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THE VASCULAR SYSTEM OF THE RHIZOME AND
LEAF-TRACE OF *PTERIS AQUILINA*, L., AND *PTERIS*
INCISA, THUNB., VAR. *INTEGRIFOLIA*, BEDDOME.

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[TEXT FIGS. 1-59.]

AS might be expected in the case of so widespread and abundant a plant, the structure of the vascular system in the common bracken fern has been frequently described and alluded to by plant-anatomists. Nevertheless, although it has long been known that both the inner and the outer rings of rhizome strands contribute to the formation of the leaf-trace, yet the exact course of the leaf-trace strands has apparently never been correctly described in adequate detail, nor has any attempt been made to bring the whole structure into its proper place in the modern theory of Filicinean vascular morphology. It is with the object of attempting to fill this gap that the present paper has been written.

HISTORICAL.

The earliest description we can find is that given by Hofmeister ('57) who made a fairly thorough investigation of the morphology and development of this plant. He describes how the single central vascular strand of the stem of the young plant at the insertion of the first leaf has a deep infolding on one side (Taf. II., Fig. 6), while after a number of leaves have been developed and the young stem has forked this bay becomes larger (Taf. II., Fig. 7) and soon the original strand is separated into two parallel band-shaped bundles (Fig. 8), which may branch, the branches again running into the main bundle. So far, Hofmeister is confirmed by Leclerc

du Sablon ('90) and Jeffrey ('00). When the length of the primary forks of the rhizome have reached about three inches, continues the description, weaker bundles branch off from the two big ones and run further out in the cortex. The uppermost of these, running above the axile bundles, is developed more strongly, almost equalling the axile ones in breadth (p. 620). The stem of a fully grown plant shews in the main the same distribution of bundles. The number of peripheral ones may rise to twelve, of which the dorsal is always the largest. The roots arise exclusively from the outer bundles.

This description of the origin of the two circles of bundles in the young plant was first shewn by Jeffrey ('00) to be incorrect. In reality the two flat strands into which the original vascular cylinder of the stem divides are not equivalent to the two similarly shaped inner strands of the adult rhizome, but give rise by branching in a tangential direction to the *outer ring* of strands, while the two inner strands are successively nipped off dorsally from the inner face of the ventrally situated outer strand ('00, p. 10 and Pl. 7.)

With regard to the insertion of the leaf-trace in the adult plant, Hofmeister's description is the fullest that we are aware of, but is partly incorrect, while his figures are inadequate for a detailed appreciation of the relations of the different strands.

Stenzel ('61) corrects Hofmeister's account in one respect. He points out that the two circles of vascular strands are often in connexion by means of cross branches passing between the two plates of sclerenchyma from the ventral inner strand to the lateral members of the outer circle (Taf. 5, Figs. 6, 17), as well as by means of occasional cross branches passing through the dorsal sclerenchymatous plate from the dorsal inner to the dorsal outer vascular strand (Taf. 5, Fig. 8), and sometimes by similar strands passing through the ventral plate (Fig. 9). He also notes that in some weak stems both the two sclerenchymatous plates and the two vascular strands of the inner ring form a closed cylinder (Fig. 12). Stenzel's description of the origin of the leaf-trace is quite general, and his figures, like Hofmeister's, fail to convey a clear and detailed picture of the facts. We cannot bear out his statement that before the leaf has separated from the stem, the foliar vascular strands are all thread-like (cylindrical).

Mettenius, at the close of his well-known paper on *Angiopteris* ('63) devotes a few words to this species, and remarks that when the lateral bud formed on the base of the petiole develops late, the vascular bundles of both petiole and lateral shoot are almost

completely separate, while if the development of the branch precedes that of the leaf and takes place higher on the petiole, then the stretch at the base, common to leaf and branch, has a structure like that of the main axis. We shall refer to these points later.

De Bary in his "Comparative Anatomy" ('77) repeats the leading points of Hofmeister's and Stenzel's descriptions, placing *Pteris aquilina* among the ferns with accessory cortical bundles, but adds nothing to our knowledge of the subject. Conwentz ('75) also follows Hofmeister, and does not advance the subject.

In 1890, Leclerc du Sablon ('90) in his well-known paper "Sur la formation de la tige dans les Fougères" described the transition from the primary root to the stem, up to the point at which the vascular system of the latter has the form of two curved plates. Leclerc du Sablon did not follow the development of the young plant to a more adult stage, but his figure of the two plates recalls so strikingly the two inner strands of the adult rhizome as to lend great colour to Hofmeister's erroneous description of the inner strands of the rhizome being directly continuous with these two primary ones, while the outer circle represented accessory cortical strands arising from the inner by branching. This conclusion was however, as already mentioned, entirely upset by Jeffrey's account ('00) of the behaviour of the vascular system of the young plant above the level at which Leclerc du Sablon's figure was taken. This shewed quite clearly that the ventral primary strand traced upwards, gives off two fresh strands in succession from its internal face, and *that it is these latter which are continuous with the internal strands of the rhizome*, while the two primary strands gradually break up at a higher level to form the outer circle.

Now while this discovery brings *Pteris aquilina* into line with the majority of ferns having a polycyclic vascular structure, in so far as it turns out to be the outer ring of strands which is the primary one, corresponding with the single ring of monocyclic ferns; yet the exceptional fact that about half (sometimes more, sometimes less) of the leaf-trace arises from the inner (secondary or additional) strands, remains to be explained. It is clear that in the hypothetical ancestor with a single vascular cylinder, the whole of the leaf-trace must have arisen from this, and it is the business of the morphologist to try to discover the steps by which the supplementary supply to the leaf originated.

The relation of the leaf-trace to the vascular system of the

stem in *Pteris* (*Litobrochia*) *incisa*, Thunb., var. *integrifolia* we believe may give the clue to the solution of this difficulty.

PTERIS INCISA.

