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LECTURES ON THE EVOLUTION OF THE FILICINEAN VASCULAR SYSTEM.¹

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LECTURE IV.

THE GLEICHENIACEÆ AND LINDSAYÆ.

[FIGS. 34—46.]

WE must now consider the Gleicheniaceæ,² a family represented by the very characteristic genus, *Gleichenia*. Two of the most aberrant species are sometimes separated as distinct genera—*G. (Platyzoma) microphylla* from North Australia, and *G. (Stromatopteris) moniliformis* from New Caledonia. Both are very xerophilous and distinctly reduced species. Of the two, *Platyzoma* has the more aberrant vascular system. Like the Hymenophyllaceæ, the Gleicheniaceæ are mainly tropical in distribution, but the different species are adapted to a much greater variety of habitat, some being quite xerophilous while others are shade plants. *G. linearis (dichotoma)* is one of the most widely spread and successful of tropical ferns, constantly covering the cleared edges of forests, roadsides, etc., with a thick, almost impenetrable growth of freely branching fronds.

The great characteristic of the fronds is their so-called "dichotomous" branching. The petiole forks into two equivalent branches; each branch may again fork into two, and so on. Pinnæ are borne either by all the branches of the rachis (Sect. *Holopterygium* of Diels) or by the ultimate ones only (*Acropterygium*). A bud is very often borne in the angle of each fork of the rachis, and this bud (especially that of the primary fork) may grow out and form a continuation of the rachis below. These buds are frequently spoken of as "adventitious," but there seems to be no real reason

¹ A Course of Advanced Lectures in Botany given for the University of London at University College in the Lent Term, 1907.

² The substance of the first part of this lecture is largely based on the excellent work of Boodle ('01B).

for regarding them as anything but (temporarily) arrested continuations of the rachis. Each bud contains a direct continuation of the primary C-shaped vascular strand of the rachis, and the vascular strands of the primary branches clearly arise from the sides of this. Boodle ('01 B) has pointed out the possibility of deriving an ordinary pinnate fern-frond from the *Gleichenia*-type, the first pair of primary pinnæ of the former being considered as equivalent to the first branches of the latter type of frond; with this view of the homology I should entirely agree. The rhizome (except in *Stromatopteris*) is always creeping and usually subterranean, the leaves being typically inserted at comparatively long intervals.

The rhizome has a single "solid" vascular cylinder; the tracheæ of the xylem, which fills up the centre of the stele, being interspersed with parenchyma. The position of the spiral protoxylems is characteristic. They are situated just below the surface of the metaxylem at about equal intervals round the periphery of the stele, which is sometimes lobed in relation to the insertion of roots (Fig. 34). This *mesarch* "protostely" is probably secondary in ferns,

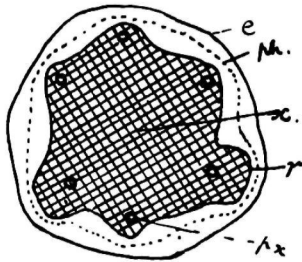


Fig. 34. *Gleichenia linearis*. T. S. of stele of internode. *e.*, endodermis; *ph.*, phloem, indicated by an interrupted line; *x.*, metaxylem, cross-hatched; *px.*, protoxylems indicated by circles; *r.*, root stele attachment. From Boodle.

The conventional indications of phloem, xylem and protoxylem are used in all the following diagrams.

and may, as we have already seen (p. 117), be derived from the endarch type and be dependent on the relation of the size and shape of the leaf-trace to that of the stele. In the rhizomes of some species spiral protoxylems are quite absent.

There are two well-marked sub-genera of the more typical *Gleichenias*—*Mertensia*, which has its pinnules more or less elongated, and *Eugleichenia*, in which the pinnules are small and rounded. The latter sub-genus is to all appearance distinctly more xerophilous than the former. The cross-section of the leaf-trace is distinctive in the two sub-genera. That of *Mertensia* is typically C-shaped as a whole, *i.e.*, the curved band of xylem is covered

with a layer of pericycle and endodermis, which follows the curve of the xylem both within and without. The phloem does not line the whole concavity of the xylem arch though it extends round the free ends. This is also the typical form of leaf-trace in solenostelic ferns, though in most cases the phloem completely lines the concavity of the xylem arch. In *G. (Mertensia) linearis*, which stands apart from the other *Mertensias* in more than one respect, the sclerenchyma in the concavity of the petiolar strand is completely enclosed by a separate internal endodermis not continuous with the external one, so that this sclerenchyma is quite shut off from the cortex (Fig. 35). This type of structure is intermediate between the *Mertensia*- and the *Eugleichenia*-types.

