A.

Fig. 1. Transverse section of stem and petiole of *Botryopteris antiqua*. st = xylem of stem; o.c. = outer cortex; pet = petiole-trace.

Slide G, 752 x 15.

Fig. 2. Transverse section of *Botryopteris antiqua*.

st = stem xylem; i.c. = inner cortex; o.c. = outer cortex; pet = petiole-trace; prx = petiolar protoxylem.

Slide 755 x 36.

Fig. 3. Transverse section of *Botryopteris antiqua*.

st = stem xylem; prx_1 = protoxylem decurrent into stem; pet = petiole-trace; prx_2 = protoxylem of petiole; o.c. = outer cortex; rt = root-trace.

Slide 590 x 15.

Fig. 4. Longitudinal radial section of *Sphaerostoma ovale*.

n = nucellus; mi = micropyle; c = chalaza; p.c. = pollen chamber; s = sinus; t = plug of tissue closing pollen chamber orifice.

x 10.

Fig. /

Fig. 5. *Physostoma sp*. Oblique section. p.c. = pollen chamber; n = nucellus; a_1, a_2, a_3, = tentacular processes forming micropyle.

x 10.

Fig. 6. *Lepidodendron Veltheimianum*, transverse section of small twig. x = axis; p = pith cavity; o.c. = outer cortex; l.b. = leaf-base.

x 10.

Fig. 7. *Lepidodendron Veltheimianum*, longitudinal section of two buds showing imbrication of leaves.

x 4.

Fig. 8. *Stauropteris burntislandica*, transverse section of petiol x = petiole trace; prx = protoxylem groups; ph = phloem; i.c. = inner cortex; o.c. = outer cortex; e = epidermis.

Slide x 30

Fig. 9. *Lepidodendron Veltheimianum*, longitudinal section of ligule. x = xylem of axis (scalariform tracheides); v.b. = bundle of leaf; lg = ligule.

Slide 227 x 50.

Fig. 10. *Lepidodendron Veltheimianum*. A few leaf bases (impressi only.)

x 2.

PLATE B.

Fig. 1. Dineuron ellipticum. Transverse section of petiole showing pinna departure. Pet. tr. = petiole trace; pin. tr$_1$, pin. tr.$_2$ = pinna traces; o.c. = outer cortex.

Slide 100 x 20

Fig. 2. Dineuron ellipticum. Section below that of fig. 1. Lettering same as before.

Slide 100A x 20

Fig. 3. Dineuron ellipticum. Section below fig. 2. Slide 100B

Fig. 4. Dineuron ellipticum. Transverse section of petiole trace. x = xylem of trace; prx = protoxylem groups; g = groove on end of petiole trace which closes in to form the island (is.) of other end; is. = island of parenchyma; b = pinna-trace bar.

Slide x 50.

Fig. 5. Dineuron ellipticum. Transverse section of petiole. x = xylem of trace; o.c. = outer cortex; sc. = sclerotic outer cortex.

Slide x 20.

Fig. 6. Sphenophyllum insigne. Transverse section of stem showing root departure. x= axis of stem (x_1 = primar wood; x_2 = secondary wood); prx = protoxylem groups /

groups; rt. tr. = root trace.

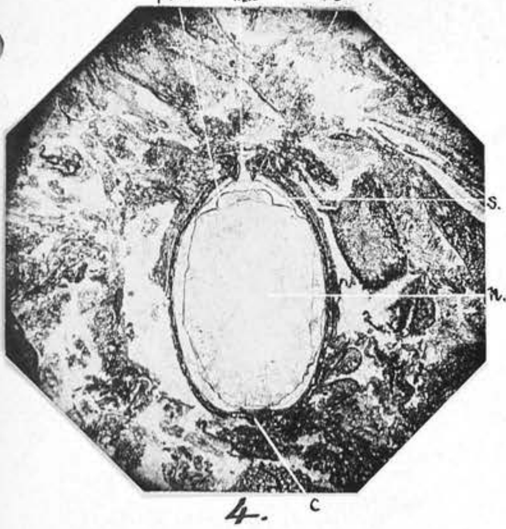
Slide x 18

Fig. 7. Stauropteris burntislandica. Transverse section of petiole to show bifurcation. x = petiole trace; prx = protoxylem groups; i.c. = inner cortex; ph = phloem; o.c. = outer cortex.