Our specimens of this plant were gathered in the woods near the top of Gunong Hijau in Perak (Malay Peninsula). They agree very well with three specimens in the Kew Herbarium, one collected by Scortechini and two by L. Wray, junr., all three also from Perak. The variety differs from the type of this very variable species in the fact of its pinnules being entire instead of wavy-edged or even pinnatifid.¹ The texture of the leaves, in our plants at least, is also more coriaceous than in the type and the plant appears to have longer and more straggling fronds. The anatomical structure of the node of our variety is also, as we shall see, considerably more complicated than in the typical *P. incisa*.

Gwynne-Vaughan ('03) in his recent important paper on the Anatomy of Solenostelic Ferns has described this species as possessing a typical solenostele from which is given off a curved leaf-trace directly facing the median dorsiventral plane of the rhizome (pp. 691-2). Since the striking complications connected with the insertion of the leaf-trace in our plant are not mentioned in Vaughan's account, he has been good enough to lend us some of his preparations to compare with our own (Fig. 4). From this comparison it is evident that there are wide differences between the vascular structure of the type and that of the variety.² Thus the internodal solenostele has a considerably greater diameter and a more wavy outline in the variety, while the leaf-trace is much larger in proportion even to the larger stem-stele and has a far more complicated outline. There are also certain histological differences, and from their anatomy one would scarcely suspect the two plants of belonging to the same species. Considering however the great differences that have come under our own observation in the anatomy of one and the same species, e.g. *Matonia pectinata*, *Lindsaya orbiculata* type, and var. *tenera*, we are not prepared to say that either of the plants under consideration has been wrongly

¹ See R. H. Beddome, Ferns collected in Perak and Penang by Mr. J. Day. Journ. of Bot. 26, 1888, p. 2; and Beddome, Scortechini's Malayan Ferns. *Idem*, 1896, p. 225.

² We are not prepared to say that the differences of vascular structure between our plant and Gwynne-Vaughan's are constant as between the type and this variety. The species is an extremely variable one, sometimes possessing leaves of enormous length, and the larger leaved individuals other than those belonging to our variety may well show similar deviations from Vaughan's simple structure.

assigned. In the specimen of which we have spirit-material, two nodes were preserved, and at each of these the stem dichotomised, the stout petiole coming off between the two branches and forming a direct continuation of the part of the stem behind the fork.

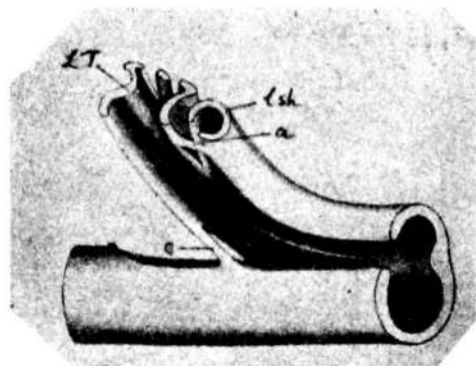


Fig. 1.

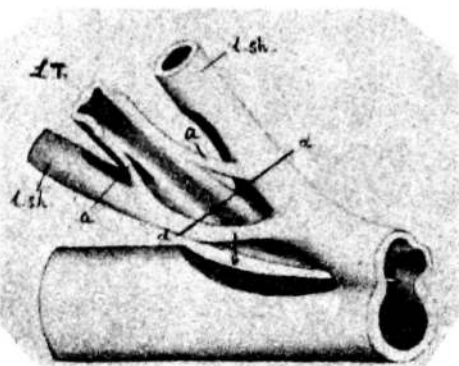


Fig. 2.

Fig. 1. *Hypolepis tenuifolia*. Diagram of vascular system of node seen from dorsal side. L. T., leaf-trace. l.sh., stele of lateral shoot. Fig. 2. Ditto of *Hypolepis repens*. a, b, c, dd, see text. (From Gwynne-Vaughan, l.c.)

In one case a shoot-bud also arose from one side of the petiole near its base, while in the other two such buds arose. Figs. 5-12 represent selected sections from a series through one of the two nodes (which were exactly alike), while Fig. 3 is a reconstruction of the stem-steles and the petiolar strand. From these it will be seen that while the stele of the internode is a solenostele, rather flattened in the horizontal plane, and wavy on the ventral side, from which roots are given off (Fig. 5), complications arise as the node is

