THE OCCURRENCE OF EUPTELEA IN THE CENOZOIC OF WESTERN NORTH AMERICA

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With three plates

IN THE EOCENE CLARNO FORMATION of north central Oregon logs and numerous fragments of silicified wood occur in association with fruits and seeds. The Clarno formation, one of a series of early Tertiary deposits in the basin of the John Day River, consists of interbedded conglomerates, tuffs, ash layers and lava flows. In very limited outcrops of the formation, in beds of siliciously cemented volcanic tuff, numerous seeds and fruits may be found. These are preserved chiefly in the form of chalcedony filled locule casts, and retain in minute detail the internal morphology and anatomical structure of a wide range of angiosperm seeds and fruits. The seed flora, insofar as it has been studied, has been described and interpreted in an intensive investigation by Scott (1954 and unpublished mss.). The tissues of the silicified logs and more abundant fragments of silicified wood which accompany the seeds and fruits are remarkably well preserved in many cases, and in both external form and internal organization the logs and fragments show evidence of silicification prior to compression failure from the weight of overlying sediments. The bulk of the preserved stems are decorticated, and commonly, in thin section, show evidence of extensive fungus attack on the wood, hence indicating conditions of aerobic decomposition preceding burial and mineralization.

The Clarno woods are being intensively studied with regard to their botanical identification and interpretation, and a number of genera have now been determined. Among the genera thus far recognized is one of unusual interest from the standpoint both of its morphology and its geographic distribution, viz., the genus *Euptelea*. As far as the authors are aware this occurrence comprises the first fossil record of the genus. The existence of *Euptelea* in the early Tertiary of western America constitutes another significant addition to the growing body of paleobotanical evidence relating the early Tertiary forest history of North America to that of southeastern Asia.

Euptelea is one of a group of small or monotypic genera extant today only in warm temperate and subtropical eastern Asia. Other members of this morphologically and geographically isolated group of woody plants include *Cercidiphyllum*, *Trochodendron*, *Tetracentron*, and *Eucommia*. These five genera have been variously associated taxonomically in the past (Swamy and Bailey 1949), but comprehensive anatomical study has revealed numerous and significant divergences in structural organization and floral morphology among them, demonstrating convincingly that each

genus is best regarded as constituting a distinct family (Tippo 1940; Nast and Bailey 1945; Nast and Bailey 1946; Swamy and Bailey 1949).

The genera constituting the Trochodendraceae, Tetracentraceae, Cercidiphyllaceae and Eupteleaceae possess in common certain ranalean characters in one or more of their organs or parts. The vesselless Trochodendraceae and Tetracentraceae are closely related, having many morphological features in common. On the other hand, the Cercidiphyllaceae and Eupteleaceae are quite distinct from each other and, likewise, quite distinct from the vesselless *Trochodendron-Tetracentron* complex. The genera included in these four families logically may be regarded as relics of ancient ranalean origin which have evolved independently at least since Upper Cretaceous time, and probably will ultimately be found to have been distinct in older Upper Cretaceous deposits. That three of these genera, excluding *Euptelea*, have been in existence in post Cretaceous time as essentially "modern" entities is well documented by their occurrence in Tertiary deposits. *Cercidiphyllum* is known from the Middle Eocene of England, the Eocene of Greenland and from numerous horizons in the early and middle Tertiary of continental United States (Brown 1939). Vesselless dicotyledonous woods conforming in structure to either or both *Trochodendron* and *Tetracentron* have been found in the Eocene of Greenland (Mathieson 1932), the Oligocene of Oregon (Hergert and Phinney 1954) and the Miocene of Washington (Beck 1941, 1944). Fruits apparently belonging to *Trochodendron* have been described from the Eocene of England (Reid and Chandler 1933).

Hence, with the notable exception of *Euptelea*, there is well documented evidence that these presently Asiatic genera once grew on the American continent and were quite probably Holarctic or circumboreal in distribution. Recognition of *Euptelea* among this assemblage of phylogenetically and geographically isolated primitive angiosperms adds measurably to our understanding of the diverse character of the woody flora of early Tertiary temperate and high latitudes in North America and accentuates the degree of depauperization which took place during the late Cenozoic. It is quite probable that further additional components of the highly diversified woody angiosperm flora currently surviving in warm temperate Asia will be found among the early Cenozoic fossil floras of temperate America. Indeed, the question may be asked whether many of these genera are not already known as leaf impressions, but are concealed in fossil floras by mis-applied binomials or form generic names, as was clearly demonstrated by Brown (1939) in the case of the American Cenozoic record of *Cercidiphyllum*.