Slide x 30

Fig. 8. Amyelon sp. Transverse section of wood. x_1 = primary wood; x_2 = secondary wood.

Plate. A.



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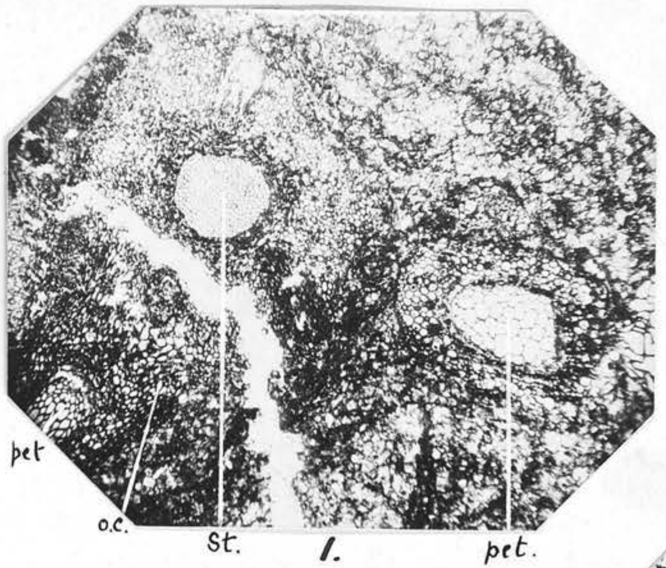

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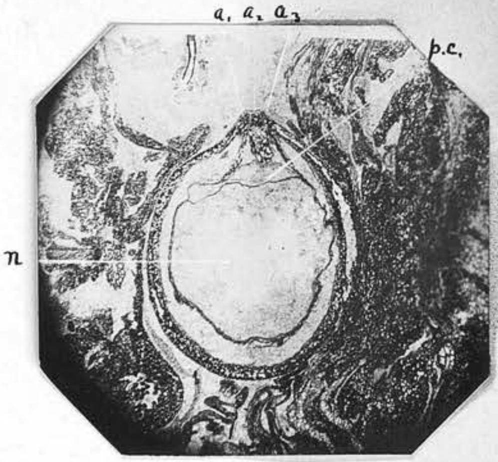

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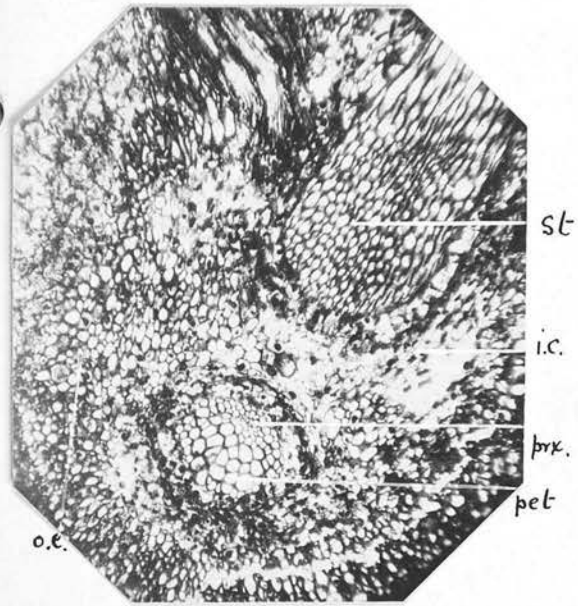