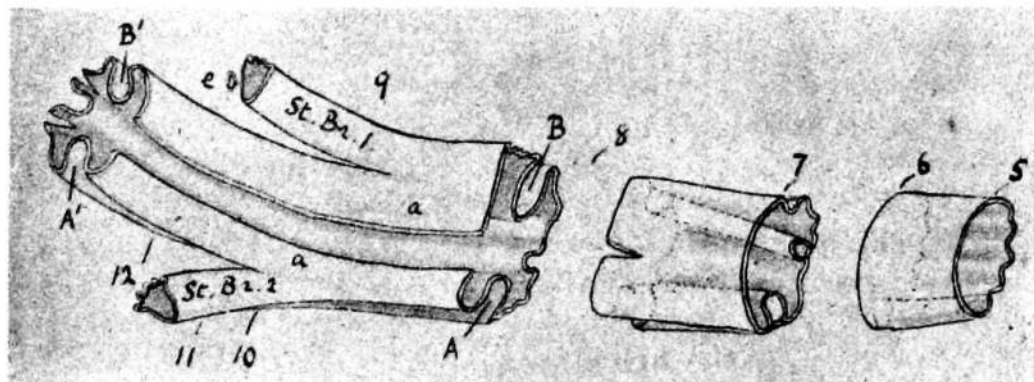
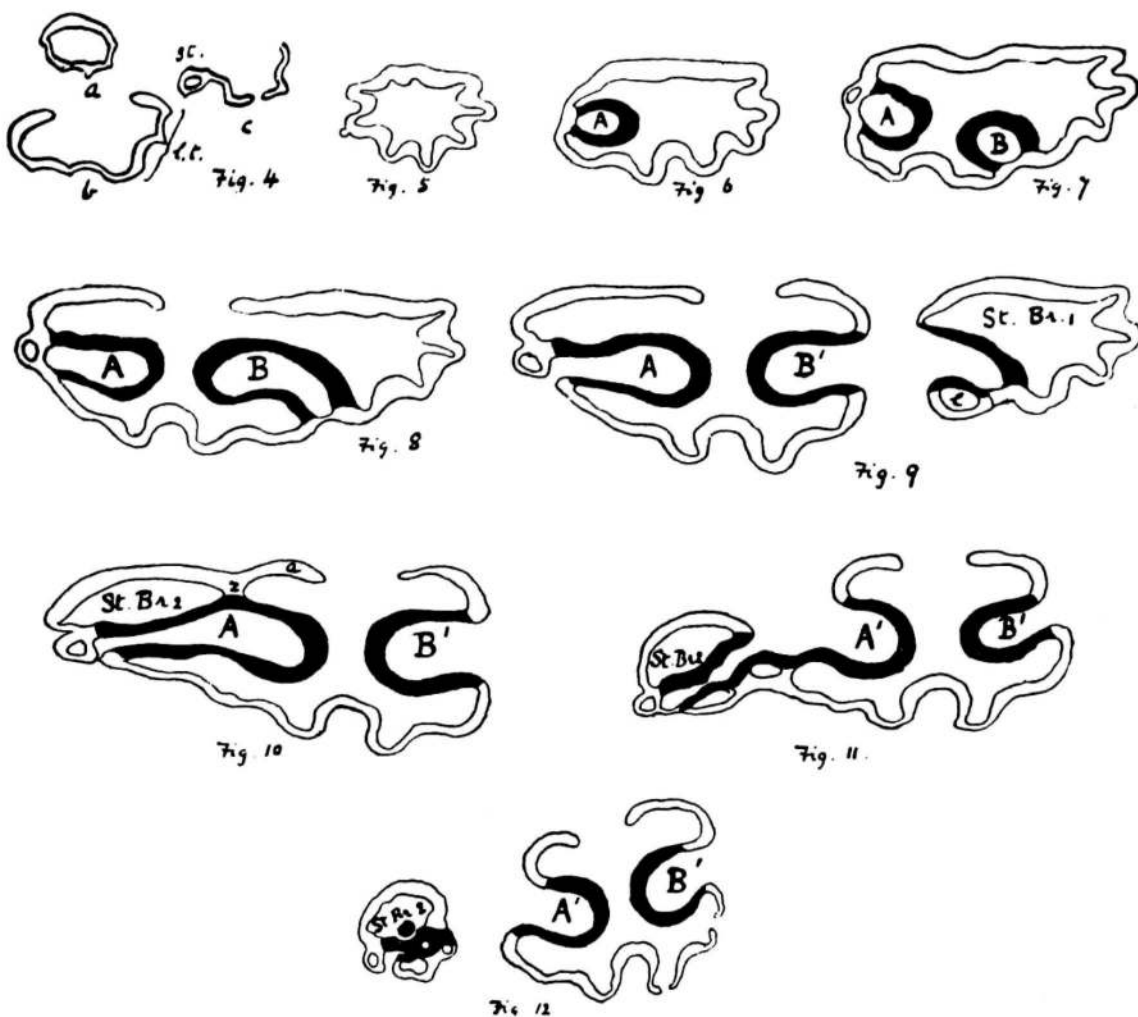


Fig. 3.

Fig. 3 *Pteris incisa* var. *integrifolia*. Diagram of vascular system of node seen from dorsal side. A, B, the two lateral folds of the stele. A', B', ditto of leaf-trace. St. Br., steles of branches of dichotomy. 5-12, planes of section of figures 5-12. a, c, see text.

approached. First an internal fold of the solenostele having the form of a closed cylinder, arises on the left side (Fig. 6,A), and shortly afterwards a similar one arises to the right of the mid-ventral line (Fig. 7,B) and shifts up till it occupies a lateral position opposite the first. At the same time both of these internal cylinders



Figs 4.—12.

Fig. 4 ($\times 6$). *Pteris incisa*, type. *a*, solenostele of internode. *b*, solenostele broken for departure of leaf-trace, *l.t.* *c*, base of petiolar strand (of another leaf) in transverse section giving off the stele (*st.*) of a lateral shoot. From Gwynne-Vaughan's preparations.

Figs. 5—12 ($\times 6$). *Pteris incisa* var. *integrifolia*. Selected sections from a series through the node. Vascular tissue of the two lateral internal folds (A, B) and the tissue continuous with them above, black. A', B', lateral folds of petiolar strand. *St. Br.*₁, stele of first branch of the dichotomy. *St. Br.*₂ stele of second branch of ditto. *a*, *z*, *c*, see text.

become open to the exterior so as to form two deep lateral bays of the stele, and the whole structure increases greatly in size. Meanwhile the vascular ring has broken in the mid-dorsal line (Fig. 8). The central ground tissue now has the form of an irregular H lying on its side, closed in all round, except in the mid-dorsal line, by the vascular ring. The dorsal limb of the H is rather longer than the ventral one.

The right-hand end of this dorsal limb, which has retained the waviness of outline of the original stele, is now nipped off as a closed ring and becomes the stele of one of the branches of the stem (Fig. 9, *St. Br.*₁). It is contributed to by a small vascular branch nipped off as a closed ring from the right-hand end of the ventral limb of the H. This quickly becomes attached to the ventral side of the branch stele, but retains its individuality for some distance (Fig. 9), eventually fusing completely with the stele to form one of the bays of its wavy margin.

The left-hand end of the dorsal limb of the H is now nipped off in the same way (Fig. 10) and becomes the stele of the other branch (*St. Br.*₂); like the stele of the former branch it is also contributed to by a strand arising from the left-hand end of the ventral limb of the H. This strand breaks up into two before joining the stele of the branch (Fig. 11.). The third strand, lying on the ventral side of this stele (Fig. 12), has taken its origin previously from the outer side of the internal fold (A) of the original solenostele (Fig. 7). The three strands now join the ventral side of the branch stele and form the three central projections of the wavy ventral side (Fig. 12).