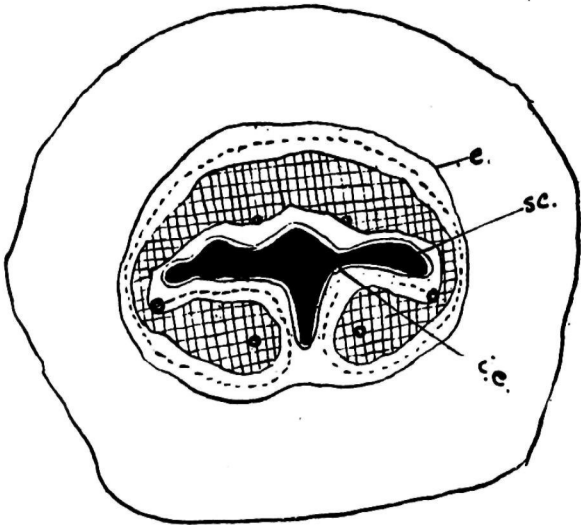


Fig. 35. *Gleichenia linearis*. T. S. of petiolar strand. *e.*, external endodermis; *i.e.*, internal endodermis; *sc.*, sclerenchyma. From Boodle.

The petiolar strand of *Eugleichenia* somewhat resembles the commonest Hymenophyllaceous type, *i.e.*, the outline of the endodermis is circular or oval in section, enclosing an arch-shaped xylem with the free ends terminating in incurved hooks. The phloem however, unlike that of the Hymenophyllaceæ, often passes in round the xylem hooks, and sometimes (*e.g.* in *G. dicarpa*) forms an almost complete lining to the xylem arch (Fig. 36). The central parenchyma of the petiolar bundle sometimes has a strand of sclerenchyma in its midst (Fig. 36), as in *Trichomanes Prieurii*. This is not bounded by an internal endodermis, as in *G. linearis*, but in the base of the petiole an isolated internal endodermis appears in some species (*G. dicarpa* Fig. 37D), *G. circinata* (Fig. 38) enclosing a strand of sclerenchyma within the main sclerenchy-

matous mass. In *G. dicarpa* this internal endodermis comes into connexion with the external one during the junction of the leaf-trace with the stele of the rhizome (Fig. 37C), thus putting the enclosed strand into open communication with the cortical ground-tissue. Almost immediately, however, the internal endodermis

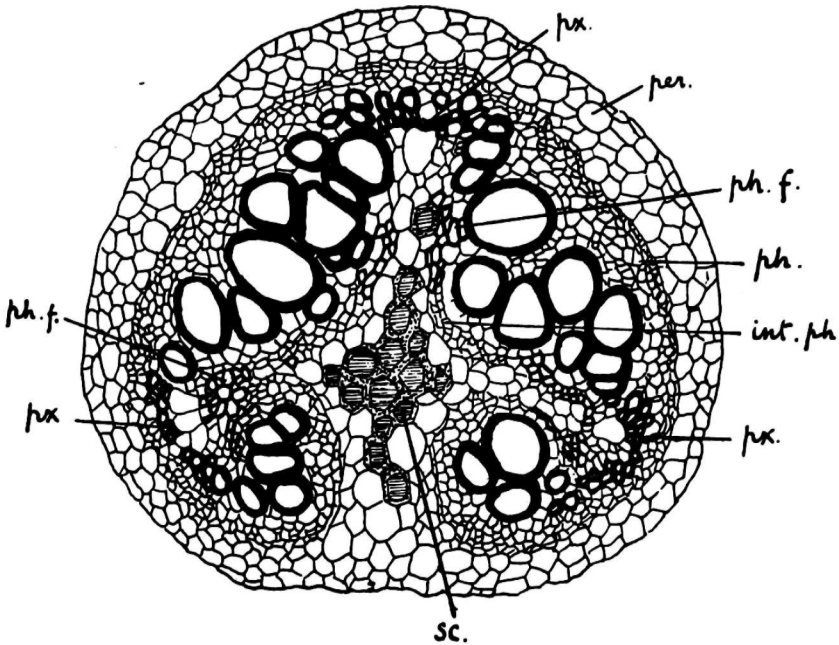


Fig. 36. *Gleichenia dicarpa*. T. S. of petiolar strand. *per.*, pericycle; *ph.*, external phloem; *px.*, protoxylem; *int. ph.*, internal phloem; *ph. f.*, internal phloem fibres; *sc.*, internal sclerenchyma. After Boodle.

again (Fig. 37B) separates from the external one, and finally dies out together with the enclosed fibres. In *G. circinata* the internal endodermis, with its enclosed fibres, dies out without making any connexion with the cortex (Fig. 38B). In *G. Boryi* there is no sclerenchyma in the concavity of the base of the leaf-trace, but the internal phloem, which in *G. dicarpa* loses itself in the external phloem of the stele during the junction, is continued down, as it is in *G. circinata*, into the xylem of the stele for a short distance, forming a "nodal island" or pocket of phloem which dies out in the xylem.

