NOTES.

ON A NEW TYPE OF FERN-STELE, AND ITS PROBABLE PHYLOGENETIC RELATIONS.—Among the alcohol-material of various Ferns, recently brought home by one of us from the Malay Peninsula with a view to the study of their anatomy, were several species of the genus *Lindsaya*. In all of these, *L. orbiculata* (Lam.), Bed. (= *L. flabellulata*, Dry.), *L. orbiculata*, var. *tenera*, Bed. (= *L. tenera*, Dry.), *L. rigida*, Sm., *L. lancea* (L.), Bed. (= *L. trapeziformis*, Dry.), we found that the rhizome presented a constant type of stele which was entirely new to us, and of such striking interest in relation to the phylogenetic problems which have quite recently become prominent in the province of Fern-anatomy, that we determined to undertake a detailed investigation of all the species of *Lindsaya* that we could obtain. *L. Guianensis*, Dry., from British Guiana, growing in one of the pits at Kew, shows the same structure¹, while *L. retusa*, Metten., on the other hand, has a typical solenostele. The nearest affinities of *Lindsaya*, as determined by soral characters, appear to be with *Davallia* § *Odontoloma*; concerning one species of this section, *Davallia repens*, Desv., a very widely distributed Fern in the Indo-Malayan region and Polynesia, it is remarked in the 'Synopsis Filicum,' p. 93: 'Quite doubtful as between *Odontoloma* and *Lindsaya*.' It was of great interest, therefore, to find that the structure of the stem of this species conformed exactly to what we will call provisionally, for convenience' sake, the *Lindsaya*-type. We have since ascertained that the stele of *Davallia repens* has already been partially described by Trécul², who, however, missed the crucial character. The reference to this paper, which we had unfortunately overlooked, was given to us by Mr. Gwynne-Vaughan, who, it appears, is familiar with this type of structure.

¹ Since the text of this note was written we have obtained fragments of the rhizomes of *L. scandens*, Hk., *L. davallioides*, Blume, and *L. (Schizoloma) lobata*, Poir. (= *L. nitens*, Blume) from herbarium-material, for which we are indebted to the kindness of Mr. R. H. Yapp, who collected it in Perak. In all these species we find the same type of stele.

² Structure du système vasculaire dans le genre *Davallia*, et en particulier dans *Davallia repens*. Comptes Rendus, t. 101, 1885.

Our object in publishing the present note (pending the preparation of a detailed paper on the anatomy of *Lindsaya*, which, owing to the difficulty of obtaining alcohol-material of other species, must occupy several months) is to call attention to the *primâ facie* inferences to be drawn from the occurrence of this type of stele in the adult stems of these Ferns. The occasion is the more opportune owing to the publication in the last number of this journal of Mr. Boodle's paper on the anatomy of the Gleicheniaceae, in which he gives a detailed account of structures already partially described by Poirault (Ann. Sci. Nat., Bot., 1893), structures having an important bearing on the phylogenetic question which we propose to outline.

The '*Lindsaya*-type' of stele, at present known in the creeping rhizomes of the five species¹ (or four species and one variety) of *Lindsaya* enumerated above, and also in that of *Davallia repens*, is a monostele showing in cross-section a central mass of xylem, consisting of scalariform tracheids intermingled with parenchyma, and surrounded by a complete ring of phloem, pericycle and endodermis, as in *Gleichenia* or *Lygodium*, but differing most strikingly from these Ferns by possessing, in addition to the external phloem-mantle, a strand of phloem completely embedded in the xylem near the dorsal surface of the latter. This strand of internal phloem consists of typical sieve-tubes mixed with parenchyma and separated by one layer of similar parenchyma from the surrounding xylem (Fig. 9).

As the node is approached from below², the strand of internal phloem forms a dorsal projection on the side corresponding to the leaf-insertion, thrusting up the dorsal 'vault' of xylem, as Trécul calls it, on that side (Fig. 10). An accumulation of parenchyma arises in the phloem-strand immediately ventral to this bay, and in the midst of this accumulation endodermal cells appear which soon come to enclose a few parenchymatous cells (Fig. 10). The dorsal bay of phloem rapidly extends laterally outwards, and at the same time the internal endodermis with its enclosed parenchyma moves up dorsally behind it, so that the phloem of the bay assumes the form of a slightly curved plate lining the inside of the thrust-out xylem arc on one side of the dorsal vault. The vault now breaks at the point near its centre where

¹ The addition of the three species mentioned in the first footnote on p. 157 raises the number to eight.

² The following description is taken from *Lindsaya orbiculata*, but the other species agree in essentials.

this arc joins the unaltered part, placing the internal and external phloem in communication: the free end of the arc rapidly raises itself, at the same time rotating laterally outwards, while its internal phloem (derived from the phloem of the bay) closely follows it, so that a wide gap is formed in the stelar tissues; as the free end of the arc moves away from the stele the internal endodermis

FIG. 9.

FIG. 10.

FIG. 11.

FIG. 12.

