

NOTE ON THE INTEREST OF ANNULAR XYLEM IN THE PSILOPHYTALES

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WHEN a body of evidence is forthcoming which leads to the view that an existing group of plants can be regarded as derived from an ancient extinct group, it is natural to dwell on the features of resemblance. A case in point is the reasonable and enlightening assumption that the existing Psilotales find their most direct relatives in the Devonian Psilophytales. It is, however, also worth while to institute critical enquiry as to features in which the fossils and the existing plants differ. When points of comparison are as numerous as they are between the Psilotales and the Psilophytales, it is easy to pass over features in which they do not agree. It is with a small point of difference between *Tmesipteris*, *Psilotum* and *Lycopodium* on the one hand, and *Asteroxylon Mackiei* and other early fossils on the other that this note is concerned. All the tracheides of the metaxylem of *Tmesipteris* exhibit typical scalariform pitting of their thickened walls; only those of the protoxylem are annular or spiral. The same holds for *Lycopodium* and other existing Pteridophyta. In contrast to this the tracheides of the metaxylem of *Asteroxylon Mackiei* and of most of the Psilophytales of the Silurian and Devonian exhibit annular thickening throughout the xylem.

It is the purpose of this note to call attention to the interest of this detail. Various circumstances have prevented an intended re-examination of the question and I have to content myself with stating it and indicating the observations that are desirable. Even this may be scientifically worth while, but it is done at present because of my desire to take part, in however small a way, in the memorial volume to Professor Sahni.

The last full investigation of one of the Psilotaceae is Sahni's paper on *Tmesipteris Vieillardii*. This was published in 1925 but, since the work had been in progress from 1915, it coincided with the period in which Halle's critical descriptions of *Psilophyton* and *Drepanophycus* (*Arthro stigma*) from the Lower Devonian of Rörägen and knowledge

of *Rhynia*, *Hornea* and *Asteroxylon* from the Rhynie Chert of Middle Old Red Sandstone age had, in Bower's words, "put theoretical morphology again into the melting-pot".

Sahni's paper is of importance not only for giving an account of a relatively robust terrestrial species of *Tmesipteris*, but in being the first descriptive study since the bearings of the Psilophytales had been recognized. Knowledge of these early fossils, and especially of *Asteroxylon Mackiei*, underlies his work on the existing plant. This emerges in his references to the various primitive features in the external morphology of the latter and especially in his account of the anatomy of the stem. He gave the first full description of the presence in the lower portion of the leafy shoot of strands of medullary xylem which "may be directly compared with the central cauline xylem in the stele of *Asteroxylon* and *Lycopodium*". Another feature, also compared with these plants, is the way in which the phloem extends deeply into the stele and more or less surrounds each individual bundle of the ring of xylem strands.

The photographs of longitudinal sections of the stele show the scalariform tracheides of the metaxylem. In contrast with these the photographs of longitudinal sections of the xylem of *Asteroxylon Mackiei* (KIDSTON & LANG, 1920, FIGS. 10, 11, 77-79; LANG & COOKSON, 1930, FIG. 43) show that the metaxylem in this plant is certainly composed of tracheides with annular thickening.

There are evidently two points for further enquiry; (1) the exact type of thickening of the tracheides in as many early vascular plants as afford material in which this can be determined critically; (2) the examination of existing Pteridophyta to ascertain whether in any of them metaxylem with annular thickening of the tracheides is found and, if so, in what organs or regions of the plant. Something can be said on the first point but little on the second; and full treatment of the subject would be inadvisable without further investigation.

The Psilophytales are not known later than the Middle Devonian and at that period seem to have formed only a small proportion of a flora which included a variety of larger and more advanced forms. The few plants of the Rhynie Chert are of outstanding importance on account of their exceptional preservation. *Rhynia Gwynne-Vaughani* with its small centrarch stele has annular tracheides of metaxylem surrounding the narrower elements of what is presumably the protoxylem. *Hornea* agrees, generally, with differences of detail. The relatively stout and complex stellate xylem of the stele in the stem of *Asteroxylon Mackiei* is composed throughout, as already mentioned, of tracheides with annular thickening; occasionally with traces of spiral thickening. There is never any indication of scalariform pitting. Incrustations of *Thursophyton Milleri*, a plant of similar organization to *Asteroxylon*, are abundant throughout the Middle Old Red Sandstone of Scotland. They rarely show any structure but in a few cases annular tracheides, resembling those of *Asteroxylon*, have been demonstrated. The other vascular plants have either as yet shown nothing of their structure (*Caulopteris*, *Protopteridium*) or, as in the case of numerous and often large incrustations of secondary wood, have tracheides with multiseriate, oval, bordered pits. In this respect they agree with the petrified specimens of *Palaeopitys Milleri*. *Dadoxylon Hendriksi* from Cornwall has circular pits with crossed pores.