Assignment of the fossil wood under consideration to *Euptelea* is as follows:

Euptelea baileyana Scott & Barghoorn sp. nov.[1] (PLATE I, FIG. 1; PLATE II, FIG. 1; PLATE III, FIGS. 1, 2, 3.)

[1] This species is named in recognition of Professor Irving W. Bailey's contributions in establishing the morphological and taxonomic position of the phylogenetically isolated genus *Euptelea*.

VESSELS: Small, mean tangential diameter 54 μ, somewhat smaller in the late wood; chiefly solitary, occasionally paired, or appearing paired as a result of overlapping of vessel elements; about 85 per sq. mm. in the early wood, somewhat more abundant in the late wood. Thin walled; oval or slightly angular in transverse section. Vessel elements up to 0.85 mm. long. Perforation plates oblique, exclusively scalariform; bars mostly narrow and widely spaced, varying in number from 5 to 35, most commonly about 15, per perforation plate. Intervascular pit pairs predominantly scalariform with narrow apertures, occasionally opposite. Pits to parenchyma scalariform, the apertures wider than those of the intervascular pits. Numerous thin walled tyloses present. Vessel distribution graded porous.

PARENCHYMA: Very scanty diffuse.

RAYS: Heterogeneous (Kribs Type IIA); multiseriate rays up to 18 cells wide and 2 mm. high, with 1 to 6 marginal rows of enlarged isodiametric or upright cells; uniseriate rays 2 to 7 cells high, composed chiefly of upright cells but occasionally including 1 or more almost procumbent cells; up to 8 per mm.

IMPERFORATE TRACHEARY ELEMENTS: Thick walled fiber tracheids, the pits with small but distinct borders.

LOCALITY AND GEOLOGIC OCCURRENCE: SE $\frac{1}{4}$ sec. 27, T. 7 S., R. 9 E., Wheeler Co., Oregon. Middle (?) Eocene, Clarno formation.

COLLECTOR: Richard A. Scott, July 1950.

MATERIAL: A single specimen of silicified, mature, secondary xylem measuring approximately 2 x 2 x 2 cm. The curvature of the growth rings indicates that the stem, of which this specimen represents a small fragment, had a diameter of at least 10 cm.

HOLOTYPE: University of Michigan, Museum of Paleontology, No. 32338, represented by three ground sections. Three ground sections are also deposited in the Paleobotanical Collections, Harvard University, No. 55572.

AFFINITIES AND DISCUSSION

Structural features of the fossil wood indicate, after extensive comparison, that its closest affinities are with the modern genus *Euptelea*. There is close agreement in all details except those noted below. The fossil wood shows a superficial resemblance to the mature secondary xylem of *Platanus*, particularly as seen in the transverse plane of section. However, the broad rays of *Platanus* are homogeneous, whereas the fossil possesses conspicuously heterogeneous multiseriate rays.

The secondary xylem of the two living species of *Euptelea*, *E. polyandra* Sieb. & Zucc. and *E. pleiosperma* Hook f. & Thoms. is characterized by small, predominantly solitary vessels. There is a conspicuous difference in diameter between the vessels of the early wood and those of the late wood (PLATE I, FIG. 2). The size and distribution of the vessels of *E. baileyana* agree with the distributional pattern in the two modern species. Mean tangential diameter of the vessels in the fossil specimen is intermediate between the measurements secured from comparable secondary xylem

of the two modern species, as follows: *E. polyandra* 52 μ, *E. baileyana* 54 μ and *E. pleiosperma* 57 μ. Thin walled tyloses, present in the vessels of both living and fossil species, appear more abundantly in the fossil. These structures tend to tear out in the sectioning and manipulation of unimbedded wood and hence for this reason there is artificially introduced a slight difference in appearance of the wood of the fossil and living forms.

