On some Climbing Davallias¹ and the Petiole of *Lygodium*.

BY

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With Plate XIV and eight Figures in the Text.

RECENT studies in the structure of the earlier fossil Filicales have lent considerable support to the theory that all the different forms of petiolar trace in the group are to be derived from a single primitive and ancestral type. This hypothetical trace is imagined as more or less round or elliptic in section, with a solid central mass of xylem of the same outline, and possessing originally a single mesarch protoxylem.

It has been shown how both the Osmundaceous² and the Zygopterid³ type of trace can be derived from this primitive form, and recently M. Paul Bertrand has shown⁴ that the Botryopterid type may also be derived from it, and, directly or indirectly, the Anachoropterid type.

As regards the living orders of Ferns, it seems probable that their petiolar traces are all variants of the Osmundaceous type with the form of an adaxially curved C. The traces of the Polypodiaceae, Cyathaceae, and Gleicheniaceae conform fairly readily with this type, and, in spite of certain difficulties, so it is believed will those of the Hymenophyllaceae and Marattiaceae. In the Schizaeaceae *Aneimia* provides us with examples of very typical C-shaped traces, but, according to the text-books, those of *Lygodium* and *Schizaea* are of quite a different type, and in no way related to the C.

¹ [The only species described in the notes is *D. fumarioides*, material of which was obtained from Bath, Jamaica, where it was collected by Professor Bower. It belongs to a group of species (Nos. 75-9) placed together by Hooker in the Synopsis Filicum, and characterized by 'fronds several feet long, usually climbing'.]

² Gwynne-Vaughan and Kidston: On the Origin of the Adaxially Curved Leaf-trace in the Filicineae. Proc. Roy. Soc. Edin., vol. xxviii, Part vi, 1908, p. 433.

³ Kidston and Gwynne-Vaughan: On the Fossil Osmundaceae, Part IV. Trans. Roy. Soc. Edin., vol. xlvii, Part iii, 1910, p. 469.

⁴ Paul Bertrand: L'étude anatomique des Fougères anciennes et les problèmes qu'elle soulève. Prog. Rei Bot., vol. iv, 1913, p. 182.

Professor C. Eg. Bertrand¹ evolved an extremely neat and ingenious theory to bring the trace of *Lygodium* into line and explain it in terms of the adaxially curved trace.

In order to test this theory and to find out whether the structural features warranted this idea, I investigated very thoroughly the traces of several species of *Lygodium* with confirmatory results, and I was led to examine the leaves of certain climbing species of *Davallia*, the near relations of which possess most typical C-shaped traces, to see whether similarity of habit had led them in the same direction of modification as appears to have been taken by *Lygodium*.

The result appears to me to be a wellnigh complete confirmation in all essentials of Bertrand's theory, with, however, a slight but interesting modification.

[Bertrand and Cornaille in their explanation of the petiolar trace of *Lygodium* started from the 'ternary chain' exhibited by the smaller traces of *Osmunda*. They based their account on the figures of *Loxsoma Cunninghami* as given by Gwynne-Vaughan,² and of *Lygodium* as given by Boodle,³ their interpretation of the structure being indicated by the symbolic notation added to the figures which they reproduced.

The change from the C-shaped trace to the type found in *Lygodium* is thus expressed: 'L'accentuation des plis inverses provoquée uniquement par un épaississement des masses du métaxylème, et l'union de ces plis inverses dans la surface de symétrie change complètement le caractère de la trace, elle n'est plus trace osmondéenne, mais bien trace onocléenne, son accentuation a produit les quadruples des *Lygodium*.'⁴

It is clear from comparison of the annotated figures of the traces of *Lygodium* and *Loxsoma* given in Bertrand and Cornaille's plate that these investigators regarded the adaxial hooks of the xylem as still constituting part of the condensed 'xylem strand' in *Lygodium*. The modification of Bertrand's theory referred to above is that (as shown by *Davallia fumarioides*) the adaxial hooks exhibit all stages in disappearance before the *Lygodium*-like condition is attained. In connexion with this it may be noted that in *Davallia aculeata* (Gwynne-Vaughan Coll., Slides Nos. 875-8), which has the same habit as *D. fumarioides*, the hooks appear to be absent throughout.

