On the Occurrence of Centripetal Xylem in *Equisetum*.¹

BY

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With Plate XLV.

AMONG living Vascular Cryptogams perhaps no group more readily attracts attention than the Horse-tails. These plants, with their odd appearance and peculiar organization, clearly proclaim themselves a stock distinct from other recent Pteridophytes. The few species, about twenty-five in all, do not vary greatly among themselves, and constitute a single genus, *Equisetum*. Although reduced in numbers in the present epoch, the Equisetales formed a large and important part of the flora of the earth during Paleozoic time. In the Devonian period well-developed and specialized Equisetaceous forms already existed; through the succeeding Paleozoic periods, especially during the Carboniferous, flourished the tree-like Horse-tails with secondary thickening, called Calamites. After the Permian age there lived other members of the Equisetales, resembling always more and more in succeeding time the existing genus. In spite of continued reduction, the living representatives of the Equisetales resemble the Calamites very strongly: form, structure, and anatomy, both of stem and reproductive branches, are in many important features very similar. From these ancient, arborescent Horse-tails, our present genus has without question descended, and of that great and flourishing group its few widespread species are the only remaining representatives. *Equisetum*, because of this isolated position among existent plants, and because of its unusual structure, has been the subject of much study. Particularly has its organization in comparison with that of Calamitean fossil remains been of interest since the latter have become better known from abundant specimens, and the cryptogamic rank of all has been firmly established. For, in the anatomical study of plants, the object, as in similar investigation in the animal kingdom, is not merely to reveal the relationship of living genera, but especially to fix phylogenetic lines. For such determinations, the preserved remains of forms that existed in long-past time must hold great interest; a knowledge of their organization becomes a necessity to a clear understanding of their evolution.

¹ Contributions from the Phanerogamic Laboratories of Harvard University, No. 19.

Most Calamitean fossils consist of fragments of stems, or of casts of these, or of their internal cavities. Where the structure of tissues can be determined, the vascular system has naturally been best preserved. This system in the Calamites has been the subject of considerable investigation, and until recently its structure, in the stem, at least, was thought to be pretty well understood. But one of the older genera has lately been shown to possess a vascular structure previously unknown in this group, and of very great importance. The plant in question is from Lower Carboniferous strata, and has been named *Calamites pettycurensis* by its discoverer, Dr. Scott.¹

The suggestion that a new genus, *Protocalamites*, be founded upon it has been provisionally accepted by Dr. Scott, although he believes it may belong to the already established genus, *Archaeocalamites*. The vascular structure of the stem is like that of other Calamites, with one important exception—the primary wood developed both outwardly and inwardly from the protoxylem lacuna. We have in this plant the most ancient of the Equisetales showing distinct *centripetal* wood in the stem.

In its anatomy *Equisetum* differs strikingly from the Calamites only in the lack of secondary wood. The secondary growth largely disappeared in the Equisetal stock at the end of the Permian period, although the Mesozoic Equisetales may have possessed it to some extent. A few even of the living species show remnants of such structure. In these cases, it occurs as a continuation in the growth of the most 'woody' portion of the stem, the 'nodal ring', best called the supranodal wood. Cormack² has shown such development in *Equisetum maximum*, Lamarck (*E. Telmateia*, Ehrh.), and Queva³ confirms its presence there, noting it also in *E. arvense*, L. In *E. hyemale*, L. and its variety *robustum*, A. A. Eaton (*E. robustum*, A. Br.), as well as in the two above-mentioned species, the writer has seen evidences of this ancestral character. Often it appears most definitely in the rhizome. Doubtless other large and well-grown terrestrial species will show such conditions. In the much-reduced or semi-aquatic species, (*E. scirpoides*, Michx., *E. fluviatile*, L. (*E. limosum*, L.), and *E. sylvaticum*, L., no clear indications of cambial activity were seen.

Since, then, our recent species possess so little secondary growth, comparison of their vascular system with that of their Paleozoic ancestors concerns chiefly the primary wood. Even here great reduction has occurred. In the internodes of *Equisetum* we find the fibro-vascular system to consist of a circle of separated bundles lying opposite the external ridges of the stem, just outside the large central cavity that occupies most of the pith.

¹ Scott, D. H. : On a Primitive Type of Structure in Calamites, Ann. Bot., vol. xv, p. 773; 1901. Studies in Fossil Botany, 2nd edition, p. 36, Fig. 11; 1908.

² Cormack, B. G. : On a Cambial Development in *Equisetum*. Ann. Bot., vol. vii, p. 63; 1893.

³ Queva, C. : Histogenèse et structure du stipe et de la fronde des *Equisetum*. Mém. de la Soc. d'Hist. Nat. d'Autun, t. xx, p. 21; 1907.