Turning again to the sub-genus *Mertensia* we find that the leaf-trace of *G. linearis*, which, as we have seen, has a petiolar structure intermediate between that of *Eugleichenia* and that of the typical *Mertensias*, affects the nodal structure of the rhizome considerably more than is the case in *Eugleichenia*. Though there is a good deal of variation in detail, in none of the cases examined

by Boodle does the internal endodermis connect with the external. It is, on the other hand, always continued down with its enclosed

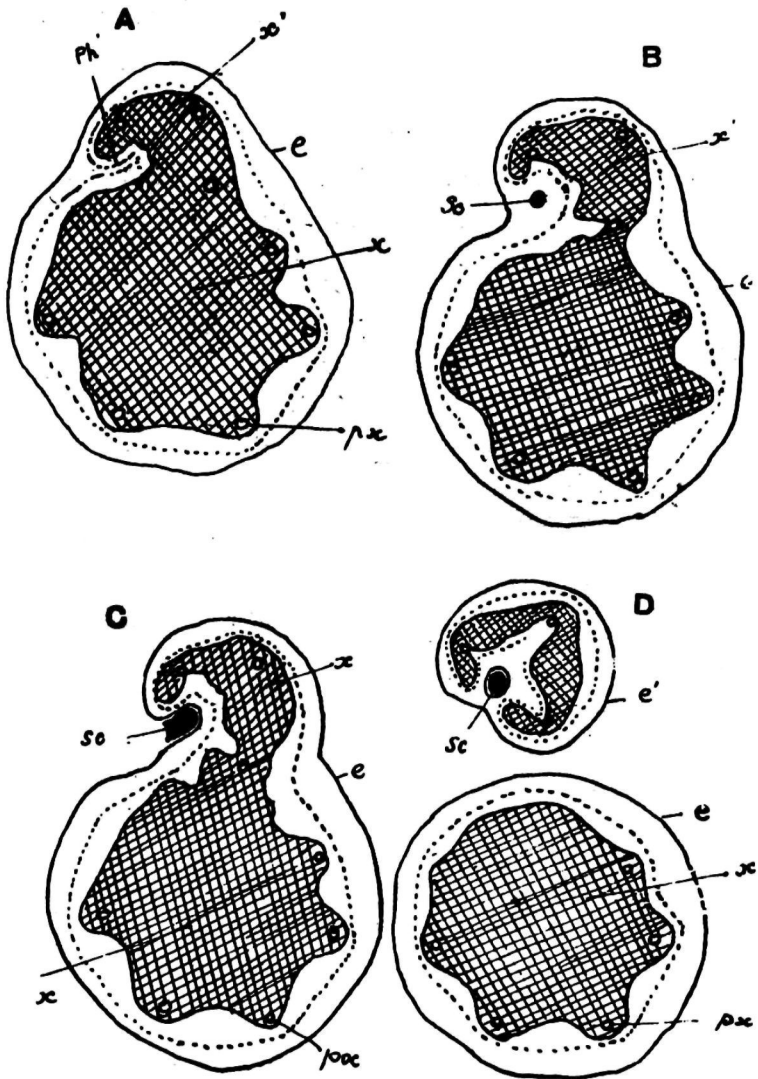


Fig. 37. *Gleichenia dicarpa*. Series of transverse sections through stele of node, showing departure of leaf-trace. From Boodle.

sclerenchyma into the xylem of the stele to form rather a bulky pocket which dies out below the node (Fig. 39). Sometimes a slight branch is also formed penetrating the xylem in an acroscopic direction (Fig. 39 C, D). The internal phloem of the leaf-trace also passes down into the pocket, forming a few sieve tubes on the side of the internal endodermis nearest the centre of the rhizome axis (Fig. 39 B, C, D). Occasionally the internal phloem connects with the

external at the insertion of the trace, but usually the leaf-trace joins the stele in the form of a closed ring, and no connexion between the internal and external tissues takes place. In *G. flabellata* (Fig. 40) the internal phloem, the internal endodermis and the sclerenchyma in the concavity of the C-shaped leaf-trace are continued down into the xylem of the stele below the node to form a bulky pocket. The sclerenchyma and endodermis first die out, leaving the internal phloem, which eventually also dwindles and disappears.