The two major differences between the vessel elements of the modern and fossil species are in the structure of the intervascular pit-pairs and in the number and spacing of the bars in the scalariform perforation plates. In both the extant species the intervascular pitting is transitional between scalariform and opposite-multiseriate, whereas in the fossil form it is chiefly scalariform. As pointed out by Nast and Bailey (1946), scalariform pitting tends to predominate in the *inner* rings of the stem wood of *Euptelea*, while opposite-multiseriate pitting is characteristic of the larger vessels in the *outer* rings of the older stemwood. However, vessels with scalariform pit pairs occasionally occur in the old wood of *E. pleiosperma*. Phylogenetically, opposite intervascular pitting is reasonably to be interpreted as evolutionarily more advanced than is scalariform pitting among woody angiosperms. In this respect the fossil species is less highly specialized than the two living species of *Euptelea*.

In the proposed new species of *Euptelea* the perforation plates of the vessel elements, however, commonly exhibit a more specialized structure than those of the two living forms. Both *E. polyandra* and *E. pleiosperma* are characterized in the mature secondary xylem by numerous fine bars (20–90) in their vessel perforation plates. The vessel perforation plates of *E. baileyana* usually possess from 5 to 35 bars, most frequently about 15. Also, in contrast to the living species the individual bars are more widely spaced (PLATE III, FIG. 2).

Very little wood parenchyma is present in the fossil *Euptelea* and its presence can be detected only because of the unusual degree of structural preservation. In living species of *Euptelea*, the wood parenchyma is distributed apotracheally and varies from fairly abundant to extremely scanty. In the range of material examined in this study it was observed that wood parenchyma is less abundant in *E. pleiosperma* than in *E. polyandra*. Terminal parenchyma, noted by Metcalfe and Chalk (1950), was not observed. The apparent extreme paucity of wood parenchyma in the fossil may be explained by a variety of factors. One of these is the difficulty of distinguishing between the effect produced by the loss of cell wall substance from the secondary walls of the tracheary elements and the true thin secondary wall and correspondingly larger lumen of parenchymatous elements. Owing to the differential rate of degradation of the various lamellae of the secondary wall various histological effects are produced in fossil plant residues which must be interpreted with this factor in view (Barghoorn 1952).

The largest ray observed in our thin sections of *Euptelea baileyana* is 18 cells in width. In *E. pleiosperma*, which has wider rays than *E. polyandra*, the largest ray observed was 13 cells in width. This is not a large

quantitative difference with respect to this structural feature in comparing the living and fossil species. The frequency of broad, multiseriate rays in the fossil wood, however, is considerably greater than that occurring in either of the two extant species of *Euptelea*. The material of *E. pleiosperma* examined, however, does not represent wood of ring development directly comparable with that of the fossil, being from wood formed in more central rings. Inasmuch as there is a marked increase in ray width during ontogeny of the woody cylinder (Barghoorn 1940) it would be desirable to compare ray width from rings of comparable radii. Wood from the outer rings of large stems of *E. pleiosperma* might show the presence of a higher proportion of large multiseriate rays. Unfortunately, material for determining this feature has not been available.

The close agreement in major diagnostic features as well as in numerous microscopic details of anatomical structure provides convincing evidence that the Clarno fossil wood is closely related to *Euptelea*. Determination of the degree of relationship necessitates careful evaluation of the three observable differences between the Eocene and the modern wood. These differences are limited to 1) the nature of the intervascular pitting, 2) the fine structure of the vessel end walls and perforation plates and 3) the proportion and size of the broad multiseriate rays. In each of these categories, the range of structural variation between the living species of *Euptelea* and the proposed fossil species is less than that which may be found, in numerous instances, among species of a single living genus. For example in *Magnolia* and *Carpinus*, among other genera, the vessel perforation plates vary from scalariform to simple. In *Platanus* and in many genera of the Lauraceae, as examples which may be drawn from a wide range of the dicotyledons, both scalariform and simple perforation plates may be observed in a single radial section. Phylogenetically, these structural differences are more quantitative than qualitative, and in our interpretation of the fossil wood we are extending the morphological range of *Euptelea* rather than proposing a new generic category of the Eupteleaceae.