The following facts relating to the vascular system of the petiole and its branches in four species of *Lygodium* are selected from notes which also deal with other features in the anatomy of this genus. They will serve as a restatement of the problem to which the structure of *Davallia fumarioides* affords the key.]

¹ C. Eg. Bertrand et F. Cornaille: Les caractéristiques des traces foliaires osmondéennes et cyathacéennes, exemples, modifications et réductions. Soc. Hist. Nat. d'Autun, 1902.

² Ann. of Bot., vol. xv, Pl. iii, Fig. 7, A-E.

³ Ibid., Pl. xix, Fig. 4.

⁴ loc. cit., p. 9.

Lygodium.

LYGODIUM SCANDENS. The petiolar bundle has the well-known peculiar form in transverse section (Text-figure 1, B); the xylem is roughly triangular, the adaxial side being slightly concave. The abaxial median protoxylem is single in young petioles, but in other cases it is apparently double; the lateral protoxylem groups are some distance in front of the lateral prominences. The abaxial protoxylem is apparently exarch, though some evidence was obtained of a mesarch position in young petioles. The protoxylem elements are annular and spiral, and are associated with distinct cavity parenchyma. At the base of the petiole the median protoxylem is not double, and the protoxylem is not crushed and consists of

TEXT-FIG. 1. *Lygodium scandens*. A. Habit sketch. B. Diagrammatic transverse section of petiolar trace. C¹⁻⁵. Primary branching of the petiole. D. Branch trace in secondary or tertiary branches. In B and D, and in some of the following text-figures, the protophloem is indicated by a line or dotted line, the sieve-tubes of the metaphloem by small circles, and the incipient phloem-fibres or small thick-walled sieve-tubes by *f*.

small elements which are probably scalariform. It is thus questionable whether there is true protoxylem in this region. Protophloem and phloem are present all round the xylem. The chief development of large sieve-tubes of the metaphloem is in the lateral and adaxial bays. Near the dorsal and lateral prominences of the xylem the small sieve-tubes have thick, soft-looking walls and may be regarded as incipient phloem fibres, the walls of which, however, are never lignified.¹

In the origin of a primary branch of the petiole one of the lateral protoxylem groups elongates (Text-fig. 1, C¹) and divides into two (Text-fig. 1, C²). The outer protoxylem is carried out as the protuberance of the

¹ Cf. Boodle, l. c., p. 368.

xylem is formed (Text-fig. 1, C³), and the inner protoxylem again divides (Text-fig. 1, C⁴), giving rise to the proximal lateral protoxylem of the branch, and the protoxylem remaining in the parent axis (Text-fig. 1, C⁴, C⁵). The median protoxylem of the petiolar bundle takes no part in the branching; if there is a true median protoxylem of the primary branch-trace it must arise *de novo*. In other respects the structure of the trace of the primary branch resembles that of the petiolar trace.

The primary branch bears two secondary branches opposite one another and then ends blindly (Text-fig. 1 A).

The origin and structure of the trace to a secondary branch are

TEXT-FIG. 2. *Lygodium japonicum*. A. Habit sketch. B. Diagrammatic transverse section of xylem strand of petiolar trace at base of petiole. C. Diagrammatic transverse section of petiolar trace in free petiole. D¹-D⁶. Departure of xylem strand to primary branch of the petiole. E¹-E³. Same, to secondary branches. F. Same, to tertiary branch.

similar to those of the trace to a primary branch, but the abaxial prominence is less marked. The outline is oval; protophloem and small sieve-tubes surround the xylem. Only one group of large sieve-tubes is present, and lies on the abaxial side; on the adaxial side and also near the lateral ends incipient fibres occur. The median prominence of the xylem is more or less obsolete, and the only protoxylems present are the two adaxial lateral groups (Text-fig. 1, D).

[A photograph of the petiolar trace of *L. scandens* giving off the trace to a primary branch is shown in Plate XIV, Photo 9.]

