Studies in the Morphology and Anatomy of the Ophioglossaceae.

III. On the Anatomy and Branching of the Rhizome of *Helminthostachys zeylanica*.

BY

WILLIAM H. LANG, F.R.S.,

Barker Professor of Cryptogamic Botany in the University of Manchester.

With Plates I-III and eight Figures in the Text.

IN the first of these studies¹ the morphology and anatomy of the rhizome of *Botrychium lunaria* was re-examined, and the anatomical relations of branches to the main axis was described. The corresponding facts for *Helminthostachys* will be dealt with in this paper. Our knowledge of this plant is fairly full and complete, but only the previous work on the rhizome and the anatomy of the stele and leaf-trace need be referred to here. Our chief source of information on these points is the account given by Farmer and Freeman². In their paper the general morphology of the rhizome, its stelar structure, and the nature of the vascular supply to the roots and leaves are all described and figured. Reference is also made to the occurrence of branches, arising as 'adventitious buds' on older portions of the rhizome, and often springing from decorticated fragments, but no details of the branching are given. To the description of the rhizome given by these investigators, Gwynne-Vaughan³ added the recognition and description of vestigial or rudimentary axillary buds, one of which is constantly present in relation to each leaf. The anatomy of young plants attached to prothalli was briefly described by myself⁴ and has been further dealt with by Campbell.⁵ Some features of the leaf-trace have been described by Bertrand and Cornaille⁶ and by Sinnott.⁷ Preliminary accounts of some of the facts to be described below have been published in the Proceedings of the Manchester Literary and Philosophical Society.⁸

¹ Ann. of Bot., xxvii (1913), p. 203.

² Ann. of Bot., xiii (1899), p. 421.

³ Ann. of Bot., xvi (1902), p. 170.

⁴ Ann. of Bot., xvi (1902), p. 41.

⁵ The Eusporangiateae (Washington, 1911).

⁶ Travaux et Mémoires de l'Université de Lille, tome x, mém. 29.

⁷ Ann. of Bot., xxv (1911), p. 168, Pl. XI, Fig. 13.

⁸ Vol. lvi, Pt. 2 (1912).

While this general reference to previous investigations on the rhizome of *Helminthostachys* will be sufficient, the main structural features, which are matters of common knowledge, may be briefly summarized. The horizontal, subterranean rhizome is definitely dorsiventral. The leaves, alternating with one another, arise in two dorso-lateral rows, while roots spring from the lower side and the flanks of the rhizome. The basal region of each leaf forms a peculiar sheath, which covers over the next younger leaf, and is broken through on the expansion of the latter. The narrow canal leading to the deeply seated vestigial bud continues backwards and inwards from the axil of the sheathing leaf-base. The rhizome has a wide parenchymatous cortex. The stele is tubular, but is not a solenostele, since there is no trace of internal phloem. It is bounded by the outer endodermis, within which come in order pericycle, phloem, conjunctive parenchyma, xylem, and pith. An internal endodermis abutting closely on the inner surface of the xylem is usually present in large rhizomes; it may be more or less incomplete, or wanting.

The cells of the pith resemble the cortical cells, and like them are often packed with starch. Cells with peculiar contents, recognized by Campbell as corresponding to the tannin cells of the Marattiaceae, may occur in pith and cortex. The xylem in adult medullated rhizomes is characteristically mesarch. Both outer (centrifugal) and inner (centripetal) xylems are well represented, their distinction being easy, as the mesarch protoxylem is often well marked. The vascular strands of the roots are attached to the sides or lower face of the stelar tube, while the upper side of the latter is disturbed by the departure of the alternating, mesarch leaf-traces. Each trace leaves a long narrow gap in the stelar tube; this usually closes just before the next leaf-gap is formed. A further complexity on the dorsal side of the tube results from a disturbance of the xylem in relation to each vestigial axillary bud; this is found, as a rule, just as the corresponding leaf-gap closes. The rhizome of the young plant shows a similar disposition of leaves and roots. Owing, however, to its more slender configuration and smaller stele, the leaves, though really in two rows, appear to spring in a single dorsal line. The stele may have a solid cylinder of xylem, or may, almost from the first, show a small pith. No definite leaf-gaps are left on the departure of the early leaf-traces, but a vestigial bud occupies the usual axillary position in relation to each leaf-trace. The transition from the slender rhizome of the young plant to the full size and usual structure appears to be a gradual one.

This summary of familiar facts will be sufficient introduction to the more critical consideration of some particular features of the rhizome of *Helminthostachys*. The difficult questions relating to the apical development and its relation to the segmental arrangement, indicated in the succession of the leaves and at least suggested by that of the roots, will

not be dealt with here. This paper will be limited to the anatomy of the developed regions of young and adult rhizomes, and the facts will be conveniently described in the following order:

1. Some points in the anatomy of the adult rhizomes. These include the relative development of centripetal and centrifugal xylem, the vascular attachment of the roots, the origin of the leaf-trace and its structure until after the first division in the cortex, variants in type of leaf-trace, and the disturbance of the vascular structure in relation to the vestigial buds.

2. The anatomical relations of actual branches to the main rhizome, and the associated development of accessory or secondary xylem.

3. The structure of the stele and leaf-trace in small rhizomes with the juvenile type of structure, whether arising as branches, or as young plants developed from an embryo; the progression from the juvenile to the adult type of structure, and condensation of stelar structure from the adult to the juvenile type.

The distinction made above, between the adult and juvenile types of rhizome and stele, is of practical convenience, but cannot of course be definite. Rhizomes, the stele of which has a pith and a clear distinction of outer and inner metaxylem, both consisting of pitted tracheides, will be classed as adult; those in which the stele is solid, or if medullated has no definite inner metaxylem composed of pitted tracheides, as juvenile. The transition from the juvenile to the adult type of stele is associated with an increase in the diameter of the rhizome, but the adult type is found in rhizomes of a wide range in thickness.

I am greatly indebted to Prof. F. W. Oliver and Prof. Bower for interesting pieces of rhizome of *Helminthostachys*.

I. SOME POINTS IN THE ANATOMY OF THE ADULT RHIZOME.

The general features of a transverse section of a large rhizome of *Helminthostachys* are illustrated in Text-fig. 1, B. This shows the proportional sizes of the rhizome and stele, and the distinction between the dorsal side of the rhizome, where the remains of the attachment of an old leaf-sheath are seen, and the ventral side, where two large laterally placed roots are attached. The section has passed through the stele, where the xylem of a nascent leaf-trace has just become detached from the stelar tube on the side away from the median line. On the other side of the median line is seen the vascular disturbance, in relation to the vestigial bud belonging to the leaf next behind. The stele is surrounded by the external endodermis, which is only interrupted in relation to the vestigial bud, while the pith is delimited by a well-marked endodermis.

The convention adopted in this figure for representing the position and extent of the various tissues is maintained in many of the other text-figures, and may be explained once for all. The external endodermis is represented by

a continuous line, the phloem by a dotted line internal to this. The outer and inner metaxylems are represented by two sets of radially directed lines; between them the protoxylem elements occur in groups, and are represented in black in relation to the leaf-trace, but are usually not specially indicated in the rest of the stele. Though diagrammatic in the representation of the tissues, these figures are based on camera-lucida drawings, and represent the position and extent of the various tissues as accurately as possible.

It will be evident that the inner metaxylem is least strongly developed at the ventral side of the stele. The greater thickness of the xylem-tube

TEXT-FIG. I. A. Section across adult rhizome near to the growing region, showing the attachment of the roots and their relation to the cortex. Only the outline of the stele and the outer limit of the xylem are indicated. B. Similar section through mature region of the rhizome. The stele of the rhizome shows a departing leaf-trace to the left of the median dorsal line, and the disturbance in relation to a vestigial bud on the left. There is an internal endodermis in the base of the root, unconnected with that in the rhizome. *l.sh.*, leaf-sheath; *R*, roots; *xy.*, xylem; *px.*, protoxylem; *x.o.*, outer xylem; *x.i.*, inner xylem; *lt.*, leaf-trace; *br'*, vascular disturbance for vestigial bud; *e.*, outer endodermis; *e.i.*, internal endodermis of rhizome; *e.i.r.*, internal endodermis of root.

dorsally is mainly, though not entirely, due to the greater development of inner xylem there, especially in relation to the vestigial bud.

Proportions of inner and outer metaxylem. In rhizomes of the adult type both xylems are always represented, but the degree of development of the inner xylem exhibits a wide range of variation. In large rhizomes, such as that just described, the inner xylem is well developed; a portion of the vascular tube of this type is shown in Pl. I, Photo 1. The tracheides of the outer xylem often show some indication of radial seriation, but this is to be related to the sequence of divisions in the procambial stage, and does not indicate a secondary development. The xylem in all normal rhizomes examined is wholly primary, though an anomalous secondary development will be described below in relation to the branching of the rhizome. The inner xylem is usually much less marked in smaller

rhizomes, and often does not form a continuous zone; a portion of a vascular tube of this type is shown in Pl. I, Photo 2. In such rhizomes the parenchyma of the pith may at places abut directly on the protoxylem (Pl. I, Photo 3). Such steles present an appearance in transverse section not unlike some steles of *Botrychium lunaria*,¹ in that the outline of the pith is rendered irregular by the scattered elements of centripetal xylem. The analysis of the primary xylem into outer and inner is, however, much easier in the case of *Helminthostachys*, since protoxylem elements are usually present at intervals in the tube of xylem, and are not confined to the region of a departing leaf-trace.

It is not necessary to enter into the histology of the xylem further than to say that, in longitudinal section, the tracheides of the inner and outer metaxylem are similar, with narrow and often multiseriate pits. The protoxylem elements are narrower and stain less deeply; they show spiral marking passing into a reticulum, in the meshes of which bordered pits appear.

The vascular attachment of the roots. The roots are developed close to the growing point of the rhizome, and the early growth of the root thus coincides with the cortex of the rhizome attaining its full thickness. In the light of this we can understand how it is that only a comparatively thin zone of the cortex is actually broken through by the emerging root; this zone corresponds in thickness to the preceding leaf-sheath. The root is thus borne on a pedicel, the inner portion of the root-stele having no cortex of its own distinct from that of the rhizome. Since the superficial layer of cortex which is broken through often wears off later, the roots on mature portions of the rhizome may appear as if exogenous. The general relations will be clear without further description from Text-fig. 1, A and B. These figures represent transverse sections close to the tip of a rhizome (A), and through a mature region (B), in both cases passing through the attachment of roots.

As Farmer and Freeman state, the pith of the base of the root may be indirectly continuous with the pith of the rhizome by means of the xylem parenchyma. This statement may be somewhat amplified. The root, especially at its base, has a wide pith, the cells of which resemble histologically those of the pith of the stem. The xylem of the root is continuous with the outer xylem of the stem-stele, and the xylem parenchyma is well marked beneath the base of the root. The pith of the root is continuous with this parenchyma, the position of which is usually between the inner and outer xylems of the rhizome, though sometimes a thin zone of outer xylem persists across the base of the root. When the inner xylem is well developed, it separates the pith of the root from that of the rhizome (cf. Text-figs. 1, B, 3, B, C, and Pl. I, Photo 4). When, however, the inner xylem

¹ Cf. Ann. of Bot., xxvi, Pl. XX, Photos 16, 17.

of the rhizome is less complete, the pith of the root appears continuous with that of the rhizome (cf. Pl. II, Photo 25). This occasional parenchymatous continuity between the pith of the rhizome and root is obviously of no significance as regards the nature or origin of the pith of the root.

It is of some interest to find that an internal endodermis may be developed in the basal region of a root, delimiting its pith. Such an endodermal layer may be more or less complete. Its position in a well-marked case is shown in Text-fig. 1, B. As in the case of the rhizome, the internal endodermis of the root may abut directly on the tracheides. There is clearly no reason to look on the internal endodermis of the root as anything but a new development, and its occurrence thus bears on the significance to be attached to the internal endodermis present in the rhizome.

Origin and structure of the leaf-trace. It has been pointed out above that the dorsal side of the stele is of special interest, since the leaf-traces depart from it, and also because of the vascular disturbance in relation to the vestigial buds (cf. Text-fig. 1, B). As is well known, the departing trace leaves a long narrow leaf-gap in the medullated stele. This gap closes before the next leaf-trace separates, so that the gaps do not usually overlap, and their mutual relation is similar to what is found in many dorsiventral solenostelic Ferns. The vestigial bud discovered by Gwynne-Vaughan is situated just in front of the closed leaf-gap to which it belongs, and the vascular disturbance in relation to the bud is found just as the gap closes. The vascular disturbance thus lies alongside the separating trace for the next leaf (Text-fig. 1, B). A series of sections through the region of separation of one leaf-trace will thus show the closure of the preceding leaf-gap on the other side of the median line, and the vascular relations of the vestigial bud. Such a series from a large rhizome is represented in Text-fig. 2; it shows to the left the earlier stages in the separation of a leaf-trace, and on the right the closure of the preceding leaf-gap, the development of the bulge of xylem in relation to the vestigial bud, and the return to the normal thickness of the vascular tube in front of this. Leaving the consideration of the vestigial bud to the next section, the origin, separation, and further history of the leaf-trace in this specimen may now be considered.

This rhizome had a complete internal endodermis, and the inner metaxylem was well developed. The first indication of the position and extent of the leaf-trace was afforded by the disappearance of the endodermal characters from the cells internal to the nascent trace. The xylem tube in the region of the trace also appeared thinner, owing to a less development of centripetal xylem. This is the condition reached at the level of the section in Text-fig. 2, A; the adjoining leaf-gap has begun to close, while the position of the nascent leaf-trace had been recognizable some distance behind the level of this section. The series of figures in Text-fig. 2 shows

the gradual arching out of the leaf-trace xylem (Text-fig. 2, A, B, C), its separation from the xylem-tube first on the side away from the middle line of the stele (D, E), and shortly afterwards on the median side also. At this level (Text-fig. 2, F) the trace is distinct from the stele as regards its xylem and phloem, but is still enclosed by the unbroken stelar endodermis. On the other side of the middle line the previous leaf-gap is seen to have closed, the disturbance of the xylem to have subsided, and the

TEXT-FIG. 2. Series of transverse sections of the stele of a large rhizome, to show the early stages of departure of a leaf-trace and the closure of the leaf-gap of the preceding leaf and the development of a well-marked vestigial branch stele. Further description in text. *lt.*, leaf-trace; *ph.*, phloem; *e.*, outer endodermis; *ei.*, internal endodermis; *x.o.*, outer xylem; *x.i.*, inner xylem; *x.o.br.*, outer xylem of vestigial branch; *x.i.br.*, inner xylem of vestigial branch; *v.b.*, inner end of canal to vestigial bud; *e.b.*, endodermis in relation to vestigial bud.

section passes through the inner end of the canal leading down to the vestigial bud.

The leaf-trace itself as it separates from the stele is mesarch, although the inner xylem is much less developed than in the stele of the rhizome. The trace in this large rhizome thus agrees with that described and figured by Sinnott, but, as will be seen below, this is by no means the only type of trace found in *Helminthostachys*.