In structure these bundles are unusual: the xylem of each is in three parts, a median inner and two lateral external portions. Among these groups of elements lies the phloem. The innermost xylem-group consists of the protoxylem, the first-formed tracheides, spiral or loosely ringed in sculpture. In a mature internode the position of this wood is occupied by a cavity, the so-called 'carinal canal', formed by the breaking-up and tearing-apart of these early-formed tracheides during elongation of the internode, and by the enlargement of the so-formed lacuna during radial and tangential growth of the surrounding cells. The more or less scattered and disarranged remnants of the disrupted cells are found in this opening in the tissues. The two other xylem-groups lie farther out, on the flanks of the canal, separated therefrom by one or more parenchyma cells. They consist of rows, or in some species of groups, of a few elements which develop considerably later than the protoxylem. In general these tracheides are scalariform, reticulate, or pitted, but occasionally annular and even spiral thickenings are found. These form the metaxylem of the bundle. Over their order of development, and the significance of the complexity of this bundle, considerable controversy has arisen. Owing to this and to the intimate relation of the leaf-trace to this bundle, the writer has made some study of the order in which the tracheides arise and the relationship of the different parts of the bundle to the whole.

In the nodal region the primary wood of *Equisetum* is much increased. The internodal strands alternate in the well-known manner. At the node they fork; each metaxylem group passes to the bundle nearest in the internode above, and, after passing the next node above, returns to the same bundle. The carinal canal disappears as the bundle approaches the node. The protoxylem, there filling the position of this lacuna, behaves in much the same manner as the metaxylem. The forking and fusion of these portions, with some enlargement or additional growth, forms a solid ring of wood just above the node. This band, the supranodal wood, projects inwardly somewhat, and externally to a considerable extent, the extension in the latter direction becoming greater when secondary growth occurs.

In structure the primary bundle of the Calamitean stem was collateral. It possessed near its inner margin a carinal canal, which, according to Williamson and Scott,¹ is identical in nature, origin, and position with that in *Equisetum*. Extending outwardly in a wedge-shaped mass from the external periphery of this lacuna is the metaxylem. As seen in radial sections its development was centrifugal. Beyond this lay the phloem, or in large or mature stems, secondary wood. The supranodal primary wood of these old plants also much resembled that of *Equisetum*. Its develop-

¹ Williamson, W. C., and Scott, D. H.: The Organization of Fossil Plants of the Coal Measures. Phil. Trans. of the Royal Soc. of London, vol. clxxxv B; 1894.

ment, as shown by the same authors, is likewise centrifugal; the protoxylem of the internodal bundles is continuous with the innermost elements of this xylem-band. In *Equisetum*, too, there has been no question raised, so far as is known to the writer, as to the centrifugal development of this supranodal wood. Certainly its innermost elements are protoxylem; many radial sections show this condition clearly.

Although it is generally agreed that the supranodal wood and the carinal strand in *Equisetum* are homologous with the similar tissues in Calamites, there has been some difference of opinion in regard to the interpretation of the remaining parts of the bundle.

The two metaxylem-groups, in the internode distinct from the clearly endarch protoxylem, have the appearance of being exarch, for the tracheides constituting them are often smallest at the outer extremity, and increase in size with some constancy inwards. Mr. Gwynne-Vaughan¹ emphasizes this fact, and bases thereon his suggestion 'that the lateral xylem strands in the vascular bundles of the existing *Equisetums* may perhaps be taken to represent the last remnants of a primitive central mass, and that this would be entirely in agreement with their apparently centripetal development, and in particular with their cauline course'. Poirault² also considers the development of the metaxylem centripetal, and Lignier³ regards it as at least partially so. The first-mentioned author at the same time doubts the integral nature of the Equisetal fibro-vascular bundle, stating that of the three groups of tracheides in each internodal bundle the carinal alone leaves the node, passing out as the leaf-trace, and 'the two lateral strands join on to the xylem of the nodal ring, and in certain species may be traced as externally projecting ridges over the nodal xylem into the internode above'. The fact that the metaxylem-groups, so definitely separated from the protoxylem, develop much later than the latter may be said also to point to the composite character of this bundle.

The study of the vascular system of *Equisetum*, both nodal and internodal, developing and mature, and of that of the reproductive axis, together with a comparison with the stele of the Calamites, has led the present writer to the conclusion that the bundle of the Horse-tails is essentially centrifugal in development and, without doubt, simple, or integral, in nature.

