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.)

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CONTENTS.

	PAGE		PAGE
Introduction	711	Summary	727
General Structure	715	Diagnosis	728
Histology :—1. Of the stem	719	Conclusions and General Considerations	728
2. Of the petiole	720	Bibliography	733
3. Of the root	726	Explanation of Plates	734

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 petrifications. 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.

* 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 *Zygopteridæ*, 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 petrifications occurring at Pettycur are either found lying loose

* K. and G.-V., *Trans. Roy. Soc.*, Edinburgh, vol. xlv. 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. $\times$ 1 ft. $\times$ 1 ft., and the other 1 ft. $\times$ 9 ins. $\times$ 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 petrifications 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

No	Stage of Pl. ii Fig. 18	Stage of Pl. ii Fig. 21	Stage of Pl. ii Fig. 24	Stage of Pl. ii Fig. 25	Stage of Pl. ii Fig. 25	Stage of Pl. ii Fig. 28	Slides
1			—————				701 - 711
2				—————	—————		713 - 733
3				—————	—————		650 - 700
4		—————	—————	—————	—————		284(a-z)-294
5	—————	—————	—————	—————			340 - 356 & 284 - 284p
6	—————	—————					335 - 338
7	—————	—————					331 - 334

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

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.

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

* 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 chequered 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

* 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 petrification. 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

* 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

FIG. 2a.—Plan of the pinnae on the rachis of *Diplolabis römeri*. The tendency to a dorsiventral arrangement is indicated.

FIG. 2b.—Elevation showing the vertical arrangement of the pinnae on the rachis. *Pet. tr.* = petiole-trace ;
pin. tr. = pinna-trace ; *aph. tr.* = aphlebia-trace.

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.

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 petrification (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.*

* "Bass. houill. et perm. d'Autun et d'Épinac," pp. 17 and 18, *Atlas 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 α, α , 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).

* 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 zygoterid 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 rœmeri* 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

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.

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).

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.e.* 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 aphebiæ. 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. 1., 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 Calcareous Sandstone (Culm) rocks, all of which contain a more ancient type of flora than that of the Permian-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 paren-

chymatous pith with a system of internal tracheides. The other known zygoterid stems are still more complicated and distinct. Thus, among the known Zygoterideæ the stem of *D. römeri* is the most primitive in its anatomy, and it is also among the earliest known zygoterids in time.

The position of this genus in the zygoterid 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 *Zygoteris 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 Zygoterideæ (if we regard simplicity of the xylem of the petiole as synonymous with primitiveness). There are thus the *Clepsydropsis*, the *Dineuron*, and the *Zygoteris* 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

* *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

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.

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.

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 *Zygopteridæ* and the *Osmundaceæ*, though the petiolar structure is not more primitive than that shown in the *Osmundaceæ*. On the whole, the *Botryopteridæ* seems much nearer the osmundaceous type than are the *Zygopteridæ*. Indeed, the *Zygopteridæ* 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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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. $\times 12$. (Slide 742.)

Fig. 2. Transverse section of stem near a dichotomy. x . = outer xylem ; x^1 = inner xylem. $\times 12$. (Slide 735.)

Fig. 3. Section following that of fig. 2. x . = outer xylem ; x^1 = inner xylem. $\times 12$. (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). $\times 10$. (Slide 737.)

Fig. 5. Longitudinal section of stem-xylem. x . = outer xylem ; x^1 = inner xylem. $\times 10$. (Slide 806.)

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

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

Fig. 8. Longitudinal section of protoxylem elements with scalariform thickenings. $\times 130$. (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. $\times 3.2$. (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. $\times 3.2$. (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. $\times 3.2$. (Slide 336.)

Fig. 12. Specimen of petiole with pinnae 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. $\times 10$. (Slide 771.)

Fig. 15. Transverse section of stem following that of fig. 14. x . = outer xylem ; x^1 = inner xylem ; *prx.*, *prx.* = petiolar protoxylems. $\times 10$. (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. $\times 10$. (Slide 773.)

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

Fig. 18. Petiolar departure, later stage than fig. 17. Petiole-trace distinct. x . = outer xylem ; x^1 = inner xylem ; *prx.*, *prx.* = protoxylem. $\times 11.6$. (Slide 740.)

Fig. 19. Petiolar departure, stage beyond fig. 18. x ., x^1 and *prx.* as before. $\times 11.6$. (Slide 741.)

Fig. 20. Petiolar departure, petiole-trace free from stem-xylem. x , x ,¹ and prx , as before. $\times 11\cdot6$. (Slide 742.)

Fig. 21. Petiole-trace—transverse section—while still in cortex of stem. Each protoxylem has divided into two. prx ,₁, prx ,₁¹, prx ,₂, prx ,₂¹ = protoxylems. $\times 7\cdot5$. (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. $\times 10$. (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?). $\times 10$. (Slide 343.)

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

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

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

Fig. 27. Stage beyond that of fig. 26. prx . = protoxylem; p ,₁, p ,₂ = united traces of a pair of reduced pinnae; the traces are connected together by a thread of xylem. $\times 7$. (Slide 719.)

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

Fig. 29. Stage following that of fig. 28. This is the normal *Diplolabis römeri* trace. prx . = protoxylem. $\times 7$. (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 petiole-trace above stage of Pl. II. fig. 22. is . = island of parenchyma. $\times 25$. (Slide 341.)

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

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

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

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

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

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

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

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

Fig. 39. Stage after fig. 38. is , is . = islands of parenchyma. $\times 25$. (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. $\times 25$. (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. $\times 22$. (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. $\times 14$. (Slide 793.)

Fig. 43. Transverse section of petiole showing the division of the pinna-trace-bar. $pin. tr.$ = pinna-trace; $aph. tr.$ = aplebia-trace; $o. c.$ = outer cortex. $\times 2\cdot4$. (Slide 789.)

Fig. 44. Transverse section of petiole showing bifurcation of aplebia-trace. $pin. tr.$ = pinna-trace; $aph. tr.$ = aplebia-trace (four of them). $\times 2\cdot2$. (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. $\times 2.2$. (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. $\times 10$. (Slide 800.)

Fig. 47. Transverse section of pinna-trace immediately after the pinna is free from the stem. $\times 10$. (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. $\times 10$. (Slide 324.)

Fig. 49. Transverse section of root-trace. *prx.* = protoxylem. $\times 36$. (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. $\times 43$. (Slide 811.)

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

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

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

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