LYGODIUM JAPONICUM. All branches of the leaf except the lowest terminate in a suppressed growing point, and bear a pair of secondary branches just below the apex (Text-fig. 2, A). The petiolar trace (Text-fig. 2, C; Plate XIV, Photo 10) agrees in general plan of construction with that of *Lygodium scandens*. The lateral protoxylems appear to be quite exarch; they very early become crushed by the surrounding parenchyma. The median protoxylem is single, and in several cases was obviously mesarch with a closed ring of centrifugal metaxylem on its abaxial side (Text-fig. 3, A; Plate XIV, Photo 10). In other cases the persistent centrifugal elements are confined to a small group immediately abaxial to the actual protoxylem and separated by parenchyma from the xylem

TEXT-FIG. 3. *Lygodium japonicum*. Diagrams showing position of abaxial protoxylem.

teeth on one or both sides (Text-fig. 3, B, C, D, E). The actual protoxylem elements are very soon crushed by the surrounding cells of the xylem parenchyma, which become somewhat enlarged. Often all the centrifugal tracheae become crushed at the same time as, or shortly after, the actual protoxylem; in this case the extremity of the median lobe is occupied by a little bay of parenchyma, which includes the crushed protoxylem and centrifugal elements and separates the two teeth composed of scalariform elements. In fact the lobe appears to be bifid and to possess two protoxylems.¹ The actual protoxylem is, however, always single, and is usually more or less attached to one of the teeth of small metaxylem elements (Text-fig. 3, D and E).

All the actual protoxylem elements are annular or spiral, but these die out when traced down to the brown basal part of the petiole, although the

¹ Cf. Boodle, l. c., Pl. xix, Fig. 4.

position of each strand of protoxylem is still indicated by a group of small scalariform elements. Towards the very base of the petiole the prominences of the xylem strand become less marked, especially the lateral ones, and the adaxial sinus disappears (Text-fig. 2, B).

The protophloem completely surrounds the xylem, but metaphloem elements only occur in groups on the abaxial flanks and in the adaxial sinus; the sieve-tubes are often in contact with the tracheae. Phloem

TEXT-FIG. 4. *Lygodium dichotomum*. A. Habit sketch. B. Diagrammatic transverse section of petiolar trace. C. Departure of xylem strand to primary branch of petiole. D. Xylem strand at third and fourth dichotomy. E. Trace of vein.

fibres were not seen, but the small sieve-tubes near the prominences are especially thick-walled (Text-fig. 2, C, f).

The pericycle is two-layered opposite the positions of maximum development of the phloem, and one-layered elsewhere.

The branching of the petiole (Text-fig. 2, D¹⁻⁴) essentially resembles that in *L. scandens*. The trace of the primary branch, which has no abaxial protoxylem, swings round (Text-fig. 2, D⁵), so that its median plane is almost at right angles to that of the main trace (Text-fig. 2, D⁶).

In the origin of each of the secondary branches a protoxylem of the primary branch elongates and divides (Text-fig. 2, E², ³), supplying a single protoxylem, which doubtless later divides into two, to the secondary trace. In this and higher branchings the plane of the branch is practically parallel to that of the mother axis (Text-fig. 2, E, F).

LYGODIUM DICHOTOMUM. The xylem of the petiolar trace (Text-fig. 4, B) has a deep adaxial indentation so as to make it almost three-lobed.

TEXT-FIG. 5. *Lygodium volubile*. A. Habit sketch. B. Diagrammatic transverse section of petiolar trace. C. Departure of xylem strand to primary branch of petiole. D', D''. Departure of xylem strand to secondary branch of petiole.

The abaxial projection has a wide sinus, and there are two distinct protoxylems facing one another, one on each tooth. This interpretation is confirmed by the presence of thick-walled sieve-tubes in the sinus in contact with the tracheae of the metaxylem. The position of the two lateral protoxylems and the distribution of the phloem are exactly as in *L. japonicum*.

Branches of the trace of the first (Text-fig. 4, C) and subsequent

(Text-fig. 4, D) orders have the same structure, and are given off in the same way as in *L. japonicum*, and, as in that species, a dorsal protoxylem is absent in the branch-traces.