Let us grant for the moment the centripetal development of the flanking metaxylem-groups in the bundle. The supra-nodal wood is centrifugal. And *into* or *over* this, fusing therewith, pass these strands. Adopting the first supposition, we find centripetal wood passing directly,

¹ Gwynne-Vaughan, D. T. : Remarks upon the Nature of the Stele in *Equisetum*. Ann. Bot., vol. xv, p. 776; 1901.

² Poirault, G. : Développement des Tissus dans les organes végétatifs des Cryptogames vasculaires. Mém. de l'Acad. Imp. des Sc. de Saint-Petersbourg, 7^e série, t. xxxvii, p. 13; 1890.

³ Lignier, O. : Équisétales et Sphénophyllales; leur origine filicinéenne commune. Bull. Soc. Linn. de Normandie, 5^e série, vol. vii, p. 114, note. Caen, 1903.

through continuous lines of tracheides, into centrifugal, as the node is reached, and *vice versa* as the node is left in passing upward along the bundle. Such a condition is difficult to imagine, and is unknown elsewhere in the anatomy of stems. Assuming the alternative view, that these 'centripetal' groups pass *over* the supra-nodal wood, an absurd condition is likewise presented, for we have *centripetal* wood, the suggested possible 'remnants of a primitive central mass' of such wood, passing *external* to *centrifugal* wood, the remains of a mass to which it formerly lay internally. Such relation obviously cannot hold. Moreover, in the two species, *E. hyemale* and *E. maximum*, in which the statement is made that such a condition exists, there has been shown to be at the point in question some cambial growth. Hence the centripetal wood there passes *outside secondary wood*! Yet, according to Gwynne-Vaughan (p. 779 of the above-mentioned paper), the view that these bundles are the vestiges of an ancestral, solid, internal stelar mass is '*entirely in agreement with their apparent centripetal development and in particular with their cauline course*'. (The italics are the present writer's.) Again, the metaxylem-groups lie externally to the protoxylem, which is granted, apparently by all, to be endarch. Can the former then, *if exarch*, be the vestiges of tissues central in position, and thus necessarily internal to the carinal canals, as is the centripetal wood in *C. pettycurensis*? The carinal canals of *Equisetum* and of the Calamites are indisputably homologous.

It is further stated that the gradation in size and the sculpture of the walls of the tracheides of the lateral groups indicate a centripetal development. Size does not necessarily indicate the order of development; and the sculpture of the tracheide-walls in metaxylem is, at least to a certain extent, independent of order of development. In his 'Observations on the Anatomy of Solenostelic Ferns', Mr. Gwynne-Vaughan¹ mentions cases in the stems of which the first-formed tracheides 'appear without order here and there throughout the whole xylem-mass, so that the differentiation is quite irregular'. Under these conditions, the sculpture is always sculariform, and 'there is no difference whatever between the first-formed elements of the xylem and those formed later on'. Plate XLV, Fig. 1, shows a somewhat similar condition in *Lycopodium*. Here, though, a definite protoxylem has first formed; lignification proceeds in general centripetally, but with much irregularity. Even in secondary wood completion of lignification does not proceed in perfect centrifugal order. This was seen by the writer, for example, in the maturing wood of *Betula*. The loss of protoplasm, indicating the completion of lignification in tracheides, is decidedly irregular.²

¹ Gwynne-Vaughan, D. T.: Observations on the Anatomy of Solenostelic Ferns. Ann. Bot., vol. xvii, p. 727; 1903.

² Special precautions were taken to assure the existence of this condition. Longitudinal sections of the wood were studied. The length of the tracheides and the shrinkage of their protoplasm in length were observed. These elements are formed in rather distinct tiers, and practically no

The development of a bundle in *E. hyemale* var. *robustum* is shown in Fig. 2. In this case, as in that of the birch wood, necessary precautions were taken in the preparation of the section. The preparation photographed came from near the centre of a good-sized piece of stem embedded in celloidin, which was not removed. Here is seen a condition which is apparently most significant. For in the rows of metaxylem-cells, which can be clearly made out flanking the carinal canal on either side, differentiation, as shown by loss of protoplasm, is seen to be centrifugal upon the right, and centripetal upon the left. The study of many sections, moreover, shows that other bundles lose protoplasm from the median tracheides first. Thus considerable irregularity of development of this tissue is established. Other phyla of living Pteridophytes show, as stated above, the same irregularity of xylem-development. Its occurrence, therefore, appears to be of no special importance in the Equisetales, the less so because a similar irregularity of development appears even in tracheides laid down by a cambium, as in the case of *Betula* cited above.