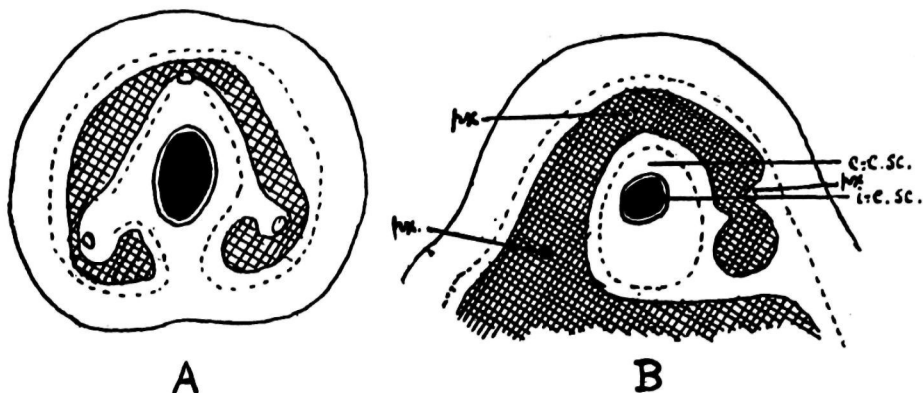


Fig. 38. *Gleichenia circinata*.

A. T. S., leaf-trace.

B. Junction of leaf-trace with stele. *e.-e.sc.*, extra-endodermal sclerenchyma; *i.-e.sc.*, intra-endodermal sclerenchyma.

G. pectinata (Fig. 41) is a solenostelic form, with a normal centrally placed sclerenchymatous pith in the internodes, surrounded by endodermis and internal phloem. A bulky "nodal island" is formed in connexion with the junction of the large C-shaped leaf-trace with the stele. This connects with the pith at the node, but is sometimes, at least, continued for some distance down into the internode in a dorsal position, independently of the pith (Fig. 41C).

Finally, *Platyzoma* has a curious and rare type of stele (Fig. 42), containing a pith surrounded by an endodermis but no internal phloem, and with quite small collateral leaf-traces, whose departure does not break the continuity of the vascular ring as it does in the normal solenostelic type.

It is obvious that the types described fall into a rough series extending from the simpler forms of *Egleichenia* on the one hand, through the types with internal endodermis at the base of the petiole only, and then through *G. linearis*, to the typical Mertensias and finally to *G. pectinata*. It is scarcely possible, however, to regard this as a progressive evolutionary series, in spite of the fact that the simpler forms have a certain resemblance to many of the

Hymenophyllaceæ, which we have seen some reason to suppose may be regarded as showing comparatively primitive types of Filicinean vascular structure. The isolated or almost isolated

