THE ORIGIN OF SIPHONOSTELE IN THREE SPECIES OF *SELAGINELLA* SPR.*

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Introduction

Several types of steles are found in the vascular plants, but in the earliest of these plants, such as, the Psilophytales, the Psilotales, several fossil and living Lycopodiales and a few of the living ferns, particularly in their seedling stages, the axes are characterised by a solid hadrocentric stele. This solid xylocentric stele is, therefore, taken to be the primitive stele or the *protostele* from which all the other types of steles are believed to have been derived in the course of phylogenetic specialisation.

One of such derivatives is the *siphonostele* with pith or medulla in the centre. Two types of siphonostele are met with, the *ectophloic siphonostele* and the *amphiphloic siphonostele.* The former has phloem only on the outside of the tubular xylem. This is by far the most common type found in the axes of Gymnosperms and Angiosperms[5] and in ferns, like Osmunda. The amphiphloic siphonostele, on the other hand, has phloem on both sides of the xylem cylinder and is represented in the living ferns, like *Adiantum, Pteris, Osmunda cinnamomea, Todea hymenophylloides,*[7] *Ophioglossum vulgatum, Botrychium Lunaria,* etc., and also in some families of herbaceous Angiosperms.[5]

So far *three* possible ways of pith formation have been suggested : (1) The pith is the included cortex or the fundamental tissue. Hence its origin is *extrasteler.* (2) The pith represents the undifferentiated xylem elements. Hence the origin is *intrastelar.* (3) The pith is partly extrastelar and partly intrastelar in origin, as in the Osmundaceæ and Ophioglossaceæ.[2]

According to Van Tieghem (1890), Jeffrey,[8] Gwynne-Vaughan,[2] Tansley,[14] and Boodle,[1] the pith is extrastelar in origin in the rhizomatous solenostelic (= siphonostelic) ferns. Jeffrey[9] further stated that *in all cases* the pith *must* be regarded as derivatives of the cortex, *i.e.,* the origin of pith in all cases is extrastelar.

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From his extensive studies of the anatomy of Pteridophytes, both fossil and living, Bower[3] generalises that the origin of the medullation is determined by two factors, *viz.*, the position of axes and insertion of the appendages. He concludes that (1) in all upright columner microphyllous stems the pith is tracheary in origin, *i.e.*, intrastelar, and he cites Lepidodendreæ and the cone of living *Selaginella spinulosa* as examples; (2) in all creeping megaphyllous shoots, *e.g.*, the rhizomatous ferns, the pith is extrastelar in origin (p. 562). Eames and MacDaniels[5], however, think that it has been established beyond doubt that in seed plants at least the pith is morphologically extrastelar; in most of the Pteridophytes the same condition obtains, probably in a few the pith is intrastelar in nature (p. 114).

Thus there is still a divergence of opinion as to the origin of pith in the microphyllous upright stem of the Pteridophytes. A great difference of opinion also prevails with regard to the origin of the internal phloem and internal endodermis of the amphiphloic siphonostele. It will, therefore, be interesting to follow the origin of pith in three of the most specialised species of Selaginella with upright microphyllous axes.

These are: *S. inæqualifolia* Spr., *S. Wallichii* Spr., and *S. canaliculata* Baker. Specimens of *S. inæqualifolia* were procured from the Orchid House of the Royal Botanic Gardens, Calcutta, and those of *S. Wallichii* and *S. canaliculata* were supplied by a student from his garden house at Dumdum, a suburb of Calcutta. All the three species were kindly identified by the Curator of the Herbarium, Royal Botanic Garden, Calcutta. The observations are based upon freehand sections cut serially from base upwards of materials preserved in formol-acetic-alcohol and stained in safranin and fast green.

Observations

S. inæqualifolia (Figs. 1–3) is tri-stelic with an accessory stele in the upright stem. The accessory stele gradually enlarges and unites with one of the lateral steles to form the siphonostele in the upper region of the stem, and in so doing encloses a mass of extrastelar ground tissue which forms the pith. In this case, therefore, the pith is distinctly extrastelar in origin.

S. Wallichii (Figs. 4–7) is also tri-stelic with an accessory stele in the lower region of the upright stem. Here also the accessory stele enlarges and unites with a lateral stele to form the amphiphloic siphonostele. In this species almost all the stages in the origin of the siphonostele from separate steles can be traced. The pith is clearly extrastelar in origin, and the character of the pith cells are strikingly similar to those of the cortical cells. The similarity in this case is certainly not " merely physiological " as is assumed by the opponents of the theory of the extrastelar origin of pith.

S. canaliculata (Figs. 8–12) resembles the other two species in having almost the same structure in the upright stem. Here also the siphonostele in the upper region of the stem has been formed by the union of a lateral and the accessory steles, and more or less a complete series in its origin can be followed. The stage shown in Fig. 12 appears to be different from any described above. It seems that a single stele has enlarged and bent in such a way that the two free ends have come to meet with the result that a mass of extrastelar ground tissue has been enclosed. A siphonostele with pith has thus been formed.

Discussion

So far as the writer is aware only two cases of medullations in living *Selaginella* have been reported : one in the creeping rhizome of *S. lævigata* Baker var. *Lyallii* Spr., reported by Gibson[6] where the stelar arrangement very closely resembles that of a typical Filicinean amphiphloic siphonostele with ramular gaps. Bower[3] admitted with Jeffrey[9] that the pith in this case is extrastelar in origin and cites the case as an illustration of his hypothesis that the origin of pith in *creeping microphyllous* form may be extrastelar by adjustment to resemble that in rhizomatous ferns.