The structure of the tracheary wall of these portions of the bundle was also studied. As the conditions of disappearance of protoplasm would cause one to suspect, there is some irregularity in structure; reticulate and pitted tracheides occupy various positions in relation to scalariform elements in *E. maximum* and *E. hyemale* var. *robustum*. The examination of a considerable number of sections is clearly necessary, for, as Fig. 2 suggests, one may show apparently clear endarch, and another as clear exarch arrangement. In the majority of cases in these two species, however, development toward the outside was manifest. In *E. arvense* an unusual condition is found. The metaxylem-tracheides of some bundles are essentially alike, only very slight differences being noticeable; those of other bundles are in part spiral and annular. Wherever this latter, not uncommon, condition occurs, the order of development is distinctly centrifugal. A possibly parallel case has been noted in *E. maximum* by Queva.¹ He figures (p. 16) a cross-section of a bundle in a long internode of the sterile stem. The metaxylem-groups are in part invaded by lacunae very similar in nature to that of the protoxylem. In the same investigation, Queva seems to have seen a rather regular development in this species. He says (p. 35), '*La différenciation est exclusivement centrifuge, mais le bois se forme en deux temps.*' His Fig. 11 shows this order. Thus, though lignification does not occur invariably in an outward direction, irregularities

longitudinal shrinkage of their contents had occurred. Transverse sections were then cut so far down into the block as to be from a region the tracheides of which could not have been torn open and their contents in any way lost during the cutting-up of the material for killing and fixing. The infiltrating material, celloidin, was not removed from the sections, thus guarding against any loss of protoplasm by 'dropping-out.'

¹ Queva, C.: Histogenèse et structure du stipe et de la fronde des *Equisetum*. Mém. de la Soc. d'Hist. Nat. d'Autun, t. xx; 1907.

in its order having in the Filicales and Lycopodiales no observable effect upon the sculpture of the cell-wall, most stress in deciding the morphological order of development must be laid upon the latter. Judged by this standard the flanking xylem-groups of *Equisetum* are centrifugal in their development.

It is consequently evident that all parts of the stem-bundle develop in the same direction. Had there been no apparent proof that the respective portions of this much-disputed bundle were of varying differentiation, doubt would not, in all probability, have been cast upon its simple nature. Gwynne-Vaughan,¹ in his statement that only the protoxylem-strand is concerned in the formation of the vegetative leaf-trace, has brought forward evidence for the complex nature of the internodal bundle. Lignier (see above-mentioned article, p. 114, note) is of the same opinion in regard to the origin of the leaf-trace. On the other hand, Campbell² and De Bary³ seem to understand the leaf-trace as connected with the entire internodal bundle. Dr. Scott's position on this point is clear. In his 'Studies in Fossil Botany' (1908), he says (p. 25): 'A single vascular bundle enters the stem from each leaf and passes straight down through one internode only. At the node below it forks.' The bundle in its entirety is clearly indicated.

Fig. 3 appears to settle this point at once. The photograph is of a portion of a radial section through the node of *E. hyemale* var. *robustum*. In this species the metaxylem is very well developed, and its share in the formation of the leaf-trace can be easily seen. In other species it is less easy to observe. Differences of opinion on this point are not hard to explain. Even though the tracheides of the metaxylem are related to those of the protoxylem at the point of origin of the leaf-trace, they are still situated upon its flanks and a radial section through the very centre, showing the departure of the protoxylem, does not usually also show well the relation of the metaxylem to the trace. And a section passing through the metaxylem might readily be cast aside as not strictly radial; especially would this be likely to occur where the metaxylem is small in amount, and the section contains none of the protoxylem. The metaxylem unquestionably takes part in the formation of the leaf-trace. In Fig. 4, which illustrates another feature of the leaf-trace, further evidence for the centrifugal development of the metaxylem is presented. The tracheides upon the right of the protoxylem are the direct continuation of the elements given to the leaf-trace by a lateral metaxylem-strand in Fig. 3. Their order of development is definitely outward.

The unit nature of the cauline internodal bundle becomes further

¹ Gwynne-Vaughan, D. T.: Remarks upon the Nature of the Stele in *Equisetum*. Ann. Bot., vol. xv, p. 775; 1901.

² Campbell, D. H.: Mosses and Ferns, p. 462; 1905.

³ De Bary, A.: Comparative Anatomy of the Phanerogams and Ferns (trans.), p. 279; 1884.

evident from the structure of the leaf-trace itself. The latter is nearly divided in its proximal portion into three parts, in position and in structure corresponding to those of the complete, cauline, fibro-vascular bundle. A connexion with all parts of the stem-bundle is here indicated. For, if the protoxylem alone passed into the leaf, we should not expect to find this simple structure dividing in such a case into three new bundles, or taking on a form indicating such a condition; especially is it difficult to conceive its forming two new bundles centripetal in development, when it, itself, is centrifugal. Whereas, if all parts of the internodal bundle unite in the formation of the leaf-trace, they would undoubtedly assume their normal position and relations, forming there a bundle of the same general structure as that of the internode.