It has been noted that the vessel perforation plates in the fossil *Euptelea* are more highly specialized than those of the living species of the genus, whereas the intervascular pitting gives evidence of a lesser degree of specialization. This apparent contradiction, however, does not seriously prejudice our assignment of the fossil form to *Euptelea*. Rather, it illustrates the observations of Bailey (1944), drawn from comparative study of the woods of the dicotyledons as a whole, viz., that the phylogenetic modifications of structural features of the vessels of the dicotyledons proceeded at more or less independent rates.

On the basis of close agreement in wood structure the Clarno fossil wood is assignable to the genus *Euptelea*. This genus occupies an isolated position, taxonomically, and possesses secondary xylem of characteristic structure. The possibility that a comparable combination of structural features has arisen quite independently in other families of the more primitive angiosperms seems extremely remote, although this possibility has been considered. Our species has been placed in an extant genus since in our

opinion no useful purpose would be served by clouding its affinities through appending "*-oxylon*" to its generic name.

The occurrence of *Euptelea* as a component of the early Tertiary forests of western United States strengthens the growing evidence that our early Cenozoic floras show stronger affinities to the woody flora now occupying southeastern Asia than has been generally recognized. It serves also to demonstrate the extreme complexity in generic composition of the early Tertiary floras and the difficulties inherent in interpreting them in terms of present day distributional patterns and associations of woody plants.

SUMMARY

A specimen of silicified wood from the Eocene Clarno formation of north central Oregon has been identified as an extinct species of the Asiatic genus *Euptelea*. The wood differs from that of the two living species in only three minor structural details: 1) character of the pitting of the vessel walls; 2) fine structure of the scalariform perforation plates of the vessel end walls; 3) occurrence of a larger proportion of broad multiseriate rays. These differences are quantitative and not qualitative in the evolutionary specialization of secondary xylem; the authors regard them as extending the morphological range of the genus rather than the basis for proposing a new genus. Accordingly, the specimen has been designated as an extinct species of *Euptelea*, *E. baileyana*. This represents the first fossil record of the genus and establishes its former existence in North America.

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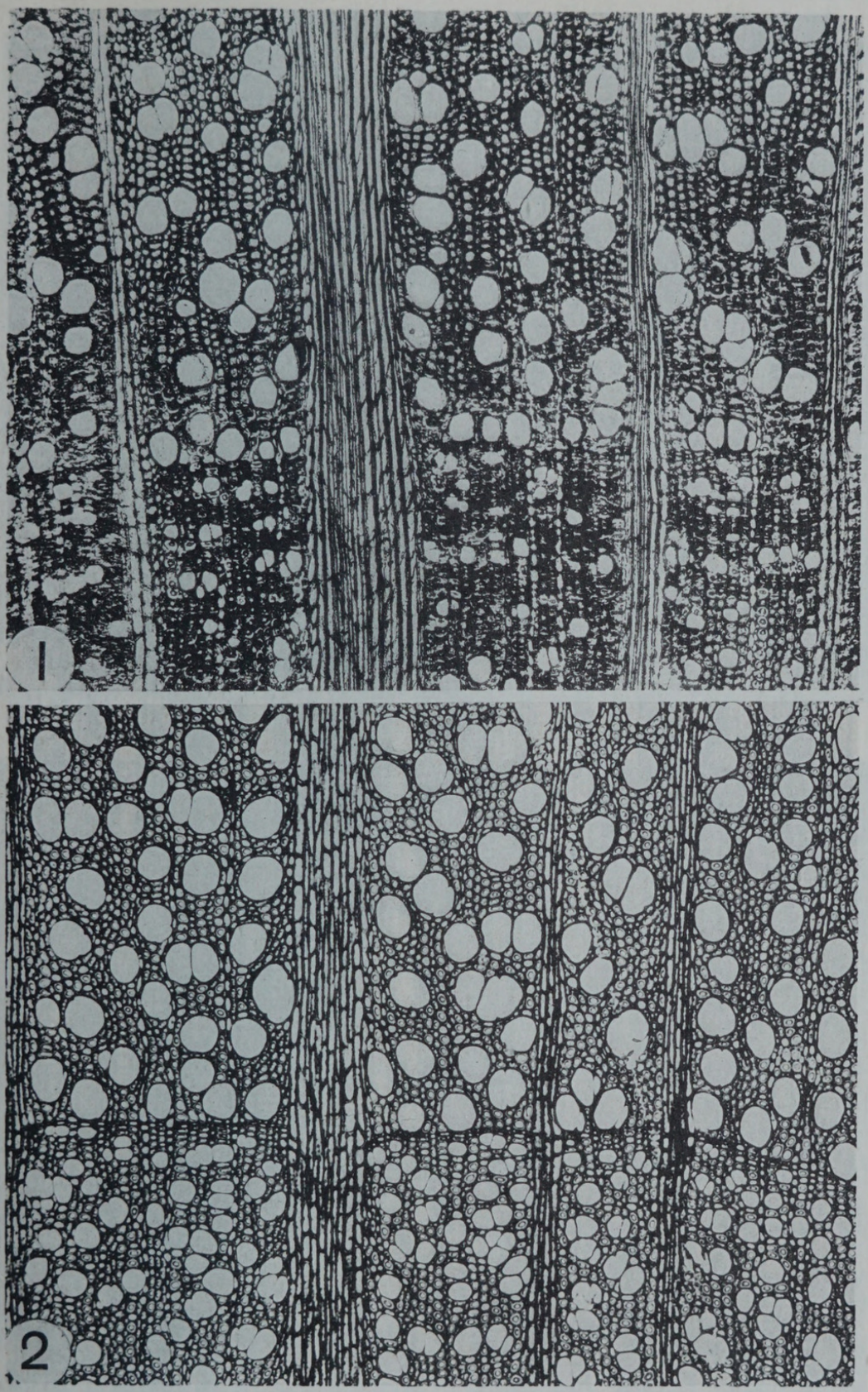
EXPLANATION OF PLATES