The abbreviated H (Fig. 12) is now the petiolar meristele. It is to be noticed that the ventral side of its ventral limb and the dorsal side of its dorsal limb (left white in the figures), *i.e.* the parts corresponding to the arch and the free edges of the primitive curved petiolar strand from which it must have been phylogenetically derived, are continuous with parts of the solenostele of the stem below, while the deep lateral bays A¹ and B¹ (black in the figures) are continuous with the folds (A and B) which arose in the solenostele as the node was approached.

The structure of the vascular system at this type of node, in which the leaf arises between the two branches of what is practically a dichotomy, is at first sight difficult to bring into harmony with a node at which the leaf-trace is directly inserted on the stele of an axis that is continued as such beyond the origin of the petiole.

A careful comparison of the figures illustrating the structure of the node of *Pteris incisa*, var. *integrifolia* with Figs. 1 and 2, which are taken from Gwynne-Vaughan's paper on Solenostelic Ferns ('03), and represent the vascular structure of the nodes of *Hypolepis tenuifolia* and *H. repens* respectively, will facilitate the interpretation of the structure under consideration in terms of the morphologically simpler case.

The leaf-trace of *Hypolepis tenuifolia* (Fig. 1) will be seen to come off from the lateral surface of the solenostele of the rhizome as a curved and folded plate, with its concavity facing the median dorsiventral plane of the rhizome. The stele opens dorsally at first, but the leaf-gap becomes lateral as soon as the leaf-trace is free.

As the trace departs it becomes deeply infolded on the basiscopic side, and the infolding so formed soon becomes separated off as a gutter-shaped strand (*l. sh.*) which closes to a cylinder and is the stele of the lateral shoot arising on the posterior side of the petiole base. Just after the gutter-shaped stele becomes free, a small strand (*a*) runs from its free edge furthest from the leaf-trace to join the basiscopic edge of the latter. Now if we imagine the stele of the main rhizome to decrease considerably in size, so that its continuation and the lateral branch arising from the base of the petiole become of about equal importance, we should have a "false" dichotomy of the stem, with the petiole arising in the angle of the fork, exactly as in the two nodes of *Pteris incisa* var. *integrifolia*. The parallel is even closer, though not perhaps so legitimate, between the node of the latter and the petiole-base with its two lateral shoots in *Hypolepis repens* (Fig. 2) if we imagine the continuation of the main rhizome to be suppressed altogether. The general resemblance between this and Fig. 3 will be obvious at once if we consider the form of the leaf-trace in cross section just below the separation of the lateral shoot-steles (*i.e.* along the line *d—d* in Fig. 2 corresponding with Fig. 8 in *P. incisa* var. *integrifolia*). Here the trace is in both cases complicated by the two deep dorso-lateral gutter-shaped infoldings most of which form the two branch-steles. In *P. incisa* var. *integrifolia*, however, the branch-stele is nipped off as a cylinder from the outer part of the infolding, *i.e.* from the end of the dorsal limb of the H, by the union of the dorsal and ventral walls of this limb at *z* (Fig. 10) so that no gap occurs either in the branch-stele or in the adjacent part of the trace, while in *Hypolepis* the stele separates as a gutter-shaped strand whose outer edge is united with the edge of the trace by means of the strand *a*

(Figs. 1 and 2), corresponding with the union of the free margin α with the deep lateral bay of the leaf-trace below at z in Fig. 10. The contributions of the *ventral* limbs of the leaf-trace to the branch-steles in *Pteris incisa* var. *integrifolia* appears to have no parallel in *Hypolepis*. They are no doubt correlated with the much greater development of these ventral limbs in the *Pteris*.

The strength of the foregoing comparison is increased by the fact that the leaf-trace of *Pteris incisa* (type, Fig. 4, *c*) is of exactly the same form as that of the two species of *Hypolepis*, but unfortunately no node of the former shewing the complication involved by branching of the stem is available for comparison. The petiolar strand of *Pteris incisa* (type) and of *Hypolepis repens* and *tennifolia* shews a slight bay or concavity on each side, but this is not decurrent into the stele of the rhizome. In *Pteris incisa* var. *integrifolia* on the other hand the petiolar strand is much more complex, and in correlation with this the solenostele of the rhizome does not become simple for some distance behind the node. The complication of the petiolar strand is mainly due to the much greater development of the two lateral bays (A^1 , B^1 in Figs. 9—12 and Fig. 3) and these are continued for some distance back in the rhizome, first as bays, then as hollow cylinders attached to the inside of the solenostele, and finally as open bays again (A and B in Figs. 6—8 and Fig. 3), which eventually die out altogether.

This increased complexity of the leaf-trace is no doubt a response to an increased demand for vascular tissue by an increased leaf-surface, and has resulted in an increased complexity of the vascular structure of the stem behind the node.

PTERIS AQUILINA.

Let us now turn to *Pteris aquilina*. It is scarcely necessary to resume the vascular structure of the rhizome, the leading points of which have already been mentioned as described by Hofmeister and Stenzel, and are well-known to every elementary student. The connexion of the petiolar strands of the base of the petiole with those of the rhizome appears, however, never to have been accurately described.

A transverse section of the base of the petiole, apart from the complications introduced by the arising of a lateral branch, shews an arrangement of the vascular strands easily derivable from the strongly curved plate which Gwynne-Vaughan has shewn to be the primitive type of leaf-trace in solenostelic ferns. In the dictyostelic

types, as he has remarked, the general outline of this is kept, though the plate is not continuous, but is resolved into a number of distinct strands.

The degree of complication of the curve varies very greatly in the species under consideration. Let us first take the elaborate petiolar system represented in Fig. 34, since this gives us the closest resemblance to *Pteris incisa* var. *integrifolia*.

