Infranodal Organs in Calamites and Dicotyledons.

BY

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With Plates VIII and IX.

I.

IN a recently published article¹ the writer has described his investigation of the development and anatomy of the genus *Equisetum*, and made some suggestions in regard to corresponding features in the structure of Calamites. During the past summer he has had the opportunity of examining several of the more important European collections of Calamitean fossils, and has been able to put to the test the suggestions made as a result of the study of the anatomy of *Equisetum*.

At the end of the article referred to above, appeared the customary summary of results and conclusions. In the fifth paragraph of the summary the statement is made: 'The branches of Calamites did not, as has been stated in recent years, arise above the nodes, but, like those of the Equisetaceae, originated either more or less exactly from the centre of the ring of nodal wood, or from its lower border.' In the sentence quoted the writer used the term node in the sense

¹ Mem. Bost. Soc. Nat. Hist., vol. v, No. 5.

in which it is ordinarily employed in the literature referring to the Equisetales, viz. as equivalent to the so-called nodal wood¹. In the memoir of Williamson and Scott² on Calamites, the term node is used in the ordinary botanical sense, viz. as marked by the exit of the leaf-traces. This different use of the term is the less apparent because these authors continue to employ the expression, 'nodal wood,' for the peculiar tracheary zone just above the insertion of the leaf-traces (i. e. node in their sense). It would seem to be preferable to abandon this term altogether and to designate the tracheary zone the supranodal wood, especially since the branches which they describe as originating 'above the node' are directly attached to the peculiar zone in question. It will be apparent from the above statement that, in regard to the mode of origin of branches in Equiseta and Calamites, there is no real difference of opinion between the writer and the authors cited above.

In the sixth paragraph of the conclusions the statement is made that 'the more conspicuous series of nodules on the medullary casts of Calamites are impressions not of Williamson's infranodal canals, but, on the contrary, of the short, cylindrical medullary cavities of modified rhizophorous branches, homologous with those of living Equiseta.' This statement rested on a number of data.

In the first place, the writer has called attention to the fact that in *Equisetum* the leaf-traces lie above the woody cylinder of the branches in the cortex of the main axis³, although they are originally below them⁴. In nearly all the figures which represent the stems of Calamites with the surface preserved (*Calamitina* of Weiss), the leaf-scars are placed below the branches. The writer argued, since 'the Calamite, so far as anatomy goes, is simply an *Equisetum* with secondary thickening⁵,' it was extremely improbable

¹ Cf. Seward, Fossil Plants, 1898, p. 251, and especially description of figure on p. 252.

² Phil. Trans. Roy. Soc., vol. clxxxv (1894), B. ³ Op. cit., Plate 29, Fig. 2.

⁴ Op. cit., Plate 26, Fig. 16.

⁵ Scott, Studies in Fossil Botany, 1900, p. 23.

that the surface of the Calamitean stem, properly orientated, should show the leaf-traces below the branches, since the opposite is the case in *Equisetum*. This view is strengthened by the fact that Weiss¹, in order to make the leaf-traces come below the branches, actually in one instance figures the scars of roots immediately above those of the branches to which they are related, whereas in *Equisetum*, as is well known, the roots always originate from the lower side of the branches. In another figure, which shows the leaves still attached to the surface of a fragment of Calamitean stem, and in regard to which, consequently, there can be no doubt as to the proper orientation, Weiss², in order to keep the leaves below the branches, is compelled to intercalate a node. In order to effect this, he interprets small rows of scars which appear along the lower margin of the cicatrices of the branches as belonging to a node in this position. The writer regards the small scars in question as representing the ochreolae or basal sheaths of leaves belonging to the branches left attached to the main stem after the removal of the latter, exactly as is the case in *Equisetum*. This view of the matter seems to be strengthened by the fact that Weiss' 'node' does not extend completely across the figure, but ends below the branch on the extreme right. The same feature is seen less clearly on the left. It has been recently shown³ that the bases of the leaves in some *Calamites* were fused to form a sheath, exactly as in the *Equiseta* of the present day. There is thus an additional reason for emphasizing the correspondence in the relation of branches and leaf-traces at the surface of the stem in the two groups. As a result of his examination of the fossils, the writer sees no reason to abandon the suggestions made in 1899, viz. the figures that represent the surface of the stem in *Calamites* are not unfrequently inverted or misinterpreted. This is, for example, specially true of those appearing in the beautiful memoirs of Weiss.

