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A COMPARATIVE STUDY OF STIGMARIAN APPENDAGES AND ISOETES ROOTS

BY

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A COMPARATIVE STUDY OF STIGMARIAN APPENDAGES AND ISOETES ROOTS [1]

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THE ROOTS of *Isoetes* and the appendages of *Stigmaria* have been studied in an effort to determine whether the stigmarian appendages are specialized leaves borne on a rhizome, as suggested by Solms-Laubach (1891) and recently entertained by Schoute (1938), or true roots arising from a rhizophore, as concluded by Lang (1923), and Scott (1920). The purpose of this paper is to furnish further anatomical evidence on this controversial question which has been discussed by many other eminent botanists and paleobotanists since the time of Williamson's monograph on the morphology and histology of *Stigmaria ficoides* (1886). Schoute (1938) has compiled a résumé of the literature concerning this problem.

MATERIALS AND METHODS.—Coal balls containing specimens of *Stigmaria* were studied from sections prepared by the nitrocellulose "peel" method, essentially the same as given by Graham (1933). The specimens studied showed excellent preservation of histological detail.

All of the coal balls are of Pennsylvanian age. They were obtained from the collection of the Illinois State Geological Survey[2] which includes specimens assembled by the late Professor A. C. Noé and by Dr. J. M. Schopf.

Living material of *Isoetes macrospora* was collected from Clear Crooked Lake in Vilas County, Wisconsin. Anatomical studies of this species of *Isoetes* were made by the author from preparations made by the paraffin method.

THE GENERAL CHARACTERISTICS OF STIGMARIA.—*Stigmaria* is a generic name applying to organs belonging to a group of fossil lycopsid plants. They are dichotomizing root-like axes and appendages of the arboreal lycopods of the Carboniferous period. Lack of notable specialized characters has thus far prevented a satisfactory classification into groups as small as those designated as genera among modern plants.

The dichotomous stigmarian axes as described by Williamson (1886) may attain a length of slightly more than 37 ft. A habit sketch is shown in fig. 1.

The surface of the axes is generally smooth with spirally arranged shallow pits which indicate the points at which the stigmarian appendages were attached (fig. 2). The habit of the stigmarian axis and appendage system suggests a broad shallow root system similar to that noted in modern swamp plants.
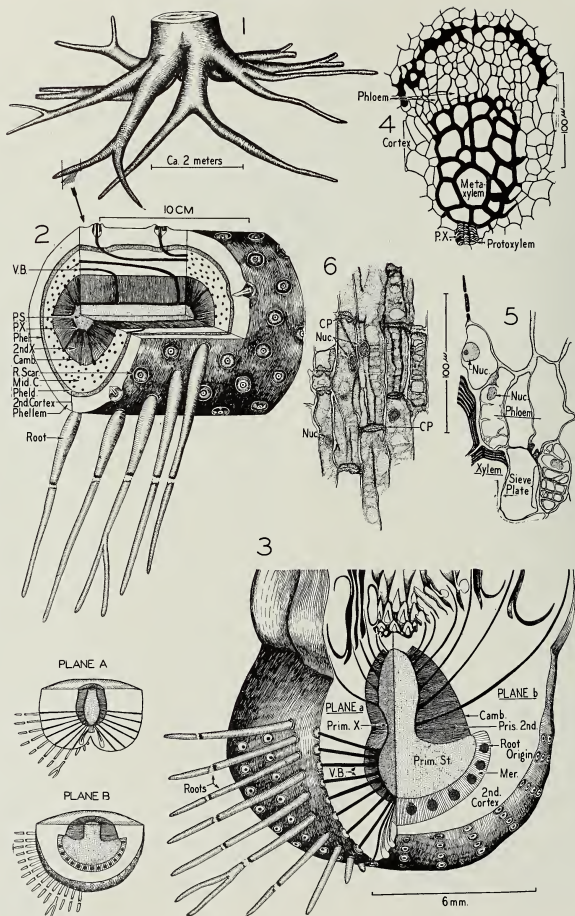
The observations made by Williamson (1886) led him to conclude that the stigmarian axes were roots. Subsequent researches have shown the stigmarian axes to have stem-like, not root-like characters. Many are similar to those of stems of *Lepidodendron* as pointed out by Leclerq (1930), Scott (1920) and Seward (1910). The aerial stems of *Lepidodendron* in common with the stigmarian axes show: (1) cambial activity producing a large cylinder of secondary wood composed of scalariform tracheids; (2) a well developed middle cortex; (3) a thick band of so-called "periderm" on the outside. These and other features have been incorporated in the diagrammatic drawing of the stigmarian axis shown in fig. 2.