The further changes undergone by the trace of this rhizome as it passes obliquely through the cortex are illustrated in Text-fig. 3; this represents the preceding trace, and is therefore on the other side of the

middle line, but otherwise continues the series of changes shown in Text-fig. 2. In Text-fig. 3, A, the endodermis is seen interrupted on the side away from the middle line, though on the other side it is continuous from the leaf-trace to the stele. The external and internal endodermal layers have become continuous round the margin of the leaf-gap. The leaf-trace is distinctly mesarch and the protoxylem elements form an interrupted band between the two xylems. In Text-fig. 3, B, the trace is completely separate, and comparison with the earlier stage will show that the arc of xylem is becoming more curved and is tending to complete the tube of outer xylem on the adaxial side. The persistence of the centripetal xylem internal to the protoxylem enables a clear distinction to be drawn between true mesarchy of the trace and this adaxial completion of the xylem. The

TEXT-FIG. 3. Series of sections from the same rhizome as Text-fig. 2, to show the later stages in departure of a leaf-trace, the adaxial completion of the xylem, and the clepsydroid stage passed through before division. Further description in text. *e.*, endodermis of leaf-trace; *ph.*, phloem; *x.o.*, outer xylem; *px.*, protoxylem of leaf-trace; *x.i.*, inner xylem; *p.r.*, pith of base of root.

trace in Text-fig. 3, B, shows preparations for division in that the protoxylem is present as two laterally placed groups; a projection of metaxylem between these is also to be noted. In the next stage figured (Text-fig. 3, C) the outer xylem has become complete adaxially and so has the endodermis; the phloem was not completed in this trace. The projection of xylem noted in the preceding stage has become continuous with the adaxial xylem, and divides the parenchyma in the concavity of the xylem into two areas. In each of these, internal to the protoxylem, centripetal xylem still occurs, though it is more poorly represented than lower down. Shortly after this, when the trace is approaching the outer part of the cortex, it divides into two. A stage of the division is represented in Text-fig. 3, D, and it will be noted that in this case the outer xylem forms a complete ring in one half of the trace and not in the other. The inner xylem is still

represented, but soon ceases to be recognizable in the bundles of the base of the leaf.

The stage represented in Text-fig. 3, C, is evidently that recognized by Bertrand and Cornaille¹ as an 'état très particulier de la trace clepsydroidé', but not described or figured in full. They describe it as 'une chaîne binaire, celle-ci est doublement fermée, étant composée de deux divergeants fermés'. The name given by these investigators to this stage will be adopted, and the significance of this clepsydroid stage will be discussed later. As a rule it is passed through rapidly, the complete division of the trace being effected in the outer part of the cortex.

The actual appearance of the large trace, the structure of which has been represented in Text-figs. 2 and 3, is shown in Pl. II, Photos 20, 21, and Pl. I, Photos 5 and 6. In Photo 21 the nascent trace is seen to the left, still forming part of the stelar tube. Photo 5 shows the adaxial completion of the xylem of the separated trace almost effected, while Photo 6 shows the trace in the clepsydroid stage. The low-power photograph in Pl. I, Photo 4 shows the trace in the clepsydroid stage in relation to the stele, from which it had departed.

This large trace, derived from a full-sized adult stele, has been described at some length, since it allows the distinction to be clearly made between the *mesarch condition*, i. e. the existence of outer and inner xylem corresponding to the outer and inner xylem in the stele of the rhizome, and the essentially different condition brought about by the *adaxial completion of the outer xylem* in the leaf-trace. Since the mesarch condition persisted until after this trace divided, the adaxial completion of the arc of outer (centrifugal) xylem could be seen to be quite distinct from the original mesarchy. The distinction of these two constructions, both resulting in the presence of metaxylem to the inside as well as the outside of the protoxylem, must be borne in mind in considering other examples, the interpretation of which is less obvious.

Different pieces of rhizome, while agreeing in the general type of construction of stele and leaf-trace, exhibited variants of the type, which were usually maintained throughout the particular piece of rhizome. These variants are of special interest in the leaf-trace and concern its mode of departure, its construction in the cortex, and its mode of division. Some examples will now be briefly described and illustrated in order to show the nature of the range.

The division of the leaf-trace often takes place without the adaxial completion of the xylem or endodermis having been effected. This is found both in the case of leaf-traces that are mesarch at their departure and in the case of smaller traces that have no centripetal xylem. An example, though not an extreme one, of a dividing trace, in which the

¹ Loc. cit., p. 179, foot-note.

adaxial extension of xylem was incomplete at division, is given in Pl. I, Photos 7–9. In such cases no definite clepsydroid stage is passed through.

Even in the large mesarch traces described above, the inner xylem was found to diminish in the region of the nascent leaf-trace (cf. Pl. II, Photo 21). As a rule, in smaller rhizomes, where the centripetal xylem is less strongly developed, the inner xylem completely disappears from the middle of the concavity of the nascent trace, so that the parenchymatous tissue is continuous from the pith to the protoxylem. The trace thus separates from the stele with xylem, which is either completely endarch or has only traces of inner xylem to the two sides. Thus there is very little inner xylem in the trace figured in Pl. I, Photos 7–9, while Photo 10 shows a purely endarch trace which had just departed from another rhizome. This latter trace divided without any indication of adaxial completion of xylem. On the other hand, the trace shown in Pl. III, Photos 47–49 was endarch at its departure, but almost at once showed adaxial completion of its xylem.

The last-mentioned specimen thus illustrates another variant in which the adaxial completion of the outer xylem of the trace takes place while the latter is still monarch (Photo 48). This was followed later by the assumption of the clepsydroid structure preceding the division of the trace (Photo 49), which took place in the outer region of the cortex.

This pre-clepsydroid condition, in which the trace is adaxially completed, but has an undivided protoxylem, may be maintained until the trace has left the cortex of the rhizome. This was the case throughout a large fragment of rhizome which bore a branch, to be described later, and the progress outwards of one trace can be followed in Text-fig. 6 from the right side of the rhizome. This trace as it left the cortex is also shown in Pl. I, Photo 11, while Photos 12 and 13 on the same plate show another trace from the same rhizome, just before the xylem was completed adaxially and after this had been effected. There is no room for doubt as to the adaxial completion of the xylem in these traces, and the reality of the process is confirmed by the accompanying completion of the phloem, which is seen in Photo 13; and this is even better shown by the next rhizome to be described.

This piece of rhizome will be referred to later in the paper as showing a rapid progression from the juvenile to the adult type of structure. The type of leaf-trace departure, which was maintained at each node, was remarkable in that the xylem of the trace was completed adaxially before or as it separated from that of the stele. As the xylem of the trace enclosed little parenchyma, it was possible on the one hand that its adaxial portion represented the very early completion of the outer xylem of the trace, or, alternatively, that it was the continuation outwards of the inner xylem of the mesarch stele. Direct observation supports the former

explanation, and this interpretation seems justified in the light of comparison with the other types of trace described above.

The main stages in the departure of one of the earlier and smaller traces from this rhizome are represented in Pl. I, Photos 14-17. The rhizome at this level was medullated and mesarch, though with the internal xylem only moderately developed. As the xylem of the trace becomes evident as a bulge on the stele (Photo 14), the protoxylem has an arc of metaxylem to the outside, and this appears almost completed on the adaxial side of the trace, which is still continuous with the xylem of the stele. Thus as the xylem of the trace becomes separate (Photo 15), it exhibits a complete ring of radiating rows of tracheides, the single group of protoxylem being in connexion with the abaxial portion of the ring, while a little parenchyma is present immediately internal to the protoxylem. The adaxial xylem at this level appears to be related to the outer xylem of the stele, and is in any case much more strongly developed than the inner xylem of the stele. At this stage the stele and leaf-trace are enclosed in a common endodermis and the phloem is still continuous. Photo 16 shows the same trace further removed from the stele. It still has a single group of protoxylem, the xylem being almost equally developed abaxially and adaxially. The interpretation given of the adaxial completion of the xylem in this trace is confirmed by the corresponding behaviour of the phloem, which is seen to form a complete tube, while the endodermis was also complete. A little further out (Photo 17) the small trace had passed into the clepsydroid stage; the endodermis and phloem were still complete. The xylem appeared dumb-bell shaped in cross-section, the protoxylem had divided into two groups, and the metaxylem elements were continuous across the constricted portion between the two halves. Shortly after this the division of the trace took place; the xylem of each half was a complete ring, and the phloem was complete around it.

The departure of the larger leaf-traces from the full-sized portion of this rhizome was essentially similar, though the trace may be mesarch at its origin, and thus have some inner xylem enclosed by the adaxial extension of the outer xylem. One of the larger traces in the clepsydroid stage is represented in Pl. I, Photo 18. While corresponding essentially to the large trace shown in Photo 6, this trace, which is at a somewhat earlier stage, has no evident remains of inner xylem. The two poles of protoxylem are clearly evident, and the adaxial arc of xylem is actually thicker than the abaxial portion. A little later the metaxylem develops in the centre of the trace connecting the abaxial and adaxial portions, and the trace then divides (cf. Text-fig. 8, E). In Pl. I, Photo 19 the left half of this trace is shown with its protoxylem in two groups preparatory to the next division.

The trace shown departing from the moderately small rhizome in Pl. III, Photo 51 agreed with those just described in having the xylem of

the trace completed adaxially before it had separated from the stelar xylem. In this case there was no difficulty in the interpretation, since the inner xylem first disappeared from within the nascent trace. In the trace figured the adaxial xylem is almost complete, and is well represented on the left side.

The variety shown by the leaf-trace in different pieces of rhizome of *Helminthostachys* is remarkable, and has necessitated the description of a number of examples. A general plan will, however, be seen to underlie the variety. The xylem of the trace is ultimately equivalent to, and derived from, an arc of the outer xylem of the stelar tube. No inner xylem may be continuous into the trace, or the latter may be mesarch at its base, the inner xylem dying out sooner or later. The outer xylem tends to be completed adaxially (though this does not always take place); the resulting construction is essentially distinct from mesarchy as we find it in the stelar tube of the xylem. In preparation for division the protoxylem separates into two groups, and the trace passes through a clepsydroid stage that is often clearly marked and striking. The monarch pre-clepsydroid condition may, however, persist until the trace leaves the rhizome. More usually the trace has divided twice before this takes place, the complex vascular system of the petiole being thus continued backwards into the cortex of the rhizome. In all cases observed, however, the trace is monarch as it separates from the stele, though the continuation backwards of the double condition seen in the clepsydroid stage would be a readily comprehensible term in the series of variants.

Parallel variants in the structure and relations of the leaf-traces will be referred to below in considering more slender rhizomes showing juvenile structure, and the whole question will be discussed at the end of the paper.

The vascular disturbance in relation to the vestigial buds. The original description by Gwynne-Vaughan¹ of the structures which must undoubtedly be regarded as vestigial or dormant lateral buds, or rather apices, was illustrated by clear diagrammatic figures. These show the course of the narrow canal extending backwards and inwards from the axil of a leaf-sheath to the neighbourhood of the stele just in front of the closed leaf-gap corresponding to the subtending leaf, and also the disturbance of the stele in relation to the vestigial structure. As his figure shows, the canal turns slightly forwards at its lower end, and, so far as I can judge, the dormant apex is situated behind this inner portion. As regards the structure of the vestigial bud itself, I can at present add little to Gwynne-Vaughan's account. It seems to consist only of a dormant apical meristem, the structure of which is difficult to make out in the absence of segmentation. It is of some interest, for comparison with the main apex, to find that the lower portion of the canal may be enlarged by the development of hairs projecting into it.

¹ Loc. cit., p. 171, Fig. 19.

As regards the vascular disturbance, Gwynne-Vaughan's figure indicates that the inner xylem first closes across the gap, and also that the increased thickness of the xylem leads to the existence of a distinct low bulge behind and below the vestigial bud itself.

The analysis of this bulge is not carried further by him, and it is of interest to ascertain the parts taken in its formation by the outer and inner xylems respectively. This was studied in the large rhizome, the departure of the leaf-trace from which has been already described, and the same series of figures (Text-fig. 2) will serve to illustrate the anatomical relations of a vestigial bud in a case in which the vascular disturbance was well marked.

After a leaf-trace has departed, the gap in the stele remains open for a considerable distance. On following a series of sections forward, the gap in the tube of xylem is seen to narrow, and its edges to thicken as preparations for closure become recognizable (Text-fig. 2, A, B). The thickening is largely due to an increase in the amount of inner xylem, which at this region becomes more strongly developed than elsewhere in the stele; there is also an increase in the thickness of the outer xylem, so that the wood bulges both outwards and inwards in the region of the closing gap (Text-fig. 2, B). The endodermis appears raised up over the margins of the gap. The closure of the gap comes about by the meeting of the edges formed by the bulges of inner xylem. This not only joins across the gap, but the inner xylem appears to extend outwards into the gap still present in the outer xylem (Text-fig. 2, C). A little further forward (Text-fig. 2, D) the outer xylem is completed over this extension of the inner xylem through the gap. Since the outer xylem also completes the xylem of the main stele, it separates the projecting portion of the inner xylem from the corresponding tissue of the main stele. At this level, therefore (Text-fig. 2, D), the vascular bulge can be regarded as a rudimentary branch stele, with its own inner and outer xylem. Still further forward the bulge of xylem is subsiding, and at this level the endodermis was completed over the parenchymatous bulge leading towards the vestigial bud (Text-fig. 2, E). The last section figured (Text-fig. 2, F) is immediately in front of the actual bud, and shows the inner portion of the canal occupied by hairs, and beneath this the forwardly bent portion of the endodermal bulge. The stele of the rhizome has resumed its normal structure, and the endodermis is complete around it.

The description of this vascular disturbance just given naturally involves a view as to the interpretation of the structure. This interpretation has been reached by comparison of a number of specimens, and will be seen below to be supported by the nature of the vascular supply to actual branches. The appearance of the vascular bulge in the specimen described is shown in Pl. II, Photos 20 and 21. Photo 20 shows the dorsal region of the stele just after the leaf-gap has been closed by the approximation of

the internal xylem, which can be traced bulging outwards into the gap. The level is therefore about the same as Text-fig. 2, C. The second photograph (Photo 21) shows the bulge with the outer xylem completed over the inner xylem and also extending across to complete the xylem tube of the rhizome. The level of this section corresponds to Text-fig. 2, D. The whole structure suggests the attachment of the base of a miniature branch stele, with its inner and outer xylem continuous with the corresponding tissues of the main stele.

The vascular disturbance in relation to the bud was exceptionally well marked in the large rhizome selected for description above, and in a number of similar pieces of rhizome (cf. Text-fig. 1, B). In other and smaller rhizomes, however, the structure was different, though such cases did not negative the interpretation of the better marked and more highly organized examples. In smaller rhizomes the closure of the leaf-gap took place by the meeting of the relatively strongly developed xylem at its edges; the inner xylem sometimes extended slightly outwards into the gap, the outer xylem not being continued across till later. But in these cases (cf. Pl. I, Photo 7) no well-marked vascular bulge was formed, and there was no indication of an organized branch stele, although the xylem ring was thicker in this region owing to the greater development of inner xylem. The endodermis was raised up and open in relation to the vestigial bud; sometimes it had previously closed around the stele, in other cases it remained open.

In small rhizomes also the bud often appears to be situated relatively further back. In the full-sized adult rhizome the transverse section showing the actual bud passes through the leaf-trace on the other side of the median line, when it has separated from the vascular tissues of the stele. This would correspond to a section between E and F in Text-fig. 2. In the small rhizomes, on the other hand, the next leaf-trace may still form part of a complete stelar tube at this level (cf. Pl. I, Photo 7), and in other cases the bud may be so far back as to lie over the unclosed leaf-gap (cf. Text-fig. 4, A). These differences in position do not affect the regular segmental succession of leaves and buds, but are of interest for comparison with what is found in rhizomes of juvenile type, and as bearing on the attachment of actual branches.

2. THE ANATOMICAL RELATIONS OF ACTUAL BRANCHES TO THE MAIN RHIZOME.

In Farmer and Freeman's paper¹ reference is made to the occurrence of 'adventitious' branches on more or less decorticated fragments of rhizome, but no account is given of the vascular relations of the branch to the main stem. Gwynne-Vaughan² suggested that such branches might be due to the vestigial buds being stimulated into action under certain

¹ Loc. cit., p. 423.

² Loc. cit., p. 173.

conditions. The following account is in complete accordance with Gwynne-Vaughan's interpretation of the morphology, the correctness of which was indeed evident from the corresponding facts since made out in *Botrychium*.