¹ Steinkohlen-Calamarien, Heft 1, p. 121.

² Ibid., Heft 2, Atlas, Plate 16, Fig. 6.

³ Scott, Studies in Fossil Botany, p. 35, Fig. 11.

Since there was, apparently, good reason for inverting the figures of the surface of Calamitean stems, the question arose whether a similar procedure should not be adopted in the case of those representing the course of the branches and leaf-traces through the secondary wood. In *Equisetum* the leaf-traces pass very quickly above the branches on their upward course in the cortex. Assuming that the disposition of the leaf-traces in *Equisetum* represents the course of the leaf-traces in the *young* Calamite, the writer was led to the conclusion that the leaf-traces should lie above the branches in the secondary wood of Calamites, since in modern plants, even where the leaves persist for several years, the course of their traces is practically that which is present in the young stem. Compare Photographs 1 and 9, Pls. VIII and IX. This view of the matter seemed to be supported by figures of Williamson reproduced in my memoir already mentioned. In these figures certain structures, imbedded for the most part in the so-called nodal wood, above the infranodal strands, are interpreted by Williamson as the beginnings of branches. Williamson and Scott subsequently announced that these were not branches, but leaf-traces. In *Equisetum* foliar traces are never found imbedded in the nodal wood, and branches do not occur over infranodal strands. By inverting these figures it became possible to regard these indications as belonging to branches. An examination of the fossils, however, has shown that the structures in question are really leaf-traces and not branches. Dr. Scott¹ has recently published an admirable figure of a tangential section of the wood of a Calamite, in which the indications are clearly recognizable as leaf-traces, which is not the case in all the earlier figures. This occurrence of the leaf-traces apparently imbedded in the so-called nodal wood, even in sections quite close to the medulla, is probably to be explained by the reduction of the metaxylem, since a similar reduction has been shown by Dr. Scott to be present in the internodal strands. It follows, of course, if the structures figured by Williamson in

¹ Studies in Fossil Botany, p. 25.

the nodal region of tangential sections of Calamitean wood, and at first interpreted by him as branches, are in reality leaf-traces, that the figures mentioned above are correctly orientated in their original position.

Another apparent reason for inverting the figures of tangential sections through the wood of *Calamites* was derived from the statement made by M. Renault, that certain organs occurring below the leaf-traces in the secondary wood bore roots. These organs he called 'organes rhizifères,' and identified them with Williamson's infranodal canals. If they were rhizophorous, it appeared to the writer that they could not well be other than reduced radiciferous branches, homologous with those of living *Equiseta*. In the *Equiseta* both the normal branches and the rhizophorous ones have the same relation to the leaf-traces, and the conclusion seemed warranted that the leaf-traces should lie above the normal branches of *Calamites* in the secondary wood, as well as above the organs described by M. Renault as rhizophorous.