Transverse sections of stele of rhizome of *Lindsaya orbiculata*. The phloem is diagonally shaded, the xylem, pericycle and endodermis left blank. The outer limit of the endodermis is indicated by a dotted line. Fig. 9. Internode. Figs. 10-12. Detachment of leaf-trace.

approaches the outer one, they touch and open, thus placing the internal strand of parenchyma, which has dilated considerably, in connexion with the cortex (Fig. 11). Meanwhile the arc of xylem, with its internal and external phloem, raises itself further from the dorsal surface of the broken stele, deepens its concavity so as to take on a gutter-shaped form (Fig. 12), finally detaches itself from the

corner of the stele, and becomes the meristele of the petiole, its plane of symmetry being now parallel with the dorsal surface of the stele. The broken dorsal vault becomes again complete before the meristele is quite detached (Fig. 12), but in such a way that a bay of the internal phloem is left, in the same position as the one below the node. This superior bay gradually dies out, and the stele returns to its internodal condition.

The first point of interest about this type of stele is its correspondence with the condition found by Leclerc du Sablon¹ in the young stems of *Pteris aquilina* (Fig. 15) and *Nephrodium molle*, and the similar condition found by Mr. Boodle in *Anemia Phyllitidis* (Anatomy of Schizaeaceae, pp. 389-390, and Fig. 26, Ann. of Bot., XV, 1901). In these Ferns the central part of the protostele of the first-formed portion of the stem consists of a solid cylinder of xylem as far as the exit of the first leaf-trace. Close above this point there arise in its centre a few sieve-tubes. The appearance of this strand of phloem in the midst of the xylem gives to the stele the same essential character as that of the internodes of the adult rhizome of *Lindsaya* (Fig. 14). At the departure of some later leaf-trace, the hollow cylinder of xylem (together with the mantle of external phloem, pericycle, and endodermis) is broken, and the endodermis dips down into the centre of the now horseshoe-shaped stele. By the closing up of the gap formed by the departure of the leaf-trace, and the inclusion within the stele of a strand of parenchyma surrounded by a layer of endodermis, the solenostelic structure is obtained (Fig. 18). Higher up still the solenostele breaks into two stelar arcs.

By the writings of Mr. Gwynne-Vaughan² and of Dr. Jeffrey³ we have recently been made familiar with the idea that solenostelic and siphonostelic structure may be phylogenetically intermediate between protostelic on the one hand, and dialystelic or astelic on the other. The solenostelic structure in the young stem of *Pteris aquilina* is ontogenetically transitional between the protostelic structure of the base of the first-formed stem, and the dialystelic ('polystelic') structure of the rhizome; and so in the

¹ Recherches anatomiques sur la formation de la tige des Fougères. Ann. Sci. Nat., Bot., 1890.

² Polystely in the genus *Primula*, Ann. of Bot. xi, 1897. Studies in the Anatomy of the Solenostelic Ferns. I. Loxsoma. Ann. of Bot. xv, 1901.

³ The Morphology of the Central Cylinder in the Angiosperms. Trans. Canad. Inst., 1900.

Type of Stele with internal phloem alone.

Type of Stele with internal endodermis enclosing parenchyma or sclerenchyma within the internal phloem.

FIG. 13.

FIG. 16.

FIG. 14.

FIG. 17.

FIG. 15.

FIG. 18.

FIG. 13. *Gleichenia flabellata* just below node (from Boodle). FIG. 14. *Lindsaya rigida*, internode. FIG. 15. *Pteris aquilina*. Transitional structure in primary stem (from L. du Sablon). FIG. 16. *Gleichenia dichotoma* just below node (from Boodle). FIG. 17. *Davallia (Microlepia) pinnata* below node. FIG. 18. *Pteris aquilina*. Transitional structure above that of Fig. 7 (from L. du Sablon). Phloem diagonally shaded. External limit of endodermis a dotted line.

adult stems of many Ferns the solenostelic structure (specially predominant in the middle grade—Prof. Bower's Gradatae—of the Fern series) is phylogenetically transitional between the protostelic structure almost certainly primitive for the Ferns, and the dialystelic condition characteristic of the great majority of the higher forms (Polypodiaceae). The young plant of these higher forms (in certain cases at least) starts by laying down the protostelic structure, but very soon this gives place to the solenostelic, which in its turn passes into the dialystelic arrangement characteristic of the adult stem. The great interest of the *Lindsaya*-type of stele is that it appears to furnish a phylogenetic link hitherto wanting in a mature stem (see Boodle, Anatomy of Schizaeaceae, p. 407, Ann. of Bot., XV, 1901) between the protostelic and the solenostelic structure; and this view is distinctly supported by the occurrence of the same type at the same stage in the ontogenetic series of the Ferns already mentioned.

