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TRANSITIONAL PITTING IN TRACHEIDS OF PSILOTUM

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Most of the anatomical studies upon *Psilotum* have been in connection with the interpretation of the spore-bearing structures and with the general organization of the stele. Accounts of the anatomical organization of the axis have been largely topographical, discussing the distribution of the cortical tissues and the differentiation of the stelar tissues, principally as seen in cross-section (Bertrand, '85, Boodle, '04, Ford, '04, Stiles, '10). The position and order of development of the wood elements have been very definitely emphasized, whereas the nature of the elements themselves has scarcely been more than mentioned. It has been stated generally that the protoxylem elements are spiral tracheids, and that the metaxylem elements are scalariform or somewhat reticulate tracheids.

Previous anatomical studies have furnished two illustrations of pitting types in the tracheids of *Psilotum.* Bertrand ('85) illustrated diagrammatically several types of tracheids which he had seen in longitudinal section in the stele of the subterranean axis. In the accompanying text he described spiral protoxylem elements and scalariform metaxylem elements with areolate pits. Boodle ('04) illustrated secondary tracheids having irregular or scalariform pitting.

In other groups of vascular plants, the development of secondary thickening types in the maturation of the primary xylem has been regarded as fundamental recapitulatory evidence of evolution. In *Psilotum,* a simple modern vascular plant that in many respects seems to hark back to the Palaeozoic for its hypothetical ancestors, a knowledge of the type of transitional pitting would be fundamentally important in determining more closely the exact phylogenetic status of the plant.

We have studied material of *Psilotum nudum* (L.) Gris. (*P. triquetrum* Sw.), which was obtained from living plants in the collection of the Missouri Botanical Garden at St. Louis. Pieces of the aerial axis were killed in formalin-acetic-alcohol, embedded in paraffin, and cut into serial longitudinal sections 10 μ thick with a rotary microtome. The sections were stained with Safranin and Fast Green FCF and photographed on Wratten M plates, using a Wratten G filter with a photoflood light.

The transition in types of secondary thickening of the xylem of *Psilotum,* passing from the protoxylem to the metaxylem, is similar to that described by Bailey ('25) as occurring in various groups of Pteropsids. Due to the small size of the actinostele in *Psilotum,* only a few cells are involved. Consequently the transition is more abrupt than that which is found in more advanced groups. In spite of the fact that only a few cells are involved, there has been observed practically every transition type that has been found in the gymnosperms.

The first formed protoxylem elements invariably are provided with loosely wound spiral or annular secondary thickenings (pl. 17, figs. 1, 7; pl. 18, fig. 9). In the succeeding exarch development of tracheids, the secondary thickening generally forms an irregular reticulate structure (figs. 7, 9). From this stage on, the formation of scalariform pits (fig. 10), of somewhat elongate bordered pits, and of true circular bordered pits is usually observed. The transition seems to follow along a number of separate lines of specialization which depend in part on the size of the elements involved. The web-like structure may give rise to more or less regular alternately arranged bordered pits (figs. 3, 4, 9), with occasional opposite pits (fig. 4), which are apparently due to irregularities in the net. In smaller cells, or those in which the secondary thickening does not assume the net structure, typical uniseriate bordered pits may be formed (fig. 1). These may be close together (araucarian) or widely spaced (abietinean).

Typical annular or scalariform thickenings (figs. 5, 6, 10) may break up to form circular bordered pits. That we are dealing with true bordered pits seems quite obvious. The overhanging thickenings forming the "dome-like" border of the pits are clearly seen in figs. 8 and 11. We have observed no thickening of the primary wall (torus) in connection with these pits.

It has been conjectured that *Psilotum* may be an extremely ancient plant which has come down through time relatively unchanged morphologically from its psilopsid ancestors, or that *Psilotum* may represent a group of plants once quite complex, but now through reduction become rather simple morphologically (Zimmermann, '30).

The display of transitional pitting seems to us to be of considerable phylogenetic significance. A general type of transition from spiral protoxylem to more definite types of metaxylem pitting has been observed in most large groups of Pteropsida (Bailey, '25). If this uniformity occurred consistently in all groups, such transition would lose significance, but, inasmuch as it is unreported in the Psilophytales, that fact seems to have specific bearing on the relation of *Psilotum* and that group.

Apparently the wood of the Psilophytales showed only annular and spiral thickenings. Kidston and Lang ('20) state definitely that they found no trace of any scalariform or pitted tracheids in the Devonian plants they studied. In *Baragwanathia longifolia,* a vascular plant of Silurian age, only ring-like secondary thickenings have been seen (Lang and Cookson, '35). In other respects the general morphology of *Psilotum* is distinctly not far removed from that of the primitive Devonian plants. It is not difficult to conceive that during the progress of their evolution these Devonian plants gave rise to *Psilotum* with its advanced stelar anatomy, and otherwise morphologically underwent little change.

If *Psilotum* approaches the simple Devonian plants by reason of reduction, one simply infers that the pit transition is vestigial. In the extreme, this line of thought might be considered to show that *Psilotum* represents a phylum of vascular plants, perhaps unrelated to the Psilophytales, in which bordered pits had evolved with or even preceding scalariform types. Then, such a series of transitional stages might be taken to mean that *Psilotum* is a greatly reduced form. Boodle ('04) has suggested that the secondary xylem which he observed in the axis indicated the possibility of origin from the type of *Sphenophyllum* or some Lycopsid.

