New Observations on *Botryopteris antiqua*, Kidston.

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With Plates LXXXI-LXXXIII and three Figures in the Text.

CONTENTS.

	PAGE
I. INTRODUCTION	1045
II. GENERAL MORPHOLOGY AND RANGE OF VARIATION	1046
III. NODE AND INTERNODE	1047
IV. THE LEAF-TRACE AND PETIOLAR BUNDLE	1047
V. THE BRANCHING OF THE DIARCH PETIOLAR BUNDLE	1048
VI. THE MONARCH PETIOLAR BUNDLE AND APHLEBIAE	1048
VII. THE ROOT-BEARING ZONES OF THE STEM STELE	1051
VIII. PSEUDO-SECONDARY THICKENING OF THE STEM XYLEM	1052
IX. BEARING OF THE NEW OBSERVATIONS ON THE AFFINITY OF THE GENUS	1053
X. SUMMARY	1054
XI. CONCLUSION AND ACKNOWLEDGEMENTS	1055
EXPLANATION OF PLATES	1055

I. INTRODUCTION.

IN 1908 Dr. Kidston published a short account¹ of a new species of *Botryopteris* from Pettycur, Fife. He gave it the name of *Botryopteris antiqua*. Unfortunately, he had inadequate material for a full description, and especially states that 'none of the stems yet met with show the departure of the leaf-trace from the stele'.²

A more abundant supply which was recently collected at Pettycur, and has been cut in the Botanical Laboratory at the Royal Holloway College, makes it possible to note the range of structure of the various organs, and affords, therefore, a better ground for comparison of this early species with those of later date.

Since the publication of Dr. Kidston's diagnosis, Professor Bertrand

¹ Kidston: On a New Species of *Dineuron* and *Botryopteris* from Pettycur, Fife. Trans. Roy. Soc., Edinburgh. vol. xlv, Part II, p. 362.

² Kidston: loc. cit., p. 363.

and M. Cornaille have published a note¹ on the *Botryopteris* type of leaf-trace in which they refer to a form which they call *Botryopteris antiqua*, 'd'Esnot'. Professor Bertrand kindly sent me a photograph of the transverse section of the petiole of this form, and states that Dr. Kidston identifies it with his species. In this photograph one of the two protoxylem groups is excellently preserved, and agrees in structure with the more detailed account I have given of the new specimens, but the other is not clearly shown. Professor Bertrand tells me that this form from Esnot has been known to him for many years and was known to Renault, but there were difficulties in diagnosing it as a species distinct from those of the Upper Carboniferous Rocks. The reasons for this difficulty I will refer to later (*vide* p. 1048).

The early date and wide distribution of the species, its variable but simple anatomy, make it an interesting subject of investigation, and I have therefore thought the following observations worthy of record.

II. GENERAL MORPHOLOGY AND RANGE OF VARIATION.

The plant consisted of a rhizome which in one region gave rise to numerous adventitious roots and was covered with uniseriate hairs. After a short interval the rhizome bore petiolar structures whose traces came off at a two-fifth phyllotaxy. Often after only two nodes the rhizome gave off more adventitious roots, which sometimes arose very close to a node. Hairs are not generally found except on the root-bearing part of the stem, but this may be an accident of preservation. The petioles varied not only in size but in character. The larger ones contained a diarch trace, the smaller only a monarch trace. The latter forms generally left the stem at the same level with a curious uninerved sheathing body, probably to be homologized with the so-called aphlebiae of the *Zygopterideae*. It will be treated of in a later section (*vide* § VI).

The stem stele varies very much in size and constitution in different parts of the same plant. In the purely leaf-bearing zone the protoxylems are concentrated into one or two centres, but in the region of root formation there are many scattered and peripheral protoxylem elements, and the transverse section of the stem is increased in size.

As in the later species of *Botryopteris* the large metaxylem elements of the petiole trace are porose, while the smaller elements and protoxylem show all intermediate phases from porose to reticulate. As a result, where no leaf-traces are being differentiated in the stem, it presents quite a different appearance from that at a node. (Cp. Pl. LXXXI, Fig. 1, and Pl. LXXXII, Fig. 13 a.)