PLATE I. FIG. 1. *Euptelea baileyana* Scott & Barghoorn sp. nov. Transverse section of the wood. × 50. Note the close agreement in major structural features to the modern wood shown below. FIG. 2. *E. pleiosperma* Hook. f. & Thoms. Transverse section of the wood. × 50.

PLATE II. FIG. 1. *Euptelea baileyana*. Tangential section of the wood. × 50. Note the larger proportion of broad multiseriate rays than in the modern wood shown below. FIG. 2. *E. pleiosperma*. Tangential section of the wood. × 50.

PLATE III. FIG. 1. *Euptelea baileyana*. Radial section of the wood. × 50. Note the numerous thin walled tyloses in the vessels. FIG. 2. *E. baileyana*. Radial section of the wood showing scalariform perforation plates. × 250. FIG. 3. *E. baileyana*. Radial section of the wood showing scalariform intervascular pitting. × 250.



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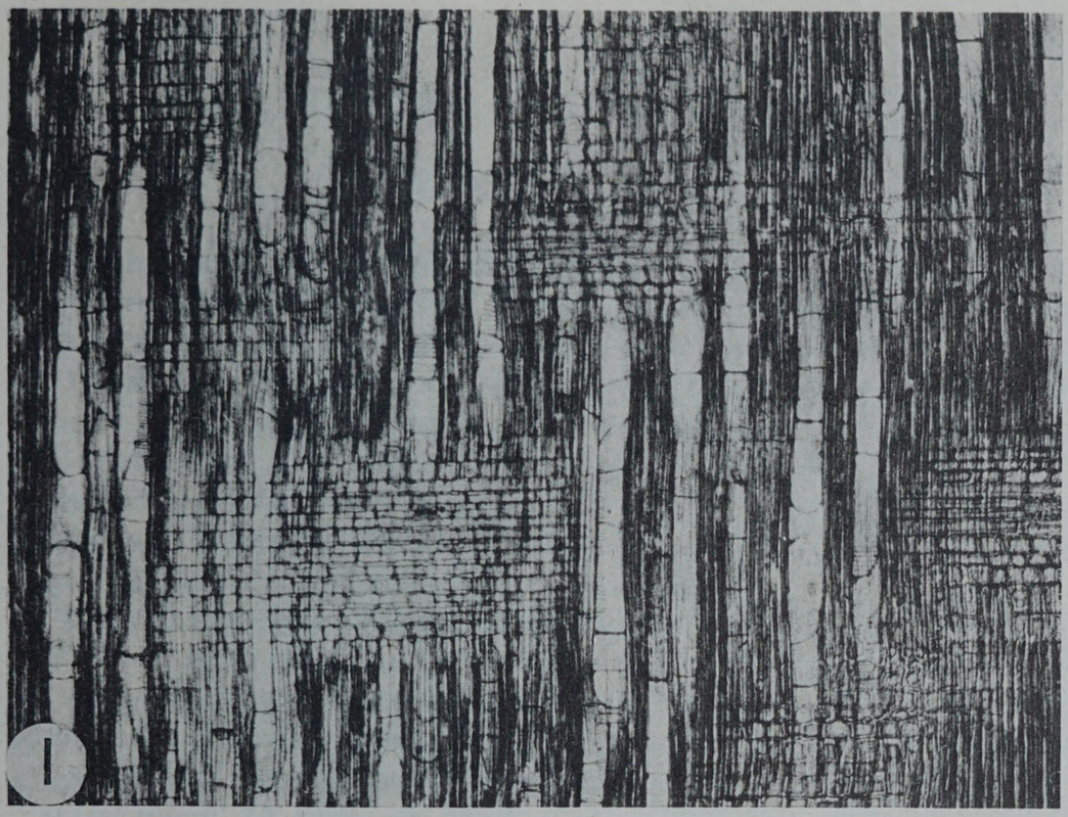

