A Fossil Solenostelic Fern.

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With Plate LVIII and a Figure in the Text.

AMONG the flora represented in the mineral nodules recently collected by Dr. Marie Stopes from the Cretaceous of Japan, is a fragment of a fern stem which is particularly interesting, since the anatomy shows it to be of the solenostelic type, and hence it seems of sufficient interest to merit description in detail. At present the only recorded example of a fossil fern with this structure is *Psaronius Renaulti*,¹ which seems essentially solenostelic, although in the sections at present known the stele is not completely closed at any one level;² thus there is still the possibility that *P. Renaulti* may be a simple dictyostelic stem.

The Japanese stem, although only about 3 cm. long, fortunately includes a node, and shows the departure of a lateral branch with its relation to the leaf-trace. The preservation of the tissues is in parts extremely good, and the structural details can clearly be seen. Although the fossil shows marked resemblances to some of the living groups of ferns, there is not sufficient evidence to identify it with or include it in any of these groups; therefore it seems necessary to form a new genus which might temporarily be used for this and any other such fragmentary portions of fossil solenostelic ferns that may be discovered, and do not show sufficient resemblance to living forms to justify inclusion with them. I therefore suggest the name *Solenostelopteris* for the genus. The species name *japonica* is given to this specimen, as it comes from the Japanese deposits.

DESCRIPTION OF THE STEM.

The fragment of the stem was from 3 to 3.5 cm. long, and from this nine transverse sections were prepared.

The Text-fig. shows the general shape of the solenostele in the various sections.

¹ Scott, D. H. ('08), *Studies in Fossil Botany*, 2nd ed., vol. i, p. 301.

² I am indebted to Dr. Scott for this information.

Sections *a*, *b*, and *c* are below the node, and the stele is here a complete ring. In section *d* the stele has opened, forming the leaf-gap. Sections *e* and *f*, in addition to the leaf-gap, show a swelling of the stele on one side, which indicates the developing lateral branch (*b*). In *g* the branch has separated from the main stele, in which the leaf-gap is still open. The two

TEXT-FIG. A series of transverse sections through an internode and part of a node of *S. japonica*.
Description in text.

remaining sections are merely of the lateral branch, the main stele having disappeared.

It seems probable that the rhizome was a dorsiventral one, the leaf-gap being on the upper surface, while the roots arose from the under surface of the rhizome both at the nodes and internodes.

Anatomy. The general view of the stem is seen in Fig. 1, Pl. LVIII. Unfortunately in most of the sections the greater part of the cortical ground tissue has disappeared, so it is impossible to determine the size of the complete stem. The stele measured about 1.8 mm. diameter.

Ground tissue. The central ground tissue (within the solenostele) is composed of cells 0.05 mm. diameter, with sclerized walls. As may be seen from Fig. 1 at *c. scl.*, the central cells are larger and less sclerized than the peripheral ones. These larger central cells are often filled with rounded bodies which were probably starch grains, such as are found in similar cells in living ferns, e. g. *Microlepia*.

Almost at the edge of the central ground tissue, separated only by one or two layers of sclerenchyma from the solenostele, is a layer of rather irregular, thin-walled cells, which in many parts are very crushed in the fossil (Figs. 1 and 2, *s.*). A similar layer of thin-walled cells amongst the sclerized ones is frequently met with in the central ground tissue of the stem of living solenostelic ferns.

The cortical ground tissue is not seen very favourably in many of the sections, and is in no case complete. Immediately surrounding the stele there is a layer of sclerenchyma about three cells in thickness (Figs. 2, 3, 4, *o. scl.*). Many of these cells, as in the case of the cells of the central ground tissue, are filled with the rounded bodies referred to above as starch grains. In most of the sections the tissues outside this sclerized ring are lost, but in some of the retained portions there may be seen, outside the sclerized ring, several rows of parenchymatous cells usually rather crushed, but which were probably of a soft, spongy nature, and had large air spaces between them. This tissue can be seen as a dark ring just outside the sclerized cortical tissue in Fig. 4, *i. c.*

The outer cortex, which was probably a much stronger tissue, is partially preserved in some of the sections—see Figs. 3 and 4, *o. c.*; but in no case can the epidermal tissues be seen. The cells composing this outer cortex, usually hexagonal in shape and averaging 0.07 mm. diameter, fit together closely, leaving no intercellular spaces.