THE STIGMARIAN APPENDAGES.—The appendages of *Stigmaria* present features of an anomalous type. They project from the axis in a spiral arrangement which is similar to a phyllotaxis (fig. 2). With the exception of their arrangement on the axis, the appendages are very root-like in external appearance. They show a dichotomous branching which is characteristic of the roots of many primitive plants. The presence or absence of root hairs and a root cap does not appear to have been determined with certainty. Schoute (1938) reports that they are absent but the evidence is not clear. There is also some controversy as to whether the appendages of *Stigmaria* were endogenous in origin as are the roots of most plants (Lang, 1923), or exogenous, similar to ordinary leaves. There is little proof of the nature of the appendages on the basis of these conventional criteria alone.

The appendage bundle.—The appendage bundle lies at a wide angle inclined slightly distal with reference to the main axis as seen in fig. 2. The first indication of the beginning of the appendage bundle is with the outward deflection of a solitary protoxylem element. The protoxylem elements lie between the pith and the larger metaxylem elements at the inner edge of the secondary wood (fig. 2). Thus the arrangement of the primary xylem of the main axis is endarch. Other protoxylem elements and larger metaxylem elements are added adjacent to the deflected protoxylem element as it traverses the broad vascular ray of the secondary xylem of the main axis (fig. 11, 13 and 14). As they pass through the vascular ray, these primary elements are in turn supplemented by pitted secondary xylem elements which are connected with the surrounding secondary wood of the main axis (fig. 11, 13 and 14). The continuity between the pitted elements of the main axis and the pitted elements of the appen-

dage bundle may indicate the origin of secondary growth in the appendage bundle.

It has been pointed out by Williamson (1886) and Solms-Laubach (1891) that the arrangement of the xylem in some of the appendage bundles appears to be diarch or even triarch, because of the presence of more than one group of small xylem elements lying adjacent to the larger metaxylem elements (fig. 8). Such "protoxylem" apparently was identified in transverse sections on the basis of size of the elements alone, without regard to the type of wall thickenings. Elements of authentic protoxylem have chiefly annular, sometimes spiral thickenings on their walls, while secondary xylem elements show characteristic scalariform pitting (fig. 7). From longitudinal serial sections which have been prepared of similar "polyarch" bundles, it has been observed that all but one of the groups of small xylem elements of a "polyarch" bundle have scalariform pitting of their walls characteristic of secondary xylem elements. Only one group of small xylem elements has spiral or annular thickenings of protoxylem elements. It is evident that the vascular supply of the stigmarian appendage is monarch as described by Scott (1920) and not a polyarch arrangement of the xylem elements.

The small secondary xylem elements of the appendage bundle connect with a layer of small secondary xylem elements at the periphery of the secondary wood of the main axis. This layer has been called the "growth zone" (fig. 12). It can be concluded that the small elements of the appendage bundle which are continuous with the cells of the "growth zone" do not constitute additional protoxylem points.

The "phloem zone."—Adjacent to the xylem of the appendage bundle on the side away from the protoxylem, there is a cap of tissue which has been designated by several writers as the "phloem zone" (fig. 4). Its identification was arrived at previously by its position in relation to the xylem of the bundle. The bundle was thus considered collateral in structure and comparable with a normal leaf trace.

A detailed study of the histology of the "phloem zone" in some exceptionally well-preserved stigmarian appendages gives positive evidence that this tissue is phloem, as described by the author (1940). Longitudinal sections show curious deposits on the end walls of the elongate cells that make up the "phloem zone." These deposits, shown in fig. 6, are interpreted as callus plugs. In the fossil material they are translucent and distinguishable from cell walls and cell contents. A cross-section of the same area shows that the end walls of some of these cells possess a network of bands which may have separated the numerous sieve fields of a compound sieve plate (fig. 5). There is some evidence that sieve areas are also present on the longitudinal walls of the phloem cells as well as on the end walls (fig. 6). These characters indicate that the cells can be regarded as sieve tube elements and may serve as a histological basis for the identification of the phloem.

Cross sections of the appendage bundles as they pass through the secondary cortex of the main axis also show the presence of phloem. The manner in which the phloem joins the main axis has not been determined, because tissues are poorly preserved around the periphery of the woody cylinder in the region of the cambium and phloem.

It is of added interest to note that in both cross and longitudinal sections of the phloem, there appear within some of the cells ovoid bodies (fig. 5 and 6). The shape, the frequency and the relative size of these bodies within the phloem suggest nuclei.