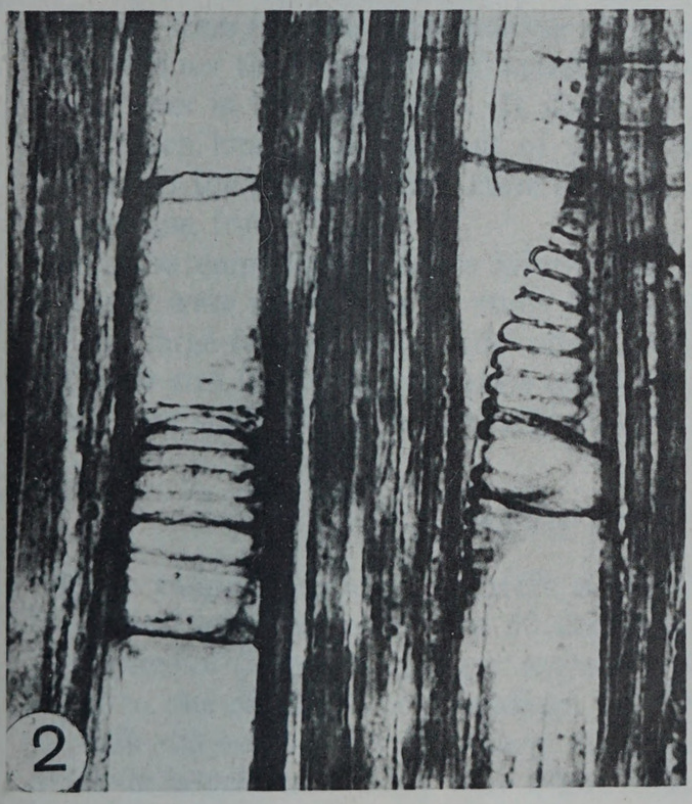

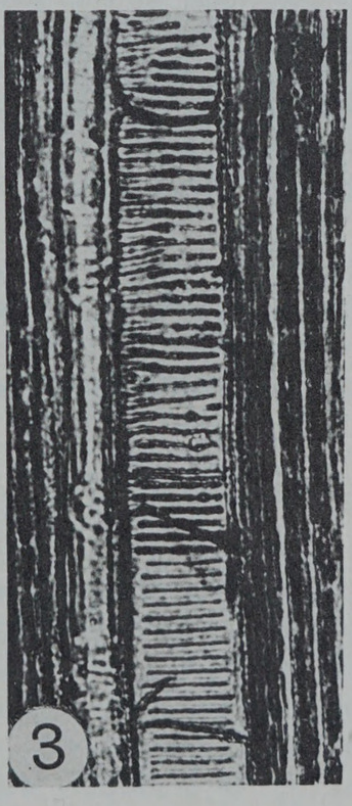

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