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## PHLOEM HISTOLOGY IN STIGMARIAN APPENDAGES

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**Introduction.**—Superficial comparisons between the fossil stigmarian appendages and the roots of *Isoetes* have been made by several authors. They noted a horse-shoe shaped cavity about a somewhat excentrically placed monarch vascular bundle (cf. Figs. 1 and 2), as characteristics common to the appendages of *Stigmara* and *Isoetes*.<sup>2,3</sup> It has been concluded by some that the location of phloem in stigmarian appendages is the same as in the roots of *Isoetes*,<sup>4</sup> but there has been no conclusive histological evidence for this identification. Since the appendages of these two plants showed striking similarities,<sup>5</sup> it was reasonable to assume that the phloem of the stigmarian appendages was located in the same relative position as it was in the

roots of *Isoetes*. The present paper provides proof of this assumption and because of the excellence of preservation in the American specimens studied, the character of the phloem in the stigmarian appendages can be described in detail.

The coal balls studied were provided by the Coal Division of the Illinois State Geological Survey. They are represented by coal balls No. 128 and No. 188 of the Illinois Survey collections. Permanent slides were made with the aid of the improved nitro-cellulose "peel" technique modified after Graham.<sup>6</sup>

**The "Phloem Zone" of the Stigmarian Appendage.**—The "phloem zone" of the stigmarian appendage is located next to the metaxylem of the monarch vascular bundle on the side away from the pro-

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<sup>2</sup>Scott, D. H. Studies in Fossil Botany, I. A. & C. Black Ltd. London, 217-239, 1920.

<sup>3</sup>Lang, W. H. On the Apparently Endogenous Insertion of the Roots of *Stigmara*, Mem. Proc. Manchester Lit. Phil. Soc. VIII, 68:101-106, 1923.

<sup>4</sup>Williamson, W. C. Monograph on Morphology and Histology of *Stigmara flooides*. Palaeontographical Society, XL:1-43, 1886.

<sup>5</sup>Eames, A. J. Morphology of Vascular Plants. McGraw, Hill & Co. New York, 354-365, 1936.

<sup>6</sup>Graham, Roy. Preparation of Palaeobotanical Sections by the Peel Method. Stain Technology, 8:65-68, 1933.

toxylem point. (Ph., Figs. 6, 7). It is a cap of tissue four to six cells thick. In cross section the cells of the "phloem zone" vary from isodiametric to rectangular in shape, as shown in figures 5 and 7, while longitudinal sections show them to be long rectangular cells with a ratio of 3-8 to 1, as in figure 4.

*The Cell Wall.*—In some appendages, the radial and tangential walls of the cells that make up the "phloem zone" are rather thick (Fig. 6), while in other apparently younger specimens these walls are very delicate (Fig. 7).

The end walls of the "phloem zone" cells are best observed in cross section. The end walls are not complete, but are marked by scalariform and reticulate thickenings (Fig. 5). In position and structure these appear to be sieve plates divided into sieve fields. Longitudinal sections show further evidence of these sieve plates by the incomplete nature of the end walls (Fig. 4).

*Cell Contents.*—Lying on both sides of the sieve plates are curious cap-like deposits of brown, glistening, translucent substance. On the basis of structure and location these may be interpreted as callus plugs of old phloem elements (CP, Fig. 4). On the surfaces of the radial and tangential walls of the cells of the phloem is a thin irregular layer of flocculent material that may be interpreted as coagulated cytoplasm. Its position, and the generally excellent preservation of the material, make this interpretation plausible. Nearly every cell of the phloem which was cut in a longitudinal direction shows the presence of a single dark ovoid body. These bodies were examined carefully by several biologists who did not hesitate to call them nuclei (Nuc., Figs. 4, 5), lending further support to the belief that this fossil material shows fairly good cytological fixation. Since the nuclear bodies do not occur in the adjoining xylem cells, it does not seem that they can be interpreted as artifacts.

*Comparison of the Phloem of Stigmairian Appendages with the Phloem of the Roots of Isoetes.*—The root trace phloem of *Isoetes* is located next to the metaxylem of the monarch vascular bundle opposite the protoxylem point (cf. Ph., Fig. 2) similar to the relative position of xylem and phloem in the stigmairian ap-

pendages. In the modern plant the phloem consists of a layer of tissue 1-3 cells thick. These cells, though much smaller than the corresponding cells of the stigmairian appendage, are similar in form. In cross section they vary from isodiametric to rectangular in shape. In longitudinal section they are long, narrow rectangular cells with a ratio of 8-10 to 1 (cf. Fig. 3). The main difference, aside from actual size (cf. scales of magnification in connection with figures), is that the cells of the *Isoetes* root phloem are relatively a little longer than those of the stigmairian appendage.