I obtained two specimens of *Helminthostachys*, each showing a small branch arising from a short piece of a main axis. The development of the branches thus appeared to be associated with arrest of the normal growth of the main axis. In this respect, as well as in the structure and position of the dormant buds, a close parallel with *Botrychium* can be traced.

The first branching specimen was a small piece of rhizome that to all appearance terminated in its apical bud. When cut into a complete series of sections, however, it proved to consist of axes of two orders. The base was a fragment of a small rhizome of adult type, including seven leaf-gaps; while borne on this, and arising from the dormant bud in relation to the most anterior leaf-gap, was a lateral branch. This had continued the line of growth of the arrested main axis. The specimen was thus particularly favourable for tracing the relations of the vascular system of the branch to that of the main stem in a series of transverse sections.

The structure of the small rhizome, which bore the branch, may be very briefly summarized (cf. Text-fig. 4, and Pl. II, Photos 22-24). The stele had a well-marked pith not limited by an internal endodermis. The xylem was mainly outer or centrifugal. In some regions the inner xylem was fairly developed, but for the greater part of the length of the fragment it was feebly represented by isolated tracheides or groups of tracheides. It was as usual best represented towards the upper side of the stele. It disappeared internal to the leaf-trace, so that the latter departed with an endarch strand of xylem (Pl. I, Photo 10). The trace passed rapidly through the cortex, dividing without adaxial closure of the xylem. A vestigial bud was present in relation to each leaf. Its general structure was as usual, but it may be noted that it was not so far in front of the subtending leaf-trace, but was situated over the leaf-gap before this had closed even in the xylem tube (Text-fig. 4, A, B). There was no definite vascular disturbance in relation to the bud. On passing forward, the vestigial bud over a leaf-gap is first met with (Text-fig. 4, A), the slit in relation to the bud then reaches the surface, and the leaf-gap closes (Text-fig. 4, B, C) before the separation of the next leaf-trace from the stelar tube commences. There is thus a region intervening between one leaf-gap and the next, in which the stele is tubular and undisturbed either by a vestigial bud or a departing leaf-trace. The appearance of a vestigial bud standing beside the separating trace for the next leaf is not seen. These differences in degree will be evident on comparing Text-figs. 2 and 4, and have to be borne in mind in considering the relations of the actual branch.

The departure of the leaf-trace subtending this branch and the vascular

TEXT-FIG. 4. Series of sections through the first branching specimen, to show the closure of a leaf-gap and the relation to it of the vestigial bud (A-C); the departure of the next leaf-trace which subtends a branch (C-E); the derivation of the outer and inner xylem of the branch stele from the accessory outer xylem and from inner xylem of the main stele (C-H); and the completion of the organization of the branch stele (I, J). The accessory xylem is cross-hatched. Further description in text. *l.t.*, subtending leaf-trace; *x.²*, accessory xylem; *x.¹*, inner xylem passing through leaf-gap; *e.br.*, endodermis of branch stele; *x.o.br.*, outer xylem of branch; *x.i.br.*, inner xylem of branch.

supply to the branch can be followed from Text-fig. 4. The first section (A) shows the preceding leaf-gap still open and the position of the vestigial bud above it. On the other side of the median line the protoxylem of the next leaf-trace is recognizable, separated by inner xylem from the pith. In B the condition is similar, but the section now passes through the canal leading to the vestigial bud, and the gap in the xylem is narrowing. In C the canal has almost reached the surface of the rhizome, and the leaf-gap is closed, although the external xylem is not of full thickness across it. On the other side of the middle line, the nascent leaf-trace is more evident, and the inner xylem has largely disappeared opposite its protoxylem. To either side of the xylem of the trace, which still forms part of the complete stelar ring, the first indication of the vascular supply to the branch is visible. At these points an additional development of tracheides has taken place immediately outside those of the normal xylem. This xylem, which is indicated in the figures by cross-hatched shading, corresponds in a sense to secondary xylem, and will be referred to as *accessory xylem*. In the next section (D) these patches of accessory xylem are much larger, and the new development extends further round the stele, though confined to its upper side. The leaf-trace is seen to be purely endarch as it departs, and the inner xylem is wanting opposite to it. The separation of the trace is further advanced in E; this shows a new feature, in that the inner xylem, which at the preceding level was well marked to either side of the nascent leaf-gap, now extends across below the gap, and also out into it. This inner xylem, together with the accessory xylem evident to either side of the leaf-gap, is destined to supply the stele of the branch subtended by the departing leaf-trace. The actual appearance of the stele about this level is shown in Pl. II, Photo 22, in which the tracheides of the accessory xylem (*x.²*), and those of the inner xylem filling up the gap (*x.i.*) will be seen to have stained more faintly than those composing the normal primary xylem of stele and leaf-trace. The next sections in Text-fig. 4 show how the xylem of the branch stele becomes constituted. At the level of Text-fig. 4, F, the leaf-trace was departing from the cortex. The endodermis has become completed over the leaf-gap, and the inner xylem has passed outwards through the gap, and come into contact with the two groups of accessory outer xylem that have extended towards the middle line of the gap. The actual appearance about this level is shown in Pl. II, Photo 23. In G, the two groups of accessory xylem have joined to form an arc of xylem, against the inner face of which lies the group of inner xylem. The xylem of this nascent branch-stele is now distinctly separated by parenchyma from the main stele, the gap in the xylem of which is seen to be still open. The outer xylem of the branch stele now becomes continued around the inner xylem, between the elements of which parenchyma has appeared. This process, begun in Text-fig. 4, H, is complete in I, although

the zone of the outer xylem is thin on the adaxial side: in J the outer xylem is more uniform in thickness, and the stele of the branch may be regarded as fully constituted. The actual appearance at this level is shown in Pl. II, Photo 24. Meanwhile, as Text-fig. 4, H, I, J, shows, endodermal markings have appeared in a layer of cells between the branch stele and the main stele, and this new-formed layer of endodermis has become continuous with the endodermis on the abaxial side of the branch stele to form the complete endodermis of the latter. By this stage, when the completed branch stele lies in the cortex beside that of the main rhizome, the leaf-gap in the xylem of the latter has closed, and the position of the next leaf-trace is evident. The end of the fragment of rhizome is, however, almost reached, and the broken stele is in great part decorticated (Text-fig. 4, J; Pl. II, Photo 24).

It is thus evident that the outer and inner xylem of the branch stele are continuous with the outer and inner xylem of the main rhizome, and that the endodermis is similarly continuous from the main stem to the branch. The same holds almost certainly for the phloem, but on account of the difficulty of distinguishing the sieve-tubes, though they could be recognized at places in these transverse sections, no differentiation has been indicated in the zone between the endodermis and the xylem of the branch stele. This zone corresponds to pericycle, phloem, and conjunctive parenchyma. Such a branch stele agrees in essentials with the stele of a young plant developed from an embryo, and its further consideration will be deferred to the next section.

Two comparative points may be indicated in passing, although they will have to be discussed more fully later. Judging by the structure of the vascular elements, the stele of the branch would naturally be described as centrarch, i. e. as having protoxylem mixed with parenchyma centrally and the metaxylem around this. The connexions of these regions of the xylem of the branch stele have been clearly seen, however, to be respectively with the inner and outer metaxylems of the stem stele. There is thus reason for distinguishing inner and outer xylem in the smaller and simpler stele of the branch.

If the connexions of the inner and outer xylem of the branch stele (Text-fig. 4) be compared with the large vascular disturbance in relation to a vestigial bud that has already been described (Text-fig. 2), a remarkable agreement will be found. The bulge of xylem behind the vestigial bud was, like the stele of the branch, composed of (*a*) inner xylem passing out through the closing leaf-gap, and (*b*) outer xylem continuous with the thickened margins of the gap in the xylem. This agreement confirms the interpretation of the marked vascular disturbance suggested in the previous section of this paper.

The second branched specimen was an irregular, discoloured, and dying

fragment of a full-sized rhizome. It bore laterally a small shoot of pale colour, with healthy-looking tissues. The parent fragment had evidently been displaced in the soil, and the developing lateral branch had adjusted its direction of growth to the new position, and had grown out almost at right angles to the main rhizome (cf. Text-fig. 5). The interpretation of the anatomical relations between the main rhizome and branch was thus more complicated than in the first specimen. The altered direction of the branch stele had, however, the great advantage of giving a view of its basal region in longitudinal section, while the parent rhizome was studied in a complete series of transverse sections.

The fragment of rhizome had the fully adult type of structure, and included portions of four leaf-gaps; the first gap was open at the basal end, while the fourth gap was not closed when the fragment ended. Vestigial buds were present in relation to the first and third gaps, while the actual branch occupied the same position relatively to the second leaf-gap. The general structure of the stele resembled that of the large adult rhizome first described (cf. Pl. II, Photo 25). Inner xylem was present, though not so strongly developed, and no internal endodermis was recognized. The peculiarities of the leaf-trace have already been described (cf. Pl. I, Photos 11-13). The vascular changes accompanying the closure of the leaf-gap resembled on the whole those in the large rhizome described, and involved the formation of a large bulge of xylem behind the vestigial bud. The bud itself, i. e. the inner end of the canal, was on this rhizome situated relatively further forward, and the branch will be seen to stand beside a leaf-trace, the departure of which is far advanced. The main features of the rhizome are shown in Text-figs. 5 and 6.

In this case, as in the first branching specimen, the influence of the development of the branch extends backwards to the region of the stele, where the subtending leaf-trace is just becoming evident. This influence is expressed in the same way, namely, by the development of accessory xylem outside the ordinary outer primary metaxylem. In the preceding specimen this was only developed in such positions that it appeared to pass off entirely as the outer xylem of the branch stele. But in this larger rhizome the development of accessory xylem was not confined to the neighbourhood of the leaf-gap, but extended all round the stele. Further, the accessory xylem did not wholly pass off to the branch, but was present for a considerable distance after the departure of the branch. It thus presented an even more striking resemblance to secondary thickening than in the former case.

It will be convenient to describe the features of this accessory xylem more in detail before considering the origin of the branch. Its distribution will be evident from Text-fig. 6, in which it is indicated by cross-hatched shading. In the first section (A) of this figure, it is seen to be represented

all round the stele, although the branch stele is not yet reached, while in the last section (F) it is still present all round the stele, although the branch has passed off and the next leaf-trace has reached the surface of the rhizome. Its appearance in this region beyond the departure of the branch is shown in Pl. II, Photo 25, which is to the same scale, and may be compared with the ordinary primary structure seen in Pl. I, Photo 4. A portion of the stelar tube, showing the accessory xylem, is more highly magnified in Photo 26 on Pl. II. It will be sufficient to refer to this last figure, which should be compared with Pl. I, Photo 1, in the following description.

The endodermal markings were not pronounced in the necrosed tissues of this rhizome, but the approximate position of the endodermis is indicated at *e*. Within this comes the pericycle, and at *ph*. the phloem is clearly evident. Within this comes conjunctive parenchyma. In an ordinary rhizome the outer metaxylem (*x.o.*), would have come next followed by the inner metaxylem (*x.i.*) and the pith. The position of these tissues is indicated in Pl. II, Photo 26, but to the outside of the outer metaxylem the irregular band of accessory xylem (*x.²*) is present in addition. This has evidently been secondarily developed as the result of tangential divisions taking place in the cells of the conjunctive parenchyma adjoining the primary xylem, and cells showing tangential division-walls are evident in the photograph. Many of the resulting elements have developed into tracheides, but others have remained parenchymatous. It is due to this that the accessory xylem is at places continuous with the primary xylem, while at other places some parenchymatous secondary tissue intervenes (cf. Photo 25, Pl. II). This xylem was clearly a secondary development after the primary structure of the stele was completed. It occupies the usual position of a normal zone of secondary xylem relatively to the primary xylem and phloem. On the other hand it is irregular, in that no definite meristematic layer or cambium is formed or persists outside the newly formed xylem. Even allowing for these peculiarities, it seems to me clear that the development of this accessory xylem should rightly come under the conception of secondary thickening. It is of special interest that in *Helminthostachys*, where no secondary thickening is normally found, we can correlate the development of this accessory xylem with the influence exerted by the development of a branch from a vestigial bud upon the completed tissues of the main stele.

Turning now to consider the relations of the branch to the main rhizome, reference may first be made to Text-fig. 5. This represents in outline a transverse section of the main rhizome, showing the branch growing so nearly at right angles to it that its stele is cut longitudinally throughout its course. The xylem is represented in black without any distinction of inner, outer, or accessory xylem. The leaf-trace after the one which subtended the branch is seen nearing the periphery of the

cortex on the right-hand side, and has left an open leaf-gap. The branch stands over the preceding leaf-gap which is now closed. The portion of the branch shown has presumably been laid down by the activity of its proper apex, and has adjusted itself to the position in which the parent fragment lay in the soil. The parent fragment had apparently been inverted in the soil, for while U indicates its upper surface, and L its lower surface, *u.* and *l.* indicate the upper and lower sides of the branch. The attachment of the stele of the first root of the branch is seen at *r.¹*, while *l.t.¹* indicates by a dotted line the course of the first leaf-trace, which was actually shown in a neighbouring section. The branch has acquired a cortex of its own in the outer part of its course through the cortex of the main rhizome, but in the more basal portion the limit is indistinct.

The sections represented in Text-fig. 6, taken together with Photos 27-29 on Pl. II, will serve to illustrate the relation between the branch and the parent rhizome in following the series from behind forwards. Text-fig. 6, A, shows the gap, left by the leaf-trace subtending the branch, beginning to narrow; the leaf-trace has already left the cortex. The xylem tube is seen to consist of inner and outer xylem, and of accessory xylem, the latter being strongly developed at the sides of the leaf-gap. The position of the nascent leaf-trace on the other side of the median line is evident, the trace still forming part of the stelar tube; accessory tracheides are wanting immediately outside the trace. The accessory xylem has been present around the stele since the first indication of the leaf-trace which subtended the gap now beginning to close.

The condition a little further forward is shown in Text-fig. 6, B, in which the nascent leaf-trace is more distinct, the closure of the leaf-gap has advanced, and the accessory xylem is very strongly developed at its margins. The inner xylem is also well developed at the edges of the gap. In the next section (Text-fig. 6, C) the endarch leaf-trace is separating, and on the left-hand side the gap in the xylem has become closed. The inner xylem is of considerable thickness in this region, and has evidently taken a main part in closing the gap. Whether the tracheides in the position marked ? are to be

TEXT-FIG. 5. Transverse section of the rhizome bearing the second branch, to show the relative position taken up by the main stem and the branch. Description in text. U, upper; L, lower side of main rhizome; *u.*, upper; *l.*, lower side of branch rhizome; *r.¹*, first root of branch; *l.t.¹*, line of departure of first leaf-trace of branch.

regarded as inner xylem protruded into the gap, or whether the outer xylem was complete across the gap, could not be determined with certainty. Comparison with the first branching specimen would favour the former

TEXT-FIG. 6. Series of transverse sections of the stele of the second branching specimen, showing the departure of a leaf-trace on the right-hand side, the distribution of the accessory or secondary xylem, and the stages in closure of the leaf-gap on the left-hand side, and the relation to it of the base of the branch stele. The accessory xylem is cross-hatched. Further description in text. *lg¹*, leaf-gap in relation to branch; *lt²*, next leaf-trace from rhizome; *xi*, inner xylem; *xo*, outer xylem; *x²*, accessory or secondary xylem; *?*, possible extension outwards of inner xylem; *xo.br.*, outer xylem of branch; *xi.br.*, inner xylem of branch; *lt.br.*, first leaf-trace of branch.

interpretation. The actual appearance in this critical region is shown in Pl. II, Photo 27, the groups of tracheides which are doubtfully regarded as projecting inner xylem being marked *?*. The photograph further shows

the great development of accessory xylem ($x.^2$) to the sides of the gap which has just closed, and also the first indication of the development of an arc of xylem connecting the accessory xylem over the region of the gap. In Photo 28, which represents the structure a little further forward, this arc of accessory xylem (marked $x.o.$ in the upper part of the figure), destined to continue as the outer xylem of the branch, is fully developed, consisting of short reticulate tracheides. Passing into the concavity of the arc of accessory xylem is seen a group of smaller spirally thickened tracheides ($x.i.$) which are continuous above with the inner xylem of the branch stele. The fact that these tracheides of the inner xylem appear to pass out from the region of xylem which was left doubtful at the preceding level (cf. Pl. II, Photos 27 and 28) adds probability to the view that here also the inner xylem was continuous between the main stele and that of the branch, though it is not possible to state this with certainty, as in the case of the first branching specimen. Comparison may be made between the condition shown in Photo 28 for the second branch, with that shown in Photo 23, and in Text-fig. 4, F, G, for the first branch.