LYGODIUM VOLUBILE. The xylem of the petiolar trace (Text-fig. 5, B) has no anterior sinus. The exarch, lateral protoxylems are some distance anterior to the lateral lobes. The posterior protoxylem is double and exarch. The method of branching of the trace (Text-fig. 5, C, D) is essentially similar to that in *L. dichotomum* and *L. japonicum*.

Davallia fumarioides, Swartz.

RHIZOME. The plant has a fairly stout creeping rhizome and shows somewhat frequent dichotomous branching. The very numerous roots arise chiefly, if not exclusively, from the under surface, and show no regular order. The leaves on the upper surface appear to stand in two rows.

One specimen was apparently quite young, the stem being small in the first formed region and the petioles slender. It seems to have grown at first erect, and later to have bent over, but the erect region seems to have been dorsiventral. Another specimen also showed a narrow juvenile region, but this was horizontal and dorsiventral.

TEXT-FIG. 6. *Davallia fumarioides*. Diagram of vascular system of rhizome including a node and the base of a leaf-trace.

The rhizome is closely beset with narrow brown paleae of very different width, continued above into a single series of cells, and terminating in a pointed non-glandular cell. The larger paleae are fairly wide at the base; others are two or three cells wide for the lower two or three tiers only, and are clearly derived from uniseriate hairs; such simple hairs are also present.

The rhizome contains a well-defined solenostele. In the earlier formed region of the stem the vascular ring is distinctly thicker on the under side than on the upper. In the later formed regions this difference disappears, or at any rate becomes less marked (Text-fig. 6).

The cortex consists of a broad outer sclerotic zone of elongated, rectangular, blunt-ended cells with brown coloured walls. The very narrow inner cortex is made up of two to five layers of cells with thin cellulose walls. The central ground tissue has very thick brown walls, and is also separated from the stele by two or three layers of thin-walled cells.

The endodermis and also the pericycle are similar on the outside and inside of the stele; the pericycle consists of two or three layers.

Phloem is present both externally and internally, but there is proto-phloem only on the outside.

The xylem has abundant xylem parenchyma; the woody cylinder is rather stout, especially on the under side, where it is six to ten tracheae thick. The smallest elements are peripheral, especially near the points of root insertion and on the back of the leaf-trace. These elements are the first differentiated, and may be regarded as an exarch protoxylem; the differentiation of the rest of the xylem is irregular. The tracheae in the stem are all scalariform, even the smallest peripheral ones.

The stem stele branches by dichotomy, the solenostele nipping into two without opening.

ROOTS. The structure of the roots varies considerably; the majority have a normal diarch stele with phloem on each side of the xylem band. In a considerable number, however, the phloem strand is markedly weaker on one side of the xylem than on the other, and the band of xylem is curved, so that the two protoxylems approach one another on the side of the weaker phloem.

In some cases the weaker phloem strand has disappeared, and the curvature of the xylem band is so marked that the protoxylems are almost confluent. In a few cases this seems actually to be the case, and the stele presents a collateral structure and shows an apparently single protoxylem; in fact in these roots a monarch collateral structure has been reached. The collateral structure is mostly found near the point of insertion, whereas farther out the structure becomes more normal.

DEPARTURE OF THE LEAF-TRACE. As may be seen from Text-fig. 6, the concavity of the departing leaf-trace faces directly to the median dorsiventral plane of the rhizome. The gap is closed as the apically directed flange of the leaf-trace is given off and does not extend beyond the departure of the leaf-trace.

PETIOLE. The petiole and its main branches are beset with little downwardly curved spinose emergences; these are composed of the somewhat elongated cells of the sclerotic outer cortex, the epidermal cells being also elongated. Within the outer sclerotic cortex of the petiole is a narrow parenchymatous inner cortex. The outer cortex is traversed by transpiration tracts almost to the base of the petiole.