Lastly, the *Botryopteridean* sporangia which are associated with these

¹ C. E. Bertrand et F. Cornaille : Les caractéristiques de la trace foliaire botryoptéridienne, t. cl, note, p. 1019. Comptes rendus des Séances de l'Académie des Sciences, 1910.

stems vary very considerably in size. Thus the sporang photographed in Fig. 18 is nearly double the size of any member of the group of four in Fig. 17. The latter show the same dimensions (275μ) and arrangement as those described recently by Dr. Scott.¹

The specimens considered occur in three different blocks of calcite, but in spite of all the range of variation they exhibit, it has not been found possible to demonstrate the presence of more than one species.

III. NODE AND INTERNODE.

In that part of the stem which is not complicated by the emission of roots, the structure of the stele throughout the node and internode is characterized by a very simple series of changes. As the leaf-trace separates from the stem xylem, the latter consists of a mass of primary tracheides with but one protoxylem group placed laterally very near the surface of separation of the trace (Pl. LXXXI, Fig. 1). In cases where the leaf-trace is equal in size to the stem stele there is little to distinguish the trace from the stele (cp. Figs. 7 and 8 *a*). The trace separates off along one margin first, and gradually increases its angular divergence until it lies at 90° to its plane of attachment (Pl. LXXXII, Figs. 11 and 12).

The protoxylem group left in the stem bifurcates, and after a very short interval (within three millimetres sometimes) two protoxylem groups are to be seen, now surrounded by metaxylem. Photographs of stem sections in this plane are shown in Figs. 2, 8 *a*, and 9 *a*. These are each from a different specimen and agree in demonstrating the formation of peripheral metaxylem elements which restores the mesarch position of the two protoxylem groups. One of these groups is the new leaf-trace group, which is thus clearly shown to be mesarch in origin.

IV. THE LEAF-TRACE AND PETIOLAR BUNDLE.

One of the two above-mentioned protoxylem groups, lying at two-fifth angular divergence from the point of departure of the last leaf-trace, may now be looked upon as destined for the next leaf. As already stated, it may pass out undivided, in which case we have a monarch trace and monarch petiolar bundle (Pl. LXXXI, Figs. 4 *a* and 9; Pl. LXXXII, Fig. 14; Pl. LXXXIII, Figs. 19 and 21).

Very frequently in the specimens under consideration the protoxylem of the leaf-trace is duplicated (Fig. 11) while still in contact with the stem xylem. An early stage in this duplication is indicated in Fig. 6 *a*, where separation is just being initiated. While the leaf-trace is passing through the cortex of the stem, all formation of strictly centrifugal metaxylem ceases, but the protoxylems line the bottom of adaxial grooves owing to the differentiation of elements of metaxylem laterally. These

¹ Scott: Sporangia attributed to *B. antiqua*, Kidston. *Annals of Botany*, 1910, Note, p. 820.

grooves, which appear like shallow pits bordered by a pair of minute cusps in transverse sections of the petiole, persist after the branching of the main rachis (Pl. LXXXIII, Fig. 24). Each groove with its projecting margins probably represents a so-called tooth of the later species, *B. hirsuta* and *B. ramosa*, although in these species the adaxial protoxylems are clearly endarch.

In this view I differ from MM. Bertrand and Cornaille, who refer to the *Botryopteris antiqua* type of petiole as tridentate.¹ This interpretation may possibly have prevented the earlier diagnosis of *B. antiqua*, 'd'Esnot'.

As is shown in the succeeding paragraph, it is only during incipient phases of branching that the Pettycur species could be described as tridentate, and it was due to the prevalence of petioles in this condition in my earlier material that I was unable to clearly distinguish the earlier from the later species until comparatively recently.