The inner cortex.—The inner cortex of the appendage surrounds the vascular bundle (fig. 15), and judging from the small size of the cells of which it is composed, this tissue is not comparable with the large cells of the secondary cortex of the main axis (fig. 21). It seems probable that this tissue was laid down by the terminal meristem of the appendage, as it grew outward through the tissues of the main axis. The inner cortex maintains its position about the appendage bundle as it traverses the secondary cortex of the main axis (fig. 21, 20, 19), and it maintains this position in the free portion of the stigmarian appendage (fig. 18).

The middle cortex.—The cells of the middle cortex of the mature appendage can first be seen within and near the periphery of the secondary cortex of the main axis. It is represented by a crescent shaped area of cells lying part way around the cells of the inner cortex (fig. 20). At this point, the appendage bundle and the inner cortex surrounding it appear to be excentrically placed. The parenchyma cells of the middle cortex of the appendage lying within

Fig. 1–6.—Fig. 1. Habit drawing of stigmarian axes showing the characteristic dichotomy of the axes and the spiral arrangement of appendages.—Fig. 2. Three dimensional diagram of a stigmarian axis segment showing the relationship of the appendages to the axis, as well as its internal anatomy. V. B., vascular bundle; P. S., protostele; P. X., primary xylem; Phel., phellogen; 2nd. X., secondary xylem; Camb., cambium; R. Scar, root scar; Mid. C., middle cortex; Pheld., phelloderm.—Fig. 3. Three dimensional drawing of the "corm" of Isoetes showing the relationship of the roots of the rhizophore to the main axis and essential details of internal structure. Camb., cambium; Pris., 2nd., "prismatic" layer made up of secondary xylem, secondary parenchyma; Mer., meristem of rhizophore; Prim. X., primary xylem; V. B., vascular bundle. Small drawings at the left show actual details of internal structure of the *Isoetes* "corm" in opposite vertical planes to correspond with the half sections (Planes a and b) combined in the three dimensional drawing.—Fig. 4. Cross-section of the vascular bundle of a mature stigmarian appendage, showing the relationship of the phloem to the xylem elements.—Fig. 5. Cross-section of the phloem of the stigmarian appendage showing the detailed anatomical structure. Nuc., nucleus.—Fig. 6. Longitudinal section of the phloem of the stigmarian appendages showing the detailed anatomical structure. C. P., callus plug.; Nuc., nucleus.

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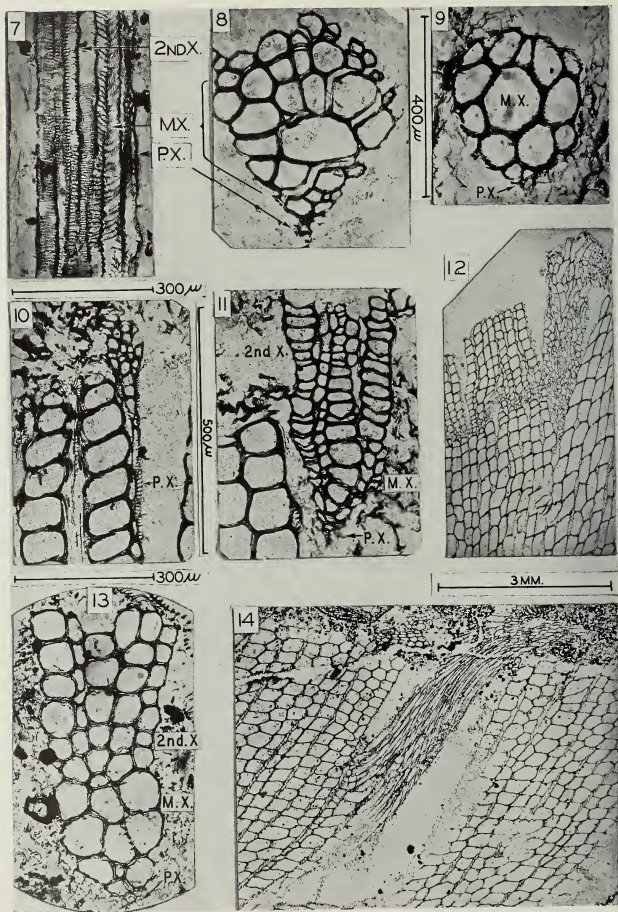
the secondary cortex of the main axis are delimited by a plate of small cells with dark contents. This plate of cells has been termed the "rootlet cushion" (fig. 16 and 20) by previous authors. The cells of the middle cortex of the appendage remain intact for only a short distance after the appendage becomes free from the tissues of the main axis (fig. 16). They then give way to an open crescent shaped cavity devoid of tissue (fig. 16 and 18) which is typical of free stigmarian appendages.