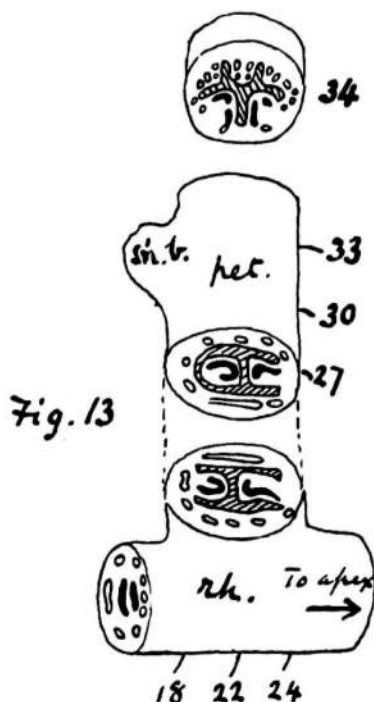
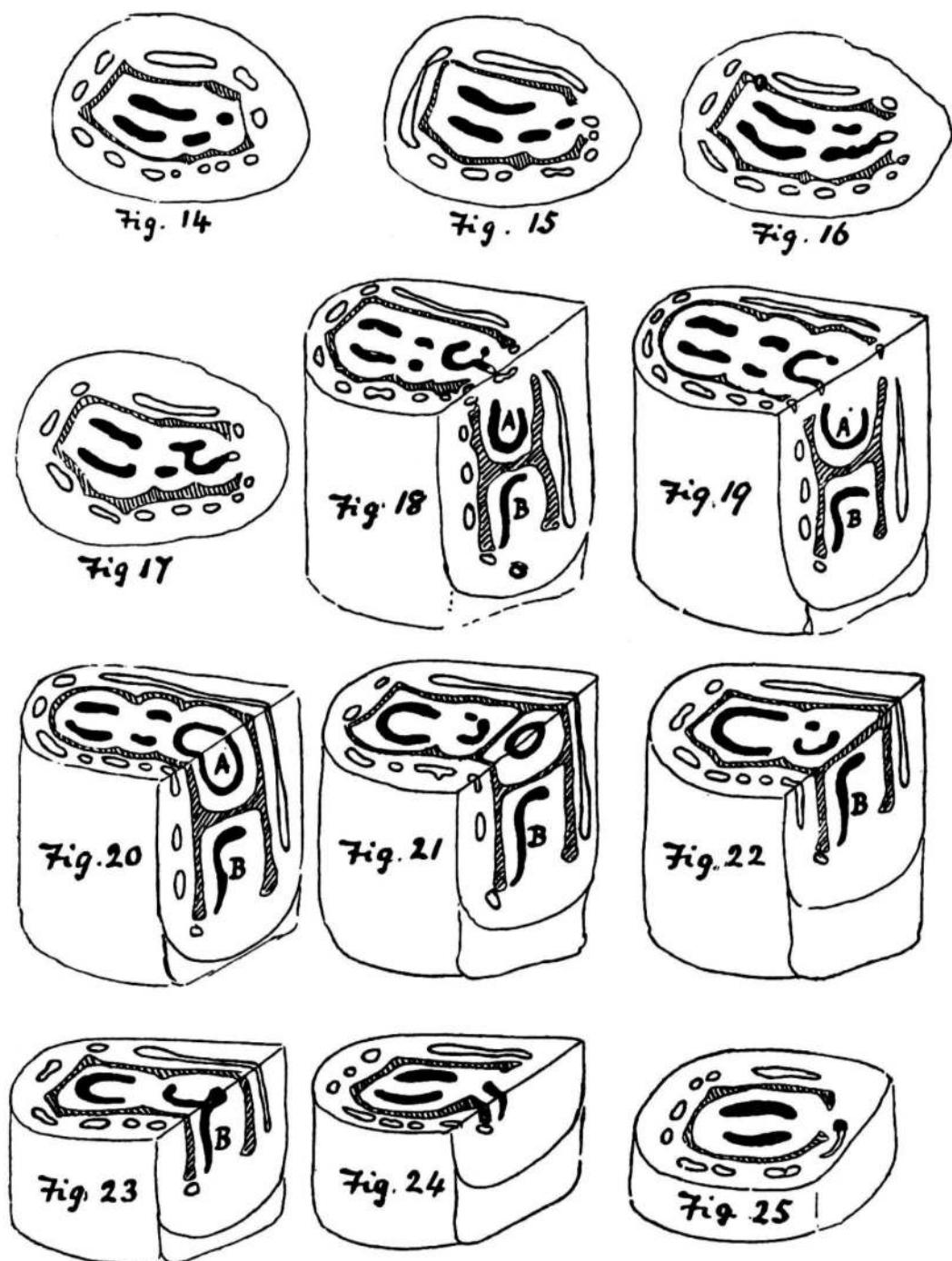


Fig. 13.

Fig. 13. *Pteris aquilina*. Diagram of node seen from ventral side. *rh.*, rhizome, *pet.*, petiole, *sh. b.*, shoot-bud. The numbers refer to the planes of section of the figures so numbered.

Fig. 34 shews the transverse section of the petiole just above the departure of the lateral branch (see Fig. 13). The petiolar strands are arranged on a figure of the general outline of an Ω with the top (abaxial side, bottom in Fig. 34, p. 12) pushed in. The resemblance to Fig. 12 is very close, the only difference in the outline of the figure being the absence of the incurvings of the free margins in Fig. 34. Furthermore the origin of the strands of the lateral shoot from those of the petiole, as shewn in Figs. 26—33 is strikingly similar to that of *Pteris incisa* var. *integrifolia*, if allowance be made for the fact that the internodal vascular system of *Pteris aquilina* consists of two circles of strands, while that of *Pteris incisa* is a simple solenostele. Compare Fig. 26 with Fig. 8, and Fig. 31 with Fig. 9.