V. THE BRANCHING OF THE DIARCH PETIOLAR BUNDLE.

When a diarch petiolar bundle is preparing to branch, a third pair of cusps appear, exactly like the original two. This, which probably owes its origin to the bifurcation of one of the two existing protoxylem groups, travels for a considerable distance in the petiole before the separation of the two metaxylem masses takes place. Hence, as already stated, in a long series of sections (Slides 390. 11-21, *vide* Fig. 24) of a branching petiole, we may have a fair semblance of the triarch type of petiole characteristic of later species. Finally, the branch, which is generally smaller than the parent rachis, passes off laterally. No equal dichotomy of a diarch petiole has been met with—the only record of a case being apparently due to an oversight.²

VI. THE MONARCH PETIOLAR BUNDLE AND APHLEBIAE.

I have no instance of two successive nodes giving off diarch traces—monarch traces apparently precede and follow the diarch trace. The monarch traces, however, apparently never come off, pass through the cortex and enter the petiole, without being accompanied by aphlebiae.

In four of the specimens figured (Figs. 8-9, 10, 19-20, and 21), monarch petiolar traces are obviously associated with minute monarch traces which come off from the stele almost simultaneously with their respective petiole traces.³ In three of these cases (Figs. 8-9, 19-20, 21), the monarch petiolar trace with its aphlebia trace follows a diarch trace, whereas in Fig. 10 there is evidence that a large trace succeeded such a pair. This figure also indicates that the aphlebia trace diverged from the petiole trace

¹ Bertrand et Cornaille: loc. cit., p. 1022. 'La trace réalise alors le facies tridenté des *B. hirsuta*, *B. antiqua*.'

² Kidston: loc. cit., Figs. 11 and 12, which appear to represent a node of a stem.

³ Cp. Kidston: loc. cit., Fig. 4, where 'pet' appears to represent the aphlebia corresponding to the petiole trace *pet*''.

when they both became free from the cortex. This is also shown in other preparations.

That the angle between the two bundles was filled by a lamella is shown in Text-figs. 1 *a* and 1 *b*, which are camera drawings from sections showing the sheathing character well. In Fig. 14 the aphlebia trace is still unseparated from the stem stele (*vide* Fig. 14, *px*). We have in this series of sections an example of the aphlebia trace coming off (Slide 393. 25, Text-fig. 1 *a*) at a considerable interval after the corresponding petiole trace (Slide 393. 28, Fig. 15).

Another curious case is afforded by the series partly reproduced by Figs. 1–5. A badly developed diarch trace comes off just before the level of Fig. 1 (Slide 407. 14). A monarch trace comes off at the next node

TEXT-FIG. 1 *a*. A camera sketch from a stem node of which the previous section is shown in Fig. 14, Pl. LXXXII. The Text-figure shows the aphlebia (*aph.*) with its sheathing base, which is attached to the monarch petiole, *p*. The stem stele (*s.s.*) is giving off various roots (*r.*, *r'*). Slide 393. 25. $\times 19$.

TEXT-FIG. 1 *b*. A camera sketch from a comparable node at a slightly higher level. *p* = petiole, *aph.t.* = aphlebia trace, *s* = stem. From a slide kindly lent for the purpose of this figure by Dr. Gordon. C.N., 1301. $\times 19$.

(*vide* Fig. 4 *a*, which is a photograph from Slide 407. 9). No evidence of an aphlebia appears with the latter until Slide 407. 7, where the petiole, now free from the cortex, shows a small branch coming off from its vascular bundle (*vide* Fig. 23). If one follows up this small branch through a series of sections of the petiole (Slides 407. 7–2), we find it flattens out and disappears, never entering an appendage of the petiole. We must, I think, regard this as a belated and abortive aphlebia trace. The phenomenon is very like the belated formation and abortion of the axillary strand in the leaf of *Trichomanes javanicum* described by Miss Chambers.¹ In this species it was shown that the axillary strand, described by Boodle² as occurring in many of the Hymenophyllaceae, may defer its separation from the leaf-trace until the latter has entered a petiole.

¹ Chambers: in the present number of the *Annals of Botany*.

² Boodle: *Anatomy of the Hymenophyllaceae*. *Annals of Botany*, xiv, 1900, p. 455.

There is no evidence that the vascular bundle supplying an aphlebia ever branched. In no single case has an aphlebia been seen in connexion with a diarch trace (cp. Pl. LXXXII, Figs. 11-13). Thus we may regard it as fairly established that diarch petioles without any aphlebia occur, succeeded by petioles with a monarch vascular bundle and a monarch aphlebia trace. This contrast between the petioles of *B. antiqua* is interesting, and probably will prove to indicate some distinction in function to which we have as yet no clue.