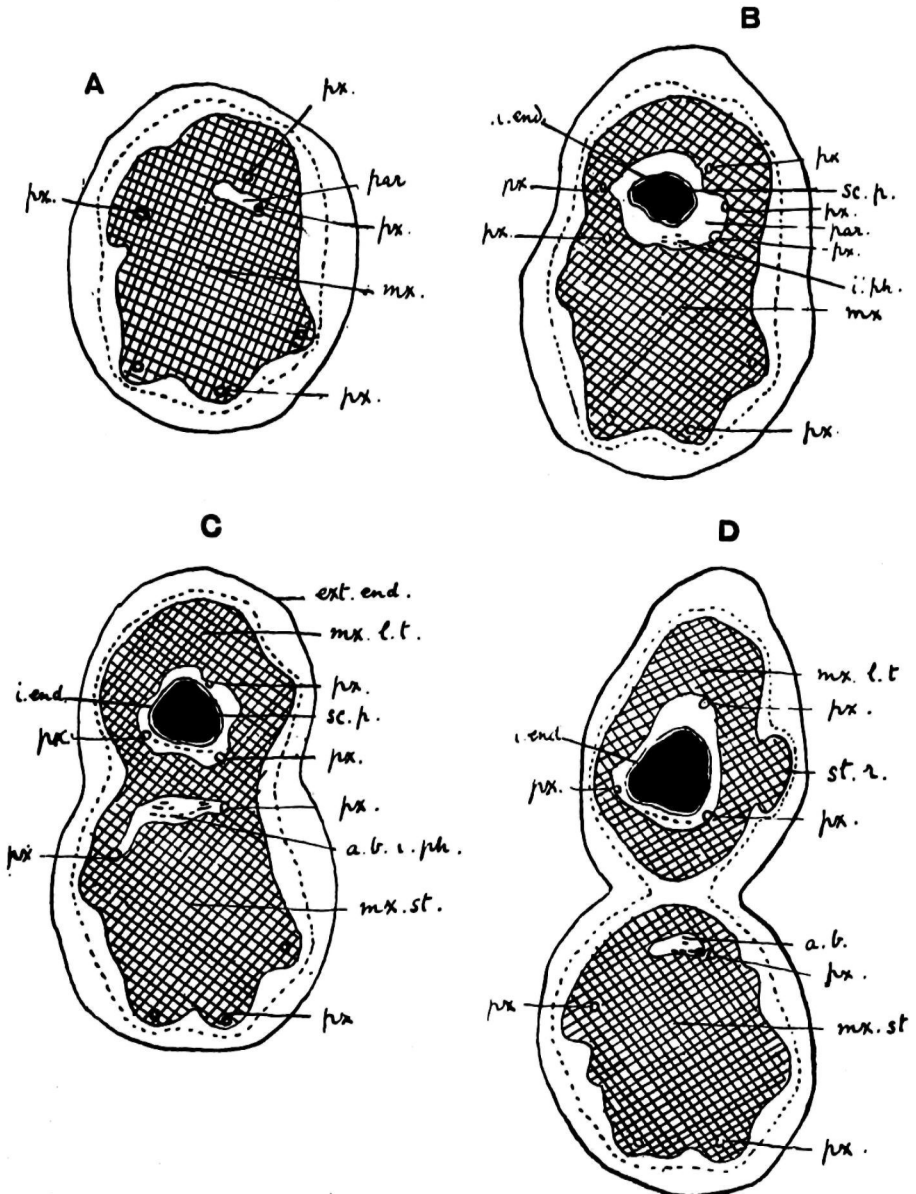


Fig. 39. *Gleichenia linearis* (*dichotoma*), Series of transverse sections through stele of node. *sc. p.*, sclerenchymatous pocket; *i. ph.*, internal phloem, confined to adaxial side of pocket; *a. b. i. ph.*, acroscopic branch of internal phloem; *par.*, parenchyma, forming lower end of pocket; *st. r.*, stele of root arising from base of leaf-trace. From Boodle.

internal endodermis of forms like *G. circinata*, *G. dicarpa* and *G. linearis* is difficult to regard as anything but a structure reduced,

from the form found in the typical *Mertensias*,¹ for it is impossible to suppose that an isolated endodermis shut up in sclerenchymatous tissue can have an actual function. Further the fact that the *Eugleichenias* compared with the *Mertensias* are xerophilous forms distinctly lends support to the theory of reduction as applied to this series.

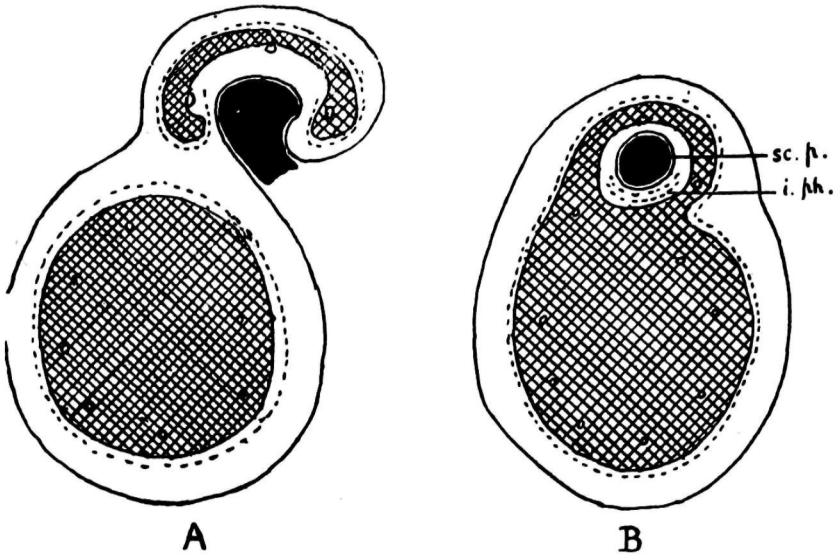


Fig. 40. *Gleichenia flabellata*. Transverse sections through stele of node. *sc. p.*, sclerenchyma of pocket; *i. ph.*, internal phloem.