The other case is the axis of the strobilus of *S. spinulosa* A. Br. reported by Bower,[3] who found pith in all stages of development in the stele in serial sections from base upwards. He regarded this to be a clear case of intrastelar origin of pith in a stem where there were no ramular or foliar gaps " to provide that continuity with the cortex without which cortical intrusion cannot take place". But a doubt certainly arose in his mind as to the real nature of this pith when a longitudinal section through the strobilus revealed the tracheidal nature of its cells (elongated), and the presence of nucleus and protoplasm in them. Prof. Bower anticipated that " it may be argued that the softer central tissues are merely the result of imperfect development of tracheids and that they would mature into tracheids later," but stated " that the tissue have the appearance of maturity while the condition of the sporangia and of the strobilus as a whole shews that further development is not to be expected." Convinced thus of the intrastelar origin of pith in the strobilus of *S. spinulosa* he cited this case as an illustration of his general hypothesis that the origin of pith in the upright microphyllous stock is always intrastelar.

Mitchell,[11] who also worked out the anatomy of the strobilus in *S. spinulosa*, on the other hand, reported that the vascular system of this organ is essentially simpler than it is in the vegetative axis. It has a single vascular chord with typically 8 marginal protoxylem groups. The metaxylem consists of small elements which are frequently not thickened towards the centre and there may be more or less a well-marked procambial area extending from the tip downwards.

It may, therefore, be suggested that the so-called pith which Prof. Bower observed in the strobilus of this species, but the presence of which has not been corroborated by other workers in the young or mature, upright or creeping stem, is a collection of undeveloped tracheids or ill-differentiated metaxylem. A comparison of the figures given by Bower (Figs. 1 and 5, Pl. XLVII), Gibson (Fig. 3, Pl. IX) and Mitchell (Fig. 9, Pl. VIII), strengthens the suggestion made here. Other examples of this type are not rare. Prof. Gwynne-Vaughan in the sporeling of *Osmunda regalis* noticed the presence of parenchymatous cells surrounding xylem tracheids, which he thought " may be undifferentiated cells in the process of differentiation as they still have well-developed nuclei." Bower's figure of the t.s. of the rhizome of *Ophioglossum reticulatum* points to the possibility of the few parenchymatous cells noticed in the otherwise solid xylem core as being still undifferentiated tracheids. The present writer's observation on the structure of the creeping stolons that are annually given off from the base of the erect rhizome of *Nephrolepis exaltata* Schott. shews that the central procambium takes a very long time to differentiate into metaxylem proper.

When the above facts are taken into account with the mode of the origin of the medullation in the upright stems of the three species of *Selaginella* described in this paper Prof. Bower's general hypothesis of the intrastelar origin of pith in the upright microphyllous forms seems to need revision. It is seen that the medullation here has nothing to do with the ramular or foliar gaps, and the pith is definitely of extrastelar origin. The presence of internal phloem and internal endodermis is satisfactorily explained as due to the origin of the amphiphloic siphonostele from the polystelic condition and as a result of fusion of more than one steles. One need not conceive of their origin (or presence) as " entirely *de novo* ", or by " decurrency through the branch gaps into the pith ", or by " involution at the leaf gap," or by " gradual encroachment upon the pith and then by invagination," or that in their origin they " crept round the edges of the branch gaps," or " have subsided into them ".

Selaginella belongs to the class Lycopsida where the steles are not characterised by leaf gaps, and there is no provision in their living representatives for secondary growth in their axes. The axes of the species under investigation grow erect and sometimes attain a great length. To meet the increasing demand for conducting and mechanical tissues the vascular cylinder here enlarges not by the activity of a cambium which is absent, but by increasing the number of steles which results in the polystelic condition observed in these species. A similar conclusion was previously reached by Scott[12] working on the origin of polystele in dicotyledons. He stated that the need for the enlargement of the vascular system is met by increasing the number of steles rather than the size of a single central cylinder. Bower[4] also developed the same idea of the expansion of the conducting and mechanical tissues in his *Size and Form in Plants*.

Conclusion

The observations recorded in the foregoing pages thus warrant the following general conclusion with regard to the origin of the amphiphloic siphonostele in *Selaginella*:

The origin of the siphonostele in *Selaginella* is correlated with the polystelic condition and the amphiphloic siphonostele originated as a result of a fusion of a number of separate steles. The polystelic condition probably originated in response to the necessity of increasing the amount of conducting and mechanical tissues in the absence of provision for secondary growth. The pith is extrastelar in origin and the presence of internal phloem and internal endodermis is directly due to the origin of the siphonostele from the polystelic condition.

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EXPLANATION OF FIGURES IN PLATES VI AND VII

All figures are photomicrographic representations

FIGS. 1–3, Plate VI. *S. inæqualifolia* Spr.—Transverse sections at different levels of the upright stem. Stages shewing the union and coalescence of the ventral lateral and accessory steles to form the amphiphloic siphonostele with extrastelar pith.

FIGS. 4–6, Plate VI and FIG. 7, Plate VII. *S. Wallichii* Spr.—Same as above. The stages are more complete.

FIGS. 8–12, Plate VII. *S. canaliculata* Baker.—Same as above. Fig. 12 shews a stage where the lateral stele alone appears to have formed the siphonostele.