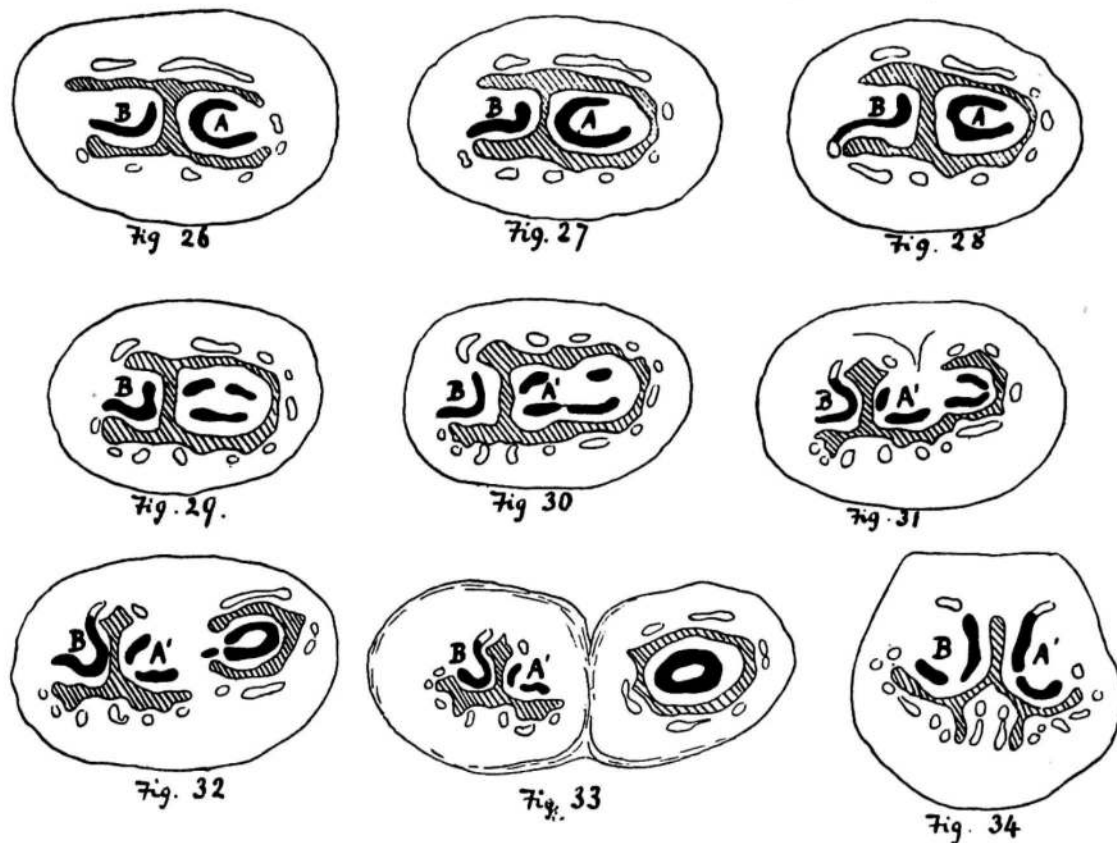


Figs. 14—25.

Figs. 14—25. *Pteris aquilina*. Selected sections from a transverse series through node (see Fig. 13). Figs. 18—24 shewing also transverse section through base of petiole, thus exhibiting connexions of vascular strands of petiole with those of rhizome. Lateral folds of petiolar system (A, B) and inner strands of rhizome, black; outer strands, white; sclerenchyma, diagonally lined.

The strands represented in black in these figures are those which

are continuous with the *inner* strands of the main stem, as may be seen in Figs. 14—25 (which represent a series of transverse sections of the rhizome passing through the node, the transverse section of the base of the petiole, in a plane at right angles to the parallel planes of the series, being also shewn in Figs. 18—24), while



Figs. 26—34.

Figs. 26—34. *Pteris aquilina*. Selected sections from a transverse series through the base of the petiole including the origin of a lateral (posterior) bud (see Fig. 13). Lateral folds of petiolar system (A, B,—above bud A', B) and inner vascular ring of bud, *black*; dorsal (adaxial) and ventral (abaxial) strands, *white*: sclerenchyma diagonally lined.

the strands left white are those derived from the outer circle of the rhizome. From an inspection of these series it is quite clear that the strands forming the lateral bays (A, B, A', B',) of the petiolar system are continuous with the inner strands of the rhizome, while the whole of the abaxial curve together with the free margins of the petiolar system are continuous with the outer strands of the rhizome. Thus while in *Pteris incisava* var. *integrifolia* the continuations backwards of the lateral bays of the leaf-trace gradually die out in the rhizome, in *Pteris aquilina* they form an inner system of rhizomic vascular strands continuous throughout the internodes, for