The internodal bundle of the Calamites has been briefly described above (p. 589). From this has come, by reduction of the metaxylem, the fibro-vascular bundle of *Equisetum*. In the reproductive axis of the latter genus the bundle-structure points to this relation. The cone-bundles of *E. hyemale* and of *E. fluviatile*, when seen in cross-section, show a condition intermediate between that of the internodal bundles of the Calamites and of the living genus. In many of them there is found the typical protoxylem-lacuna. Spreading externally from this is a considerable body of elements that are clearly seen to be metaxylem in radial sections. They are not solidly packed, but have many parenchyma-cells intermingled with them. There is a marked tendency for these metaxylem-tracheides to form groups outwardly flanking the protoxylem. In the cone of *Equisetum* we have accordingly repeated the Calamitean primary bundle well started on its way in reduction toward the condition found in the vegetative stem of the living descendants of the group.

An analogy of some value can be drawn between aspects of the vascular system of two groups of plants which are believed to be much reduced, the Horse-tails and the Monocotyledons. The ancestors of both undoubtedly possessed secondary growth; in the living members this is found only as a remnant. It is a striking fact that this growth, as observed by Dr. Chrysler¹ in the Gramineae, is in exactly the same situation as it appears in *Equisetum*—slightly above the node. The resemblance of the primary wood in the bundles of these two widely separated groups has been noted by many writers. It is, indeed, close; in both are found a canal containing broken-down protoxylem and two externally flanking metaxylem-groups, to a greater or less extent separated therefrom.

The internodal bundle, then, of *Equisetum* is, without doubt, centrifugal throughout in its development, and is structurally a fibro-vascular unit, a much reduced Calamitean bundle.

Paleobotanists have recognized a close relationship between the

¹ Chrysler, M. A.: The Nodes of Grasses. Bot. Gazette, vol. xli; 1906.

Equisetales and the *Sphenophyllales*. The latter possess a stolid stele of centripetal wood. *Calamites pettycurensis* has a considerable amount of centripetal xylem; and even the axial bundles of *Equisetum* show clear centripetal wood in some cases.

Cross-sections of the cones of *E. hyemale* and *E. fluviatile* show bundles as described above (p. 594) with this addition: upon the inner side of the lacuna are often found, adjacent to the canal, or separated therefrom by a few parenchyma cells, from one to four or five tracheides. Radial sections (Fig. 6 of *E. hyemale*) show these to be metaxylem, scalariform or reticulate elements, situated on the inner side of the broken-down spiral and ringed elements of the protoxylem. With its considerable body of metaxylem upon the external side of the lacuna, the reproductive branch possesses fibro-vascular bundles of the type that has been called 'mesarch'.¹

The reproductive axis of *Equisetum* gives accordingly some evidence of the derivation of the genus from Calamitean forms similar to *C. pettycurensis*. Still stronger evidence is provided, however, in the foliar traces emanating from this region. The strobilus consists of a continuation of the stem, with much shortened internodes bearing, at the nodes, whorls of modified leaves, the sporophylls. The bundles of the sporophylls were studied in transverse and longitudinal sections in the following species:—*E. maximum*, *E. hyemale*, *E. fluviatile*, *E. arvense*, *E. palustre*, *E. sylvaticum*, and *E. scirpoides*. In all save the last two strongly-marked mesarch strands appear. In external appearance the sporophylls vary but slightly. Their fibro-vascular system, however, shows considerable difference in development, due to the great range of habitat found in the genus—from xerophily in *E. scirpoides* and *E. arvense* to hydrophily in *E. fluviatile*. But even in the latter the cone is not weak in vascular elements. In nearly all species a lateral fusion of sporophyll-peduncles occasionally occurs, and the union of their flattened distal ends is often found. Figs. 7 and 8 show cross-sections of sporophylls of *E. maximum* and *E. fluviatile* respectively, the former near the middle of the stalk, and the latter through the trace as it leaves the cortex of the strobilus. Both show well-defined lacunae in the centre of the bundle. Above and below, and to some extent also upon the sides, are tracheides. The longitudinal sections were cut in the dorsiventral plane of the sporophyll. Looking now at such a section (Fig. 9) from the fertile leaf of *E. fluviatile*, the structure seen in transverse section is explained. The elements upon the left are ventral, corresponding to the upper group in the cross-section; those upon the right are dorsal tracheides. Between, is a partially open space, the