Beyond this level the base of the branch stele bends away from the line of the axis of the main stele, as has already been described. The swollen base of the branch stele with its xylem distinguishable into outer xylem (continuous with the arc of accessory xylem) and inner xylem, the origin of which has been referred to above, is still in continuity with the accessory xylem of the stele in Text-fig. 6, D. Still further out, the stele of the branch, which has been seen in Text-fig. 5 to be followed longitudinally, narrows. The connexion between the basal transitional region and the narrow stele is shown in Pl. II, Photo 29, which shows the distinction between the outer xylem of the branch and the tracheides of the inner xylem, forming together with parenchyma a kind of 'mixed pith'; the photograph further shows how the isodiametric tracheides of the accessory xylem are continuous with the elongated tracheides of the branch, where it has grown in length by the activity of its proper apex. The next section of the series (Text-fig. 6, E) is mainly of interest as showing the departure of the first leaf-trace from the branch stele, the direction of which was indicated in Text-fig. 5, *l.t.*¹ The xylem of the base of the branch now appears completely separate from that of the main stele, but the other tissues of the branch still show continuity. In the last section (Text-fig. 6, F) all sign of the branch has gone, the stele of the rhizome is complete, save for the next leaf-gap in relation to the trace which has just left the cortex, but it is noteworthy, as already stated, that the zone of accessory xylem is still well marked, and only ceases to be developed after this leaf-gap has closed.

If the actual connexions of the vascular system of the two branches to their respective steles be compared, an essential agreement will be found

to exist. Omitting some qualifications as to the continuity of the inner xylem in the second specimen made in the detailed accounts above, the important feature appears to be the continuity of the inner and outer xylems from the main stele to the branch. In the case of the outer xylem, this involves the secondary development of accessory outer xylem, which may be limited to the connecting tracts necessary, or may form over the whole stele for a distance of more than two leaf-gaps. Were the branch developed at or close to the apex, the connexions would probably be expressed in a continuity of the primary tissues, as is the case in the vascular disturbance in relation to some vestigial buds. This has been shown above to be comparable with the simpler case presented by the vascular connexions of the first branch. In describing the structure, it is impossible to avoid the metaphor of departure of tissues from the stele, but in interpreting it the other point of view of influences extending backwards from the more or less active bud is essential. Similar considerations had to be entertained in studying the vascular connexions of branches developed from vestigial buds on the rhizome of *Botrychium lunaria*.¹

3. RHIZOMES OF JUVENILE TYPE. PROGRESSION FROM JUVENILE TO ADULT TYPE. CONDENSATION FROM ADULT TO JUVENILE TYPE.

In the preceding pages the structure of rhizomes with medullated and distinctly mesarch steles has been described, the origin of the leaf-trace and its progress through the cortex has been followed, the vascular disturbance of the stele in relation to the vestigial bud has been analysed, and the vascular connexions of branches developed from such buds have been described. This section will be devoted to the structure of the stele and leaf-trace in small rhizomes of the juvenile type, and to the relations between the adult and juvenile types of anatomy.

The available material has consisted of the two small rhizomes arising as lateral branches, of a number of young plants undoubtedly developed from embryos, and of some small rhizomes which might have come either from small branches, or by further development of embryonic plants. The uncertainty (in the absence of the characteristic basal region) is due to the fact that the structure of small branches and of plants of embryonic origin is essentially similar. Branches of *Helminthostachys* have not been described in detail, though Fig. 2 of Farmer and Freeman's paper gives the external appearance of a shoot of this nature, and the small rhizome, the stele of which is figured in Fig. 23 of the same paper, was presumably a branch. The anatomy of young plants has been described by Campbell and by

¹ Ann. of Bot., xxvii, p. 235.

myself. Some redescription is however necessary, since I am unable to agree with Campbell's interpretation of the structure, or with his view of the constitution of the stele of the young and old plants.

Anatomy of the branches. Both the branches, the connexions of which with their main stems have been described, were much smaller than their respective parent rhizomes. Their stelar anatomy approximated to that of embryonic plants, but was easier of interpretation, since the vascular elements were more numerous. They had the further interest of a known continuity of the tissues of their steles with the corresponding regions of the parent stele. The first branch was followed in a complete transverse series, while the lower region of the second branch (including the origin of the first leaf-trace and first root) was cut longitudinally, and the remaining portion transversely.

The origin of the first branch has been traced to the stage at which its stele (just before attaining a definite cortex of its own) lay beside the decaying broken end of the parent fragment (Text-fig. 4, J; Pl. II, Photo 24). The stele of the branch, thus completely organized, had a cylinder of xylem slightly oval in transverse section, and around this a zone of tissue some five or six cells deep, enclosed by the complete endodermis. Presumably pericycle, phloem, and conjunctive parenchyma were represented in the zone between the endodermis and the xylem, and the sieve-tubes soon become recognizable in the transverse section. The chief interest is, however, in the constitution of the xylem. This was solid, in the sense of having no definite pith, though parenchymatous cells were scattered through it. There was a clear distinction between outer and inner or central xylem. The tracheides of the zone of outer xylem (Photo 24, *x.o.*) were larger, and showed a roughly radial arrangement like that found in the outer xylem of the adult type of stele; their walls were pitted. The tracheides of the inner xylem (Photo 24, *x.i.*) were smaller, stained less deeply, and their walls were reticulately or spirally thickened.

Judging by the appearance of the elements of xylem, it would be natural to regard the stele as centrarch, i. e. as having a central group of protoxylem elements surrounded by a zone of metaxylem. The backward connexion of these two components of this stele has, however, been shown to be with the inner and outer (accessory) xylem of the main axis, respectively. That this connexion indicates the right interpretation of the stele of the branch is confirmed as soon as preparations for the departure of the first leaf-trace become evident. A small group of elements now recognizable at the limit between the outer and inner xylem is undoubtedly the protoxylem of the nascent trace, and its position demonstrates the mesarch construction of the small stele. This stage is represented in Pl. III, Photo 30. The leaf-trace xylem is thus derived from a small arc of the outer xylem, with a protoxylem group on its inner face, and as

it separates from the xylem of the stele (Pl. III, Photo 31), the outer xylem becomes at once complete around the inner xylem. A little further on (Pl. III, Photo 32) the leaf-trace and stem-stele are still enclosed by the common endodermis, but the xylem of the leaf-trace has become completed adaxially, in a similar fashion to what has been seen in larger rhizomes. The xylem of the stele is almost solid, with outer xylem surrounding a small central core of inner xylem mixed with parenchyma. This condition is maintained for some distance after the trace has definitely separated from the stele, as is shown in Pl. III, Photo 33, where the section passes through the vestigial axillary bud (*v.*) in relation to the departed trace. The stele already shows the first indication of the position of the protoxylem for the second leaf-trace. The xylem of this trace is seen still forming part of the stele in Pl. III, Photo 34, and it will be evident that a small definite pith is present, the inner xylem being practically replaced by parenchyma. It is unnecessary to follow the anatomy of this branch node by node, especially as it showed no further advance towards the adult type. Indeed, after the departure of the second leaf-trace, the stele, though usually showing a small pith, was smaller than at the base of the branch, and more like that of a young plant.

While the departure of the first leaf-trace from the stele of the first branch has now been examined in transverse section, the corresponding region of the second branch was shown in longitudinal section. The general relations of the inner and outer xylems of this branch to the stele have already been described and discussed. As shown in Pl. II, Photo 29, the base of the branch had a well-developed outer xylem composed of pitted tracheides, and centrally a 'mixed pith', consisting of narrower tracheides, with spiral and reticulate markings, and rather abundant parenchyma. The same structure was traceable as the stele became more slender, and it was evident that this branch, while corresponding in the position of inner and outer xylem to the first branch, tended to have the inner xylem largely replaced by parenchyma. It was possible to prove also, from the longitudinal sections, that the leaf-trace departed from the outer xylem only, and that the stele was to be regarded as mesarch. Pl. III, Photo 35, shows the base of the departing leaf-trace, and it will be clear that while a gap is left for some distance in the cylinder of outer xylem, the inner xylem (*x.i.*), consisting of long spiral tracheides, can be traced straight on within this gap, just as it can on the lower side of the stele. The behaviour of the inner xylem here is thus essentially similar to what held for the first branch, allowing for the fact that in this case more medullary parenchyma is present. The facts seem inconsistent with regarding the centrally placed tracheides as protoxylem, while they agree with regarding it as the representative of the inner xylem, a view which its basal connexion has already suggested.

The stele of the second branch had from its base more central parenchyma than that of the first specimen, and even before the departure of the first leaf-trace may be said to have a definite pith. This is clearly marked above the leaf-trace departure, and it may be noted that nothing in the arrangement of the cells suggests 'intrusive' origin of the pith, which is indeed enclosed within the peripherally placed remains of the inner xylem. A short distance further on (cf. Text-fig. 5) the first root springs from the ventral side of the branch, and from that level onwards the stele is much larger, and has a wide pith surrounded by a tube of xylem. There is little indication of inner xylem in this region, the pith occupying its position, though occasional tracheides occur.

The distal portion of the basal region of this branch, as seen in longitudinal section, naturally corresponds to the appearance of the next portion cut transversely. In Pl. III, Photo 36, the first leaf-trace (*lt.*¹) is seen just after it has undergone division. The endodermis is complete around the stele, which shows the relatively large pith surrounded by a tube of xylem. This is almost entirely outer (centripetal) xylem, though occasional single tracheides of the inner xylem were found. Dorsally, the xylem for the second leaf-trace is recognizable in the stelar ring, its protoxylem, in the absence of inner xylem, abutting on the pith. The next photographs (Pl. III, Photos 37-39) show the interesting histological changes associated with the departure of this leaf-trace. Photo 37 shows the endarch xylem of the trace just separated from that of the stele. The gap in the tube of outer xylem, which is left by its separation, is partially bridged across by the development of a number of tracheides of inner xylem. In Photo 38 the development of inner xylem across the gap in the outer xylem is much more marked, and inner xylem is also present in the lower part of the stele. The leaf-trace is still within the common endodermis. In the next stage (Photo 39) the trace and stele have their respective endodermal layers complete, the trace shows only slight indications of adaxial extension of its xylem, and the stele has almost returned to the condition from which we started (cf. Photos 39 and 36), in having almost no tracheides of inner xylem developed in the central parenchyma or pith. The position of the protoxylem of the nascent third leaf-trace is recognizable at *px.*³ The attachment of the second root is seen at the ventral side of the stele in Photo 38.

The rhythm exhibited in the disappearance and reappearance of the inner xylem in this small medullated stele will be discussed later, after the corresponding facts for young plants have been described. The two branches described show agreement in essentials of construction, though medullation by replacement of the inner xylem was earlier and better marked in one case than in the other. Both show, however, that the small stele is to be regarded as mesarch, although the inner xylem consists

of spiral or reticulate tracheides, and may fail to develop in some regions of the stem. The leaf-traces in the first branch showed adaxial completion of their xylem, while in the second branch this was only slightly indicated. Another interesting difference, for comparison with young plants, was that the first leaf on the one branch was an arrested structure, while in the second branch it was shown by its vascular supply to have been normal.

Anatomy of young plants. The anatomy of young plants developed from embryos will be dealt with as briefly as possible. The main facts are recorded by Campbell and myself in the existing literature, but not in the form required for comparison with the branches and the rhizomes of adult type. What is further necessary may be brought out by following a series through part of a well-developed young plant, such as that figured in outline in the previous paper of this series.¹ Such a plant would show the large foot at the base, the primary root with its vascular system continuous with the base of the stem stele, but not in the same straight line as this, and the strictly dorsiventral construction of the further growth. The plant actually selected for description had borne four expanded leaves dorsally, and a number of roots (in addition to the differently placed primary root) ventrally.

Transverse sections of this plant at various levels are represented in Text-fig. 7, the external outline, the endodermis, and the xylem only being shown. The scale did not allow of a distinction being made in these figures between the inner and outer xylem. In Text-fig. 7, A, the continuity between the stele of the first root and the base of the stem-stele is seen, and this root is seen to differ from all the later ones in standing on the morphologically dorsal side of the plant. B and C show the hypocotyledonary stele, while D, E, F, G show the departure of the first leaf-trace, the slit leading down to the first vestigial bud being evident in G. The second root is seen in F. The departure of the second leaf-trace extends from H to K, the last section passing through the vestigial bud; L shows the third root and the preparations for departure of the third leaf-trace, while in M this trace is seen with its axillary canal. In N the fourth leaf-trace is distinct from the stele, and the attachment of the fourth root is seen. Beyond this, the stele passes into a more meristematic condition, the last tracheides visible in P being a dorsal group in relation to the young fifth leaf, and a ventral group belonging to this region of the stele; in connexion with this, the fifth root is developing.

The more important structural features of the stele of this plant are illustrated by Photos 40-46, on Pl. III. The xylem of the hypocotyl exhibited a central group of tracheides surrounded by a more or less definite zone of somewhat larger tracheides. This zone is rather irregular at the level figured (Pl. III, Photo 40), but became more regular and closer

¹ Ann. of Bot., xxviii, p. 30, Text-fig. 9 A.

a little higher up, before any indication of the departure of the first leaf-trace was evident. Longitudinal sections of this region in other plants showed that the central xylem consisted of spirally thickened tracheides, while the peripheral ones were pitted. Owing to this structure, the stele was described in my earlier accounts as centrarch, the inner xylem being regarded as protoxylem, which it resembles histologically. For reasons that will be further evident below, I am now led to distinguish even in these slender steles between inner and outer xylem, as in the case of the branches previously described, and to correct in this sense my earlier statements.

TEXT-FIG. 7. Series of transverse sections of the rhizome of a small plant, developed from an embryo, to show the relative positions of the various organs. The outline of the rhizome is given, that of the stele is a dotted line, the xylem is black. Description in text. L^1, L^2, L^3, L^4, L^5 , successive leaves or leaf-traces; r^1, r^2, r^3, r^4, r^5 , successive roots; vb^2 , second vestigial bud. The slits leading to other vestigial buds are also shown.