The petiolar trace is at first an open wedge-shaped C (Text-fig. 7, A¹). On passing upwards the concavity gradually closes from the abaxial to the adaxial side (Text-fig. 7, A²; Plate XIV, Photo 1). A small island of one or two cells surrounded by endodermis is often isolated on the adaxial side as the closure proceeds. The xylem strand is hooked, although the trace is not. The hooks are short and stout, with enlarged club-like ends

three to five tracheae thick. The flanks are very stout and have quite distinct external lateral bays. At some distance from the stem three protoxylem groups are present, but these die out before the trace enters the cortex of the stem. The protoxylem strands have usually well-marked groups of cavity parenchyma in front of them. In weaker petioles the xylem of the hooks diminishes till it may be represented by a single series of tracheae.

Within the endodermis of the petiolar trace is a pericycle two or three layers thick on the abaxial and concave surfaces, and three to five layers thick at the sides opposite the bays. The phloem extends all round, but the protophloem is confined to the outer side, being entirely absent in

TEXT-FIG. 7. *Davallia fumarioides*. A¹. Diagrammatic transverse section of petiolar trace at base of free petiole. A². Same, some distance up. B. Trace of primary branch at base of the branch. C¹⁻³. Departure of xylem strand to a secondary branch. D. Primary branch trace above its second branch. E^{1, 2}. Traces in secondary and tertiary branches.

the concavity; the phloem is in greatest quantity opposite the lateral bays and in the bays of the hooks.

When the trace is closed up and has become reniform in transverse section, the middle of the strip of tissue between the halves of the xylem strand consists of pericycle which is often somewhat lignified; this is lined on either side by phloem. Farther up, when the xylem masses of the flanks begin to approach each other, the pericycle disappears, and the centre is occupied by a strip of phloem. Still farther up the phloem is reduced to a single row of sieve-tubes separated from the tracheae on either side by cells of the xylem sheath.

The fact that the petiolar trace of *Davallia fumarioides* appears to be more open in the basal region is not surprising. The climbing habit is not immediately impressed upon the petiole. At first its structure is like that

of an ordinary petiole; climbing adaptations would only be developed in this region after some time.

BRANCHING OF THE PETIOLAR TRACE. For a short distance below a branch the hook separates off from the margin of the xylem strand (Text-fig. 8, A¹), and the internal phloem becomes continuous with the outer. The protoxylem divides, and the outer protoxylem moves out on the xylem of the branch-trace, which at the same time elongates laterally. The protoxylem divides again, and a second protoxylem also moves out. Before the branch-trace is free the xylem of the hook joins up with that of the flank on the outside of the remaining protoxylem; it also seems to join up on the inner side of the protoxylem, so that the latter is temporarily immersed (Text-fig. 8, A²); soon, however, about half an inch above, the protoxylem again becomes clearly endarch (cf. Plate XIV, Photos 2, 3).

In weaker leaves the hooks of the xylem strand separate off from the flanks some distance (even as much as one or two inches) before the branch departs (Text-fig. 8, B¹), and after its departure (Text-fig. 8, B³) they do not again join on to the outside of the protoxylem till a long way above; the distance over which the hook remains separate below and above the departure of a branch-trace increases on passing up the rachis. In these weak petioles the hook never joins on to the flank on the inside of the protoxylem, so that the latter is never mesarch (cf. Plate XIV, Photos 4, 5).

TEXT-FIG. 8. *Davallia fumarioides*. A¹⁻³. Departure of trace to primary branch of the petiole. B¹⁻³. The same in a weaker leaf.

The trace of the primary branch, when in the cortex of the rachis, is always very bluntly triangular in outline (Text-fig. 7, B; cf. Plate XIV, Photo 3), and its median plane is parallel to that of the rachis. The xylem has the form of an ellipse. There are only two protoxylem groups; these lie on the adaxial side of the xylem, one at each end of the ellipse. At the base of the free primary branch the trace is the same, but the xylem is more nearly triangular (Plate XIV, Photo 6). At first there is no sign of a dorsal protoxylem, but one begins to appear, either just below the first lateral branch or not until the branch-trace is free. At first it is completely mesarch and near the dorsal surface (Text-fig. 7, C¹); the protoxylem elements may be surrounded by a small island of parenchyma (Text-fig. 7, C²; Plate XIV, Photo 7).