¹ The term 'mesarch' was first applied to such structure by Count Solms-Laubach. This type of arrangement in bundles has since been used to a considerable extent in the determination of relationships among the groups of Vascular Cryptogams.

lacuna of the cross-sections. The origin of the latter is the same as that of the carinal canal of the stem. The elements outside the disarranged spiral and annular tracheides of the lacuna are closely ringed or scalariform. This is, then, a mesarch bundle. The dorsal elements are of course centrifugal, the ventral, centripetal. It might, perhaps, be objected that this arrangement of elements in the sporophyll-bundle is due to the concentric arrangement of the sporangia. But this is not the case. The strand continues in the general form shown in Fig. 8 until it approaches the base of its flattened end. There occurs a division into a number of bundles corresponding to the number of sporangia. Fig. 10 shows this condition in *E. maximum*. In the lower portion the undivided bundle is seen. Its resemblance to that of *E. fluviatile* is close. There is a central mass of distorted protoxylem bounded by unbroken tracheides. As the bundle passes outward division is made into several parts, only two of which, of course, lie in the plane of section. The separation is made from the very centre, a portion of the protoxylem passing to each branch-strand. The latter immediately forms metaxylem upon its inner face. At the very top of the figure this can be seen. And this mesarch structure in each of these small bundles can often be traced clear to the base of the sporangium. The arrangement of the sporangia upon the tip of the sporophyll cannot, then, control the form of the main bundle, causing it to simulate mesarch structure. The protoxylem of the two species discussed above consists chiefly of loose-ringed tracheides. Two other species are interesting in comparison: *E. arvense* (Fig. 11) shows portions of a spiral tracheide in the protoxylem; the central elements of *E. palustre* (Fig. 12) are spiral throughout.

The sporophyll fibro-vascular bundles appear not only to be mesarch but concentric, a condition which may also be regarded as a relic of ancestral structure.

Jeffrey¹ has shown that 'the Equisetaceous strobilus perpetuates both the non-alternating strands and the complete absence of foliar-gaps of the oldest Calamitean forms'. These figures make it probable that it also retains, so far as the sporophylls are concerned, the bundle-structure of ancestors contemporary with *C. pettycurensis*.

In the trace of the vegetative leaf the mesarch condition is also found. Investigations were made by means of radial sections of complete nodes with leaves attached, by cross-sections of the stem just above the origin of the traces, and by tangential sections at the outer limit of the supranodal wood. Well-marked centripetal wood was found in *E. maximum*, *E. hyemale*, *E. hyemale* var. *robustum*, *E. arvense*, and *E. scirpoides*. In *E. sylvaticum* and *E. fluviatile*, species of shaded and aquatic situations, the

¹ Jeffrey, E. C.: Are there foliar Gaps in the Lycopsidea? Bot. Gazette, vol. xlv, p. 254, 1908.

xylem-system is much reduced, particularly in the leaves. Yet indications of the mesarch structure of the leaf-trace were seen even in these two last-named species.

A brief description of the course of the trace will aid in understanding the conditions presented. As shown in the first part of this paper, the leaf-trace is formed by a continuation of the various elements of the internodal bundle. The carinal canal becomes discontinuous as it approaches the node. The protoxylem occupying that space enlarges, extending radially, then passes upward and forms the innermost tracheides of the supranodal wood. Just before that xylem-mass is reached, a 'branch' to the leaf is sent off more or less horizontally. Each of the metaxylem-groups enlarges somewhat, and gives off a small strand which passes upward and slightly outward, joining the protoxylem of the leaf-trace a short distance outside the point where the latter is first seen clearly. These three strands fuse more or less, and form the leaf-trace. Fig. 4 shows the structure of such a trace in *E. hyemale* var. *robustum* as it passes through the cortex. (The leaf lies above to the right.) Centrally are seen the scattered rings of protoxylem; to the right is metaxylem that is clearly formed centrifugally, its outermost elements being pitted. Another group of metaxylem is seen upon the inner side, centripetally developed. Thus the trace is mesarch. Parenchyma cells occur scattered through the xylem. Fig. 3 of the same plant does not show centripetal wood for the reason that it is not strictly median as to the bundle, but passes to one side of the centre, so as to show the attachment of the metaxylem. *E. maximum* (Fig. 5) shows very similar conditions—disorganized protoxylem with metaxylem both external and internal thereto. The strongly sclerified cells are those in the axil of the leaf-sheath. Mesarch structure in these two species appears close to the origin of the trace, and continues nearly to the end of its xylem. *E. hyemale* resembles its variety *robustum* very closely in the organization of the leaf-trace. In *E. arvense* no distinction was noticed among the tracheides until the trace had left the stem, but throughout the leaf proper mesarch conditions are well defined. Even in that most reduced species, *E. scirpoides*, with stems only a few millimetres in diameter, the foliar bundle is distinctly mesarch.