The stelar xylem in the hypocotyl can be regarded, as in the further regions of the shoot, as composed of a dorsal portion destined to continue outwards as the first leaf-trace, and a ventral portion which is more strictly cauline. At the level of the section represented in Pl. 3, Photo 41, the arc of outer xylem destined for the leaf-trace is rendered distinct from the lower portion of the stele by the group of parenchyma immediately within its endarch protoxylem. The true protoxylem for the trace was evidently placed immediately within the outer xylem, thus indicating the mesarch

nature of the stele in the hypocotyl. On the separation of the leaf-trace xylem (Pl. III, Photo 42), the outer xylem becomes complete around the inner xylem of the stele, which again forms a solid cylinder. For some distance the stele, now belonging to what may be termed the first internode of the epicotyl, maintains this appearance. Then parenchyma again appears in the central xylem, replacing many of its elements, and shortly after this the second leaf-trace becomes clearly recognizable, forming the dorsal half of the stele (Pl. III, Photo 43). In this section the xylem of the leaf-trace is again seen to be endarch, and to be continuous with the outer xylem of the stele. This outer xylem is one or two tracheides thick in the lower portion of the stele, and surrounds the small 'mixed pith', consisting of a number of parenchymatous cells, and some three or four tracheides of the inner xylem (*x.i.*). The separation of the leaf-trace xylem would evidently leave a gap in the outer xylem, but before this takes place (Pl. III, Photo 44) the inner xylem is found to be much more strongly developed, rendering the stem portion of the stele almost solid again. Indeed, before the leaf-trace xylem completely separates (Pl. III, Photo 45), the outer xylem in the stem stele becomes continuous, so that on the departure of the trace, the stele is left with a complete solid xylem strand consisting of inner and outer xylem. In the preparations for the departure of the third leaf-trace medullation again takes place by replacement of the inner xylem by parenchyma. Thus in Pl. III, Photo 46, the xylem of the nascent third trace is recognizable, forming the dorsal portion of a stele that has a small pith, scattered tracheides of inner xylem round this, and a continuous tube of outer xylem.

It is unnecessary to follow the changes node by node, for the facts just given will be sufficient to show the rhythmical nature of the changes in the stele associated with the leaf-trace departures. It should be mentioned, however, that this stele never became quite solid above the departure of the third trace, a small pith persisting. The second root arose from the ventral surface of the rhizome, just after the first leaf-trace separated from the stele, and the third root was inserted shortly after the stage reached in Pl. III, Photo 46. The leaf-traces of this plant were endarch, and showed no adaxial completion of the xylem, but cases in which this was effected have been observed in other young plants.

The progression from the juvenile to the adult type of rhizome. The comparison of the stelar structure of young plants and branches on the one hand, and of rhizomes of different diameters, but with the usual adult type of stele, on the other, reveals an essential correspondence. The chief differences in the adult type, apart from size, concern the definite and persistent medullation; the development of the elements of the inner xylem as pitted tracheides and the occurrence of an internal endodermis.

The origin of the pith in the seedlings and other small rhizomes

studied shows no indication of being intrusive. The pith arises by the greater or less development of parenchyma in the central region of the stele. There is no indication of conversion of tracheidal elements to parenchyma, but this phrase expresses in a general way the mode of origin of the pith, since different plants or regions exhibit completely solid inner xylem, inner xylem with scattered parenchymatous cells, mixed pith with parenchyma predominating in the central region, and lastly a small pith where the central region is free from tracheides. It may therefore be stated definitely that a pith, such as that shown in Pl. III, Photos 36, 39, 46, is purely intrastelar and in no way due to intrusion.

None of the seedlings, branches, or juvenile rhizomes of uncertain origin showed the actual progression to the fully adult type of stele with an internal endodermis, but comparison of rhizomes of different sizes of both juvenile and adult type gave a series which lent no support to the view that at a later stage of development an intrusive pith was present in addition to the primary intrastelar pith. To draw the line on the appearance of an internal endodermis would be wholly artificial, as this may be present, incomplete, or absent in rhizomes of various sizes. The value of the internal endodermis in this plant as an indication of the limit between stele and intrusive cortex is further discredited by the occasional appearance of an internal endodermis in the base of roots, as described earlier in this paper.

With regard to the change in inner xylem from spiral or reticulate to pitted tracheides, the latter characterizing the inner xylem of the adult type of rhizome, the evidence of direct transition in any one piece of rhizome is also lacking. But it has been shown, in considering the branches and young plants, that the inner xylem of the juvenile rhizome behaves like the inner metaxylem of the adult rhizome in the region of the leaf-gap, and also that in the case of branches there was continuity between the inner xylem of the main rhizome and the branch. The question of the transition between the two histological types in the ontogeny, though it would be interesting, is not vital to the morphological interpretation of the stele. That there is a transition at a certain stage may reasonably be assumed.

Since none of the slender rhizomes of juvenile type, though some of them consisted of a considerable number of nodes, showed the advance to the adult type, it is clear that this is not necessarily (or perhaps even usually) attained quickly. In one piece of rhizome, however, a rapid transition from the condition with a stele with a solid xylem to the fully adult structure was exhibited, and, though peculiar in some ways, this rhizome may be briefly described. It was probably a branch, since, while much thicker than any young plant, the first leaf-trace was imperfectly lignified and supplied an arrested leaf. The character of the leaf-traces and their departure have already been described (see Pl. I, Photos 14-19), and

all that need be done is to refer to the progress in size and in stelar complexity.

This piece of rhizome measured about an inch and a half in length, and rapidly increased in diameter from the narrow basal end till its full diameter was attained and then maintained. Its diameter at the base was slightly over 2 mm. and the diameter of the adult region was about 7 mm. A transverse section at the base (Text-fig. 8, A) showed the xylem of the first leaf-trace already separate from the stelar xylem, but within the common endodermis. The xylem of the stem stele was complete, showing no indication of a gap, and at this level was practically solid, only a few parenchyma cells being scattered among the more central tracheides. There were indications of a distinction between somewhat smaller tracheides of the inner xylem and the zone of outer xylem, though the limit was not easy to decide definitely from transverse sections. Where the sections were slightly oblique, it could be seen that the inner tracheides were spirally thickened and those of the outer xylem pitted. The stele at this level, though larger than the other examples described, was thus of the juvenile type. The xylem of the departing first leaf-trace was clearly endarch. It did not show adaxial completion, and indeed as it became further removed from the stele ceased to be lignified; it was evidently related to an arrested leaf.

Meanwhile, parenchyma had become more definitely present in the central region of the stele, replacing some of the inner xylem and forming a small pith, around which a broken ring of elements of the inner xylem remained. The distinction between the outer and inner xylem was evident on the appearance of the protoxylem of the second leaf-trace, which had elements of inner xylem internal to it. Then the inner xylem disappeared opposite to the nascent endarch trace, the pith being continuous into the concavity of the latter. The xylem of the trace, derived from the outer xylem only, almost closes round as it separates from the xylem of the stele (Text-fig. 8, C). The adaxial closure becomes complete later, and this trace passed through the usual clepsydroid stage and divided just before it departed from the cortex. While the separation of the second trace has been proceeding, the stele has enlarged and is provided with a greater definite pith. The inner xylem is especially well represented as the gap closes.

It is unnecessary to follow the elaboration of the stelar structure further in this rhizome, but this portion is of interest in showing how, between the departure of the first and second leaf-traces, the xylem passed from the solid condition with inner and outer xylem to the definitely medullated condition found in small rhizomes of the adult type of structure. It is impossible to state at what level the inner xylem was composed of pitted tracheides, but it was evidently by now or not much further on. The

relative size of the rhizome and stele after the departure of the third leaf-trace is seen in Text-fig. 8, D. The rapidity of the transition in this rhizome can be associated with the greater size of the stele even at the base, and presumably with more effective conditions of nutrition. The comparative sizes of stele and rhizome from the base to the attainment of the full diameter can be followed in the diagrams in Text-fig. 8. When the full size was attained (Text-fig. 8, E) the stele showed the size and complexity of the fully adult type, but had no internal endodermis.

Condensation of stelar structure from the adult to the juvenile type. It is usual to find the primary structure of a young plant or a branch continuing on the up-grade of elaboration until the adult type is reached and then maintained. It was of interest, as bearing on the significance to be

TEXT-FIG. 8. Selected transverse sections to show the progression in size and stelar complexity in a rapidly widening piece of rhizome. A, B, showing departure of the first leaf-trace; C, at the level of the first vestigial bud and showing the second leaf-trace on the left; D, the leaf-trace at the clepsydroid stage; E, the full-sized rhizome showing a dividing leaf-trace at the periphery of the cortex. l^1 , l^2 , l^3 , leaf-traces of the first three leaves; r^1 , stele of the first root; $l.t.$, dividing leaf-trace of full-sized region; $px.$, protoxylem group of next leaf-trace.

attached to this progressive elaboration of the stele in the ontogeny, to find a converse change exhibited by certain rhizomes, in which a condensation or reduction from the adult to the juvenile type of stele could be traced. This was associated with diminution in size of the rhizome as a whole, and may reasonably be regarded as due to growth under less favourable conditions of nutrition.

The amount and nature of the condensation will be evident on comparing transverse sections of the stele of the same rhizome at different levels, photographed to the same scale. Thus Photos 51 and 52 on Pl. III are respectively further from and nearer to the apex of the same piece of rhizome. The former shows the usual structure of a small rhizome of adult type, with a definite pith surrounded by a xylem-tube with well-developed outer and irregular inner xylem. This rhizome actually had an imperfect internal endodermis. Passing towards the apex of the piece of rhizome

there was a progressive diminution in thickness, and the stele exhibited changes similar to those seen in the ascending series of complexity traced in rhizomes of increasing size, but in a converse direction. At the level shown in Photo 52 the stele agreed in size and organization with those of small branches or young plants in which the scattered elements of inner xylem formed, with the cells of the central parenchyma, a mixed pith. The stele had returned to the juvenile type, and the changes in relation to the departure of a leaf-trace agreed with this. A corresponding, though less extreme reduction, is seen on comparing Photos 48 and 50 from another piece of rhizome. Both pairs of photographs show that there is a corresponding reduction in the size of the leaf-trace.

Such specimens seem to indicate clearly that the simpler type of stele characteristic of normal young stages in the ontogeny of *Helminthostachys* is to be associated with small size and less efficient nutrition. The same juvenile structure can be resumed when from any cause an adult rhizome becomes again feeble and more slender.

4. ON THE INTERPRETATION OF THE CONSTRUCTION OF THE RHIZOME AND STELE IN *HELMINTHOSTACHYS*.

In the preceding parts of this paper a number of facts have been described which amplify our knowledge of the anatomy of *Helminthostachys*. In the description of the facts theoretical interpretations have been touched upon as lightly as possible. Some general considerations may fitly be placed here, and are necessary in order to properly discuss Professor Campbell's views on this plant.

If the descriptions of the adult rhizome, the branches, and the young plants are compared, an essential similarity in construction will be found to underlie the differences presented by rhizomes of various sizes. As regards general morphology the rhizome is throughout dorsiventral, the ventral region bearing roots but no leaves, while the dorso-lateral leaves alternate, as shown by their leaf-traces, to either side of the middle line. In relation to each leaf is its vestigial axillary bud, which may be more or less displaced in front of the leaf-trace—in adult rhizomes usually by the whole length of the leaf-gap. There is thus a general indication of a segmental repetition of the parts of the shoot which will need to be considered further below.

The essential agreement in stelar construction between the juvenile and adult rhizomes must first be made clear. If the series through the adult rhizome (Text-fig. 2) be considered, it will be evident that while the large pith is continuous from node to node it is unequally encroached upon by xylem at different levels. This especially concerns the inner xylem. The inner xylem, on the one hand, diminishes in amount (and often disappears),

internal to the protoxylem of a nascent leaf-trace, by the development of parenchyma replacing more or less completely the xylem elements. On the other hand, the pith is diminished immediately above a leaf-gap by an increased development of inner xylem forming a marked bulge inwards.

When this rhythm is considered in the light of the stelar structure of small rhizomes it gains in significance. Thus in steles with a small pith like that shown in Photos 36–39 we find the inner xylem least developed just before the leaf-trace begins to separate, while on the separation an increase of the inner xylem takes place, which is especially marked on the dorsal side of the stele below the gap in the outer xylem. In this case, as in the adult rhizome, the pith persists even where the inner xylem is at its greatest development, and this is on the dorsal side of the stele below the closing leaf-gap. In other cases, and especially in the basal nodes of the young plant (Photos 42–46), the inner xylem is less developed as the trace prepares to separate, and the subsequent increase of inner xylem leads to total filling up the centre of the stele so that the pith is interrupted at the base of each internode.¹ Whatever be the ultimate explanation of it, the rhythm in proportional development of inner xylem and pith is the same in large and small rhizomes.

The pith can be seen to arise in *Helminthostachys* by the increase in the amount of parenchyma in the centre of the stele. Usually scattered elements of parenchyma are present in the inner xylem, though this may consist of tracheides only, and all grades between this and the complete replacement of inner xylem by parenchyma may be found in juvenile steles. The rhythmical variation in amount of the inner xylem appears in some cases to negative the idea of the pith being of 'intrusive' origin. Thus, in such cases as those shown in Photos 35 and 38, the pith is cut off from the outside by the inner xylem,² the leaf-gap only affecting the outer xylem. It is only in the adult rhizomes with larger leaf-gaps that continuity between the cortical and medullary parenchyma is marked, and it is in these regions that an internal endodermis is often developed. The appearance of this is not suggestive, however, of its being a morphological limit between an intrusive cortical pith and the stele;³ the occasional presence of an internal endodermis in the root is further evidence against attaching morphological importance to it in the stem. A still further argument against regarding the pith as extra-stelar is afforded by its reduction and the distribution of tracheides through it when the stele exhibits condensation from the adult to the juvenile type (cf. Photos 51, 52).

Though the inner xylem differs in its histological features in the

¹ A similar return to a solid stele after a leaf-trace departure is described for a small plant of *Botrychium lunaria* by Bower (Ann. of Bot., xxv, p. 541).

² Cf. *Botrychium lunaria*, Ann. of Bot., xxvii, p. 221, Pl. XX, Photo 14, and the discussion and comparison with *Osmunda* there.

³ A similar conclusion was reached in the case of *B. lunaria*. Ibid., p. 217.

juvenile and adult rhizomes, critical consideration shows that even the small rhizomes with their central elements spirally thickened are to be regarded as mesarch. The mesarchy is shown where the protoxylem for the leaf-trace appears (cf. Photo 30). This interpretation is supported by the behaviour of the spirally thickened tracheides of the inner xylem at such leaf-trace departures as those in Photos 35, 37, and 38, a behaviour quite inconsistent with regarding them as protoxylem.

An essential similarity is thus seen in the small and large steles, though the actual construction differs in rhizomes of different size. It is usual to find the primary structure of a young plant or a branch continuing on the up-grade of elaboration until the adult type is reached and maintained. This is natural and intelligible whether the ontogenetic progression is to be looked upon as a phylogenetic recapitulation or as an expression of the cumulative increase in strength and nutritive power of the plant. The fact that in *Helminthostachys* the earlier grades in the progression may be maintained for many nodes of a rhizome, or, on the other hand, may be rapidly passed through, suggests that the physiological explanation may be the more important. This is further shown by the juvenile structure being resumed when rhizomes of adult type become more slender under unfavourable conditions of nutrition. Thus the usual progression must be regarded as an expression of physiological differences, and its use as an index of phylogenetic history must be critically considered in this light. In *Helminthostachys* at least the physiological interpretation seems inevitable, whatever phylogenetic value may be attached to the different manifestations of the underlying type of construction.

The essential structural fact appears to be the existence of two components in the xylem, inner xylem and outer xylem. Various indications suggest that this may be a distinction of fundamental importance in the general morphology of the conducting system of a shoot. Not to go into detail here, it may be mentioned that a similar distinction has been made in the case of the independently evolved conducting system of Mosses,¹ and that it is exhibited by the stele of the Lycopodiales, Equisetales, and Sphenophyllales. It is present in the stele of the adult stem in some Ferns (e. g. Gleicheniaceae) and is indicated in others. The distinction is clearly suggested in the slender basal region of the stems of many young Ferns. But the most interesting cases in the Pteropsida are found in a number of relatively archaic groups, such as the Osmundaceae, the Coenopterideae, especially the Zygopterideae, and also in some Cycadofilices.