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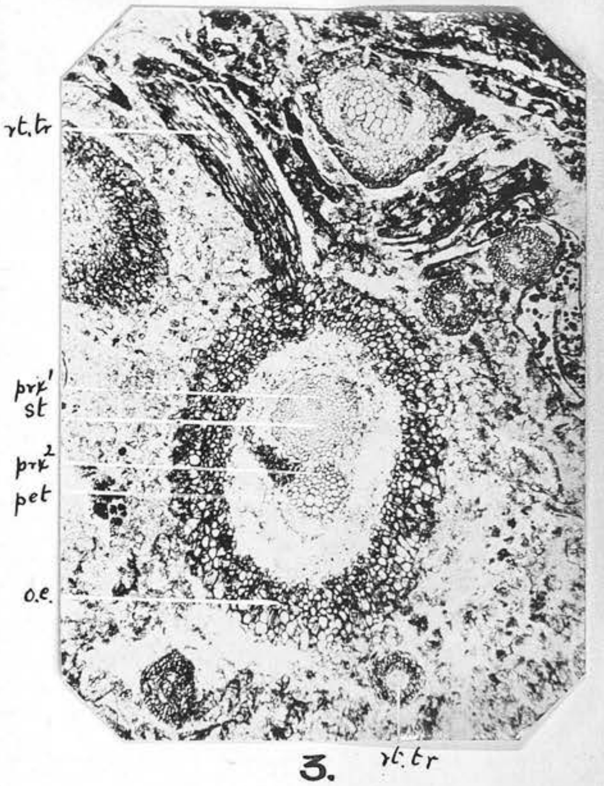

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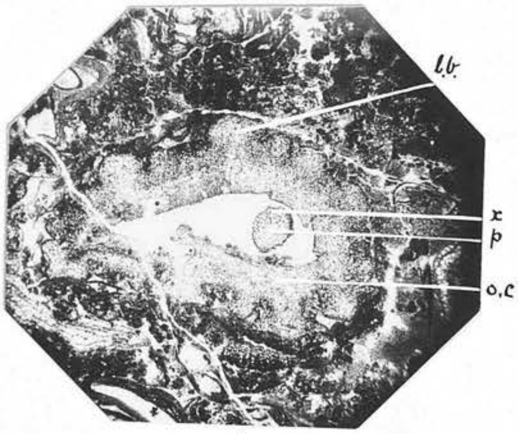

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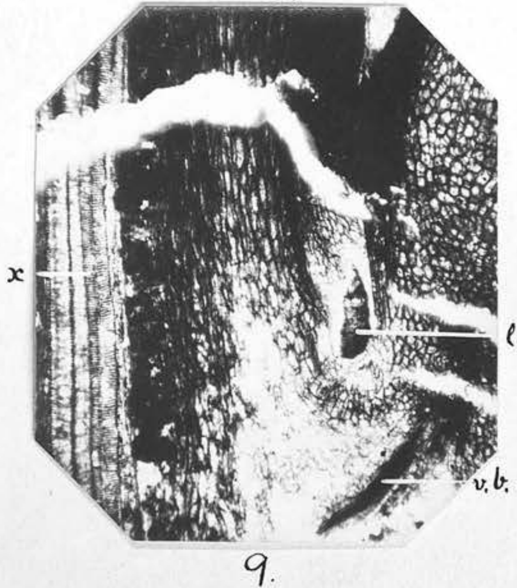

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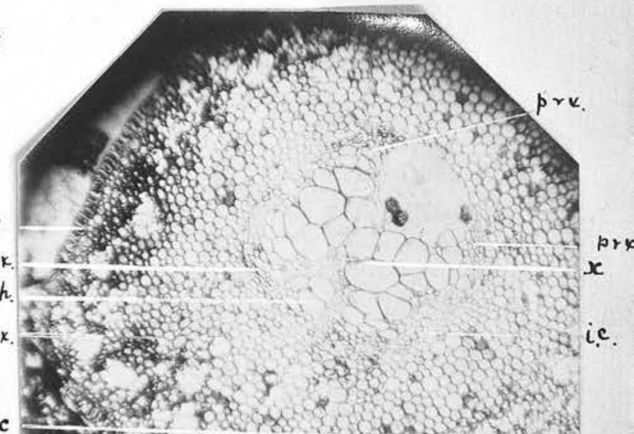