The connective.—The connective is a band of parenchyma found in the free appendage, connecting the outer cortex with the more or less centrally placed vascular bundle and inner cortex (fig. 15 and 18). It is derived from the cells of the middle cortex of the appendage as a remnant which persists after the remainder of the middle cortex cells has broken down. There is little histological difference between the tissues of the middle cortex and the connective. The tissue of the connective may also break down and it is not demonstrable in many of the appendages, particularly those poorly preserved or at a distance from the main axis. The connective is often characterized by stray protoxylem elements some of which are continuous with the protoxylem point of the vascular bundle and some of which are continuous with scattered transfusion elements lying in the tissue of the outer cortex at the base of the connective, indicated diagrammatically in fig. 15.

The outer cortex.—The outer cortex is persistent the entire length of the free appendage. It is composed of isodiametric parenchymatous cells which are somewhat differentiated into two poorly defined layers (fig. 18). The outermost layer, which is three to four cells in thickness, is made up of small cells which are continuous with the outermost tissues of the secondary cortex of the main axis. The inner layer is composed of larger cells five to six cells in thickness, and is continuous with the larger, deeper lying cells of the secondary cortex of the main axis. No epidermal layer is definable, nor is any cuticle in evidence in the mature appendage. There is no indication of root hairs or any sort of trichomes extending from the outer cortex and it does not seem that there was any special adaptation for water absorption. If these plants were growing in

swampy environment, as has been suggested, the absorbing surface presented by the smooth appendages would probably have fulfilled the water requirements of the plant.

THE STIGMARIAN "PERIDERM."—As previously stated, the outer cortex of the appendage is continuous with the peripheral tissues of the main axis (fig. 16). This peripheral axis tissue has been called "periderm" but study of the stigmarian axis shows that it has features which do not wholly coincide with the present day conception of periderm tissue. The "periderm" of stigmarian axes (fig. 2 and 17) consists of three layers which have been called respectively phellem, phellogen, and phelloderm by Kisch (1913).

The phellogen in *Stigmaria* is represented by a poorly defined single row of flattened cells which lies just inside the phellem (fig. 2 and 17). Besides producing phellem centrifugally (fig. 2 and 17), the phellogen produces a relatively narrow band of phelloderm centripetally. The cells of the phelloderm are small, they lie in radial rows, and apparently do not undergo further division after their formation by the phellogen.

The phellem of living plants is characterized by compact radial rows of dead cells, whose walls are highly suberized. Study of the stigmarian phellem indicates that the cells of the phellem apparently retained their capacity for growth indefinitely and underwent repeated divisions after their formation by the phellogen. They form an outer layer of loosely arranged parenchyma cells whose walls show no signs of thickening. Among the living lycopods, the secondary cortex of *Isoetes* offers a close analogy to this condition (fig. 3 and 28). The suggestion of A. C. Seward (1910) that the term secondary cortex is applicable to the outer band of secondary parenchyma tissue of the mature stigmarian axis, seems entirely appropriate and should therefore replace the term "periderm" in this connection.

COMPARISON OF STIGMARIAN APPENDAGES AND THE ROOTS OF ISOETES.—The roots of *Isoetes*, which have been described by Scott and Hill (1900), Stokey (1909) and many other authors, are much smaller than the appendages of *Stigmaria*. They both have dichotomous branching (fig. 3). The arrangement