The study of transverse sections of these bundles in the larger species completes the understanding of their structure. The leaf-trace of *E. hyemale* var. *robustum* just before it leaves the cortex has a strong resemblance to the axial bundle of the cone. It is made up as follows: centrally, or often a little to one side, is a protoxylem-lacuna; external to this are the centrifugal tracheides arranged largely in two groups upon its flanks; directly inward from the centre are the centripetal elements, from three to seven in number. *E. maximum* presents much the same conditions. The protoxylem-lacuna is well developed in the proximal portion of the

trace. Queva, in his study of leaf-development in this species, however, did not find it.

Equisetum shows, therefore, centripetal wood, not only in the traces of the sporophylls, but also in those of the vegetative leaves. The descent of this genus from ancient Calamites of the type of *C. pettycurensis* is thus made highly probable. The centripetal wood in the leaf-trace of the Equisetales, together with many other characters, seems to indicate a clear relation of these plants to the Sphenophyllales, and through them, perhaps, to the Lycopodiales, which the latter resemble in anatomy.

The Lycopodiales and the Sphenophyllales possess centripetal wood in their stem structure. In *C. pettycurensis*, alone among the Calamites, small arcs of centripetal xylem remain in the stem-bundles. The stem proper of all other known Equisetales has completely lost it, and it has persisted only in the more conservative organs, the reproductive and vegetative leaves. The structure of the foliar traces of the Tertiary, and especially of the Mesozoic, Equisetales should prove very interesting. Some of the Equisetaceous fossils of the latter era have recently been shown¹ to be interesting in other respects—in the number and course of the stem-bundles and in the markings of the spores. Doubtless, when well-preserved material is available, they will show considerable centripetal xylem in their foliar traces. In the stems of the living members of this class secondary growth has nearly disappeared; the centrifugal primary wood has largely become parenchymatous, and the centripetal has completely vanished.

Through the countless generations of Equisetaceous plants, from the Lower Carboniferous Period to the present day, the vegetative leaf has continued to form centripetal wood. This places new and strong emphasis upon the conservatism of that portion of the vascular system which supplies the leaves. Its value in this respect has often been noted, but has perhaps not yet received the attention it deserves. A few instances in different groups of plants may be cited. The Cycads present a case parallel in many respects to that of *Equisetum*. Mettenius, in 1860, discovered mesarch structure in their leaf-bundles. Dr. Scott² has shown that the peduncles of several genera have mesarch bundles; also that the traces of the vegetative leaves and, to a less extent, of the sporophylls have centripetal growth. The vegetative stems of the Cycadaceae, however, have only centrifugal wood. Yet their probable ancestors among the Pteridospermeae had mesarch bundles in the stem. Among the Cordaitales the most ancient forms had mesarch stem and mesarch leaf-bundles; later forms had the same leaf-structure, but endarch structure had become the

¹ Halle, T. G.: Zur Kenntnis der mesozoischen Equisetales Schwedens. Uppsala und Stockholm; 1908.

² Scott, D. H.: The Anatomical Characters presented by the Peduncle of the Cycadaceae. Ann. Bot., vol. xi; 1897.

rule in the stem. Still another example occurs in the lower Gymnosperms. The bundles of the cotyledons of *Ginkgo*, and also of the vegetative leaves to a slight extent, have been shown by Worsdell¹ to be mesarch. Its ancestors were probably allied to the primitive Gymnosperms and possessed mesarch stem-structure. Further, Jeffrey² has recently shown that the leaves of a primitive pine-like Gymnosperm, named by him *Prepinus*, also had well-marked centripetal xylem. Thus in many places we find foliar organs retaining the typical xylem-structure of the older vascular plants.

Lately there has been some objection to the division of Vascular Cryptogams into the Pteropsida and the Lycopsidea, on a basis, in part, of the presence or absence, respectively in the two groups, of foliar gaps. *Equisetum* among the Lycopsidea has been regarded by some writers as varying from other members of the series in possessing leaf-gaps. In the examination of leaf-trace structure in this genus, a large number of sections, both transverse and radial, through the points of origin of traces, both of vegetative and reproductive leaves of several species, has been studied by the writer. In no case did a gap exist. The strands of the cone continue upward without sign of interruption after giving off the sporophyll-trace. Immediately over the origin of the vegetative leaf-trace, and connected with all portions of the internodal bundle, lies the unbroken ring of supra-nodal wood. Even in the much reduced vascular system of *E. fluviatile*, this xylem-mass is unbroken; in the tiny *E. scirpoides* it likewise completely shuts off the leaf-trace from the so-called 'gap' above.