During or after the departure of the second lateral branch the xylem

parenchyma and the phloem on the adaxial side of the xylem of the primary branch encroach on it so as to form a sinus which eventually reaches the protoxylem (Text-fig. 7, C³; Plate XIV, Photo 8). The protoxylem thus becomes endarch, the xylem now having the form of a C; this remains open through subsequent branchings (Text-fig. 7, D). When the trace to a secondary branch is given off, a small xylem strand departs from the end of the arm of the C, and is supplied successively with two protoxylems (Text-fig. 7, C¹⁻³; Plate XIV, Photo 7). The trace of a secondary branch never obtains a dorsal protoxylem (Text-fig. 7, E¹), and the trace to a branch of the next higher order has only one adaxial protoxylem (Text-fig. 7, E²).

SUMMARY.

[1. Bertrand and Cornaille's interpretation of the petiolar trace of *Lygodium*, as derived by the union of the inverse folds of the metaxylem of a C-shaped trace, is confirmed.

2. In *Lygodium japonicum* the dorsal protoxylem of the petiolar trace, consisting of annular or spiral elements, is not exarch but mesarch, being more or less completely enclosed by centrifugal metaxylem.

3. In the petiolar trace and branch-traces of *Davallia fumarioides* all stages between the open C-shaped trace and the condition present in *Lygodium* are found.

4. In this condensation of the C-shaped trace of *Davallia fumarioides* the adaxial hooks of xylem completely disappear. It may be inferred that they are absent in the trace of *Lygodium* also.]

DESCRIPTION OF THE FIGURES IN PLATE XIV.

Illustrating Professor Gwynne-Vaughan's paper on *Some Climbing Davallias and the Petiole of Lygodium*.

(All these figures are from untouched photographs.)

Photo 1. Transverse section of the petiolar trace of *Davallia fumarioides* four inches below the first branches; cf. Text-fig. 7, A². Slide No. 2148. (× 46.)

Photo 2. Transverse section of the petiolar trace of a strong leaf of *Davallia fumarioides* just preparing for the departure of the trace to the first primary branch on the left; cf. Text-fig. 8, A. Slide No. 2149. (× 46.)

Photo 3. Section of the same petiolar trace with the trace to the first primary branch just separated on the left; cf. Text-fig. 8, A. Slide No. 2149. (× 46.)

Photos 4, 5. Transverse section of the petiolar trace of a weaker leaf of *Davallia fumarioides* just below the separation of the trace to one of the second lowest pair of primary branches and during the separation of the xylem of the trace; cf. Text-fig. 8, B. Slide No. 2160. (× 46.)

Photo 6. Transverse section of the trace of a primary branch of *Davallia fumarioides* near the base of the branch; cf. Text-fig. 7, B. Slide No. 2154. (× 67.)

Photo 7. Transverse section of the trace of a primary branch of *Davallia fumarioides* which has just given off to the left the trace to the first secondary branch; cf. Text-fig. 7, c². Slide No. 2154. (× 67.)

Photo 8. Transverse section of the trace of a primary branch of *Davallia fumarioides* above the departure of the first pair of secondary branches; cf. Text-fig. 7, c³, D. Slide No. 2164. (× 67.)

Photo 9. *Lygodium scandens*. Transverse section of petiolar trace, showing the trace to the second primary branch going off on the left; cf. Text-fig. 1, c⁴. Slide No. 2073. (× 46.)

Photo 10. *Lygodium japonicum*. Transverse section of petiolar trace, showing the abaxial protoxylem enclosed by centrifugal metaxylem; cf. Text-figs. 2 C, 3 A. Slide No. 2095. (× 67.)

The general resemblance between the petiolar trace and the origin of a primary branch-trace in *Davallia fumarioides* and in *Lygodium scandens* will be evident on comparison of Photos 3 and 9, while a still closer similarity can be traced between the petiolar trace of *Lygodium japonicum* (Photo 10) and a particular stage of the primary branch-trace of *Davallia fumarioides* (Photo 7). These pairs of figures have been placed together on the plate to facilitate comparison.

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Gwynne-Vaughan, D. T. 1916. "On some climbing Davallias and the petiole of *Lygodium*." *Annals of botany* 30, 495–507.

<https://doi.org/10.1093/oxfordjournals.aob.a089620>.

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