The aphlebia is simpler in structure than the bodies described under this name in the Zygopterideae, for the latter receive a bundle which 'divides into two, three, or four strands',¹ whereas in *Botryopteris antiqua* I have met with no example of the branching of an aphlebia bundle.

In one respect the diarch petiole resembles the monarch petiole with its aphlebia, e.g. they each receive a vascular supply, including two protoxylem groups. Perhaps on this ground we may regard the diarch petiole as equivalent to the monarch with its appendage.

As is well known, Dr. Paul Bertrand regards *Botryopteris* as having been derived from Anachoropterid ancestors by the shifting of the two fundamental poles of the leaf-trace to an adaxial position. Such a theory involves the assumption that the leaf-trace in *Botryopteris* was primarily diarch. The new observations appear to introduce some difficulty in the acceptance of this view because, if the diarch type were the older, we should be under the necessity of regarding it as already undergoing disintegration or reduction in *B. antiqua*—the oldest known species of the genus.

The argument in Bertrand and Cornaille's recent account of the characteristics of the Botryopteridean trace is based primarily on the 'forensis' type. They suggest the 'ramosa' type to be a reduction form, since they compare it² with the reduction form met with in the upper part of the frond of the 'forensis' type. They also refer to the *B. antiqua* trace as having 'le facies tridenté'. If *B. antiqua*, 'd'Esnot,' has a tridentate leaf-trace it cannot be identified with *B. antiqua* of Pettycur. Except in branching diarch petioles, I have never seen a tridentate trace from Pettycur. If the authors of the above note homologize each of the minute cusps limiting a group of protoxylem with the tooth of *B. ramosa*, then the *B. antiqua* trace is respectively either quadri- or bidentate. The identification of a single protoxylem group in *B. antiqua* with a correspondingly single protoxylem group in the latter type of trace seems absolutely necessary, even though in the former it may be slightly mesarch or sunk between two cusps, and in the latter it is endarch and projects as a single point. It will be simpler, therefore, to refer solely to the number of pro-

¹ Scott : Studies in Fossil Botany, p. 314.

² Bertrand et Cornaille : loc. cit., p. 1022.

toxylem groups, in which case *B. antiqua* may be said to have either a monarch or diarch, while *B. ramosa* and *B. hirsuta* have a diarch or triarch trace.

Since this is the case the trend of evolution in the genus *Botryopteris* would seem to be towards a multiplication of the protoxylems rather than towards a reduction. If we accept the monarch type of leaf-trace as the older, and regard the diarch type as derived from it, we may explain the diarch type as due to arrest of branching at a primary phase. Such a view could be extended to the derivation of the later triarch forms, which may well bear the same relation to the diarch forms as the latter to the monarch. The series would then be continuous, and is represented diagrammatically in Text-fig. 2. In this figure the gradual protrusion of the protoxylem is simultaneously indicated.

TEXT-FIG. 2, *a, b, c, d, e*. A series of diagrams of transverse sections of petiole bundles or leaf-traces of *Botryopteris* (*vide text*). *a* = the mesarch form of the monarch trace which is found while the trace is still only partially separated from the stem stele (cf. Fig. 2) in *Botryopteris antiqua*. *b* = the very common monarch petiole bundle of *B. antiqua*. *c* = the diarch trace of *B. antiqua*. *d* = the branching diarch petiole bundle of *B. antiqua* (cf. Fig. 24). *e* = the unbranched petiole bundle of *B. ramosa*. The position of the protoxylem is indicated by hatching, and is shown to be mesarch at one end of the series and endarch at the other.

In support of this view we may add the facts (*a*) that diarch petioles are known fairly commonly among the later triarch forms, and (*b*) that with the exception of the slightly mesarch position of the protoxylems (Fig. 24), it would not be easy to distinguish, as already stated, a branching diarch petiole of *B. antiqua* from a non-branching triarch petiole of *B. ramosa*.

