Telephragmoxylon and the Origin of Wood Parenchyma.¹

BY

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With Plate III and three Figures in the Text.

IN Jeffrey's 'Anatomy of Woody Plants', published in 1917, a theory of the origin of wood parenchyma is advanced. From a study of living woods, and particularly those of the Coniferae, the author was led to the conclusion that this important element originated from the so-called septate tracheide and that its first appearance was at the end of the annual ring.

While the book just mentioned was still in the press an interesting and further confirmation of the theory came to light through the discovery of a new wood from the Comanchean deposits of Texas. A certain histological feature was judged of sufficient importance to justify a new generic name—*Telephragmoxylon*.

The technical description of the wood, along with many others derived from Mesozoic and Tertiary deposits, has been embodied in a memoir which will appear later. The reason for taking the genus from its original setting for individual treatment may be explained by a quotation from a recent letter of Professor Jeffrey's: 'It seems to me extremely desirable that you should write a special article on *Telephragmoxylon*. The genus is so important and so interesting that it should be brought to attention in one of the general journals.'

It is commonly known that Texas is well favoured with immense deposits of Tertiary lignite which are of considerable economic importance. On the other hand, it is probably known only to geologists that in far more ancient deposits of the same state, namely, those of the Triassic and Lower Cretaceous or Comanchean, may be found scattered and very local masses and fragments of lignitized and partially silicified woods.

In the fall of 1917, while collecting near Weatherford, Texas, the writer came upon fragments of charred and flattened trunks of a wood which seems to be new to science and to afford a striking justification of the theory

¹ Contribution from the Laboratories of Plant Morphology of Harvard University.

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just mentioned: namely, that wood parenchyma arose by the septation of tracheides at the end of the annual ring. Two species of the wood have been recognized. The following description is based upon *T. brachyphylloides*.

From an examination of the microtome sections, the first and most obvious fact is that we are dealing with a wood belonging to the Araucarian complex which dominated the Mesozoic forest. The bordered pits on the tracheides are uniseriate and are commonly tightly pressed against one another, though on larger tracheides biseriate alternation is not uncommon. The pit mouths are elongate and oval.

The rays are manifestly Araucarian; in tangential aspect they show themselves as either uniseriate or biseriate. Their cells show a slight gummy inclusion. The lateral tracheide field (as seen radially) is impressed with few to ten small pits which have either oval or circular openings. These Araucarian features are well shown in Fig. 1, Pl. III. Traumatic vertical resin-canals are present—a fact very suggestive of the phylogeny of the Araucarians, but one with which we are not now concerned. They are shown in Fig. 2, Pl. III. The wood at this point is poorly preserved, but it came from the same blocks that have exhibited the feature which makes the wood distinctive.

In sections inclined slightly from the true tangential plane towards the transverse, so that summer as well as spring wood may be included, there is manifest in many of the *terminal tracheides* of the annual ring successive and apparently double diaphragms which cross their lumina. These diaphragms are the end walls of short tracheides whence the middle lamella has disappeared. Each bears from one to three bordered pits. In other words, we are dealing with a condition of initial septation of the tracheides at the terminus of the annual ring: hence the generic name *Telephragmoxylon*. That these plates and their pits are very abundant and definite is evidenced by our microphotographs.

In Fig. 3, Pl. III, is seen a cross-section of the wood. Stretching obliquely across the field is a darker band of tracheides. The darker colour is due to the fact that a lucky section has cut at least five successive tracheides at such a point that their cross-diaphragms are visible. On one of these septa a pair of bordered pits is seen; and evidence of the same is visible on three others.

In Fig. 4, Pl. III, of a tangential section, an oblique band of septated tracheides runs across the field. Even with the low magnification employed it is evident that bordered pits are present in the septa. Fig. 5, Pl. III, shows a detail of these same tracheides under higher magnification.

In Text-fig. 1 is shown a stereogram reconstruction of a small block of *Telephragmoxylon* wood. In Text-fig. 2 we have a similar figure of the allied genus *Brachyoxylon*. The essential difference is obvious.

To those who are familiar with the modern theory of the origin of wood parenchyma it is at once clear that we have here direct testimony from a fossil form as to the correctness of that view. It has been shown that in *Spruce* wood, for example, elements are laid down at the end of the

TELEPHRAGMOXYLON

TEXT-FIG. 1.