Leaving phylogenetic considerations out of the question for the present, the Ophioglossaceae appear to find their place with the last-named groups, as regards the general comparative morphology of the stele. The Ophioglossaceae are of peculiar interest on account of the range of variants of the

¹ Cf. Tansley and Chick: *Ann. of Bot.*, vol. xv, p. 1.

same essential type of primary construction they present. In *Helminthostachys* the inner xylem is better represented than in any other existing medullated plant. Indications of inner xylem are found in *Botrychium*, and a mixed pith may occur as a result of traumatic disturbance. In *Ophioglossum* tracheides may be developed throughout the pith in branching rhizomes, while strands of tracheides occur normally in the pith of some specimens of *Ophioglossum pendulum*.¹

In attempting to get a deeper insight into this distinction of inner and outer xylem, it must be borne in mind that the descriptive statement that a leaf-trace 'departs' from a stele is metaphorical. The vascular system has no such individuality or power of branching. In the light of development it must be regarded as laid down along certain tracts, determined partly by the meristematic construction, and partly by influences proceeding backwards from the growing points of the main axis, or of lateral leaves or branches. While our knowledge of the necessary facts is too imperfect to make any inference more than tentative, it is suggested that the central region of a stele may be directed from the main apex, while the peripheral region is largely influenced from the developing leaves. In support of such a conception of the vascular structure, it may be pointed out that the study of the Ophioglossaceae has shown clearly the reality of such backward influences along more or less predetermined tracts, in the case of the vascular connexions of the branches. This was evident in the study of the branches of *Botrychium lunaria*, and has been shown above for *Helminthostachys*. In the latter plant we see further that such an influence may extend to the main stele, and modify its structure all round and for a considerable distance; the extensive development of accessory or secondary xylem in the second branching specimen was clearly due to the influence of a developing branch upon the mature primary structure of the stele.

In the preceding considerations, the stem with its stele has been regarded as the unit. It is possible, however, to regard the rhizome of *Helminthostachys* as exhibiting a segmental construction from three rows of segments, two dorso-lateral and one ventral. The distinction of the dorso-lateral segments is pretty clear, since each bears a leaf and its related vestigial bud; the distinction of the ventral segments which do not bear leaves, and on which the roots are borne, is less evident. Such a construction differs in the existence of a ventral region not having leaves, from the radial construction exhibited by *Botrychium*, where each segment bears a leaf and a bud. The difference here shown between these dorsiventral and radial types of rhizome is of course present in Ferns at large, but this preliminary consideration may be confined to the Ophioglossaceae.

The radial and strictly dorsiventral types of shoot, with the general appearance of a segmental construction, as seen in *Botrychium* and

¹ Petry: Bot. Gazette, vol. lvii, p. 183, Figs. 12, 13.

Helminthostachys, are paralleled by the independently evolved shoots of the sexual generation of Mosses and leafy Liverworts respectively. In the case of the Bryophyta we know that the construction of the mature shoot is directly related to the apical segmentation. To what extent such a relation holds in the case of the more massive shoots of Ferns is, in my opinion, an open question which requires fuller investigation. The view has been expressed on the one hand that the leaf-development in Ferns is independent of the apical segmentation.¹ On the other hand, we know that in certain cases, such as *Ceratopteris*, the relation between apical segment and leaf holds, and this is also stated to be the case for the dorsiventral rhizome of *Polypodium vulgare*.² The appearance of the mature regions of both radial and dorsiventral shoots is at least consistent with assuming such a relation to hold, and is otherwise insufficiently explained. If such a segmental relation holds for *Helminthostachys*, for example, it would explain the regular succession of the lateral members in a way that does not involve the acceptance of any view that denies the existence of an axis. On such lines we should be prepared to find that the stele of the rhizome could be regarded, in part at least, as cauline, though influenced profoundly by the leaves.

The segmental construction with two rows of dorso-lateral and one row of ventral segments is indicated, not only in the general morphology of the rhizome of *Helminthostachys*, but also in the stelar structure. It is shown most clearly in smaller rhizomes, where the whole of each dorso-lateral segment of the outer xylem of the stele is continuous with the outgoing leaf-trace. Since the segmental construction is of the rhizome as a whole, the vascular system being developed along certain tracts through this, only two of the segments may be evident in the stele itself, the third being indicated by the departing leaf-trace. In the less extended adult type of stele all three segments are represented in any one section.

Thus the three components of the stele are represented in a large rhizome, such as that in Text-fig. I, B, by the ventral portion where the roots are borne, the right dorso-lateral portion concerned with the vestigial bud, and the left dorso-lateral portion concerned with the next leaf. In small steles the distinction of three parts is shown in Photo 32, where the ventral portion and the right dorso-lateral portion are evident in the stele of the stem, while the left dorso-lateral segment is represented by the departing leaf-trace. The same thing is shown in Photo 52, where the dorso-lateral segments are indicated by the leaf-trace (*l.t.*), and by the region with the protoxylem group (*px.*) of the next trace already evident. The rest of the stele corresponds to the ventral segment.

If the stele be traced into the meristematic region behind the apex,

¹ Cf. the discussion of this question in the Land Flora, pp. 175-7.

² Klein : Bot. Zeit., 1884, p. 646.

the same distinctions can be drawn so far up as the procambial strand exhibits any lignified elements. Pl. III, Photo 53 shows a transverse section of a stele at this level; the outline of the procambial cylinder can be traced, and in it two groups of protoxylem elements are lignified; one of these marked *l.t.* corresponds to the leaf-trace supplying the youngest developing leaf, while the other (*px.v.*) is the early formed xylem of the ventral segment. A corresponding independence of the ventral region of the xylem has been traced to close behind the apex in a number of small rhizomes.

We are now in a position to consider the divergent views expressed by previous investigators of *Helminthostachys*, as to the evidence for or against the stele, or a portion of it being cauline.

According to the work of Farmer and Freeman¹ on adult rhizomes, the stele can be followed to the apex of the stem beyond the youngest leaves and roots, and hence is cauline. These investigators further emphasize the evidence afforded by the ventral side of the dorsiventral rhizome, from which leaves are absent, while the vascular tissue can be traced up to the apical meristem. With this view, according to which there is a stem with a stele which in part at least is strictly cauline, I am in essential agreement.

Campbell, who has investigated the question mainly on young plants, a number of which he describes in some detail, comes to a very different conclusion, which will be clear from two quotations, remembering that he takes as his starting-point 'the single axial strand of collateral structure throughout cotyledon and root', as found in the young plants of some species of *Ophioglossum*. From such strands he derives directly the dictyostelic arrangements in *Ophioglossum* and Marattiaceae. After considering these he continues: ² 'The second type of skeleton is that found in *Botrychium* and *Helminthostachys*. This is a solid, hollow cylinder, with inconspicuous leaf-gaps, resulting from the union of the broad leaf-traces which fuse completely to form this hollow stele. That the cylindrical bundle, or siphonostele, is not due to the formation of a pith within the protostele is clearly shown by the development of the bundle in the young sporophyte of *Botrychium*, where it can easily be seen that the component bundles are separate at first, and that the pith, so called, of the siphonostele is merely a portion of the ground tissue that is included between them, and which later becomes entirely separated from the cortical tissue. A similar condition of things may be found in tracing the development of the vascular cylinder in the young stem of *Helminthostachys*.'

In describing the structure near the tip of the young rhizome of *Helminthostachys*, Campbell says ³ earlier in the same work: 'From this study of the development of the leaf-traces, following them from the stem

¹ Loc. cit., p. 428.

² Loc. cit., p. 214.

³ Loc. cit., p. 78.

apex downwards, it appears that the cylindrical stele in *Helminthostachys* arises in precisely the same way as that of *Botrychium*, viz. by the union of the leaf-traces. The appearance of procambium upon the ventral side of the stele, which in longitudinal section appears to be derived directly from the stem apex, can thus be explained by the ventral extension of the broad leaf-traces, which meet on the lower side of the stem as well as above, and the cylindrical stele is thus developed. It is not impossible that the root-traces may also contribute to some extent to the development of this ventral portion of the stele.'

If the last sentence is taken to mean that a ventral portion of the stele not derived from leaf-traces is always present, this view would not differ so fundamentally from the segmental analysis of the rhizome and stele indicated above, though the idea of root-traces 'contributing' to the stele is even less satisfactory than that of entering leaf-traces.¹ It is clear, however, from the context, from the description of particular plants, and from the view of the nature of the pith expressed in the first quotation above, that Campbell recognizes steles of young plants as resulting entirely from the union of successively older leaf-traces. This view leads him to interpret certain structural appearances in a way that I am unable to accept.

Thus, if the description of a young plant given on pp. 71-3 of 'The Eusporangiatae' and illustrated by Figs. 49 and 50 be referred to, it will be found that the anatomical relations of the leaves and stems are followed from above downwards. The bundle from the youngest leaf is traced inwards from above the level of the stem apex to a plane below this. Not even a meristematic or procambial equivalent of the stem stele is recognized as present below the apex for the trace to join on to, but this leaf-trace is regarded as forming the whole of the stele present in the rhizome below the apex. On to this the trace of the next older leaf is followed, so that the stele below is regarded as made up by the union of the first and second leaf-traces, no stem portion other than this being recognized. The double nature of the xylem in this stele below the entry of the second trace is figured in detail (Fig. 50), and explained as being due to the portions of xylem derived respectively from the two leaf-traces.

The difficulties which have led to this interpretation of the facts seem to be due partly to the extreme closeness of the apex to the youngest developing leaf, and partly to the fact that the actual apex is sunken and ventrally displaced. Thus the leaf-trace is met with above the level of the apex, and below this level may be lignified, while the cauline component of the stele is still procambial. The double nature of the xylem of the stele behind the junction of a leaf-trace is readily seen, and is accurately figured by Campbell, but the lower of the two components is not traceable to the next younger leaf, but, as shown above, is the ventral and cauline

¹ Roots and leaves might both be regarded as influencing the differentiation of the stele.

portion of the stele. This is most clearly seen on following the changes in the stele from below upwards, and this method also shows the intrastelar development of the pith which is naturally called in question on Campbell's view.

A further argument against Campbell's interpretation is afforded by the vascular structure of the hypocotyl. In this region also the stele appears composed of a dorsal portion continuous with the first leaf-trace, and of a ventral portion. Apart from the fact that the ventral portion is not traceable into the second leaf (as would be necessary on Campbell's view), it would appear a strained interpretation of the ventral and often larger portion of the stele below the first leaf, to regard it as due to the vascular strand entering from the next younger leaf; the latter was probably not developed when the vascular structure of the hypocotyl was determined.

This question has been discussed at some length because the interpretation of the vascular structure of the *Ophioglossaceae* given by Campbell has wide bearings on the general morphology of vascular plants. His view is in accordance with a phytonic theory, and while applicable with some difficulty to the stelar structure in *Ophioglossum*, meets with greater difficulties in the stele of the shoot of *Botrychium*, which is also radially constructed. It appears to be almost negatived when the attempt is made to apply it to the dorsiventral shoot of *Helminthostachys*, where there is a ventral component not bearing leaves.

On the alternative view held in this paper, the segmental construction of the shoot is recognized, but is not regarded as inconsistent with the primary existence of an axis upon which the leaves arise as lateral appendages. Both the segmental construction of the shoot and its morphological unity require to be recognized. Phytonic theories may be said to over-emphasize the first feature, while opposing views tend to minimize the reality of segmental construction. This general aspect of the question cannot, however, be further discussed here.

5. CONCLUDING REMARKS.

In the first number of these studies,¹ the direction which a number of features of the rhizome of *Botrychium lunaria* indicated for the relationship of the *Ophioglossaceae* to other plants was very briefly considered. The general view expressed was that 'the stelar structure, the medullation, the construction of the leaf-trace, and the nature of the branching, are all consistent with a relationship of the *Ophioglossaceae* to the ancient Fern stock, the general features of which are indicated in the relatively primitive groups of Ferns, such as *Zygopterideae*, *Botryopterideae*, *Osmundaceae*, *Hymenophyllaceae*, &c.' This is in general accord with the views expressed by Renault and Scott,² and with the position now given to the group by

¹ Loc. cit., p. 240.

² Studies in Fossil Botany, p. 640.

Bower,¹ and will not be further discussed here. It is confirmed by this study of *Helminthostachys*.

Without dwelling on the question of actual relationship of the group, some of the main data for comparison afforded by this plant may be reviewed, and possible comparisons indicated. In doing this it is necessary to extend the field of comparison to some of the Cycadofilices. The main features of importance for comparison in the rhizome of *Helminthostachys* are (a) the presence of inner and outer xylem, (b) indications of secondary thickening, (c) peculiarities of the leaf-trace, (d) axillary branching and the vascular relations of the branch. These may be briefly discussed in order. The comparisons indicated are not to be taken as necessarily implying actual relationships.

(a) The distinction of inner and outer primary xylem is, as has long been known, exceptionally clear in the large adult rhizomes of *Helminthostachys*. An essentially similar construction has been shown in this paper to hold for small rhizomes, where, however, the inner xylem does not consist of pitted tracheides; it may be solid or form a mixed pith. The progressive elaboration exhibited by the stele of *Helminthostachys* is particularly instructive, as the zone of inner xylem is preserved even in the large rhizomes. Thus comparing *Helminthostachys* with other Ophioglossaceae we have an interesting range of variants on a fundamental type of construction. In the one direction we have the *Ophioglossum* type with a reticulum of collateral bundles, consisting of outer primary xylem and phloem, all trace of inner xylem having usually disappeared. On the other hand, we have the *Botrychium lunaria* type with only traces of inner xylem round the pith, but with a well-marked zone of primary outer xylem passing on the outside into the zone of secondary xylem in large stems. In other species of *Botrychium*, e. g. *B. virginianum*, the radial arrangement of the elements of xylem begins at once, so that in this respect no equivalent of the primary outer xylem of *B. lunaria* or *Helminthostachys* is recognizable. In the species of *Botrychium* we find the same problem of what is to be regarded as primary xylem that faces us in the higher Gymnosperms. The same general direction of elaboration of a monostele appears to have been followed independently in several lines of Filicales, and in the Lyginodendreae, while parallels can be traced in other groups such as the Lepidodendreae.

As to how far the distinction of inner and outer xylem can be usefully followed in the Filicales, cannot be discussed here. Among existing Ferns it is clearly seen in such forms as the Gleicheniaceae, and the same line of interpretation can be applied to the Schizacaceae, where the elaboration is in many respects parallel to the Ophioglossaceae. The distinction is also

¹ Handwörterbuch der Naturwissenschaften (1913), Bd. iii, p. 935. The full statement of the alternative view of a relationship to the Lycopodiales is in the Land Flora (1908).

suggested in the case of the Marattiaceae when the young plants are considered. The most interesting comparisons are, however, with the extinct Zygopterideae and Botryopterideae, and with the Osmundaceae, which have been shown by recent investigation to show signs of a common origin with these. It would lead too far to follow the comparisons in detail at present, but it may be pointed out that the closest comparisons can be drawn between *Helminthostachys* and those forms in which the inner xylem consisted of elongated tracheides mixed with parenchyma, rather than with those in which a gradual conversion of actual elements of the inner xylem into short parenchymatous cells is suggested. The two processes are, however, probably not fundamentally distinct. *Osmunda* appears to still possess a zone of inner xylem around its pith, and is thus comparable with *Helminthostachys*. The parallel is even closer between *Helminthostachys* and some Zygopterideae, notably *Metaclepsydropsis duplex*, *Ankyropteris Grayi*, and *A. corrugata*, although a central pith is not present in them. The steles of these plants with mesarch decurrent protoxylems are, in fact, paralleled by the condition found in the smaller stems of *Helminthostachys* with a mixed pith, the inner tracheides being histologically different from those of the outer xylem. The condition in *Helminthostachys* with a mesarch but solid xylem may be compared with what is sometimes found in *Botryopteris*.¹ Whether the comparison can be extended to some other Botryopterideae and to the Hymenophyllaceae, where the narrow inner elements of xylem appear, on our present knowledge, to be really protoxylem, is not so clear. The protoxylem may possibly be central in some very slender young plants of *Helminthostachys* where the inner metaxylem is practically wanting, but in all strong plants the metaxylem was mesarch as described.