Fig. 7–14.—Fig. 7. Longitudinal section of the vascular bundle of the stigmarian appendage showing the relationship of the secondary xylem and metaxylem to the single protoxylem point. The scalariform pitting of the secondary xylem, the spiral thickening of the metaxylem, and the annular thickening of the protoxylem can be noted.—Fig. 8. Cross-section of the vascular bundle of the appendage of *Stigmaria* showing the small peripheral secondary elements, on the side away from the protoxylem point, which have been misinterpreted as additional protoxylem elements.—Fig. 9. Cross-section of the typical stigmarian appendage bundle. Note the absence of secondary xylem. M. X., metaxylem; P. X., protoxylem.—Fig. 10. Cross-section at the periphery of the secondary wood of the main axis of *Stigmaria* showing a small appendage bundle leaving the secondary wood. Note that there is no sign of any secondary thickening in this appendage bundle. P. X., protoxylem.—Fig. 11. Cross-section at the periphery of the secondary wood of the axis of *Stigmaria* showing a large appendage bundle leaving the secondary wood. In contrast to fig. 4, there is a large amount of secondary wood present in this bundle. 2nd. X., secondary xylem; M. X., metaxylem; P. X., protoxylem.—Fig. 12. Cross-section of the secondary wood of the main axis of *Stigmaria* showing the smaller, peripheral elements making up the "growth zone."—Fig. 13. Cross-section of a stigmarian appendage bundle in the middle cortex of the main axis showing the relationship of the xylem elements. P. X., protoxylem; M. X., metaxylem; 2nd. X., secondary xylem.—Fig. 14. Cross-section of the secondary wood of the main axis of *Stigmaria* showing the vascular bundle leaving the secondary wood. Secondary elements of the bundle connect with those of the stele.
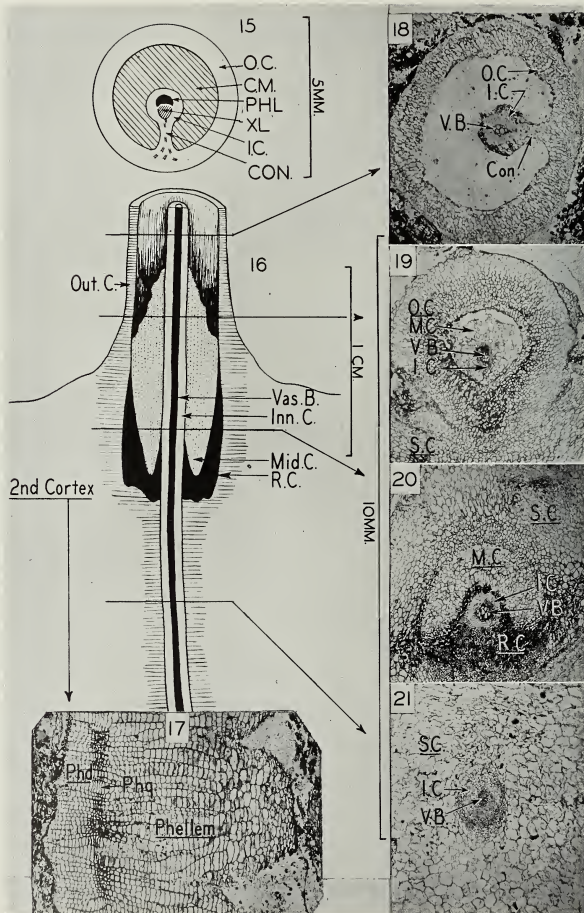
of the tissues of the roots of *Isoetes* shows an organization very similar to that found in stigmarian appendages as illustrated in pl. 3 and 4. The vascular strand of the root of *Isoetes,* diagrammed in fig. 26, shows the same monarch arrangement of the primary xylem as described for the stigmarian appendage. The roots of *Isoetes* are borne on the base of the "corm" in a regular sequence unlike that found in any other living plant (fig. 3). Their arrangement is suggestive of the regularity of the arrangement of the stigmarian appendages, but whether it is to be interpreted as a spiral sequence or not, is difficult to establish. If the "corm" of *Isoetes* is homologous with the stigmarian axis, the diversity of size is enormous and a close morphological agreement cannot be expected. If the organs are actually homologous, it is evident that the mere difference in size is such that the structure of the "corm" of *Isoetes* must have been profoundly altered in the process of reduction.

The phloem.—The phloem in the root of *Isoetes* can be seen in cross section as a group of sieve tube elements lying adjacent to the metaxylem and opposite the protoxylem point. The arrangement of the xylem and phloem of the vascular strand is collateral in the root of *Isoetes* (fig. 26). The position of the phloem within the tissue of the root is always to the inside of the metaxylem (fig. 26). As has been pointed out above the collateral arrangement of the vascular strand and position of the phloem to the inside of the metaxylem are characteristics of the stigmarian appendage. It is evident that there is a striking similarity between the roots of *Isoetes* and the stigmarian appendage as to the position of the phloem.

It is of interest to note that the collateral strand of a root of *Isoetes* and a stigmarian appendage is like that of a leaf trace. In *Isoetes,* however, there can be no question that the appendages produced on the base of the "corm" are roots. They not only have the endogenous insertion of a normal root, but they carry on the physiological and mechanical functions characteristic of roots, not of leaves.

The inner cortex.—The inner cortex of the mature root of *Isoetes* can be seen in cross section as a poorly defined layer of parenchyma cells lying around the vascular strand (fig. 22–27). The inner cortex is persistent from the point of the endogen-

ous insertion of the root at the edge of the protostele of the main axis (fig. 3) to the meristematic region of the root tip.