BRACHYOXYLON

TEXT-FIG. 2.

TEXT-FIG. 3. *Picea*. Origin of parenchyma.

growing season which at an early stage 'become transversely septate, and in the segments so set off the protoplasm sometimes persists (when a typical parenchymatous element of the wood is the result); at other times it disappears with the complete differentiation of the walls surrounding it (in the case of so-called short tracheides)'. Text-fig. 3 illustrates this condition in a diagrammatic manner, while Fig. 6, Pl. III, is introduced to show by an

actual photograph a cross-section of *Spruce* wood and the position of wood parenchyma among the summer tracheides. In *Picea*, then, the midmost point of the differentiation of long tracheides into parenchyma has been reached. Yet logic requires us to suppose that the initial step in the process was the septation of the long tracheide into short tracheides, all of which were essentially similar. Such a situation appears not to have been detected in living woods, but in the fossil form under discussion just that condition is strikingly manifest.

That it belongs to a different genetic series is of no consequence. We are here dealing with the origin of wood parenchyma, not with the origin of *Picea*, and we know that this element of the wood has originated several times and independently.

It has been suggested that fully developed wood parenchyma at the end of the ring serves as a storehouse for foods which may be directly available to the developing cambium in the succeeding spring; and that its differentiation was correlated with the progressive refrigeration which characterized the last part of the Mesozoic Period.

Without bringing in a teleological explanation, we may believe that the original tracheide septation, as exemplified by the genus discussed in this article, constituted a superior mechanism for facilitating the rapid, radial transference of water and food-materials to the cambium at the same critical period of growth.

It should be pointed out that a wood of this character has once before been discovered. In 1913 Miss Ruth Holden found, among the fragments of lignitic wood from the Jurassic deposits of Yorkshire, a specimen of *Brachyoxylon* which, to quote her own words, is 'unique in the possession of large numbers of septate tracheides at the beginning (?) of each annual ring. The significance of these cells it is difficult to infer. Whether they represent incipient parenchyma or are related to an injury it is impossible to say, but the latter supposition is rendered improbable by their appearance in several successive years and the lack of any twist in the grain which would indicate proximity to a wound.'

Hence we are fairly certain that wood of the genus *Telephragmoxylon* was growing in Europe in the period which preceded the one in which our own specimens have been discovered.

As to its taxonomic position, *Telephragmoxylon* is a member of the sub-tribe Brachyphylloideae of the tribe Araucarineae, family Pinaceae.

SUMMARY.

From a study of living coniferous woods the theory has been advanced that wood parenchyma arose by septation of long tracheides, and that its first position was among the terminal cells of the summer wood. Pro-

gressive differentiation and diffusion through the ring was intimately related to the progressive refrigeration of the later Mesozoic.

From the Comanchean deposits of Texas have recently been obtained two woods of Araucarian affinities which exhibit the incipient stages of tracheide septation demanded by the theory. These have been placed in a new genus, *Telephragmoxylon*.

In conclusion, the writer expresses his indebtedness to Professor E. C. Jeffrey for assistance in the photographic work and for permission to use Text-figs. 1, 2, and 3.

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LITERATURE CITED.

- JEFFREY, E. C. : The Anatomy of Woody Plants. Chicago, 1917.
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EXPLANATION OF PLATE III.

Illustrating Mr. R. E. Torrey's paper on *Telephragmoxylon* and the Origin of Wood Parenchyma.

Fig. 1. Radial section of the wood of *Telephragmoxylon brachyphylloides*, showing the characteristic ray and tracheide pitting.

Fig. 2. Cross-section of the same, showing the Brachyoxylloid traumatic resin canals.

Fig. 3. Cross-section of the same, showing the horizontal and pitted walls of the short tracheides.

Fig. 4. Tangential section of the wood, exhibiting the septated tracheides at the end of the annual ring.

Fig. 5. Detail of the last under higher magnification.

Fig. 6. Cross-section of the wood of *Picea sp.* to show the position of the wood parenchyma on the face of the summer wood.

1.

2.

3.

4.

5.

6.

Huth coll.

TORREY—TELEPHRAGMOXYLON.