Obviously, the argument in the last paragraph turns on whether the 'organes rhizifères' of M. Renault (infranodal canals of Williamson) were really radiciferous or not. Through the kindness of Dr. D. H. Scott the writer has had the opportunity of studying two beautiful series of tangential sections through bases of Calamitean branches bearing roots. Such specimens are extremely rare. An examination of the series showed that the roots were not attached to the infranodal organs, although the latter were present in abundance. The writer owes to the courtesy of M. Renault the opportunity of examining the Calamitean sections in the collections of the Jardin des Plantes. Although some of the preparations showed roots imbedded in the secondary wood, the writer was unable to discover that in any case they were related to infranodal organs. M. Renault's statement that roots were attached to the infranodal organs possibly depends on the observation of Weiss, that the infranodal tubercles are absent on the medullary casts of aerial portions of *Calamites*. Grand'Eury also, in one of his older articles on *Calamites*,

notes that the infranodal tubercles occurred on the medullary casts in subterranean parts of *Calamites*, and gradually disappeared as the stem passed above the surface of the soil. The subterranean position of the infranodal organs probably suggested to M. Renault their relation to roots. In a recent account¹ of the casts of *Calamites*, Grand'Eury has described more fully the distribution of the infranodal tubercles. He states that they are absent on the horizontal rhizomes, although these are abundantly provided with roots, and that they occur only on the ascending portions of the subterranean stems of *Calamites*. It is apparent from these recent observations that there is no necessary relation between the presence of roots and the occurrence of infranodal tubercles. It follows from the various data introduced in this paragraph that the infranodal organs of *Calamites* were not rhizophorous, and further, that, as a consequence, they were not radiciferous branches. Hence they do not supply an argument for the inversion of figures representing tangential sections through the secondary wood of *Calamites*.

Convinced by the study of the fossils that the infranodal organs of *Williamson* were not to be explained as the equivalents of the rhizophoric branches of the *Equiseta*, the writer has still felt that it was improbable that they should be without analogues in living plants. He has devoted his attention particularly to marsh-plants with fistular medullary cavities separated by diaphragms, with a large number of leaf-traces passing off in the region of the nodes, and with considerable secondary wood. The result has been the discovery of structures which appear to differ in no important respect from the infranodal canals (lenticular organs) of *Williamson*. Some account of these is given in the following paragraphs.

II.

Potentilla palustris is a plant which is particularly characteristic in respect to infranodal organs. Photograph 3, Pl. VIII,

¹ Forêt Fossile de *Calamites Suckowii*, Comptes Rendus, 1897.

shows the structure of the woody cylinder of a biennial stem of this species a little below the region of a medullary diaphragm. It is evident that the continuity of the woody zone is interrupted at approximately equal intervals by broad parenchymatous bands running from the persistent zone of medullary tissue just inside the fibrovascular cylinder to the cortex. Photograph 4, Pl. VIII, represents one of these parenchymatous organs more highly magnified. Certain dark-walled elements may be distinguished among the parenchymatous cells; these are moribund cells corresponding to those of the fistular portions of the pith. In Photograph 5, Pl. VIII, is to be seen a radial section through one of these parenchymatous organs. The zone of secondary wood maintains its full thickness above the organ, while below it becomes narrower in passing upwards. On the right above is the medullary diaphragm. Photograph 6, Pl. VIII, shows the parenchymatous organ more highly magnified. Externally is to be seen a layer of periderm. Certain of the cells of the parenchymatous organ are dead, and show dark in the photograph. On the lower side of the parenchymatous organ a leaf-trace may be seen passing upwards and outwards. Photograph 7, Pl. IX, is of a tangential longitudinal section of the nodal region of the woody cylinder. Two parenchymatous organs are to be seen, and at their lower margins may be made out two corresponding leaf-traces in oblique transverse section. The parenchymatous interruptions of the woody cylinder illustrated in the photograph described above occur always opposite the leaf-traces and a little below the medullary diaphragm. They cause the only breaks in the continuity of the woody zone, and are, as the writer will attempt to show subsequently, to be regarded as the upper ends of the foliar lacunae which have not been closed up by the formation of secondary wood.