In the Middle Devonian of Germany there was a similar abundance of advanced plants which do not concern us here. The plant known as *Asteroxylon elberfeldense* is, however, of great interest. Though not preserved as clear petrifications Kräusel and Weyland have ascertained a good deal as to its vascular structure (KRÄUSEL & WEYLAND, 1926, PL. 4, FIGS. 1, 2; PL. 6, FIGS. 2, 3, and 1929, PL. 1, FIGS. 4, 5). The interest of their results is that they explicitly describe the tracheides as scalariform and speak of the walls as having "treppentüpfel". It is not easy for anyone, dependent on the study of illustrations only, to come to a decision as to this, but the photographs exhibit some features which support the views of the investigators. Should further work confirm the scalariform pitting of the tracheides in this plant, it will be of extreme interest in contrast to the undoubted annular thickening of the metaxylem in *Asteroxylon Mackiei*.

The tracheides with multiseriate circular pits with crossed pores found in the stellate xylem of *Schizopodium Davidi*, an Australian fossil of Middle Devonian age, is a more profound difference and need not be discussed further here (HARRIS, 1929).

From the Silurian to the summit of the Lower Devonian the vascular plants that are known as regards the nature of their tracheidal thickening are all Psilophytales. In all in which the pertinent features can be clearly ascertained the tracheides of the metaxylem seem to have annular thickening. Nothing is known as yet as to the vascular plants from the Silurian of Britain. In Victoria, Australia, however, *Baragwanathia* (a plant of considerable size not unlike *Drepanophycus*) from the *Monograptus* Beds of Lower Ludlow age has shown the structure of its stellate stem-stele and leaf-traces. There is clear proof from observations by reflected light, by film-pulls and ground sections (LANG & COOKSON, 1935, PL. 31) that the metaxylem of this Silurian plant has the same annular thickening of all the tracheides as was found in *Asteroxylon Mackiei* from the Middle Devonian.

The same seems to hold for slender axes, presumably belonging to *Cooksonia*, from the Downtonian (LANG, 1937, FIGS. 23, 35, 36) and for the leafless axes of *Zosterophyllum myretonianum* (LANG, 1927, FIGS. 11, 12) and of *Gosslingia* (HEARD, 1927, PL. 14, FIGS. 6, 7) from the Lower Devonian. From Lower Devonian rocks also incrustations of *Psilophyton princeps* and of *Drepanophycus* have demonstrated clearly the annular thickening, both from Scotland (LANG, 1932, FIGS. 14, 16, 74, 75) and from Norway (HALLE, 1916, PL. 1, FIGS. 19, 20; PL. 4, FIGS. 14a, 14b). Similarly in the Australian sequence, which begins in the Silurian with *Baragwanathia*, xylem with clear annular thickening occurs in the Centennial Beds which are now regarded as definitely Lower Devonian (LANG & COOKSON, 1930, FIGS. 30-36).

It seems likely that other types of tracheidal thickening will become known in these early rocks with further investigation, but the persistence of the annular type in the Psilophytales can hardly be disturbed by this. A remarkable fact is the lack so far of evidence of early Pteridophyta with scalariform pitted walls. The only case in which this question has been really raised is that of *Asteroxylon elberfeldense*. While, as

has been shown, there is now a considerable body of information concerning the xylem elements of early vascular plants there is still need of additions to our knowledge and its critical evaluation.

The other point on which enquiry is needed, the question whether metaxylem with annular thickening, as critically distinguished from scalariform pitting, occurs in any existing Pteridophyta requires further work before any statement can be made. It may, however, be said that a preliminary inspection of a few available preparations, not made for the purpose, has suggested that there are grounds for careful enquiry though the results of this may well prove negative.

It is a little remarkable that nothing suggestive has been noticed as yet in *Tmesipteris* or *Psilotum*. In some species of *Lycopodium* with considerable metaxylem in their leaf-traces the features of the tracheides of this seem more than suggestive. Preliminary enquiry also suggests that *Equisetum* and *Helminthostachys* are worth study, especially their sporangiophores.

The remarks in this note are directed only towards clearing up the objective description of certain facts. From these we might be led to the consideration of the causal factors underlying various types of tracheidal thickening but I have of course nothing to say on this deeper problem.

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