VII. THE ROOT-BEARING ZONES OF THE STEM STELE.

Sections of stems bearing numerous roots occur both in transverse and longitudinal planes. This part of the stem is covered with delicate

uniseriate hairs with a slightly enlarged base. The roots pass out of the stem rather abruptly, and resemble those of later species of *Botryopteris*. When the xylem of a stem stele is about to give rise to roots, the diagrammatic arrangement of protoxylems and metaxylem described above for the leaf-bearing stem (Pl. LXXXI, Figs. 1–3) is interfered with. The protoxylem becomes at first more scattered (Figs. 12 *a* and 13 *a*), and small peripheral groups are formed at irregular intervals. Meanwhile the xylem increases considerably in bulk, and consists mainly of elements of a smaller size and less definitely porose marking than those supplying the leaf-trace (*vide* Fig. 22). Different examples of such stems are shown in Figs. 4, 6 *a*, and 9 *a*. It is in this region that sections of the stem, e.g. Fig. 13 *a*, show considerable resemblance to those of the root-bearing regions in *Botryopteris ramosa*, and possibly admit of some comparison with those of *Diplolabis* and *Metaclepsydropsis* recently described by Dr. Gordon.¹

VIII. PSEUDO-SECONDARY THICKENING OF THE STEM XYLEM.

As already observed, the xylem of the stem increases its dimensions very rapidly after giving off a leaf-trace, especially if it is about to give off roots (cp. Figs. 11 and 13).

In Fig. 13 two roots are being given off, and we may safely conclude that in Fig. 14 (cp. Figs. 15 and 14) and in Fig. 9 (cp. Figs. 7 and 9) roots would have been demonstrated if the series could have been prolonged.

This increase in size is brought about partly by the differentiation of parenchymatous elements which divide irregularly, as commonly occurs in primary xylem. Partly, however, the serial mode of division of a common mother-cell obtains, examples of which are seen in Figs. 4, 12 *a*, and 15. This mode of developing new xylem appears to be intermediate between the irregular division of normal primary mother-cells and the regular formation of secondary wood from a definite meristem. The resemblance is more striking when several contiguous cells lay down tangential walls in the same plane, as may be seen in Fig. 12 *a*. There is no reason to think this is a vestigial character, as no older nor contemporary form of the *Botryopterideae* has been described with normal secondary thickening.² If primitive it is very suggestive of the way in which secondary meristems may have arisen, and thus seems worthy of record. For such cases of cellular increase as these the term 'pseudo-secondary' is suggested. They are of course exceedingly common, occurring in the stem of *Metaclepsydropsis duplex* and *Diplolabis Römeri*,² among contemporary Ferns and in many recent plants.

¹ Gordon: *Diplolabis Römeri*, 1910; *Metaclepsydropsis duplex*, 1911. Trans. Roy. Soc., Edinburgh.

² Gordon: loc. cit., 1911, Fig. 8. Since writing this Dr. Gordon tells me he has found a striking case in a new stem from Pettycur.

In some cases it may coexist in the same bundle with the more advanced type, i. e. that brought about by the divisions of a definite meristem. Thus pseudo-secondary wood is found at the nodes of *Protocalamites*, where an abrupt increase in the centripetal primary wood takes place, but the centrifugal primary wood of the same bundle is added to by the agency of a normal cambium (Fig. 25).

IX. BEARING OF THE NEW OBSERVATIONS ON THE AFFINITY OF THE GENUS.

In Dr. Paul Bertrand's admirable monograph¹ on the frond of the Zygopterideae, he not only accepts the view that *Botryopteris* is a reduced type, but suggests the mode of its origin. Thus on page 278 he says: 'The Anachoropterideae seem to be derived from the ancient Zygopterideae by the loss of the accessory plane of symmetry. The Botryopterideae form a series parallel to the Anachoropterideae, from which they are derived by the approximation of the two fundamental poles to the anterior face of the foliar trace.'

If this view be accepted we must interpret the simplicity of structure met with in *Botryopteris antiqua* as due to reduction, and not to its relatively primitive character. As already pointed out, this view involves the assumption that the diarch type of petiole is older than the monarch, and the species is in process of simplification. This result is not easy to harmonize with the fact that later forms of *Botryopteris* petiole are triarch.