The stele conforms to the definition of a solenostele given by Gwynne-Vaughan,¹ for 'the vascular tissue is arranged in a single hollow cylinder with phloem and phloeotermata on either side . . . the complete continuity of which is interrupted only by the departure of the leaf-traces; the gaps thus produced are closed up in the internode above, before the departure of the next leaf-trace'. There is only one node and a portion of an internode in the fossil fragment, but those parts are in agreement with the above

¹ Gwynne-Vaughan ('01), Observations on the Anatomy of Solenostelic Ferns (Part I). *Annals of Botany*, vol. xiv, March, 1901.

description, and it is reasonable to assume that the whole of the rhizome was of this solenostelic type.

The *xylem* is composed of a ring of tracheides, one or two layers deep, in the ventral portion of the stele (Figs. 1, 2, and 3, *x.*), but becoming five or six layers deep in the dorsal portion in connexion with the outgoing leaf-trace (Figs. 1, 3, and 4, *a*). A few parenchymatous cells occur here and there among the woody elements. Protoxylem elements of the spiral and annular type are not found in the stem, but fairly frequent exarch groups of scalariform elements are found around the ring of metaxylem (*p. x.*, Fig. 2), quite similar to the 'protoxylem elements' described for recent solenostelic ferns.¹ Unfortunately there are no longitudinal sections of the rhizome, but in some of the oblique parts of the transverse sections it may be seen that both the protoxylem and metaxylem are composed of scalariform elements, which possess a single series of pits on each wall. In some of the better-preserved and uncrushed parts of the rhizome distinct pits can be seen (Fig. 5) between the walls of adjacent xylem elements, such as Gwynne-Vaughan² has described in the fossil Osmundaceae, and has since shown to exist in the xylem elements of many of the living ferns.

The *phloem* forms a continuous ring on either side of the xylem (Fig. 2, *i. ph.* and *o. ph.*), but unfortunately, as is the case with the other soft tissues in the stem, it is usually so crushed that the structure is not very clearly seen. In the better-preserved parts one can recognize two or three layers of sieve-tubes, but no distinction into protophloem and metaphloem. The phloem layer is separated from the xylem on each side by an irregular layer of parenchymatous cells (Fig. 2, *par.*). Surrounding both the inner and outer bands of phloem is a single layer of pericycle cells (Fig. 2, *i. per.* and *o. per.*), often rather irregularly arranged. The solenostele is limited on each side by a well-marked endodermis, which is clearly shown in all sections, since the cells, unlike the surrounding ones, are usually filled with masses of black, carbonized material. They are slightly elongate tangentially—that diameter being 0.02 mm. (Fig. 2, *o. end.* and *i. end.*). There are no undulations on the radial walls of the cells, but the corners are slightly thickened. This endodermal layer is remarkably well defined and recognizable for a fossil.

THE LEAF-TRACE AND BRANCH.

As was mentioned previously and shown in the Text-fig., the continuity of the solenostele is interrupted in some sections by the outgoing leaf-trace. The lateral shoot of the rhizome, as in living solenostelic ferns,

¹ Gwynne-Vaughan ('03), Observations on the Anatomy of Solenostetic Ferns (Part II). *Annals of Botany*, vol. xvii, 1903.

² Gwynne-Vaughan ('08), On the real nature of the Tracheae in the Ferns. *Annals of Botany*, vol. xxiii, July, 1908.

is inserted upon the base of the petiole and attached to one margin of its vascular strand. An attempt has been made in Fig. 6 to represent a node of the rhizome with leaf-gap, and to show the relations between it and the leaf-trace and adjacent lateral branch. The restoration is in part hypothetical, for although its position is obvious the actual leaf-trace is not seen in any section, and therefore its shape, direction, &c., are merely suggested, and possibly not the actual ones. A comparison of Fig. 6 with the series represented in the Text-fig. will show the general arrangement of the various parts. At *a*, Text-fig., which is a section below the node, the solenostele is seen to be of uniform thickness; *b* represents a section a little higher and nearer to the node. Fig. 1, Pl. LVIII, is a photograph of this same section. The solenostele is no longer of uniform thickness around its circumference. The dorsal portion which will very soon open to form the leaf-gap is slightly thicker than the remaining part of the stele. Diagram *c*, Text-fig., shows this dorsal thickening more markedly. In the next section, represented at *d*, the solenostele has become open in preparation for the departure of the leaf-trace, and the free margin of the leaf-gap is seen to be considerably thickened, owing to an increase in the number of tracheides at this point. The xylem ring at this point is at least twice as thick as in any other part, so that the free margin of the leaf-gap projects considerably towards the centre of the stem.

This thickening of the margin is of interest, a similar development having been described in several species of *Dicksonia* and *Davallia* by Gwynne-Vaughan.¹ It is regarded by him as a preliminary step in the formation of internal steles. A further step in this direction is seen in *Dipteris conjugata*, described by Seward and Dale.² In this fern the thickening of the margin of the leaf-gap extends through the internodes as well as the nodes, and this portion of the xylem has become almost completely separated off from the solenostele.