By way of contrast the continuity of the inner cortex of the stigmarian appendage has not been traced to the woody cylinder of the main axis; it can be seen about the vascular strand as it traverses the tissues of the secondary cortex of the main axis (fig. 20 and 21). The cells of the inner cortex of the appendage are small and they are distinct from the large cells of the secondary cortex of the stigmarian axis. It is probable that the inner cortex of the appendage was derived from a terminal meristem as it passed through the tissues of the main axis. This would indicate an endogenous insertion of the stigmarian appendage comparable to the insertion of the root of *Isoetes.*

The middle cortex.—Near the periphery of the secondary cortex of the main axis of *Isoetes,* the middle cortex of the root can first be seen as a crescent-shaped mass of parenchymatous cells lying around the eccentrically placed vascular strand and its surrounding inner cortex (fig. 24 and 27). The middle cortex of the root persists for only a short distance. It gives way to a horseshoe-shaped cavity as can be seen in fig. 23, 22 and 27. The vascular strand with its surrounding inner cortex maintains its eccentric position throughout the extent of the root.

A comparison of fig. 20 and 16 of pl. 3 to fig. 24 and 27 of pl. 4 will show that the middle cortex of the root of *Isoetes* can be seen at the same relative level within the tissues of secondary cortex of the main axis as the middle cortex of the stigmarian appendage. The comparison between these figures will also show that the middle cortex of the *Isoetes* root gives way to the horseshoe-shaped cavity of the free root (fig. 22) at about the same relative level as does the middle cortex of the stigmarian appendage (fig. 18). Fig. 20 and 24 also show the eccentrically placed vascular strand of the stigmarian appendage and the root of *Isoetes.*

Cells adjacent to the middle cortex of the root of *Isoetes* are not differentiated into a "rootlet cushion" as described for the stigmarian appendage (fig. 20).

The outer cortex.—The outer cortex of the mature root of *Isoetes* becomes apparent as the root

Fig. 15–21.—Fig. 15. Diagrammatic cross-section of a free stigmarian appendage. O. C., outer cortex; I. C., inner cortex; Phl., phloem; Xl., xylem; Con., connective; C. M., horseshoe-shaped cavity.—Fig. 16. Diagrammatic longitudinal section of the base of a stigmarian appendage, showing levels at which various sections were taken. Out. C., outer cortex; Vas. B., vascular bundle; Inn. C., inner cortex; Mid. C., middle cortex; R. C., "rootlet cushion."—Fig. 17. Cross-section of the secondary cortex of the main axis of *Stigmaria.* Phd., pheloderm; Phg., Phellogen.—Fig. 18. Cross-section of the appendage of *Stigmaria* after it has emerged from the secondary cortex of the main axis. O. C., outer cortex; I. C., inner cortex; Con., "connective," V. B., vascular bundle.—Fig. 19. Cross-section of the stigmarian appendage just leaving the secondary cortex of the main axis, showing the beginning of the disintegration of the middle cortex of the appendage. O. C., outer cortex; M. C., middle cortex; V. B., vascular bundle; I. C., inner cortex; S. C., secondary cortex.—Fig. 20. Cross-section of the stigmarian appendage, traversing the peripheral tissues of the secondary cortex of the main axis, showing the horseshoe-shaped middle cortex and the vascular bundle which is eccentrically placed in relation to it. S. C., secondary cortex; M. C., middle cortex; I. C., inner cortex; V. B., vascular bundle; R. C., "rootlet cushion."—Fig. 21. Cross-section of the stigmarian appendage traversing the deep tissues of the secondary cortex of the main axis, showing the small celled inner cortex of the appendage surrounding the vascular bundle. S.C., secondary cortex; I. C., inner cortex; V. B., vascular bundle.
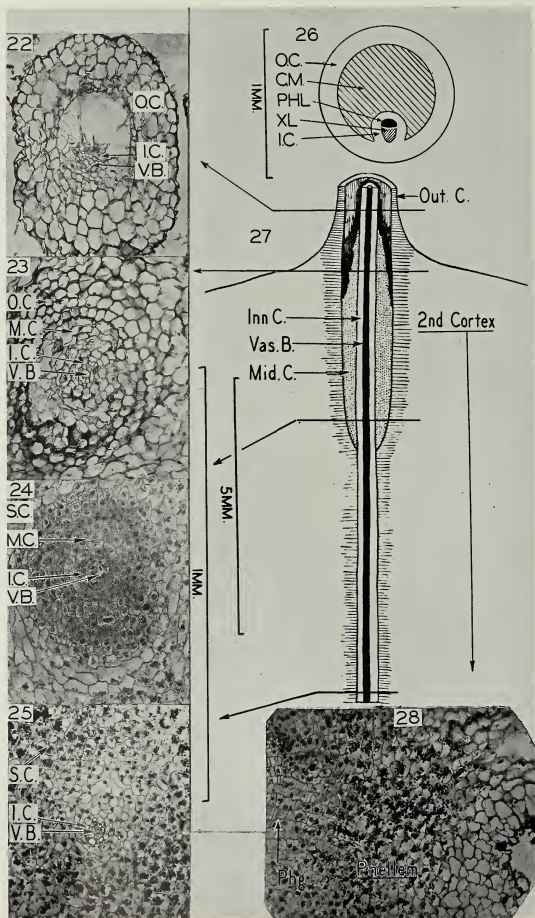
leaves the main axis (fig. 22 and 23). At this point it can be seen that the cells of the outer cortex of the root are continuous with the cells of the secondary cortex of the main axis (fig. 27). This feature has been described above for the stigmarian appendage.