Unless pitting types, such as we have demonstrated in *Psilotum,* at some future time are found in the simpler Devonian plants, the evidence seems to suggest strongly that *Psilotum* is more highly evolved with respect to these characters than are the Psilophytales.

For the drawings we are indebted to Dr. Gladys E. Baker.

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Explanation of Plate

PLATE 17

Photomicrographs of types of secondary wall thickening and pitting in xylem of *Psilotum.*

Fig. 1. Elements with loose spiral, spiral thickenings, and bordered pits.

Fig. 2. Elements with annular, reticulate and spiral thickenings.

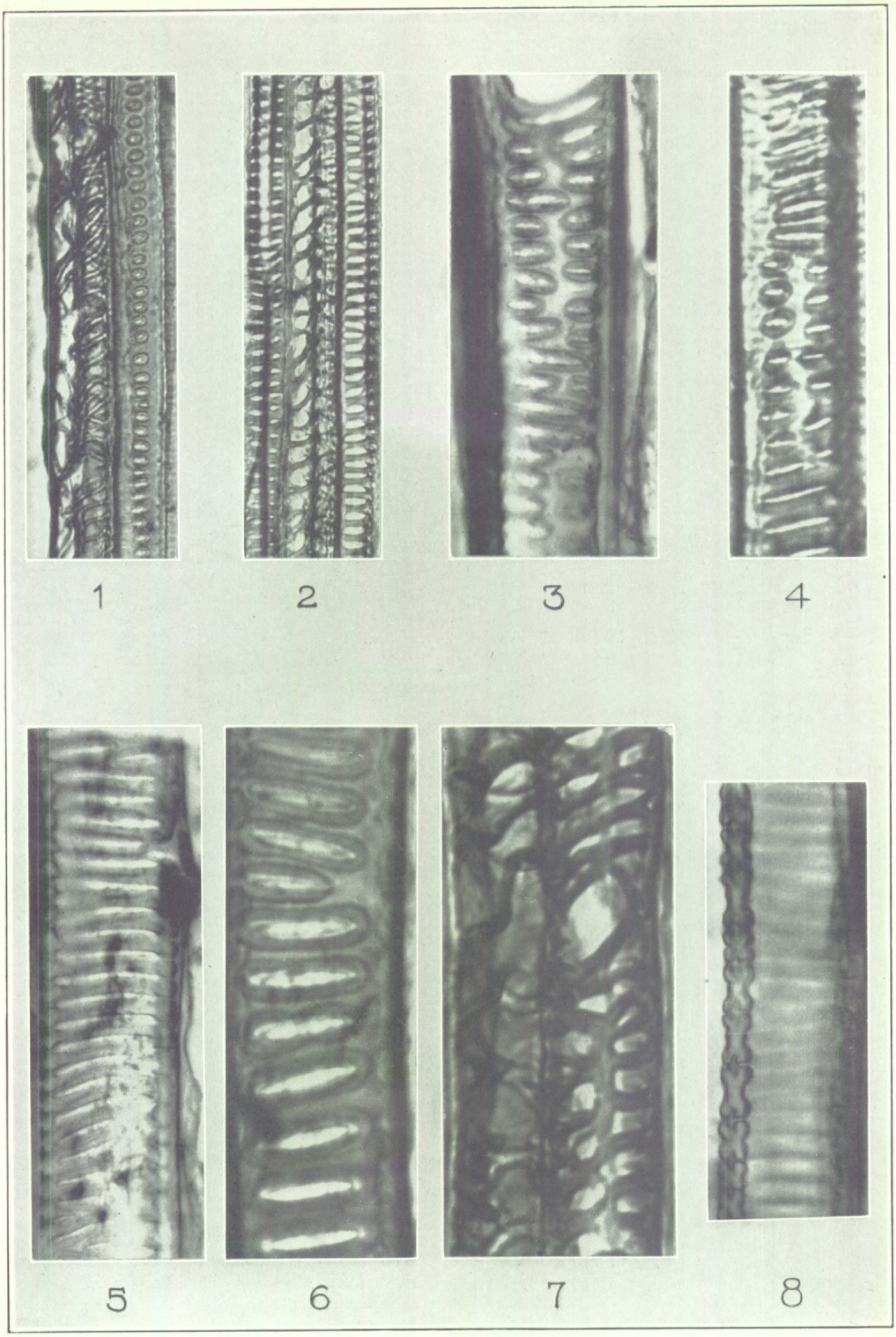
Figs. 3 and 4. Transition from elongate scalariform bordered pits to alternate biseriate bordered pits.

Fig. 5. Typical scalariform metaxylem thickening.

Fig. 6. Elongate bordered pits.

Fig. 7. Spiral thickenings and transition from spiral to reticulate structure.

Fig. 8. Section of tracheid wall showing overarching walls of the bordered pit-pairs.



MOORE AND ANDREWS—TRACHEIDS OF PSILOTUM

Explanation of Plate

PLATE 18

Camera-lucida drawings of tracheids of *Psilotum.*

Fig. 9. Transition stages in development of secondary thickenings from irregular ring-spirals to irregular reticulations to scalariform bordered pits.

Fig. 10. Scalariform element showing development of occasional bordered pits.

Fig. 11. Structure of bordered pits as seen in longitudinal section.