The parallel may be extended to the primary structure of some Cycadofilices, where the inner xylem is of the *Heterangium* type, and outer primary xylem is seen in the leaf-traces. The significance of smaller remains of centripetal xylem, as in *Lyginodendron*, will be referred to below in connexion with the leaf-trace structure.

(b) Secondary thickening. In *Helminthostachys* there is normally no secondary growth, though (as is also seen in the Zygopterideae and some other Ferns) there may be an approach to an irregular radial serration of the tracheides. As is shown by the pieces of rhizome which bore branches, however, a localized development of tracheides in the normal position of secondary xylem can take place long after the primary structure was mature. Though there is no regular persistent cambium, this must be regarded as a special case of secondary thickening, all the more interesting because something is known of the stimulus that starts the process. It may, on the one hand, be compared and contrasted with the more regular secondary thickening in *Botrychium*, and, on the other, with the secondary

¹ Cf. Benson, Ann. of Bot., xxv, Pl. LXXXII, Fig. 13 A.

thickening known in the stems of some Zygoterideae. The marked secondary thickening in *Botrychioxylon* appears more closely comparable to what occurs in *Botrychium*, but the stem of *Ankyropteris corrugata* appears to offer features suggesting a comparison with *Helminthostachys*. It may not be without significance that the only specimen of *A. corrugata* in which secondary thickening has been described and figured was branching. The secondary growth, described as 'only a local formation superadded to the normal woody zone',¹ is most marked in the larger of the two steles shown in the cross-section of the branching specimen. The few existing Ophioglossaceae afford examples of all grades of replacement of the primary wood, with both centripetal and centrifugal xylem, by the secondary wood, and raise the same difficulties in homology and nomenclature as are met with in the case of Cycadofilices and Gymnosperms.

(c) The peculiarities of the departing leaf-trace of *Helminthostachys* afford data for comparison with long-extinct plants, which are remarkable features to find in an existing plant with no known fossil history. These features make it easier to compare the leaf-trace of *Helminthostachys* with the Zygoterideae and such Cycadofilices as *Calamopitys* and *Lyginodendron* than with other existing Ferns, except perhaps the Osmundaceae. No detailed comparisons will be made here, and this is the less necessary since the main points to which reference must be made are raised in recent works on the Zygoterideae, and were summarized by Dr. Paul Bertrand in the 'Progressus Rei Botanicae' for 1912.

It must be borne in mind that while the leaf-trace as it arises from the stele is monarch in the Ophioglossaceae, Osmundaceae, and the Cycadofilices mentioned, it already possesses two groups of protoxylem where it separates from the stele in those Zygoterideae in which the leaf-trace departure is best known. This is not an essential distinction, since the two protoxylem poles in the Zygoterideae may be regarded in some cases at least as derived by division of one, and since further there is some reason to regard the traces of the simplest known Zygoterid trace (*Clepsydropsis*) as having been monarch at departure. It is a question of how far down into the stem the double nature of the leaf-trace is continued.

Dr. Paul Bertrand and Kidston and Gwynne-Vaughan agree in comparing a stage in which the departing leaf-trace of such an Osmundaceous plant as *Thamnopteris* exhibits two protoxylem groups immersed in the metaxylem of the trace, with the structure exhibited by the petiolar bundle of *Clepsydropsis*. The traces of *Asterochlaena*, *Metaclepsydropsis*, and *Diplolabis* pass through a similar stage. Those of *Ankyropteris Grayi* and *A. corrugata* only differ in having a small central extension of the inner xylem or mixed pith of the stele. This soon dies out, and the central portion of the trace xylem becomes solid. This clepsydroid stage is of

¹ Scott : Trans. Linn. Soc., vii, 1912, p. 376, Pl. XL, Fig. 19.

importance as affording a simple expression of the double leaf-trace which assumes such complicated forms in the petioles of the Zygopterideae. If the origin of the trace of *Clepsydropsis* itself, as described by Bertrand, be included in the comparison, we can contemplate a preceding stage in which the xylem of the departing trace includes a single protoxylem. In any case this monarch stage is realized in *Thamnopteris*, and may be spoken of as the pre-clepsydroid stage.

Dr. Bertrand's interpretation of these structures differs considerably from that of Kidston and Gwynne-Vaughan.¹ The essential point for our purpose is brought out by the nomenclature used by the former investigator, who describes all these traces as 'divergeants fermés'. This idea of a closed divergent appears to imply that the outer xylem of the trace is completed adaxially. It may or may not include a portion of the mixed pith or inner xylem, but except in so far as it does this it is not mesarch in the sense in which this term applies to the stelar tube of *Helminthostachys*, i. e. as being composed of outer and inner xylem. This conception of a closed divergent plays an important part in the detailed accounts of Fern anatomy by Bertrand and Cornaille, and has recently been more directly applied to the Cycadofilices by Chodat. The clepsydroid stage is on this view naturally regarded as composed of two closed divergents.

While the other Ophioglossaceae² have leaf-traces that are most readily compared with the C-shaped trace of many recent Ferns, *Helminthostachys* in the variety of its leaf-trace departure comes into line with the plants referred to above. As has been shown in the detailed descriptive account, its leaf-trace exhibits every degree of adaxial completion of the arc of outer xylem with which it is continuous in the stem. It goes far to justify the conception of the closed divergent as distinct from the mesarchy exhibited by the stelar tube of xylem. The inner xylem may or may not extend for some distance into the departing trace, being included within the closed divergents of the pre-clepsydroid or clepsydroid stages. As in the case of *Ankyropteris*, the inner xylem soon disappears from the trace, but its presence enables a clear distinction to be drawn between the adaxial completion of the xylem of the trace and true mesarchy. There is a striking resemblance between the clepsydroid stage of the departing trace in *Helminthostachys* and that in *Clepsydropsis* and the various Zygopterideae mentioned above. The pre-clepsydroid stage in *Helminthostachys* is comparable to the similar monarch stage in *Thamnopteris*, especially when the adaxial completion of the xylem takes place before separation from the stelar xylem.

¹ P. Bertrand: *Progressus Rei Botan.*, vol. iv, p. 182; Kidston and Gwynne-Vaughan: *Proc. R. S. Edinb.*, vol. xxviii, p. 433, and *Trans. R. S. Edinb.*, vol. xlvi, p. 654, and vol. xlvii, pp. 469 ff.

² The occasional adaxial completion of the xylem in *Botrychium lunaria* must be remembered in this connexion. *Ann. of Bot.*, xxvii, pp. 223 and 239.

It would lead too far to extend the comparison in detail to the Cycadofilices and the Cycadaceae, but it must be pointed out that there is a close resemblance between the monarch stage of the leaf-trace in *Helminthostachys* and in *Calamopitys*, a resemblance extending to the stage of division of the trace in the cortex. This comparison may be also applied to *Lyginodendron*, and the reality of the adaxial completion of the xylem in *Helminthostachys* supports the interpretation of the 'mesarch' bundles of *Lyginodendron* as closed divergents.¹ This view does not necessarily prevent a comparison of the bundles of the latter plant with those of Cycads, for one way of regarding them would be as derived from such a closed divergent.

These comparisons, without fully treating the subject, will indicate that the leaf-trace of *Helminthostachys* resembles those of the Osmundaceae, Zygopterideae, and Cycadofilices more than it does those of the more modern leptosporangiate Ferns.

(d) The branching of *Helminthostachys* also affords suggestive points of comparison with the Zygopterideae and Cycadofilices. The branching is definitely axillary, and buds or branches in this position are known in some Zygopterideae and in *Lyginodendron*. Among other Ferns axillary branching is only known in the Hymenophyllaceae. This position of the lateral branches is the characteristic one in the Cordaitales and in the modern Conifers and Angiosperms.

The branching of *Helminthostachys* may first be compared with that of *Botrychium*. In both these genera of Ophioglossaceae there is a regular development of dormant lateral growing points or vestigial buds in an axillary position. From these, when the normal correlation is disturbed by the arrest of the growth of the main axis, lateral branches may develop. In *Botrychium lunaria* the vascular system of the branch is in relation with the adaxial side of the subtending leaf-trace. In *Helminthostachys*, on the other hand, while the relative position of the branch and the subtending leaf-trace is the same, the vascular connexion is with the stele of the rhizome some distance above the level of the leaf-trace departure. In the case of one branch at least it has been proved that the inner xylem of the branch stele was continuous with the inner xylem of the rhizome, while the outer xylem was continuous with an accessory or secondary development of the outer xylem of the main stele. Had the branch developed at once, instead of after the stele of the rhizome was mature, the inner and outer xylems would both doubtless have been continuous from the main stele to that of the branch. This primary relation is indicated in the structure of the vascular disturbance behind some vestigial buds.

The vascular connexion of the axillary branch in *Botrychium lunaria*

¹ Chodat: Arch. d. Sc. Phys. et Nat., 1908. Cf. also P. Bertrand: Études sur la Fronde des Zygoptéridées (Lille, 1909), pp. 264 ff.

is comparable to what is found in the Hymenophyllaceae and in some Zygoterideae, such as *Ankyropteris Grayi*. On the other hand, the relation of the branch-stele in *Helminthostachys* to the stele of the main axis, and not to that of the subtending leaf-trace, is comparable to what is found in some other Zygoterideae, where, however, a relation of the branching to a leaf-axil is not established. Thus the branching in *Botrychioxylon*, *Ankyropteris corrugata*, *Diplolabis Römeri*, and *Metaclepsydropsis duplex* is described as dichotomous, 'using the word in the somewhat loose sense, which is inevitable when dealing with fossils'. The facts regarding the branching of the Zygoterideae have been recently summarized and discussed by Scott, and it is only necessary to refer to his recent papers.¹ It is clear that in this group of plants we meet both with branches standing in the leaf-axils and connected with the meristele of the subtending leaf, and with branches the steles of which were related directly to the stem. In the latter cases, to which the term dichotomy is applied, the two branches were sometimes equal, and in other cases the appearance was of a smaller stele attached laterally to a main one. Dr. Scott leaves it open whether the dichotomy is the more primitive condition, the axillary association with leaves being secondary and derived, or whether the dichotomies may be really cases of modified lateral branching. The regular presence of dormant axillary apices in *Botrychium* and *Helminthostachys* appears to be in favour of the relation between leaf and branch being part of the primary construction of these plants. The vascular relations of the branches in *Helminthostachys* are directly with the stele of the rhizome. It is easy to see how with greater separation of the branch from its subtending leaf, and somewhat stronger development of the branch, a state of affairs would result indistinguishable from what is described as dichotomy in some Zygoterideae. Were a branch rudiment to develop close to the growing point of the rhizome of *Helminthostachys*, the main rhizome continuing its growth, an appearance of equal dichotomy would probably result.

In any case there is a striking parallel both in the variety in the vascular relations of the branches to the main shoot, and in the details of the vascular connexions, between the Zygoterideae and the Ophioglossaceae. The regular presence of lateral branches or suppressed buds in some of these plants must be given due weight in considering the general question of whether lateral monopodial branching is primitive or derived from dichotomy. The case of the Ophioglossaceae appears to support the former view.

The argument for a relationship of Ophioglossaceae with Zygoterideae is clearly stated and advocated from the side of the extinct plants in Dr. Scott's paper on *Botrychioxylon*. More detailed study of *Helminthostachys* strengthens the case for this affinity from the side of the existing

¹ Ann. of Bot., xxvi (1912), pp. 57-60; Trans. Linn. Soc., 2nd ser., Bot. vii.

plants by revealing additional and unsuspected resemblances in the morphology and anatomy of the stem and leaf-trace. If our knowledge of the anatomy of *Helminthostachys* was based on the four pieces of rhizome illustrated in Text-figs. 2, 3, Text-fig. 4, Text-figs. 5 and 6, and Text-fig. 8, it may reasonably be stated that we should find our closest comparisons not among existing Ferns, but with the palaeozoic Zygopterideae and Cycadofilices. If these resemblances indicate the true affinities of the isolated group of the Ophioglossaceae, the latter present an interesting contrast, as regards the evidence, to the Osmundaceae, which there is also reason to trace back to the ancient Fern stock. In the case of the Osmundaceae we have fossil remains extending our knowledge of the group back to Permian times. In the Ophioglossaceae the conclusion that there is a true affinity with Zygopterideae seems, if anything, more inevitable in the light of the primary structure of the stele, the secondary thickening, the structure of the leaf-trace, and the nature of the branching. The evidence is here derived from comparative anatomy with a practical absence of any historical record between the early palaeozoic Ferns and the Ophioglossaceae of the present day.

SUMMARY.

1. The rhizome of *Helminthostachys* exhibits a general segmental construction, and may be regarded as composed of three series of segments, one ventral and two dorso-lateral. The insertion of a leaf, with its stipular sheath and axillary bud, corresponds to each dorso-lateral segment, the leaves alternating right and left of the median line. The ventral segments do not bear leaves. This arrangement holds throughout the plant.

The transition from a leaf into its region of the stem is a gradual one, and it is hardly possible to speak of definite internodes in the adult plant. In the slender shoots of young plants the leaf insertions are more separate and internodes may be distinguished, at least in the stelar anatomy.

It is not stated that the segmental construction of the rhizome is related to the cell-segmentation at the apex, though it would be consistent with such an explanation.

2. The stele of the adult rhizome has a large pith, and the tube of xylem around this is mesarch, i. e. consists of outer and inner xylem, the protoxylem elements being found between them. The inner xylem may be more or less extensively represented; in smaller rhizomes there may only be scattered tracheides at the periphery of the pith, and sometimes the latter abuts directly on the protoxylem.

3. The roots are endogenous, but only penetrate a comparatively thin zone of cortical tissue. The xylem of the root is continuous with the outer xylem of the stele of the rhizome, and when the inner xylem of the latter

is poorly developed there may be a more or less direct continuity of the parenchymatous pith of the root and rhizome. The pith in the root base sometimes has a well-marked internal endodermis independent of that often found in the rhizome.

4. The dorsal side of the stele is disturbed by the leaf-traces and in relation to the vestigial buds.

The leaf-trace exhibits considerable variety in its mode of departure, structure, and mode of division in the cortex. In large rhizomes it may depart as a mesarch portion of the stelar tube, though the inner xylem is always less developed within the trace, and gradually dies out as the latter departs. In other cases the inner xylem disappears from the nascent leaf-trace, which departs with an endarch xylem.

The leaf-trace, whether mesarch or endarch, may divide into two in the cortex without adaxial completion of the outer xylem or the other tissues. More usually, this adaxial completion of the xylem takes place before division, and the phloem as well as the endodermis may also be completed. Adaxial completion may take place just before division of the trace; in other cases the xylem is completed adaxially while the trace is still monarch, and sometimes even before its xylem is free from that of the stele. This condition, in which the monarch trace has a complete ring of outer metaxylem surrounded by phloem and endodermis, may persist until the undivided trace leaves the rhizome. Usually, however, division of the trace is effected, and just before this the leaf-trace has a dumb-bell-shaped outline with a protoxylem group in each half, the metaxylem being continuous from the abaxial to the adaxial xylem between the two protoxylem groups. This has been termed (following C. E. Bertrand and Cornaille) the clepsydroid stage.

In leaf-traces which are mesarch and also show adaxial completion of the xylem, a clear distinction can be drawn between the two conditions; they both involve the presence of metaxylem to the inside and outside of the protoxylem, but are essentially different. The leaf-traces of small rhizomes are always endarch at departure, and may or may not exhibit more or less complete adaxial extension of the xylem.