SUMMARY AND CONCLUSIONS.

In *Equisetum* the development of the xylem of the vegetative stem is *centrifugal throughout*.

The internodal bundle does not consist of three united bundles, representing different portions of an ancestral stele: it is a *unit* in structure, and represents the much-reduced internodal primary bundle of the Calamites. The strobilus shows in its axial bundles conditions intermediate between those in the vegetative stems of the Calamites and of *Equisetum*.

The vegetative leaf-trace does not arise solely from the protoxylem-strand of the internodal bundle; all three parts of the xylem of the latter contribute to its formation.

Through Dr. Scott's discovery of an ancient Calamite with centripetal wood in the stem-bundle, a link has been formed between the Equisetales and the Sphenophyllales, and possibly through the latter with the Lycopodiales. The most primitive Equisetaceous forms doubtless possessed well-developed centripetal wood. Early in the history of the series this

¹ Worsdell, W. C.: On Transfusion Tissue. Trans. Linn. Soc. of London. Series 2, vol. v; 1897.

² Jeffrey, E. C.: On the Structure of the Leaf in Cretaceous Pines. Ann. Bot., vol. xxii; 1908.

disappeared. *Equisetum* shows signs of relationship to these ancient plants in the possession of centripetal wood in regions recognized as conservative of ancestral characters. The axial bundles of the strobilus are weakly mesarch; those of the sporophylls, strongly so. This condition in the sporophyll-trace is not due to the concentric arrangement of the sporangia upon the scutes, for the subdivisions of the trace, one of which passes to each sporangium, are themselves equally mesarch throughout their course. The traces of these fertile leaves are likewise concentric. The traces of the vegetative leaves show well-developed centripetal wood, in some species throughout their course. In no case does the passage of a foliar trace from the stele leave a gap.

Equisetum presents additional and very strong evidence of the conservatism of the leaf-trace, thus emphasizing its value in phylogeny.

Centripetal wood is now known to exist in all the large groups of Vascular Cryptogams. In all those in which it is well developed it is continuous with the protoxylem; where it no longer appears at all, as in the higher plants, or where only vestiges are found, as in *Equisetum*, the protoxylem usually becomes continuous with the centrifugal xylem. The formation of xylem adaxially from the protoxylem is, therefore, a Cryptogamic character. Moreover, bundles in which both centripetal and centrifugal xylem are present cannot be said to be characteristic of any one group of the Vascular Cryptogams, as, for example, of the Ferns, nor can such bundles in higher plants be of other phylogenetic value than as indicating general Cryptogamic affinities.

This work has been carried on in the Phanerogamic Laboratories of Harvard University, and to Dr. E. C. Jeffrey the writer is much indebted, both for abundant material and for advice and guidance throughout the investigation.

DESCRIPTION OF PLATE XLV.

Illustrating Mr. Eames's paper on Centripetal Xylem in *Equisetum*.

Fig. 1. *Lycopodium*, sp.; transverse section of part of the central cylinder during lignification of the xylem. $\times 180$.

Fig. 2. *Equisetum hyemale*, var. *robustum*; transverse section of a developing internodal bundle. $\times 500$.

Fig. 3. The same; radial section through the origin of the vegetative leaf-trace, showing connexion with both protoxylem and metaxylem. $\times 100$.

Fig. 4. The same; radial section through vegetative leaf-trace passing through cortex, showing mesarch structure. $\times 500$.

- Fig. 5. *Equisetum maximum*; radial section through vegetative leaf-trace as it leaves the cortex. $\times 500$.
- Fig. 6. *Equisetum hyemale*; radial section through an axial bundle of the cone. $\times 500$.
- Fig. 7. *Equisetum maximum*; transverse section of sporophyll-trace. $\times 1100$.
- Fig. 8. *Equisetum fluviatile*; transverse section of sporophyll-trace. $\times 1100$.
- Fig. 9. The same; longitudinal section of sporophyll-trace. $\times 500$.
- Fig. 10. *Equisetum maximum*; longitudinal section of the sporophyll-trace, showing forking at base of scute and the mesarch structure of the branch-bundles. $\times 180$.
- Fig. 11. *Equisetum arvense*; longitudinal section of sporophyll-trace. $\times 500$.
- Fig. 12. *Equisetum palustre*; longitudinal section of sporophyll-trace. $\times 500$.

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Eames, Arthur J. 1909. "On the occurrence of centripetal xylem in Equisetum." *Annals of botany* 23, 587–601.

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