G. pectinata, on the other hand, is best regarded as derived from the *Mertensia*-type by the evolution of a regular pith. The co-existence in some cases of the nodal island, or, as it is better called, the nodal pocket, with the ordinary pith in this species is a curious feature scarcely compatible with the derivation of the *Mertensia*-type by reduction from a normal solenostelic form. *Platyzoma* again, with its extreme xerophily and anomalous leaf-traces may almost certainly be regarded as reduced from the solenostelic type.

We are therefore led to the conclusion that such a form as *G. flabellata* on the whole represents the most primitive type of the genus, and it is interesting to note that not only do the branching of the fronds and the form of the pinnules but also the large number of spores in the sporangium (Bower, '99) tend to corroborate this view.

THE LINDSAYA-TYPE.

The next type of Filicinean vascular structure, naturally connecting with the *Mertensia*-type as seen in *Gleichenia flabellata*,

¹ This view was put forward by Boodle ('01 B).

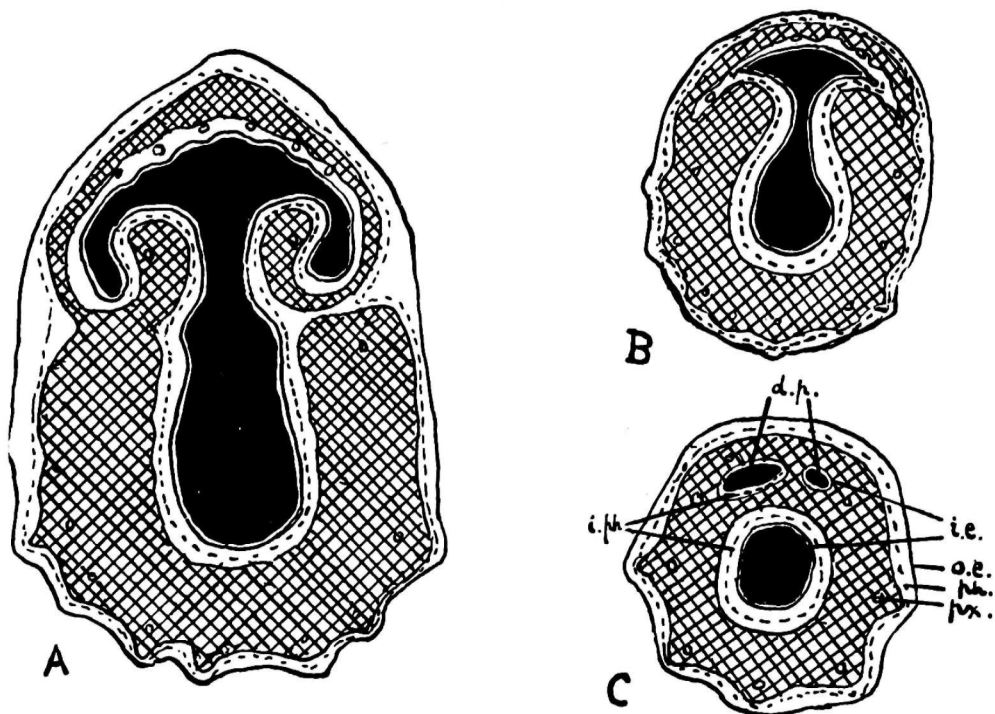


Fig. 41. *Gleichenia pectinata*.

- A. Junction of leaf-trace with stele of rhizome.
- B. T. S., behind node showing connexion of dorsal pocket with pith still open.
- C. T. S., further back, showing dorsal pocket, (*d.p.*) split into two and separate from pith.

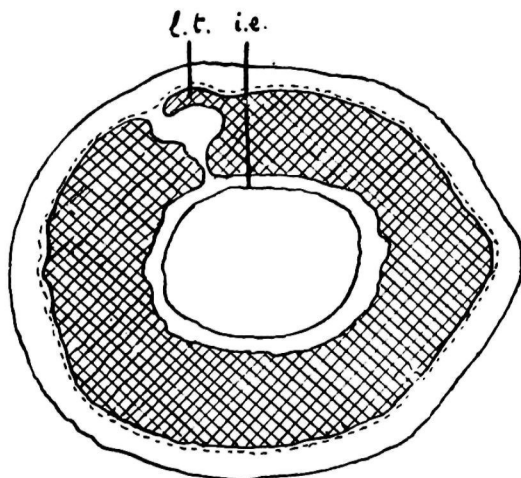


Fig. 42. *Platyzoma microphylla*. Diagram of stele of rhizome showing internal endodermis (*i.e.*) with pith, but no internal phloem. Only a single leaf-trace (*l.t.*) is shown leaving the xylem. As a matter of fact the leaves are polystichous, and in any given section a number of traces would be seen. Modified from Boodic.

is the *Lindsaya*-type, characteristic, though not exclusive, in the genus *Lindsaya*, and also found in *Davallia* (*Odontoloma*) *repens*.