The chief objection to this hypothesis of the morphological position of the *Lindsaya*-stele is the fact that the Lindsayeae are relatively advanced Ferns so far as their sori are concerned, coming into Prof. Bower's highest grade, the Mixtae, with a flat receptacle, no definite order of development among the sporangia, and a nearly if not quite vertical annulus. The great majority of the rest of the Mixtae (Polypodiaceae in the wide sense) have dialystelic structure. There is, however, evidence that the *Lindsaya*-type is not wanting among the more immediate allies of the Lindsayeae, the Davallieae, while the Dennstaedtiaceae, which appear to come immediately below in the series, are predominantly solenostelic; whether they will supply evidence of similar transitions we do not as yet know. It is not to be supposed that all the morphological characters of the Ferns will evolve strictly *pari passu*, and if an anatomical character of a relatively low grade is well adapted to general conditions of habit and the like, there is nothing surprising in its being retained in plants in which evolution of the sorus has advanced considerably. This, however, is a large question, which we hope to treat more fully in our detailed paper. We may expect also a considerable elucidation of the whole of these relations as a result of Mr. Gwynne-Vaughan's extended researches on the solenostele, the second instalment of which, dealing with the Cyatheaceae in the wide sense, and the Davallieae, we may hope to see published within the next few months.

Meanwhile we may point out that there are not wanting

indications of the steps by which protostelic structure was changed into the *Lindsaya*-type. Mr. Boodle has described in his last paper¹ the structure of the stele of the node of *Gleichenia* (sub-genus *Mertensia*) *flabellata*. As the node is approached from below, a 'nodal island' of parenchyma, in the midst of which are some sieve-tubes, appears in the xylem of the stele near its dorsal surface, so that at this level the structure of the stele in the essential relations of xylem and phloem is identical with that of *Lindsaya*. The description of the arrangement of tissues above this point, involving the detachment of the leaf-trace, strikingly agrees with the facts we have described in the case of *Lindsaya*, the main differences being the much bulkier and sclerotic strand of tissue enclosed by the internal endodermis in *G. flabellata*, and the fact that the two endodermes join in the latter only after the xylem and phloem of the meristele have become detached from the stele at the other end; in this last respect *G. (Eugleichenia) dicarpa* is much more like *Lindsaya* (see Boodle, Fig. 22).

The petiolar meristele of *Gleichenia* is, we are inclined to believe, primitively collateral in structure, i. e. with phloem belonging only to its outer (lower) side. The internal phloem, which passes round the incurved ends of the meristelic xylem, as seen in cross-section, and in extreme cases (*G. dicarpa*) becomes almost continuous round the concave side of the dorsal bay of xylem, may be regarded as an inward extension of the external phloem, developed to meet the increasing needs of conduction. But such an extension had to be provided with an attachment to the phloem of the stele. At first its attachment to the ordinary external phloem of the stele seems to have been mediated by the downward extension of the bay of the meristele (*G. dicarpa*, Boodle, Fig. 20), which in its lower part contains phloem alone (cf. our Fig. 11). In other cases we must suppose the downward extension of this bay became completely enclosed in the xylem of the stele, forming a 'nodal island' consisting not only of phloem but also of a downward extension of the central parenchyma or sclerenchyma of the meristele, enclosed by an internal endodermis. Of what precise benefit to the plant this blind downward extension of the internal phloem (or its corresponding upward extension, described by Mr. Boodle in *G. dichotoma*) may be, it is difficult in the present state of physiological anatomy to guess. But if we imagine the

¹ Boodle, Gleicheniaceae, p. 723.

phloem of the inferior and superior nodal islands continued respectively through the lower and the upper internodes till they meet corresponding extensions from the next nodes below and above, it is clear that we have reached the *Lindsaya*-type, and have obtained an internal stelar phloem-system forming a satisfactory attachment for the internal phloem of the meristele, which has now become completely concentric.

Finally, with regard to the change from the *Lindsaya*-type to that of the solenostele, we have the strand of parenchyma or sclerenchyma surrounded by its own endodermis in the concavity of the meristele, already usually carried down into the 'inferior phloem island' in *Gleichenia*, and into the 'inferior phloem-bay' in *Lindsaya* (Fig. 10). We have only to imagine it continued down in the centre of the internal phloem, till it reaches the next node, and the change is made. In *Davallia* (*Microlepia*) *pinnata* we have found this change apparently in progress. Immediately above the node the stele has the *Lindsaya*-type with internal phloem alone, but a stout strand of sclerenchyma continuous with that lying in the concavity of the horse-shoe-shaped open meristele, and surrounded by an endodermis, penetrates the internal phloem of the stele, ending blindly some little distance above the next node below (Fig. 17). The appearance presented corresponds strikingly with Boodle's Fig. 17, which we have reproduced as Fig. 16, of the node of *Gleichenia dichotoma*, representing a section taken just below the separation of the xylem of the leaf-trace.

The above is a very brief indication of our ideas as to the probable phylogenetic meaning of the new facts. In this preliminary note they are necessarily expressed imperfectly and somewhat dogmatically. Detailed qualification would be out of place, but we may perhaps point out that we do not intend to convey the impression that in our opinion the method we have roughly sketched is necessarily the *only* way in which the solenostele has arisen in evolution. Doubtless in some cases the pith may have come before the internal phloem, and in such a case the stage represented by the *Lindsaya*-type would not be passed through at all.

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