The anatomy of the fossil shows that *Solenostelopteris* must have occupied a similar position as regards the development of internal steles to *Dicksonia apiifolia* among recent ferns. In both these ferns the development is limited to a nodal thickening of the xylem of the free margin of the leaf-gap, without any indication of a separation of the thickened part of the xylem from the solenostele, as is seen in *Dicksonia adiantoides* and more clearly in *Dipteris conjugata*.

Section *e* shows a further change in the shape of the stele preparatory to the formation of the lateral shoot given off in connexion with the leaf-trace. The stele is seen to be considerably stretched in the horizontal plane, the region marked *b* being destined to form the branch. The limits

¹ Gwynne-Vaughan ('03), l. c.

² Structure and Affinities of *Dipteris*, &c. Phil. Trans., Series B, vol. cxciv, p. 499, and Fig. 4, 1901.

of the margins of the leaf-gap in this section cannot be accurately given, since the fossil is broken along the part indicated by dotted lines in *e*. The thickened margin is possibly almost complete, and did not differ much from its form in the previous section, *d*.

The other margin to which the leaf-trace must have been attached is probably more seriously damaged. The next section, *f*, of which Fig. 3, Pl. LVIII, is a photograph, shows the stele still more stretched, and the part *b* which is to form the branch is larger, but the actual leaf-trace is not preserved.

Section *g*, Text-fig. and Fig. 4, Pl. LVIII, shows the lateral branch now free from the main stele, though it is still joined up to the main stem by cortical tissues. The branch evidently became detached from the main stele by a gradual constriction of the xylem ring in quite a similar way to the departure of the branch in *Microlepia*. From an examination of the main stele it is obvious that at this level the leaf-trace had not yet departed, for the leaf-gap shows no signs of closing, and the free margin is still considerably thickened (Fig. 4, Pl. LVIII). It is suggested from a comparison with *Microlepia*, which *Solenostelopteris* resembles in many respects, that the leaf-trace would probably be a hook-like mass of xylem attached at the end of the elongated portion of the stele on the side of the branch, at about the point where the xylem is broken (Text-fig., *e* and *f*). The branch was thus on the same side of the rhizome as the leaf-trace, and became free from the main stele shortly before it. The vascular anatomy of the lateral shoot (Fig. 4 and Text-fig., *g*, *h*, *i*) is exactly like that of the main stem.

ROOTLETS.

Rootlet bundles are seen in many of the sections at different points on their way out through the cortex. In all cases they arise from the lower surface of the solenostele, i. e. the side remote from the leaf-gap. They are of the usual fern type—a diarch plate of xylem forming an almost circular mass with phloem on either side, a pericycle and clearly marked endodermis around (Fig. 8, Pl. LVIII).

While passing through the ground tissue of the stem the rootlets possess no ground tissue of their own, a feature noted by Gwynne-Vaughan in recent solenostelic ferns. The rootlet represented in Fig. 8 is the one seen at *r* in Fig. 3, in the sclerized tissue outside the solenostele. The groups of protoxylem (*p. x.*) show clearly at either side, also the development of metaxylem between. Unfortunately, in this particular rootlet, all tissues between the xylem and endodermis, which is quite similar to that surrounding the stele of the stem, are lost. The diarch plate of xylem is placed with its long axis tangential to the circumference of the solenostele, as is usual in recent ferns. The mode of origin of the rootlet is easily seen in

the various sections. A bulging of the xylem on the outer side of the ring is seen, which causes the phloem, pericycle, and endodermis to project outwards considerably. As this excrescence of the xylem grows it gradually becomes separated from the main mass of xylem (Fig. 7), the endodermis of each side of the rootlet bundle joins up, forming a complete ring, and so the rootlet becomes free from the solenostele.

A solenostelic fern very similar to but rather smaller than the one just described appears among the Japanese preparations in Dr. Stopes's possession, but unfortunately in only one slide of a series. The tissues of this stem agree very closely with those of *Solenostelopteris japonica*. As there is no gap in the solenostele, the section must have been taken through the internode of the rhizome. The xylem ring is composed of an irregular row of scalariform elements with scattered groups of smaller elements towards the outside in some parts. On each side of the xylem ring there is a well-marked layer of parenchymatous cells separating the xylem from the ring of phloem, which is made up of several layers of small sieve-tubes. The pericycle and endodermis can be seen on either side of the solenostele, the endodermis showing the same black, carbonized contents as were described in *S. japonica*. At one point a rootlet is seen arising from the stele in the manner described above. It seems probable, from a close comparison of the tissues, that this fern is merely a fragment of a smaller branch of the fern rhizome described.