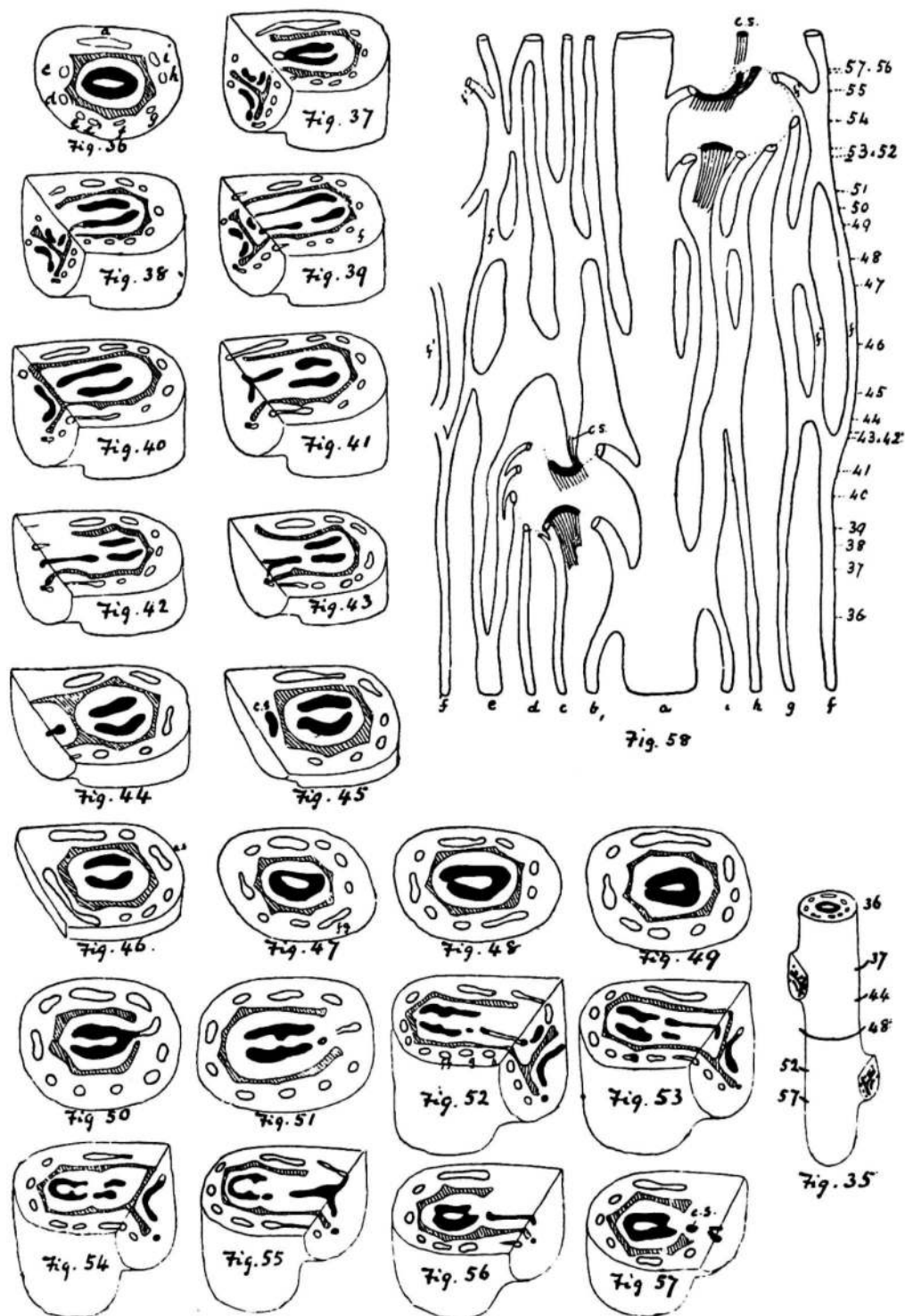
the most part independent of the outer primitive system, but, as Stenzel shewed, having occasional connexions with it. It is noteworthy that these connexions, according to Stenzel, are mainly, though not exclusively,¹ *lateral*, i.e. in much the same position as the connexion between the internal cylinders and the solenostele in *Pteris incisa* var. *integrifolia* (compare Figs. 16 and 50, with Figs. 6 and 7). Figs. 36—57 represent selected sections from a series through two successive nodes of the rhizome diagrammatically represented in Fig. 35. The petiolar system is in this case considerably simpler than that of the node represented in Figs. 14—34, and hence its resemblance to *Pteris incisa* var. *integrifolia* is much less marked, but it will be seen that the relations of the petiolar and rhizomic strands is identical with that already described. These relations in fact appear to be perfectly constant.

It is difficult to resist the conclusion that the vascular system of *Pteris aquilina* has passed through a stage like that now represented by *Pteris incisa* var. *integrifolia* on the way from its monocyclic ancestor. It does not of course follow that this intermediate stage was solenostelic; dictyostely may have arisen at any point in the series.

A few words must be devoted to the relation of the insertion of the leaf-trace to the branching of the rhizome. Two distinct types of branching exist in this species, first, ordinary dichotomy, in which the vascular system of the rhizome typically divides into two approximately equal parts,² and which has no necessary relation to the origin of a petiole; and secondly, the lateral origin of a shoot-bud from the posterior side of the base of a petiole (Figs. 13 and 26—33), in which the vascular system of the bud is derived entirely from that of the petiole. It is, however, very common for the weaker branch of the dichotomy to bear a leaf on the inner side more or less close to the fork of the rhizome. If the insertion of this leaf is sufficiently removed from the fork, the petiolar strands arise from the rhizome branch-system in the ordinary way. This seems to be Mettenius' second case, referred to above, but why he should consider the stretch from the base of the petiole to the fork as belonging to the *petiole* is not obvious. If the insertion of the leaf is closer to the angle, the strand forming the lateral fold of the

¹ We have not seen the dorsiventral connexions of the inner and outer strands figured by Stenzel ('61. Taf. V., Figs. 8 and 9), but it appears that they occur in larger rhizomes than those we have worked with.

² The division is however very often far from being equal, see below.



Figs. 35—58.

Fig. 35. *Pteris aquilina*. Diagram of piece of rhizome seen from ventral side with two nodes. The numbers refer to the planes of section of the figures so numbered.

Figs. 36—57. *Pteris aquilina*. Selected sections from a transverse series through the piece of rhizome represented in Fig. 35, shewing the departure of two successive leaf-traces. Vascular strands and sclerenchyma represented as in previous figures. *c.s.*, compensation-strands, see below.

Fig. 58. *Pteris aquilina*. Diagram of the course of outer vascular strands of piece of rhizome in Fig. 35 represented as spread out in a plane, the dorsal strand in the middle. Sections of the leaf-trace strands are shewn where they pass out of the plane of section, those derived from the inner strands of the rhizome black. An inner strand (*c.s.*) passes into the outer circle as a "compensation-strand" and helps to close each leaf-gap.

petiolar system on the basiscopic side may arise directly from the inner strands of the rhizome behind the fork and run independently of the branch system, though the rest of the leaf-trace arises directly from the latter. This is a frequent case. Finally, if the leaf is inserted actually in the angle of the fork, its trace arises from the rhizome strands behind the fork quite separately from the branch. The last two types are apparently covered by Mettenius' first case.