Cicuta maculata is another marsh-plant with numerous leaf-traces passing out in the nodal region, and with a considerable secondary growth of the ligneous zone. Photograph 8, Pl. IX, represents the nodal region of a woody

cylinder which has been deprived of its cortex and phloem by maceration. The cylinder has been split and the two halves placed side by side. A row of lenticular cavities may be seen crossing the axis, each of which subtends a leaf-trace. In Photograph 9, Pl. IX, is represented a radial section passing through one of the parenchymatous organs. Above, on the left, is the medullary diaphragm. Passing obliquely outwards is a leaf-trace which originates from the lower node and passes upwards, opposite the secondary wood, to make its exit just below the higher node. This photograph shows clearly that the parenchymatous organs under discussion are really the upper ends of the foliar lacunae, and at the same time are infranodal.

Photograph 10, Pl. IX, is of a transverse section of the stem of *Cornus stolonifera* at the height of exit of the leaf-traces. The parenchymatous gaps are six in number in this case, three for each leaf. The lacunae are here very small in size, as is usually the case with plants with more slender stems and denser texture than those described in former paragraphs. In Photograph 10, Pl. IX, the same stem is shown in transverse section at a region considerably below the node, and indentations may be seen in the woody zone corresponding to the leaf-traces. Photograph 12, Pl. IX, shows the same stem at a point just above the region where the woody cylinder is interrupted by the exit into the cortex of the leaf-traces of the next lower phytomere. The foliar indentations in the woody cylinder have disappeared. This section is to be regarded as passing through the nodal region; for just above it the leaf-traces begin their upward and outward course in the secondary wood, which is only completed immediately below the next node. The gaps in the woody cylinder in this case also correspond to the outgoing leaf-traces, and are likewise below the node.

The writer has made similar observations in a number of other cases, and it appears to be not uncommon in plants possessing secondary growth that the leaf-traces should pass upwards in the secondary wood, and outwards into the cortex

near a higher node. On the other hand, in some instances the foliar strands may pass to the higher node in the cortex, e.g. *Menyanthes trifoliata*, &c. It seems unnecessary to go further into this matter at the present time. It is worth while, however, to emphasize in this connexion that the only criterion of the node in plants with secondary growth is the point of exit of the leaf-traces from the primary wood.

The interesting feature of these observations seems to be that parenchymatous organs, lenticular in shape and infranodal in position, occur in a number of Dicotyledons with secondary growth. Where the leaf-traces are verticillate and medullary diaphragms are present, these organs resemble most strikingly the infranodal organs of the *Calamites*. If a very large stem, possessing the structure of that of *Potentilla palustris*, were to have its parenchymatous parts macerated away and its medullary cavity filled with mud, the latter would produce a cast not unlike the very characteristic casts of *Calamites*. The only essential difference would be the fact that the constrictions in this case would really be infranodal, and not represent rings of tracheary tissue above the nodes, as in *Calamites*.

The infranodal organs of certain palustrine Dicotyledons differ morphologically from those of the *Calamites* in the fact that they are the upper ends of foliar lacunae of the woody cylinder, whereas those of *Calamites*, as the writer has attempted to show, are the upper open ends of ramular lacunae. This is an important difference from the phylogenetic standpoint, since it unites the Angiosperms with Filicinean ancestors, whilst for the *Calamites* a Lycopodiaceous ancestry is indicated. It is interesting that analogous structures should appear in groups genetically so remote, under similar conditions in life, and affords a striking example of the efficiency of homoplasy in originating similar structures.

In conclusion, a few words should be said on the relation of branches and roots to the lenticular organs, although it is not necessary to go into this matter at length, since Dr. Scott will doubtless deal with it sufficiently in his

description of the newly discovered root-bearing stems of *Calamites* in his possession.

In *Equisetum*, as is well known, the branches occur immediately above the medullary rays, and since the roots in this genus are always attached to the bases of the branches, they consequently occur in the same position. In *Equisetum hiemale* it not unfrequently happens, in the case of deep and vigorous rhizomes, that the rhizophorous branch almost completely aborts, and the single very large root, which it bears, is attached directly to the supranodal wood, thus lying immediately over the large ramular medullary ray. What occurs exceptionally among the *Equiseta* seems to have been the rule in the case of the *Calamites*; for in the latter it is quite unusual to find a branch with roots attached. Weiss figures only one example of this sort.