*The Cell Wall.*—The cells which make up the root phloem of *Isoetes* are true sieve tube elements.<sup>7</sup> Their thin radial and tangential walls are covered with lattices where they come in contact with another sieve tube element. The end walls of these sieve tube elements show scalariform sieve plates, essentially similar to the sieve plates illustrated in the phloem of the stigmairian appendages.

*The Cell Contents.*—Callus plugs have not been reported in the root phloem of *Isoetes*. This is probably due to the fact that the roots last for only one growing season of about seven months, and then are shed along with the old secondary cortex of the main axis. Since callus plugs are characteristic of old phloem cells, it seems probable that the stigmairian appendages were longer lived than the roots of *Isoetes*.

The cytoplasm is peripheral, similar in location to the apparent cytoplasm of the cells of the stigmairian phloem.

An unusual feature of all the phloem cells of *Isoetes* is the presence of degenerate nuclei which are about half the size of a normal nucleus. They stain a brilliant red with safranin and appear to be extremely dense (Nuc., Fig. 3). If the nuclei of the cells that make up the phloem of the stigmairian appendages were of this same dense degenerate nature, their preservation in well preserved fossil material would not be unlikely.

*Conclusions.*—On the basis of this detailed anatomical study of the phloem cells of stigmairian appendages, which showed the presence of callus plugs, sieve plates, cytoplasm and nuclei, it is evident that this tissue is true phloem composed chiefly if not entirely of sieve tube

<sup>7</sup>West, C. and Takeda, H. On *Isoetes japonica*. Trans. of Linn. Soc. London 8:333-369, 1913.