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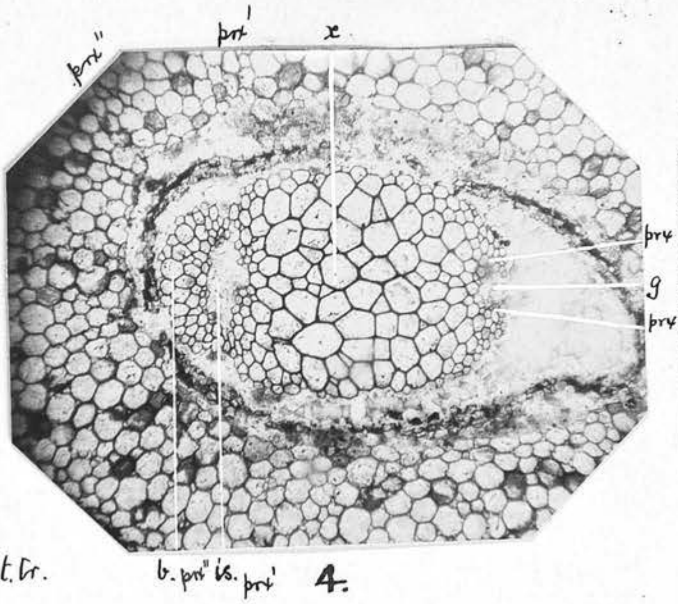
Plate B.

1.



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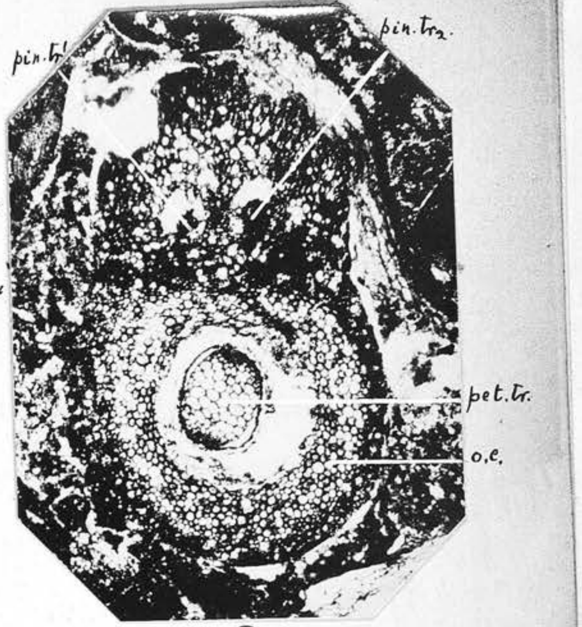

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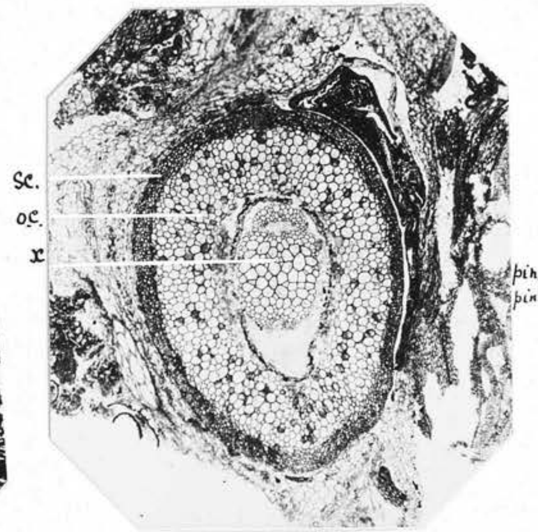