DIAGNOSIS.

Solenostelopteris, gen. nov.

Rhizomes of fossil ferns, vascular system a solenostele.

S. japonica, sp. nov.

Rhizome dorsiventral, solenostele 1.8 mm. diameter (without cortex). Xylem elements scalariform, with one series of pits on each wall. Protoxylem exarch, scalariform. Internal and external phloem. Pericycle and endodermis well marked. Central ground tissue sclerized, with a layer of thin-walled cells separating it from the stele. Cortex with sclerized layer a short distance outside the stele, followed by thin-walled parenchymatous cells, probably with air spaces between; the outermost cortex consisting of hexagonal parenchymatous cells without intercellular spaces. Xylem of free margin of leaf-gap considerably thicker than the rest of the xylem ring, lateral branch given off on same side of stele as, and in connexion with, the leaf-trace.

Horizon. Upper Cretaceous.

Locality. Hokkaido, Northern Japan. Collected by Dr. M. C. Stopes.

Type. Stopes's Collection, Nos. I YA. 16-24.

AFFINITIES.

From the small fragment of the stem available and without any indication of what the external characters were, it is impossible to determine the definite affinities of the fern. The vascular anatomy is the only ground to work from, and the exact value of that as a factor in classification of ferns is yet hardly known; moreover, there is much necessary information concerning the vascular anatomy lacking, for the structure of the petiole and its connexion with the stem are not known. Many of the anatomical features resemble those in the more typical solenostelic forms of the Davallieae, in particular *Microlepia*. The marginal thickening of the xylem of the leaf-gap, which seems a point of considerable interest and importance, is developed to a similar extent in *Microlepia hirta*. The distribution of sclerenchyma, arrangement of xylem and phloem, &c., are also very similar in this species. Owing to our ignorance of the soral and sporangial characters, and the incompleteness of this, the only specimen of the plant, this account of *Solenostelopteris japonica* is necessarily a purely descriptive one. The specimen is interesting as affording an example of a definite stelar type common in recent ferns, but not previously described in detail among fossils. It also adds a new type to the Cretaceous Flora, as described by Stopes and Fujii.¹ We may perhaps venture to go so far as to recognize it as probable that the affinities of the fossil are with the typical solenostelic members of the Davallieae.

I wish to express my sincere thanks to Dr. Marie Stopes for so kindly placing her material at my disposal, and also for the helpful interest she has shown. To Dr. Lang, also, I am indebted for many useful suggestions.

DESCRIPTION OF PLATE LVIII.

Illustrating Miss Kershaw's paper on a Fossil Solenostelic Fern.

Fig. 1. Photograph of the solenostele below the leaf-gap, showing at *a* on the dorsal side of the stele the greater thickness of the xylem. *c. scl.*, central sclerized ground tissue; *s.*, thin-walled cells amongst sclerized ones; *x.*, xylem. (Slide I YA 17.)

Fig. 2. Drawing of a small part of the solenostele, showing details of anatomy. *o. per.*, *i. per.*, outer and inner pericycle; *o. end.*, *i. end.*, outer and inner endodermis; *o. ph.*, *i. ph.*, outer and inner phloem; *p. x.*, protoxylem; *par.*, parenchymatous cells. (Slide I YA 16.)

¹ Stopes and Fujii ('10), Studies on the Structure and Affinities of Cretaceous Plants. Phil. Trans. Roy. Soc., London, Series B, vol. cci.

Fig. 3. Photograph of the rhizome, showing leaf-gap with one margin considerably thickened, and the beginning of the lateral branch. *o. c.*, outer cortex; *i. c.*, inner cortex (crushed); *r.*, rootlet in cortex (enlarged in Fig. 8). Other lettering as in Figs. 1 and 2. (Slide I YA 21).

Fig. 4. Photograph of the rhizome, showing main stele with leaf-gap still open, and the stele of the lateral branch now separate. (Slide I YA 22.)

Fig. 5. Group of xylem elements, showing pits between adjacent vessels.

Fig. 6. Diagram of the probable relation of stele, leaf-trace, and lateral branch at a node of *Solenosteleopteris japonica*.

Fig. 7. Drawing of stele of rootlet which is about to become separate from the solenostele.

Fig. 8. Rootlet in cortex; the stele surrounded by endodermis but with no cortex of its own.

Hoth, lith et imp

Kershaw, Edith May. 1910. "A fossil solenostelic fern." *Annals of botany* 24, 683–691. <https://doi.org/10.1093/oxfordjournals.aob.a089299>.

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