If we hold Bertrand's view we must grant that not only do the two Anachoropteridean 'fundamental poles approximate to the anterior face of a foliar trace', but that very frequently they are represented by one pole only throughout the main rachis of the petiole in the oldest known species of the genus (Fig. 14).

Our new knowledge of the stem structure and nodes of the older Zygopteridean Ferns, *Metaclepsydropsis duplex* and *Diplolabis Römeri*, which we owe to Dr. Gordon, leads us to regard these forms as possessing a less specialized type of stem structure than later Zygopteridean species, e. g. *Ankyropteris corrugata*. The nodal form of the petiolar bundle, i. e. the leaf-trace, is also comparatively simple, exhibiting in transverse section a tangentially extended band of primary xylem with a mesarch protoxylem group at either end. This structure appears to offer the best basis of comparison between the Zygopterid and Botryopterid types.

The section of the stem of *B. antiqua* shown in Fig. 13 a is not unlike the type found in *Metaclepsydropsis*, except that the peripheral larger centrifugal elements are continuous all round the periphery in the latter.

¹ P. Bertrand: Études sur la fronde des Zygoptéridées, 1909.

There is no vestige of a stellate character in the transverse section of the stem stele of either genus. The smaller internal elements do not contribute to the trace in either. In *Botryopteris* there are far fewer mesarch groups of protoxylem; hence the giving off of a leaf-trace approximates very closely to a simple dichotomy, and resembles what one would expect to find in a primitive Pteridophyte.

We cannot but regard *Botryopteris* as having a close affinity with the Zygopterideae, in spite of the outstanding contrast in the mode of branching of their petioles. The presence of aphlebiae, now for the first time recorded in a species of *Botryopteris*, is a new feature of resemblance. If the *Botryopteris* type does not owe its simplicity to reduction, then the Zygopterid type must owe its complexity to elaboration.

The fundamental difference may possibly be traced back to the origin of the Zygopterid leaf-trace, from parts which in their ancestors gave rise to more than one trace, but we must wait for more facts before the problem of the common origin of the mono- and bisymmetric type of petiole can be solved. That the more complex type is the derived type is suggested by the ontogeny; the gradual series of changes which occur in a single petiole of *Metaclepsydropsis* or *Diplolabis* (so beautifully represented in Dr. Gordon's figures¹) as it passes from the nodal form to the upper part of the main rachis may possibly be regarded as representing in some degree the phases in its evolutionary sequence.

X. SUMMARY.

A considerable amount of new material of the Pettycur species of *Botryopteris* having become available, it has been possible to give details of its structure, especially with regard to its stelar anatomy and the presence of aphlebiae at the base of its smaller leaves.

Botryopteris antiqua, Kidston, is a form which, though variable, is often as large and well differentiated as *Botryopteris ramosa*. The protoxylem elements of the leaf-trace before it leaves the axis are mesarch, and later are aggregated into either one or two adaxial grooves, and are not evenly distributed. Heterophylly obtained, for those petioles which are supplied by a monarch trace are found to possess a uninerved sheathing organ which is regarded as of the nature of an aphlebia. The diarch petioles show no trace of this organ.

The axis was of the nature of a rhizome which at intervals gave off numerous adventitious roots.

The xylem of the stem stele is differentiated differently in the leaf-bearing part and the root-bearing part. The distribution of the protoxylem has been clearly shown in both types of structure and the departure of

¹ Gordon: loc. cit.

leaf-traces, both monarch and diarch, has been traced in detail. The preservation of the phloem elements is unsatisfactory, but indications of the characteristic large sieve tubes seen in later species can be made out surrounding the xylem of the petiolar bundle.

Reasons are adduced against the theory that the *Botryopteris* type of petiole is derived from the *Anachoropteris* type.

XI. CONCLUSION AND ACKNOWLEDGEMENTS.

I have had the privilege of discussing the problem of the aphlebiae with Dr. D. H. Scott.

All the slides were cut and, with two exceptions, all the micrographs taken by C. H. Wells, my laboratory attendant.

Help towards the expenses of the work was received from the Royal Society Government Grant.