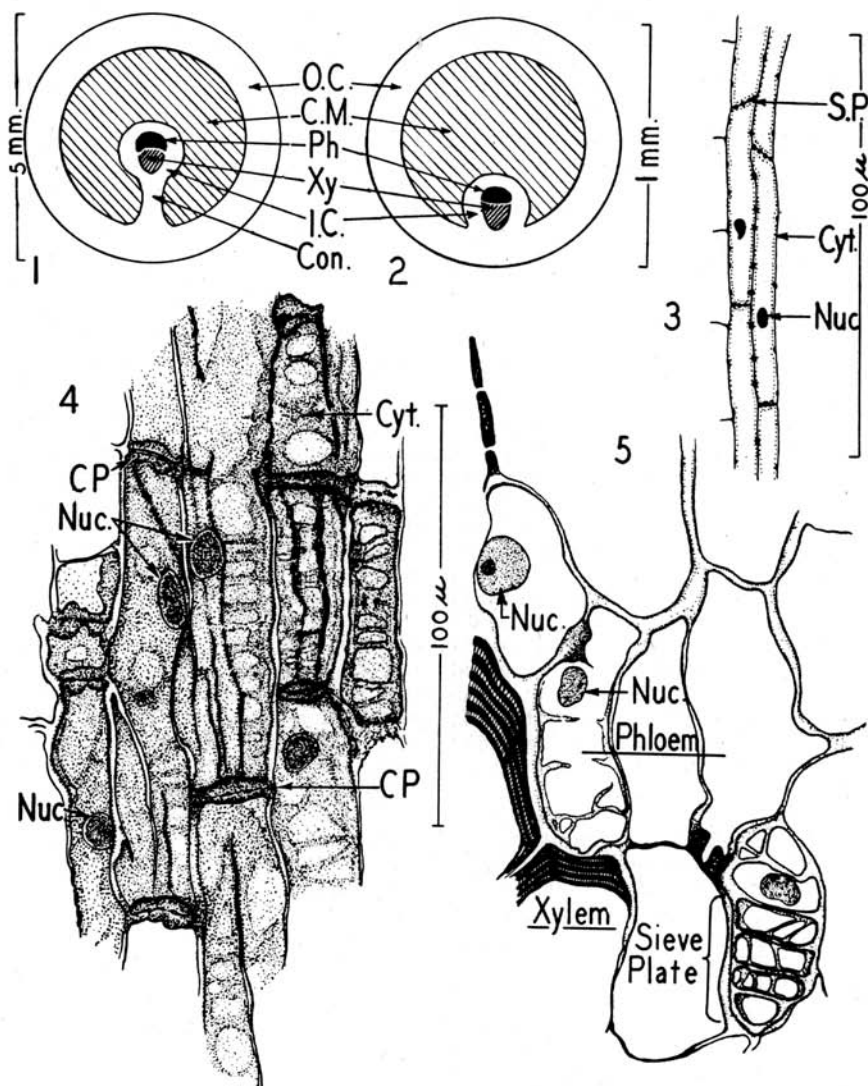


Fig. 1. Diagrammatic cross section of a stigmarian appendage. O.C., outer cortex; C.M., cavity of the middle cortex; Ph, phloem; Xy, xylem; I.C., inner cortex; Con., connective.

Fig. 2. Diagrammatic cross section of a root of *Isoetes*. For abbreviations see Fig. 1 above.

Fig. 3. Longitudinal section of the root trace phloem of *Isoetes*. S.P., sieve plate; Cyt., cytoplasm; Nuc., nucleus.

Fig. 4. Longitudinal section of the phloem of a stigmarian appendage. From 128B (T1) Ill. Geol. Survey collection. C.P., callus plug; Nuc., nucleus; Cyt., cytoplasm.

Fig. 5. Cross section of the phloem of a stigmarian appendage. From 188B<sub>1</sub> (T1), Ill. Geol. Survey collection. Nuc., nucleus.

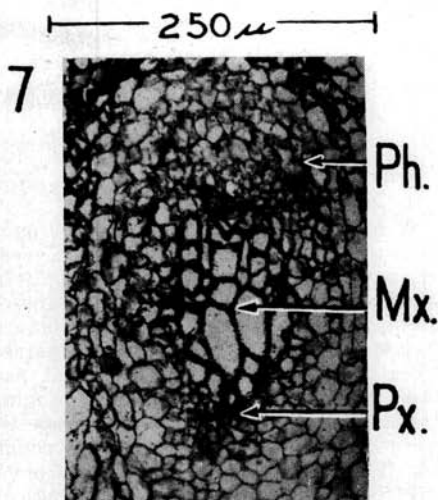
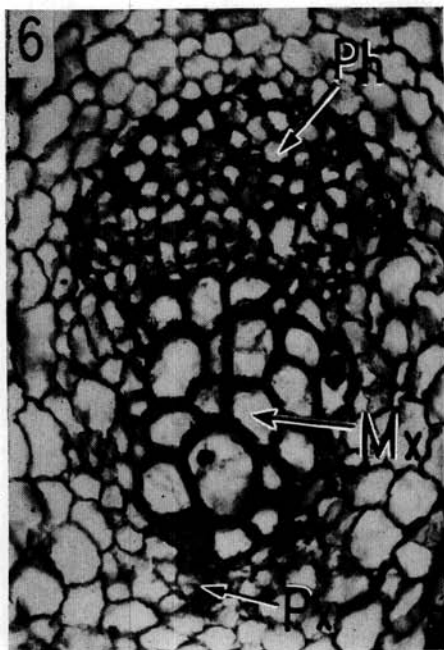


Fig. 6. Cross section of the vascular bundle of a stigmarian appendage showing the cap of thick-walled phloem and its relation to the xylem. From 188C<sub>1</sub>(T3). Ph., phloem; Mx., metaxylem; Px., protoxylem.

Fig. 7. Cross section of a small vascular bundle of a stigmarian appendage showing a cap of delicate thin-walled phloem and its relation to the Xylem. From 188C<sub>1</sub>(T1). Ph., phloem; Mx., metaxylem; Px., protoxylem.

elements. The position and shape of the cells, the scalariform sieve plates on the end walls of the cells, the presence of nuclei in the cells, all are characteristics duplicated in the root phloem of *Isoetes*, which lacks companion cells.

The greatest point of disparity between *Isoetes* roots and stigmarian appendages is in the absolute size, both in gross

anatomy and in the cells themselves. In addition to the similarity of phloem reported above, there are many other points of agreement between *Stigmaria* and *Isoetes* which are to be dealt with in a more extensive paper. The evidence is strongly in favor of a homologous interpretation of stigmarian appendages and *Isoetes* roots.