Photograph 2, Pl. VIII, represents a tangential section through the wood of *Polygonum amphibium* in the nodal region. Above is to be seen the parenchymatous medulla of a branch, and immediately below the latter is a lenticular organ with a leaf-trace causing a toothed projection on its inferior margin. In nearly the same horizontal plane on the left is another lenticular organ (infranodal canal). In the lower part of the photograph a root is seen in cross-section. So far as the writer has been able to observe, the roots of the *Dicotyledons* have no fixed position in regard to either the nodes or the branches. The relation of the branch to the infranodal organ in the *Dicotyledons* exactly simulates the relation of the roots to the similar organs of the *Calamites*; for in the latter the roots occupied the same position as branches just as they do exceptionally in *Equisetum hiemale*.

The results of the present investigation may be summarized as follows:—

1. Some of the existing figures of the surface of *Calamitean* stems are inverted and others are misinterpreted.
2. The infranodal organs of Williamson were not rhizophorous.

3. The structures figured by Williamson apparently imbedded in the supranodal wood of *Calamites* are not branches, as he originally stated, but, on the contrary, are leaf-traces, as subsequently suggested by Williamson and Scott.

4. As a consequence of paragraphs 2 and 3, and other minor considerations, the writer's earlier suggestion that the figures of tangential sections of the secondary wood of *Calamites* should be inverted is not to be accepted.

5. Analogues of Williamson's lenticular organs (infranodal canals) exist in certain palustrine Dicotyledons of the present day.

The writer is under great obligations to Sir William Thiselton-Dyer and Dr. D. H. Scott for the hospitality of the Jodrell Laboratory at Kew, and to the latter for free access to his collection of fossil plants. Thanks are also due to Dr. Henry Woodward and Mr. Newton of the Museum of Natural History, South Kensington, for the opportunity of examining the large series of palaeobotanical sections in their charge. Last, but not least, he wishes to express his gratitude to M. Renault, of the Museum at the Jardin des Plantes, for very kindly permitting him to examine his preparations illustrative of Calamitean anatomy.

DESCRIPTION OF THE PHOTOGRAPHS IN
PLATES VIII AND IX.

Illustrating Dr. Jeffrey's paper on Infranodal Organs.

PLATE VIII.

Photograph 1. Radial section through the wood of *Abies balsamea*, showing the course of a leaf-trace. $\times 30$.

Photograph 2. Tangential section of the subterranean stem of *Polygonum amphibium*.

Photograph 3. Transverse section through the infranodal region of the stem of *Potentilla palustris*; the woody cylinder is interrupted by parenchymatous stripes. $\times 8$.

Photograph 4. The same, showing one of the parenchymatous stripes more highly magnified. $\times 40$.

Photograph 5. Radial section through a parenchymatous stripe of the same species, which shows that it is situated below the medullary diaphragm. $\times 10$.

Photograph 6. Radial section showing the parenchymatous stripe more highly magnified. $\times 40$.

PLATE IX.

Photograph 7. Tangential section through the wood of *Potentilla palustris*, showing two parenchymatous stripes (infranodal organs). $\times 10$.

Photograph 8. Superficial view of a split stem of *Cicuta maculata*, showing the infranodal lenticular organs; the cortex and the bast have been macerated away. $\times 2$.

Photograph 9. Radial section passing through two nodes of the same species, showing the oblique course of the foliar bundle. $\times 7$.

Photograph 10. Transverse section through the region of exit of the foliar traces in *Cornus stolonifera*. $\times 10$.

Photograph 11. Transverse section of the same, some distance below the node, showing the indentations in the secondary wood caused by the leaf-traces. $\times 10$.

Photograph 12. Transverse section through the nodal region of the same species; the indentations have disappeared. $\times 10$.

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