Near the root tip the outermost cells of the outer cortex form a well defined epidermis which is soon sloughed off as the root develops. In addition, the root tip produces a poorly defined root cap. Root hairs have also been observed as a feature of the roots of *Isoetes*.

Probably due to poor preservation of their delicate cells, the growing tips of stigmarian appendages have not been found. As a result the presence or absence of a root cap and root hairs has not been determined.

THE RHIZOPHORE OF ISOETES AND THE STIGMARIAN AXIS.—The stem of *Isoetes* may be characterized as a small two to three lobed stem or "corm" with a growing point at both the apex and base of the stem. The stem, in turn, may be divided into two general regions, the upper portion which bears the sporophylls and the lower portion which bears the roots (fig. 3). The root bearing portion of the stem is commonly called the rhizophore (fig. 3, plane A and B).

The apical growing point of the stem is located in a cup-like depression and is surrounded by the spirally arranged sporophylls (fig. 3), while the growing point of the rhizophore lies above and parallel to the furrow formed at the line of union of the lateral lobes of the "corm" (fig. 3, plane A and B). The roots arise endogenously from this rhizophore meristem. Divisions in both the apical and rhizophore meristems are infrequent and this accounts for the slow rate of growth of the stem in length. On the other hand, the lobes of the "corm" are formed by the comparatively rapid divisions of an anomalous cambium which lies between the secondary cortex and the "prismatic" layer of the stem (fig. 3). The secondary cortex and the "prismatic" layer are the products of the activity of the cambium. The secondary cortex is formed to the outside of the cambium, while the "prismatic" layer is formed to the inside.

The "prismatic" layer is known to be composed of cells of secondary xylem, secondary parenchyma and possibly secondary phloem. All of the cells of the "prismatic" layer show a typical radial arrangement. There is nothing comparable to this type of secondary thickening in any of the other living lycopods.

In spite of the great discrepancy in size between the rhizophore of *Isoetes* and the stigmarian axis (*cf.* fig. 1 and 3) they show many characteristics in common. Among these which have been discussed are the regular sequence in which the appendages of both are borne on their respective axes and the similarity of the "periderm" of the stigmarian axis to the secondary cortex of *Isoetes*. In addition, the anomalous cambium of *Isoetes* may also be a point of similarity to the cambial activity in the stigmarian axis.

As has been indicated the stigmarian axis must have had two cambial layers, one the phellogen which formed the tissues of the secondary cortex, the other, the cambium which was active in producing the secondary wood centripetally and a "phloem zone" centrifugally. As yet the "phloem zone" has not been identified on a histological basis. Between the "phloem zone" and the secondary cortex of the stigmarian axis is the middle cortex (fig. 2).

If the small rhizophore of *Isoetes* and the large stigmarian axes are phylogenetically related it is conceivable that during the course of the great reduction in size, accompanied by shortening of the axes, the middle cortex as represented in the stigmarian axis may have been eliminated. If such were the case it would not be difficult to visualize the phylogenetic origin of the anomalous cambium of the rhizophore of *Isoetes*. It can be seen, by examining fig. 2 that by eliminating the middle cortex of the stigmarian axis the phellogen would be brought into close proximity with the cambium producing the centripetal secondary wood. The final step would be the merging of these two cambia to form an anomalous type of cambial activity as represented in the modern plant *Isoetes*.