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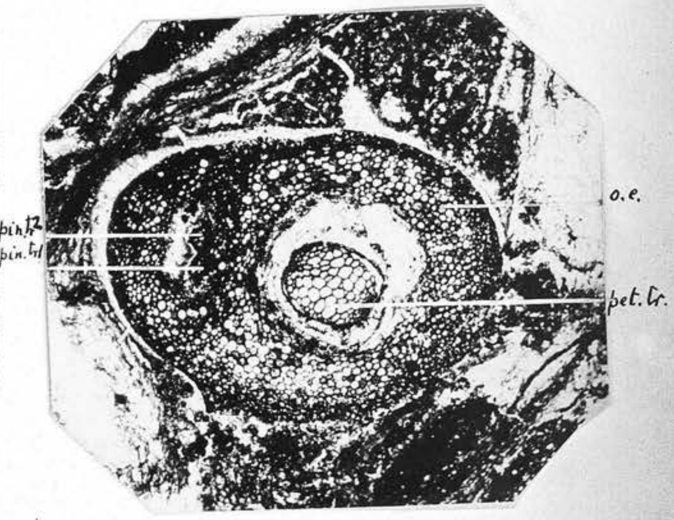

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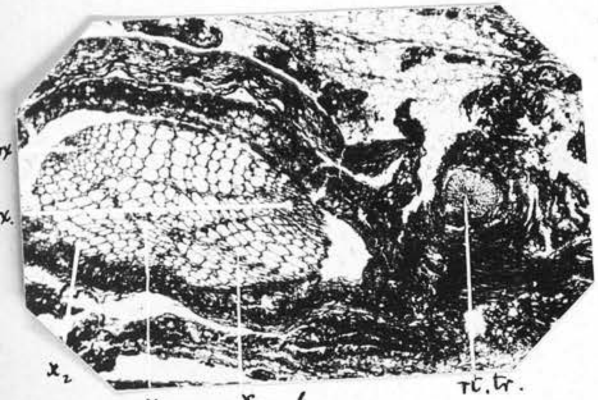

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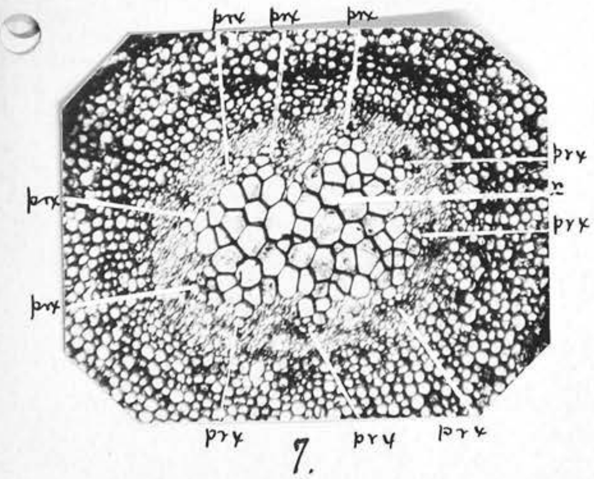

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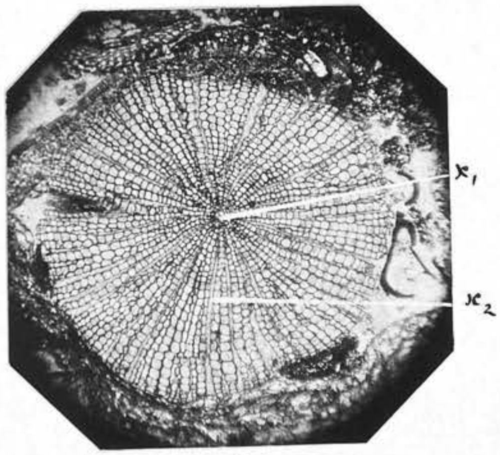

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