Lindsaya is a tropical genus showing a preponderance of shade-forms and with an unmistakably "mixed" sorus; it is usually placed in a separate family Lindsayæ, closely allied to the Davallieæ, and, by its foliage and the position of its sorus, to Adiantæ also. Gwynne-Vaughan's work ('03) has shown that certain species which are placed by Hooker and Baker (Synopsis Filicum) in the genus *Davallia*, agree closely with the *Lindsaya*-type of anatomy, and since these species have all been put, at various times, by one authority or another, in separate genera, and their general characters also sufficiently agree with *Lindsaya*, we

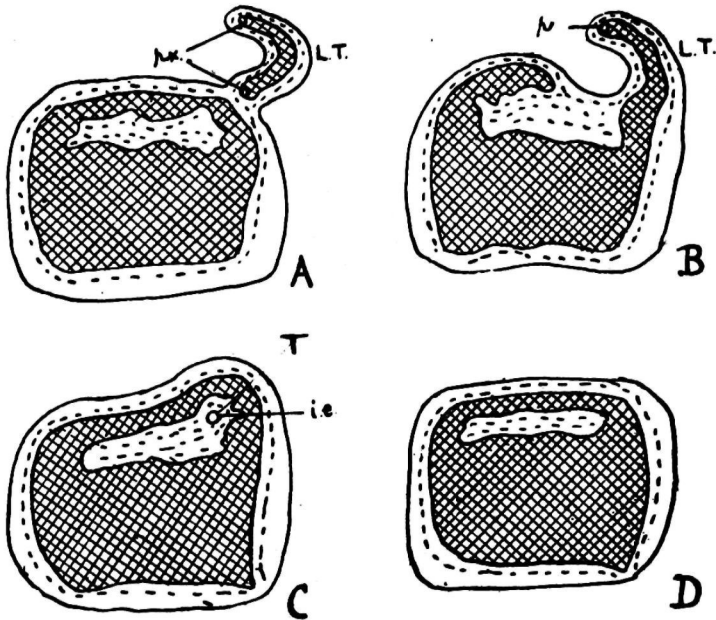


Fig. 43. *Lindsaya scandens*. Series through node, showing internal phloem and mode of attachment of leaf-trace.

seem fully justified in associating them under separate generic names in the family of Lindsayæ.

The internode of a typical *Lindsaya* (Tansley and Lulham '02) shows a dorsiventral stele with mainly "solid" xylem, but with an internal strand of phloem running close to its dorsal surface (Fig. 43D). The xylem has a good deal of intermixed parenchyma, as in *Gleichenia*, but no spiral protoxylem.

The petiolar strand is "subrotund or cordate" in cross section, the xylem consisting of two more or less distinct arms inclined to

one another at an acute angle, approaching to a right angle, which is of course directed away from the stem-axis (Fig. 44). "The protoxylem groups are distinct and endarch; one occurs at the end of each arm of the xylem, and sometimes a third is also present at its apex. The arms of the xylem-strand are sometimes prolonged past the two lateral protoxylems, curving inwards towards the plane of symmetry of the petiole so as to form two small hooks. These

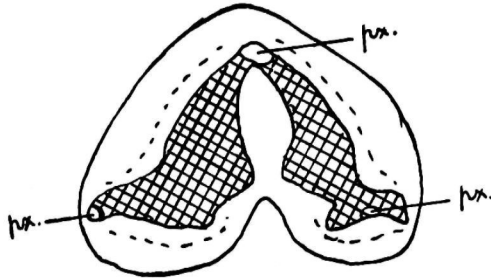


Fig. 44. *Odontoloma repens*. T. S. of petiolar strand. After Gwynne-Vaughan.

hooks are included in the phloem of the bundle, which is perfectly continuous all round the xylem-strand" (Gwynne-Vaughan, '03). The leaf-trace leaves the stele by the breaking of the dorsal arch of xylem which covers the internal phloem, and the passing off of tracheids, together with surrounding tissue, from one side of the arch, which soon re-closes. The internal phloem of the stele is therefore continuous with that of the trace, and the whole structure is essentially what would result if the nodal pocket of phloem in *Gleichenia* were continued down through the internode to join that of the node below. Owing to the somewhat different shape of the leaf-trace the concavity is much less marked, and the ground tissue surrounded by endodermis is not carried down so far into the stele as is the case in *Gleichenia flabellata*, but in some cases there is a short endodermal pocket extending into the internal phloem below the node (Fig. 43 C).