DISCUSSION.—Lang (1923), Scott (1920), Walton (1935), Leclercq (1930), Eames (1936) and others have compared stigmarian axes and their appendages with the *Isoetes* rhizophore and its roots. They have concluded that these structures are homologous and that *Stigmaria* and *Isoetes* are phylogenetically related. The stem-like characters of the stigmarian axes have long been accepted; however, agreement has not been reached as to the

Fig. 22–28.—Fig. 22. Cross section of the root of *Isoetes macrospora* free from the secondary cortex of the "corm." O. C., outer cortex; I. C., inner cortex; V. B., vascular bundle.—Fig. 23. Cross-section of the root of *Isoetes macrospora* at the outermost edge of the secondary cortex of the "corm," showing the disintegration of the middle cortex of the appendage. O. C., outer cortex; M. C., middle cortex; I. C., inner cortex; V. B., vascular bundle.—Fig. 24. Cross-section of the root of *Isoetes macrospora* passing through the peripheral tissue of the secondary cortex of the main axis, showing the differentiation of the horseshoe-shaped middle cortex about the excentrically placed vascular bundle. S. C., secondary cortex; M. C., middle cortex; I. C., inner cortex; V. B., vascular bundle.—Fig. 25. Cross-section of the root of *Isoetes macrospora* passing through the deep tissues of the secondary cortex of the axis. The cells of the inner cortex of the appendage can be seen surrounding the vascular bundle. S. C., secondary cortex; I. C., inner cortex; V. B., vascular bundle.—Fig. 26. Diagrammatic cross-section of a mature *Isoetes macrospora* root showing the relationship of parts. O. C., outer cortex; I. C., inner cortex; Phl., phloem; XL., xylem; C. M., horseshoe-shaped cavity. —Fig. 27. Diagrammatic longitudinal section of the root base of *Isoetes macrospora*, showing the levels at which the various cross-sections are taken. Out. C., outer cortex; Inn. C., inner cortex; Vas. B., vascular bundle; Mid. C., middle cortex.—Fig. 28. Cross-section of the secondary cortex of *Isoetes macrospora*. Phg. phellogen.

nature of the appendages. Solms-Laubach (1891) and Schoute (1938) have homologized the stigmarian appendage with modified leaves and not with roots. It is argued, on this basis, that the stigmarian axis is a rhizome (leaf-bearing stem) and not a rhizophore (a root-bearing stem) such as is found in *Isoetes*.

If the interpretation given by these authors is correct, no homology could exist between roots of *Isoetes* and the appendages of *Stigmaria;* the similarities that exist must in that case be due to homoplastic adaptations. However, from the evidence presented it appears more reasonable to regard the roots of *Isoetes* and the appendages of *Stigmaria* as strictly comparable. Even the minute anatomical structure of the phloem, inner cortex, middle cortex, outer cortex, etc., show many similar features. The point of greatest contrast is only in size so far as can be accurately established. It seems that the comparison is so exact, in spite of the extreme diversity of size between the fossil and the living plant, that it could not have arisen out of homoplastic convergence in structure. It is thought that the evidence presented justifies the conclusion that the stigmarian appendages and *Isoetes* roots are strictly homologous and that the term root should be applied to the spirally arranged appendages borne on the stigmarian axis. It follows that the stigmarian axis is a root-bearing stem or rhizophore. The rhizophore of *Stigmaria* shows a regular arrangement of its roots, it has centrifugally developed secondary cortex and shows the formation of secondary xylem due to cambial activity. The only group of living lycopods that has these characteristics is *Isoetes*.

The results of this study are in substantial agreement with conclusions reached by LaMotte (1936) on the basis of his study of the embryology of *Isoetes*. He concludes that *"Isoetes* by means of its adaptive reduction remains the sole living representative of a long [phyletic] line." From the evidence presented, a phylogenetic relationship between *Isoetes* and *Stigmaria* seems to be established.

SUMMARY

Further evidence for the anatomical similarity between the roots of *Isoetes* and the appendages of *Stigmaria* is presented. The greatest difference between the two is the size of the respective structures.

The arrangement of the primary tissues in the vascular strand of the stigmarian appendage is identical with the arrangement of these tissues in the root of *Isoetes*. The primary xylem is monarch in the vascular strands of both. The phloem has been identified in the vascular strand of the stigmarian appendage on a histological basis. Its position, like that in the root of *Isoetes*, is adjacent to the metaxylem and is always centripetal. The vascular strands of their respective appendages are collateral.

The outer cortex of the stigmarian appendage is continuous with the secondary cortex of the main axis. This characteristic also applies to the outer cortex of the root of *Isoetes*. The middle cortex within the root of *Isoetes* can be seen to occupy the same relative position as that within the stigmarian appendage.

The close homology between the roots of *Isoetes* and the stigmarian appendages has led to the conclusion that in the case of *Stigmaria* the term root should be applied and that the stigmarian axis bearing the roots should be called a rhizophore.

The secondary cortex of the rhizophores of *Stigmaria* and *Isoetes* shows a striking similarity in their structure. Both rhizophores show marked cambial activity. A hypothesis is presented for the phylogenetic origin of the anomalous cambium of the *Isoetes* rhizophore.

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