5. The disturbance of the stele in relation to the vestigial axillary buds varies in degree, being most marked in the case of large adult rhizomes, and wanting in many smaller ones. In all cases, however, the endodermis remains open, or opens again, in relation to the dormant lateral apex. In well-marked examples, the bulge of xylem behind the bud corresponds to the stele at the base of a lateral branch in consisting of inner xylem surrounded by outer xylem, both being continuous with the corresponding tissue of the main stele.

The vestigial bud is in relation to the subtending leaf, and exhibits some variety in position relatively to the corresponding leaf-gap; it is

usually at the level of the separation of the next leaf-trace, but is sometimes further forwards and in smaller rhizomes nearly always further back.

6. The vascular relations of two branches, developed from lateral buds, to their parent rhizomes are described, and place the nature of the dormant buds beyond doubt.

The xylem of the stele of the branch is composed of a central strand of tracheides of the inner xylem surrounded by a zone of outer xylem. The inner xylem is continuous with the corresponding tissue of the main stele, while the outer xylem of the branch is continuous with the outer xylem of the rhizome, or rather with a secondary development of this, to which the name 'accessory xylem' has been given.

This accessory xylem has the characters of an irregular secondary thickening of the stele of the rhizome, and may be developed not merely in the direct tract backwards of the branch stele, but all round the main stele and before and after the branch departs.

7. The inner xylem is unequally developed at different levels in the adult rhizome, and exhibits a regular rhythm of decrease and increase in the dorsal region of the stele. It diminishes or disappears opposite the nascent leaf-trace, and is especially strongly developed as the leaf-gap closes.

A corresponding rhythm is traceable in slender juvenile rhizomes. The inner xylem may be largely replaced by parenchyma before a leaf-trace begins to separate, but increases again in amount as this happens, bridging across the gap left in the outer xylem by the departing trace. In small rhizomes this increased development of the inner xylem may lead to the stele becoming solid on the departure of a leaf-trace, to become medullated again as the next trace is initiated.

8. The structure of slender rhizomes with the juvenile type of stele is described both for plants developed from the embryo and for branches. These show essential agreement, with differences in detail depending partly on the strength of the shoot, and partly on the earlier or later development of a pith by replacement of most of the inner xylem by parenchyma.

The inner xylem in the young plant and the slender basal region of the branches consists of spirally thickened tracheides, and histologically resembles protoxylem. Its real nature is shown when the true protoxylem is distinguishable between outer and inner xylem in relation to a nascent leaf-trace, and by the behaviour of the inner xylem at the separation of the trace. That the more central xylem of the branch, in spite of its histological characters, is to be regarded as inner xylem is further shown by its continuity with the inner xylem of the main axis.

9. The juvenile type of anatomy may be maintained for many nodes, and no example showing the transition from the seedling structure to the adult type has been studied. Rhizomes of different sizes show, however, that the change from the juvenile type of structure to the adult condition

(in which the stele has a large and definite pith and a well-developed inner xylem consisting of pitted tracheides) is to be regarded as a process of further expression or elaboration of the structure found in the more slender rhizomes. It is probably related to increased strength and nutrition of the plant.

An exceptionally rapid transition from a condition with a solid stele to the fully adult type is described in what was probably a large well-nourished branch.

10. That the juvenile type of structure is to be regarded as an expression in miniature of what is found in full-sized rhizomes, and is to be explained on physiological grounds, rather than as a necessary phylogenetic recapitulation in the development of the individual, is further shown by full-sized rhizomes which become more and more slender. In such cases, presumably dependent on poorer nutrition, the stele with adult structure assumes in the slender continuation of the rhizome the juvenile size and structure. A condensation of structure is shown in such cases, the converse of the expansion or elaboration exhibited in the normal ontogeny.

11. The segmental construction of the rhizome, referred to in the first paragraph of the summary, is more or less clearly reflected in the stelar anatomy. Corresponding to the ventral segments, a lower, purely cauline portion of the stele is recognized. By tracing the tissues towards the apex this is confirmed. The stele is regarded as in part at least cauline, and not as made up of the united leaf-traces enclosing between them a portion of the ground tissue as the pith, as on Campbell's interpretation. Both the segmental construction of the shoot and its morphological unity, as expressed in recognizing axis as well as leaves, have to be taken into account.

12. Comparisons are made with the Zygopterideae and Cycadofilices as regards the outer and inner xylems, the secondary thickening, the peculiarities of the leaf-trace, and the nature of the branching, and confirm the general view of a relationship between the Ophioglossaceae and the more primitive Ferns.

DESCRIPTION OF FIGURES IN PLATES I-III.

Illustrating Professor Lang's paper on *Helminthostachys zeylanica*.

(All these figures are from untouched photographs.)

e., endodermis; *e.i.*, internal endodermis; *ph.*, phloem; *x.o.*, outer xylem; *x.i.*, inner xylem; *px.*, protoxylem; *ab.*, abaxial portion of xylem of leaf-trace; *ad.*, adaxial portion of xylem of leaf-trace; *x.²*, secondary or accessory xylem.

PLATE I.

Photo 1. Portion of vascular tube of a rhizome of adult type, showing the well-developed inner xylem. × 67.

Photo 2. Similar portion of the vascular tube from a smaller rhizome; the inner xylem is represented by scattered elements. $\times 67$.

Photo 3. Similar portion of the vascular tube from a rhizome with irregularly developed inner xylem; in the centre of the portion figured the protoxylem abuts on the parenchyma of the pith. $\times 67$.

Photo 4. Transverse section of a large adult rhizome, showing the stele, from which a leaf-trace has departed, leaving the leaf-gap. The leaf-trace is seen in the clepsydroid stage in the cortex. The basal connexions of two roots with the stele are shown. $\times 25$.

Photo 5. Leaf-trace from the adult rhizome figured in Photos 4 and 1, and Plate II, Photos 20, 21, showing an advanced stage of the adaxial extension of the xylem. The protoxylem of the trace has divided in preparation for the division of the trace; internal to each of the two groups of protoxylem, a small amount of inner xylem persists. $\times 67$.

Photo 6. Same leaf-trace as in the preceding photograph, but a little further out (cf. Photo 4). The outer xylem is complete adaxially, and a band of tracheides connects the abaxial and adaxial portions, dividing the central parenchyma into two portions. In each of them remains of the inner xylem are still present in front of the protoxylem groups. $\times 67$.

Photo 7. Dorsal portion of a stele of a small rhizome, showing to the right the disturbance of the endodermis in relation to a vestigial bud and on the left the arc of xylem for a leaf-trace; the inner xylem is almost wanting within the protoxylem of the trace. $\times 67$.

Photos 8, 9. Two stages in division of the leaf-trace seen in Photo 7. The division takes place without adaxial completion of the xylem, though a number of metaxylem elements are present internal to the protoxylem groups. $\times 67$.

Photo 10. Transverse section of a leaf-trace from a small rhizome (that in Text-fig. 4), showing endarch xylem with no adaxial completion of the outer xylem. $\times 67$.

Photo 11. Transverse section of the leaf-trace shown departing from the cortex of the large rhizome in Text-fig. 6. The trace is monarch, the xylem has closed round to form a complete tube, and the protoxylem is separated from both the adaxial and abaxial regions of the xylem by parenchyma. $\times 67$.

Photo 12. Transverse section of another leaf-trace from the same rhizome, showing the monarch trace, the absence of inner xylem, and the adaxial extension of the outer xylem still incomplete. $\times 67$.

Photo 13. The same trace as in Photo 12, a little further out. The adaxial extension of the xylem is complete, and the phloem also forms a complete tube. $\times 67$.

Photo 14. Dorsal portion of the stele of the rhizome in Text-fig. 8, showing the preparation for the departure of the third leaf-trace. The adaxial extension of the outer xylem is happening as the arc of xylem separates. $\times 67$.

Photo 15. Further stage than Photo 14. The adaxial xylem is complete, but is still continuous with the xylem of the stele. $\times 67$.

Photo 16. The same leaf-trace in the cortex, showing the complete tube of phloem. The xylem of the trace is still monarch. $\times 67$.

Photo 17. The same leaf-trace in the clepsydroid stage. $\times 67$.

Photo 18. Similar but larger leaf-trace from the same rhizome in the clepsydroid stage. $\times 67$.

Photo 19. One of the halves into which this trace divided (cf. Text-fig. 8, E), showing the preparation for the next division. $\times 67$.

PLATE II.

Photo 20. Dorsal portion of the stele of the rhizome represented in Text-fig. 2, C. To the left the nascent leaf-trace is seen with the inner xylem diminished in amount but not wanting. To the right is the closed leaf-gap with the greatly developed inner xylem continuous across and extending outwards into the gap still present in the outer xylem. Above this the endodermis is raised and open in relation to the vestigial bud. $\times 67$.

Photo 21. Similar section, corresponding to Text-Fig. 2, D, showing the full development of the bulge of xylem in relation to a vestigial bud. The bulge consists of inner xylem covered by outer xylem, while the outer xylem is also extending across below to complete the xylem ring of the main stele. $\times 67$.

Photos 22-24. Stages in the departure of the vascular supply from the first branching specimen.

(Cf. Text-fig. 4.) In Photo 22 the endarch leaf-trace is departing, its protoxylem being seen at *px*. *x.²* indicates one of the two groups of accessory xylem, while *x.i.* points to the inner xylem extending into the leaf-gap and destined for the branch. In Photo 23 the inner xylem has passed through the gap and approximated to the uniting groups of accessory xylem. In Photo 24 the stele of the branch is fully constituted and lies beside the broken-down stele of the parent fragment of rhizome. $\times 67$.

Photo 25. Transverse section of the stele of the second branching specimen after the branch had passed off. The stele shows outer and inner primary xylem, and outside the former accessory or secondary xylem is present all round the stele. $\times 25$.

Photo 26. Portion of a similar section more highly magnified, showing the relations of the accessory or secondary xylem to the primary xylem. $\times 67$.

Photos 27-29. Stages in the departure of the vascular supply from the second branching specimen. (Cf. Text-fig. 6.) $\times 67$. Photo 27 shows the great development of accessory or secondary xylem to the sides of the closed leaf-gap. It is uncertain whether the xylem marked ? is to be regarded as inner xylem passed into the gap, as in the first branching specimen. Photo 28 shows the arc of accessory xylem destined to form the outer xylem of the branch completed over the closed gap. Extending into it are the narrow tracheides of the inner xylem mixed with parenchyma. Photo 29 shows the basal region of the stele of the branch in longitudinal section, and the continuity of its outer and inner xylem respectively with the tissues recognized in Photo 28.

PLATE III.

Photos 30-34. Stele of the first branch in transverse section, showing the preparation for the separation of the first leaf-trace and the position of its protoxylem (Photo 30); a later stage on the separation of the xylem of the first leaf-trace (Photo 31); the first leaf-trace, with its xylem completed adaxially, lying beside the xylem of the stele of the branch, which has now regained its complete structure (Photo 32); the stele of the branch after departure of the first leaf-trace and at the level of the vestigial bud (Photo 33); and a later stage in the preparation for departure of the second leaf-trace, the protoxylem of which was evident in the preceding photograph (Photo 34). $\times 67$.

Photo 35. Longitudinal section of the basal portion of the second branch, showing the departure of the leaf-trace, which leaves a gap in the outer xylem; the inner xylem is continuous along the gap and separates the pith from the parenchyma in the angle of the departing trace. The inner xylem consists of spiral tracheides, while those of the outer xylem are pitted. $\times 67$.

Photos 36-39. Stele of the second branch in transverse section, showing the stages in initiation and departure of the second leaf-trace. In Photo 36 the first leaf-trace is seen divided in the cortex, the stele is medullated, and the protoxylem of the second leaf-trace is recognizable in its xylem; the inner xylem is almost entirely replaced by pith. In Photo 37 the endarch xylem of the second leaf-trace has separated, and elements of inner xylem have developed below the gap left in the tube of outer xylem. In Photo 38 this development of inner xylem is still more marked, and inner xylem is seen in the lower part of the stele, where a root is attached. In Photo 39 the leaf-trace is separate and has its complete endodermis; the inner xylem of the stele, which has returned to the condition shown in Photo 36, has largely disappeared, and the protoxylem of the third leaf-trace is evident in the xylem tube. $\times 67$.

Photos 40-46. Transverse sections of the stele of a young plant developed from an embryo, showing the changes involved in the separation of the first and second leaf-traces. Photo 40 shows the stele low down in the hypocotyl, with a central group of inner xylem surrounded by an irregular zone of outer xylem. Photo 41 shows the group of parenchyma cells internal to the arc of outer xylem destined for the first leaf-trace; the protoxylem of this is endarch. In Photo 42 the first trace has separated, and the xylem of the stele has again become solid. In Photo 43 most of its inner tracheides are replaced by parenchyma, while the second leaf-trace is initiated as an endarch arc of the outer xylem. Photo 44: the trace is not separate, but the increased development of inner xylem in the stem stele has filled up the gap to be formed in the outer xylem when separation takes place, and rendered the stem stele almost solid. Photo 45 shows a slightly further stage, the trace xylem not being completely free, while the outer xylem of the stem stele is reconstituted around the central group of inner xylem. In Photo 46 pith is again appearing by the replacement of most of the inner tracheides by parenchyma; the protoxylem of the third leaf-trace is evident. $\times 130$.

Photos 47-49. Separation of a leaf-trace from a stele of a small medullated rhizome of adult type. The trace is endarch at origin (Photo 47); the outer xylem becomes completed adaxially, while the trace is still monarch (Photo 48); and the trace later passes through the clepsydroid stage (Photo 49). × 67.

Photo 50. Stele of the same rhizome as Photo 48, at a level nearer to the apex, showing the condensation in size and structure. × 67.

Photo 51. Stele of a small adult rhizome, showing a departing leaf-trace, the xylem of which becomes adaxially completed before separation from that of the stele. × 67.

Photo 52. Stele of the same rhizome as that in Photo 51, but nearer to the apex, photographed to the same scale as Photo 51. The stele exhibits condensation or reduction to a purely juvenile type, with scattered tracheides of inner xylem in the undefined pith. × 67.

Photo 53. Transverse section of the stele of a young plant somewhat behind the apex. The outline of the stele is evident in the procambial condition, and the first-formed tracheides are seen to occur both dorsally (*lt.*) in relation to the youngest leaf-trace, and ventrally (*px.v.*) in relation to the lower purely cauline portion of the stele. × 67.

W.H.L. photo.

ei.

20.

21.

22.

24.

23.

25.

20.

21.

28.

22.

24.

27.

23.

25.

26.

29.

30.

31.

32.

36.

37.

38.

40.

41.

42.

43.

44.

45.

39

5

46.

W.H.L. photo.

30.

31.

32.

33.

34.

35.

xo. xi. xi.

36.

37.

38.

39.

52.

51.

48.

40.

41.

42.

53.

50.

49.

44.

45.

46.

47.

43.

WHL photo.

Lang, W. H. 1915. "Studies in the morphology and anatomy of the Ophioglossaceae: III. On the anatomy and branching of the rhizome of *Helminthostachys zeylanica*." *Annals of botany* 29, 1–54.

<https://doi.org/10.1093/oxfordjournals.aob.a089532>.

View This Item Online: <https://www.biodiversitylibrary.org/item/243629>

DOI: <https://doi.org/10.1093/oxfordjournals.aob.a089532>

Permalink: <https://www.biodiversitylibrary.org/partpdf/320049>

Holding Institution

Smithsonian Libraries

Sponsored by

Biodiversity Heritage Library

Copyright & Reuse

Copyright Status: Not in copyright. The BHL knows of no copyright restrictions on this item.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.