The boulder from which the sections shown in Figs. 16, 22, 24, and 25 were cut was kindly presented to me by Professor I. B. Balfour.

EXPLANATION OF PLATES LXXXI-LXXXIII.

Illustrating Dr. Margaret Benson's paper on *Botryopteris antiqua*.

Abbreviations used: *aph.* = aphlebia, *c.* = cusp limiting the protoxylem group of a leaf-trace, *m.l.t.* = monarch leaf-trace, *d.l.t.* = diarch leaf-trace, *p.s.* = pseudo-secondary thickening, *p.x.* = protoxylem, *r.* = root, *s.s.* = stem stele.

All the figures are photomicrographs from slides in the Royal Holloway College Collection.

PLATE LXXXI.

(Figs. 1-9.)

Figs. 1-5 represent successive transverse sections through a stem stele. Slides 407. 12-8.

Fig. 1 shows the condition of the stele in a leaf-bearing zone immediately after the liberation of a diarch trace. The single protoxylem (*p.x.*) is about to bifurcate. Slide 407. 12. $\times 95$.

Fig. 1 *a* is a low-power micrograph of the whole section from which Fig. 1 was taken. $\times 20$.

Fig. 2 shows the completed duplication of the protoxylem (*p.x.*, *p.x.*') shown in Fig. 1. Slide 407. 11. $\times 95$.

Fig. 3. The next leaf-trace (*m.l.t.*) is preparing to leave the stem stele. Slide 407. 10. $\times 95$.

Fig. 4. The leaf-trace shown in the stem stele in Figs. 2 and 3 has now just become free (*m.l.t.*). The stem stele is rapidly increasing in size by pseudo-secondary thickening (*p.s.*). Slide 407. 9. $\times 95$.

Fig. 4 *a* is a low-power micrograph of the whole section from which Fig. 4 was taken. It shows both the leaf-traces still in the cortex. $\times 20$.

Fig. 5 is a low-power micrograph of the next section of the same series, showing the two petioles supplied by the above traces just leaving the stem. Slide 407. 8. $\times 20$.

Fig. 6. A micrograph of a stem giving off a root and a leaf-trace. The stem stele which shows an early stage in the liberation of another trace is shown enlarged in Fig. IV *a*. Slide 405. 16. $\times 20$.

Fig. 6 *a*. An enlarged view of the stem stele shown in Fig. 6. The protoxylem of the leaf-trace appears to be dividing (cp. a corresponding stage in the protoxylem of the stem in Fig. 1).

The contrast in character between the metaxylem of the leaf-trace and that of the stem is well shown. The stem is partially in a root-bearing phase. $\times 95$.

Fig. 7. A transverse section of a diarch petiolar bundle. This petiole should be compared with the stem in Fig. 8*a*. The cusps are not as well preserved as in the petiole shown in Fig. 16. Slide 407.8. $\times 95$.

Figs. 8 and 9 are low-power micrographs from two successive sections transverse to a stem which first gives off a large diarch trace and later an aphlebia trace (Fig. 9), to be followed by a monarch petiolar trace. This succession is shown also in Figs. 19, 20, and 21. Slides 407.24-25. $\times 20$.

Fig. 8*a* is a high-power micrograph of the stem stele from Fig. 8 and is comparable with that shown in Fig. 2. $\times 95$.

Fig. 9*a* is a high-power micrograph of the stem stele from Fig. 9, and shows the separation of an aphlebia trace (*aph.*) and origin of a monarch petiolar trace, while the rest of the stem stele is preparing for the emission of roots. This series should be compared with that shown in Figs. 19 and 20, and with Fig. 21. $\times 95$.

PLATE LXXXII.

(Figs. 10-18.)

Fig. 10. An obliquely longitudinal section through a stem bearing a small petiole with its aphlebia (*aph.*). In the upper part of the section can be seen a large leaf-trace in its attached part. Slide 416.4. $\times 20$.

Figs. 11-13 represent three sections from a series through a stem bearing at first a diarch trace and later roots. Slides 417.2-5. $\times 30$.

Figs. 11*a*, 12*a*, and 13*a* are high-power micrographs of the respective stem steles. $\times 95$.