It is noteworthy that the vascular system of the petiole, when it arises in the actual angle of the dichotomy, does not in this species ever become so important in relation to that of the rhizome as to form a direct continuation of the latter, the branches of the dichotomy being nipped off from its sides, as in the case of *Pteris incisa* var. *integrifolia*. On the other hand, though we have not found cases shewing intermediate vascular structure, it is easy to see how the weaker branch of the dichotomy which in this type is developed late and is much smaller than the stronger one, could, by a still further delay in its development, be carried up onto the petiole and so lead to the type in which a bud arises from the posterior side of the petiole base. In this way it is possible to suppose that this type of branching, not uncommon in ferns, may have been derived from primitive dichotomy in which a leaf arose on the inside of one of the branches. This appears to have been Stenzel's view ('61, p. 40 and footnote). In any case it is significant of some genetic connexion that where in this species there is branching in the neighbourhood of leaf-insertion, the relation of position between the stronger branch, the weaker branch and the leaf is constant. The whole subject of the morphology of branching in ferns and its relation to vascular structure—a subject which occupied a considerable amount of attention about the middle of last century—deserves re-investigation.

Fig. 58 is a representation of two nodes and the intervening internode, the cylinder formed by the outer rhizomic system being spread out on a plane; the inner strands (black in section) are

only put in where, at the nodes, they pass through the plane of the cylinder. If this figure be compared with the similar figures of Mettenius it will be readily seen that the outer rhizomic system is a much dissected dorsiventral dictyostele in which there remains one constant broad dorsal strand, representing a dorsal strip of the original solenostele, as for instance in *Polypodium latipes* (Mettenius '63, Taf. IX., Fig. 6). See Gwynne-Vaughan ('03, pp. 694—698).

We conclude, therefore, that the vascular system of *Pteris aquilina* is a dorsiventral dictyostele of the *Polypodium*-type with an internal system of accessory strands developed in connexion with lateral elaboration of the leaf-trace.

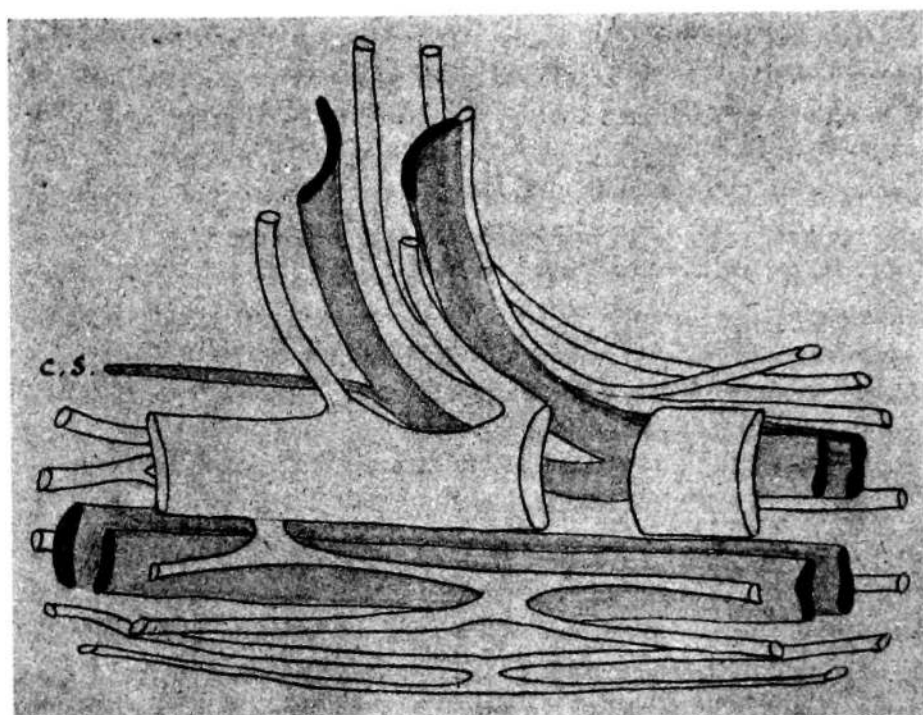


Fig. 59,

Fig. 59. *Pteris aquilina*. Diagram of the course of the vascular strands at a node, somewhat simplified, seen from the dorsal side. Inner strands of rhizome and lateral folds of leaf-trace shaded. A part of the dorsal outer strand is supposed to be removed, thus shewing the branching of the inner ones. c.s., compensation-strand.

Fig. 59 is a diagram of the vascular system of the node of *Pteris aquilina*, drawn for comparison with Figs. 1—3. It is represented as somewhat simpler than any node we have actually seen, so as to avoid confusion. The inner strands of the rhizome and the petiolar strands in connexion with them are darkly shaded.

The probability of the modification of vascular structure at the node of a plant, in relation to an alteration of the leaf-trace, and the effect of leaf-traces in modifying stem-structure generally, has been pointed out in one form or another by nearly all recent writers on vascular morphology. In ferns the principle of the decurrency of such a new structure from the node into the internode below, and its eventual establishment throughout the internode to join a similar structure at the next node below was tentatively suggested by Boodle ('01, pp. 737-8) and by ourselves in reference to *Lindsaya* and *Davallia pinnata*.¹ These suggestions have been confirmed and greatly extended by Gwynne-Vaughan ('03). There can now be little doubt that we have here a principle of very wide application, at least within the Filicinean series. The particular instance of it described in the present paper is of special interest, since it brings before us a mode of origin of an internal system of rhizomic vascular strands differing from that described by Gwynne-Vaughan in a number of types. Whereas the internal ridges and strands in the *Dicksonias*, in *Cyathea*, and in *Pteris clata* var. *Karsteniana* arise at the node as a local thickening of the leaf-gap, those of the plants we have described arise as lateral elaborations of the leaf-trace itself.

¹ Tansley and Iulham. On a New Type of Fern-Stele, Ann. of Bot., XV., 1902.

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