The *Lindsaya*-type of stele is found in all the species which have been examined of *Davallia* §*Odontoloma* and §*Stenoloma* (Synopsis Filicum) except *Davallia* (*Stenoloma*) *aculeata* (see Gwynne-Vaughan, '03). This last named species, which has been put in a separate genus *Lindsayopsis* by Christ, and *Davallia pinnata*, which has been separated as *Wibelia* by Christ, show a further modification of the *Lindsaya*-type.

Wibelia pinnata (Fig. 45) has a strand of sclerenchyma in the concavity of the leaf-trace (Fig. 45 A) and this is continued down

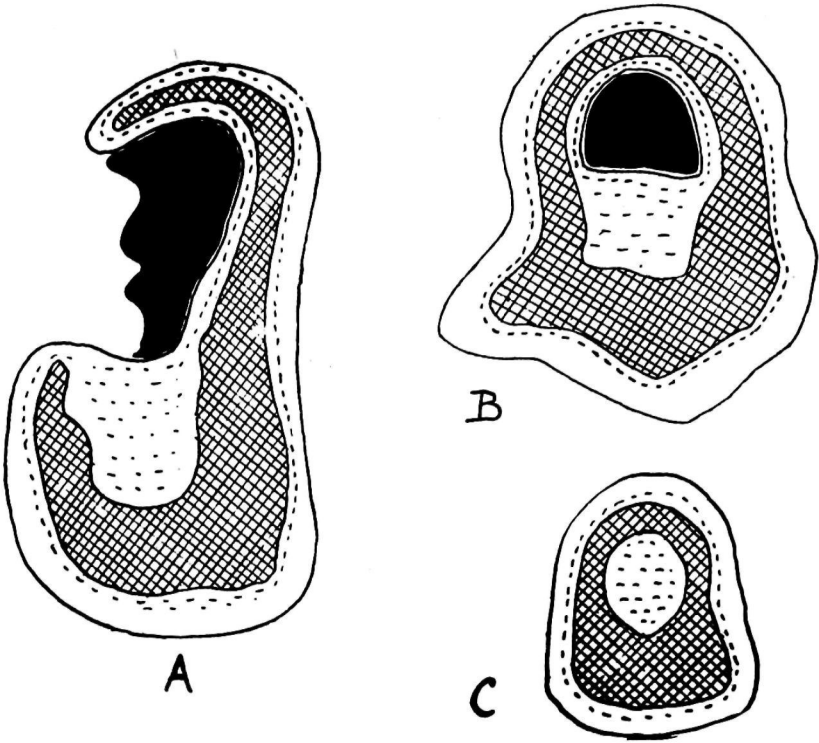


Fig. 45. *Wibelia pinnata*.

- A. T. S. of stele at node showing attachment of leaf-trace with strand of sclerenchyma in its concavity.
 B. T. S. of stele just below node, with internal sclerenchyma and endodermis.
 C. T. S. of stele above node.

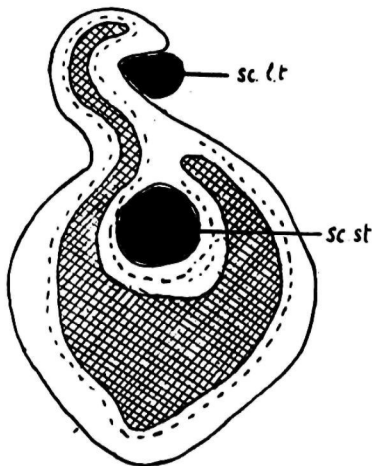


Fig. 46. *Lindsayopsis aculeata*. T. S. of stele of node; *sc. lt.*, sclerenchyma of leaf-trace concavity; *sc. st.*, sclerenchymatous pith of stele.

as a fairly bulky strand surrounded by an endodermis into the internal phloem of the stele (Fig. 45 B). It is persistent through most of the internode but gradually dwindles and disappears before the next node below is reached. A transverse section just above the node therefore shows the pure *Lindsaya*-type (Fig. 45 C).

In *Lindsayopsis aculeata* (Fig. 46) the internal sclerenchyma reaches the next node and joins the incoming strand belonging to that leaf-trace, so that a regular solenostele is formed. This differs however from a perfectly typical solenostele, owing to the fact that the xylem on the ventral side of the internal phloem is considerably thicker than the dorsal arch of xylem; though this difference is not so extreme as in certain species of *Lindsaya* and *Odontoloma*. Finally in two species of *Lindsaya*, *L. cultrata* and *L. retusa*, a typical solenostele is present.



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