The series shows diagrammatically the change in character of the stem as it passes from a purely leaf-bearing zone into a root-bearing zone, and should be compared with Figs. 1-4.

Fig. 11*a* shows the duplicated protoxylem of the stem which is characteristic of internodal structure, and corresponds with that shown in Figs. 2 and 8*a*.

Fig. 12*a* shows the rapid increase in diameter of the stele in preparation for root formation and pseudo-secondary (*p.s.*) development of new metaxylem.

Fig. 13*a* shows a stem section in marked contrast to such a one as is shown in Figs. 1, 2, 8*a*, and 11*a*. It may be regarded as bearing some resemblance to the stem of *Diplolabis Römeri* and *Metaclepsydropsis duplex*. The bulk of the tracheides have a small diameter.

Figs. 14 and 15 represent two sections from the same series. Slides 393.26 and 28.

Fig. 14 shows a monarch trace entering the base of the petiole and the stem in a root-bearing phase. At *px.* can be seen the protoxylem of the aphlebia trace. Cf. Text-fig. 1. (Roots were numerous in the next section, 393.25.) Slide 393.26. $\times 20$.

Fig. 14 is a high-power micrograph of the node from which the above monarch trace took its origin. It shows the single protoxylem group characteristic of a purely leaf-bearing node (*vide* Fig. 1) and the addition of new primary xylem by pseudo-secondary formation. Slide 393.28. $\times 95$.

Fig. 16 is a high-power micrograph of the adaxial part of a diarch petiolar bundle. The minute cusps with intervening protoxylem elements can be clearly seen. The phloem elements are as usual badly preserved. This figure should be compared with the branching diarch petiole seen in Fig. 24. Slide 320.11. $\times 95$.

Fig. 17 is a high-power micrograph of part of a group of four 'Botryopteridean' sporangia measuring on an average $275\ \mu$ across. Slide 326.2. $\times 95$.

Fig. 18. A single larger 'Botryopteridean' sporange represented at the same magnification as those of Fig. 17. Such sporangia occur in all the three blocks from which the specimens figured have been obtained. Slide 400.x. $\times 95$.

PLATE LXXXIII.

(Figs. 19-24.)

Figs. 19 and 20 are micrographs of two successive sections of a stem at a node. The leaf-trace which is just becoming free in Fig. 19 is shown as the petiole bundle in Fig. 20, and the small aphlebia trace (*aph.t.*) not yet detached from the stem stele in Fig. 19 is now (in Fig. 20) found passing into the base of an aphlebia.

Fig. 19 shows in the upper part of the photograph evidence of the stem having recently borne a large trace which has perished. Slides 402. 35 and 34. $\times 20$.

Fig. 19a is a high-power micrograph of the stem stele from Fig. 19. It shows the details of the aphlebia trace which is destined to go off almost simultaneously with the monarch petiolar trace just given off. Slide 402. 35. $\times 95$.

Fig. 21. A low-power micrograph of a stem stele (s.s.) showing simultaneously a diarch leaf-trace (d.l.t.), a monarch leaf-trace (m.l.t.), and an aphlebia trace (aph.). Slide 417. 15. $\times 11$.

Fig. 22. A longitudinal section of the tracheides of a well-developed stem stele in a root-bearing region. They are reticulate and show various intermediate conditions between the porose marking met with in the metaxylem of the leaf-trace and the spiro-scalariform marking of the protoxylem elements. Slide 302. 19. $\times 95$.

Fig. 23. A transverse section of the petiole which may be seen leaving the stem on the left of Figs. 4a and 5. The vascular bundle gives off a small group of tracheides which later become flattened out and do not leave the rachis (*vide* text, where it is suggested they represent an abortive aphlebia trace). Slide 407. 7. $\times 20$.

Fig. 24. A transverse section of a diarch petiole showing an early phase of branching. The pinna-trace separates off in the next section and eventually supplies a branch. Slide 390. 12. $\times 20$.

Fig. 25. A transverse section of one bundle or a node of *Protocalamites* showing in the upper centripetal part pseudo-secondary thickening. Slide 306. 7. $\times 95$.

12.

13.

12 a

13 a

17.

18.

Huth, coll.

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