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EDITORIAL

This is the first IAWA Bulletin issued from the Netherlands. We hope it meets with your approval. Within the limits of our technical and financial resources the format and lay-out have been kept as close as possible to what we have grown accustomed to. Frequent changes of format are impractical and unpleasant for our library subscribers as well as for our membership, and the success of the Bulletins issued from Syracuse has certainly inspired us to try to retain the high quality of recent years. The only desirable change in format for the future is an increase in the number of pages per issue. This depends on your contributions, and although it may sound monotonous, we once more urge you to submit manuscripts for publication as well as notes and requests.

It is our sincere hope that this editorial column will soon be superfluous, and that the editors can restrict the voicing of opinions to occasions when they really have something important to say about recent developments in the wood anatomical world.

Meanwhile it is gratifying to notice that our membership has been increasing steadily, as well as the number of libraries which subscribe to the IAWA Bulletin. This safeguards future accessibility of the numerous relevant scientific contributions from our members. It has been stated that the IAWA Bulletin cannot be regarded as a really serious scientific periodical because of its limited size and the fact that it so much carries the image of a 'club journal'. This 'club journal' aspect is something unique for our Bulletin, since it offers possibilities for the exchange of views and for the publication of news and requests. It is essential to preserve this aspect because it fosters a sense of informal colleagueship and stimulates contacts. This is precisely the *raison d'être* of the International Association of Wood Anatomists. However, the 'club journal' aspect is fully compatible with a serious scientific periodical. In fact, from its first appearance the Bulletin has almost always contained high quality scientific papers, albeit usually of short length. A scientific periodical of long standing like our Bulletin deserves full recognition. Its importance must be realized by institutional libraries who cannot afford to do without a subscription to the IAWA Bulletin, and scientific workers must realize that the Bulletin can be seriously considered for the publication of short papers. We usually publish rapidly, and although there is still room for improvement, we can guarantee a good worldwide distribution. Wood anatomy is a vigorous and strong discipline at present. It deserves a worthy periodical all to itself!

Pieter Baas

Peter B. Laming

VESTURED SIMPLE PERFORATION PLATES

by

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Twenty-nine woods indigenous to New Zealand known to have simple perforation plates (Meylan and Butterfield, 1975 and unpublished data), and vestured vessel pits (Meylan and Butterfield, 1974 and unpublished data) were selected for examination. Small cubes of wood were prepared for examination by our usual technique (Exley, Butterfield and Meylan, 1974) and examined using a Cambridge stereoscan 600 scanning electron microscope. At least 100 perforation plates were checked for the presence of vestures in each species.

The results of our observations are listed in Table 1. Out of the 29 species belonging to 10 genera of 7 families examined, vestures were found along the perforation plate borders in 9 species belonging to 4 genera of 3 of the families. In five woods: *Leptospermum ericoides, Metrosideros excelsa, M. fulgens, M. robusta* and *M. umbellata* (all members of the Myrtaceae) vestured perforation plates were frequently observed in all of the wood samples examined of each species. In *Fuchsia excorticata* (Onagraceae), *Coprosma australis, C. repens* and *C. rotundifolia* (Rubiaceae) vestures were found in only about 3% of the perforation plates and even then they were not present in all the wood samples of each species. Their occurrence is therefore described as rare. Non observation of vestures in the perforation plates of the other *Metrosideros* and *Coprosma* species does not preclude the possibility of their existence. When present, the perforation plate vestures show a marked similarity in architecture to those found in the vessel pits in the same wood. In some cases the vestures line the borders on each side of the perforation plate (Fig. 1), while in others they may line only one of the two borders (Fig. 2). The depression between the borders in each perforation plate, however, is always free of vestures (Fig. 3). This depression marks the position where the perforation partition, made up of the primary walls and intervening middle lamella, formerly separated the adjoining vessel members. This partition is removed enzymatically during vessel member differentiation (Meylan and Butterfield, 1972).

The absence of warts and vestures from this depression suggests that these features are deposited prior to the removal of the perforation partition.

Vestures are outgrowths or deposits in the apertures and chambers of vessel and fibre pits. They occur in some of the members of a limited number of dicotyledonous families: Metcalfe and Chalk (1950), citing Bailey (1933), record some 24 families where vestured pits were known to occur in some or all of the members. Vestured vessel and fibre pits have also been observed in a member of the Proteaceae (Butterfield and Meylan, 1974a), a family not normally listed as possessing this character.

In the wood of certain species, the vestures occur only in the pit chambers and apertures (e.g. in some species of the Loganiaceae, Onagraceae, Papilionaceae and Rubiaceae) whereas in others they may spread out onto large areas of the inner wall surface of the cell (e.g. in some species of the Myrtaceae and Proteaceae) (Meylan and Butterfield, 1974). They have also been found between the bars of scalariform vessel perforation plates in *Neomyrtus pedunculata*, a New Zealand member of the Myrtaceae (Butterfield and Meylan, 1974b). This note records the observation of vestures in the openings of simple perforation plates.

Vestures were also observed lining the border on the simple half-plate side in simple to scalariform combination perforation plates in *Coprosma rotundifolia* (Rubiaceae) (Fig. 4). Combination perforation plates comprise less than 1% of the perforation plates in the species, the majority being simple.

The observation of vestures lining the borders of simple and simple to scalariform combination perforation plates reinforces our earlier belief (Butterfield and Meylan, 1974b) that these structures need not be confined to pit apertures and chambers. Vestures are already known to spread out from the pit aperture onto the lumen surface of the cell wall in a number of species (Meylan and Butterfield, 1974). The similarity in appearance of vestures and the particles of the warty layer has been noted by Côté and Day (1962) and

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Table 1

Twenty-nine New Zealand woods known to have both simple perforation plates and vestured pits in their vessels. Woods where vestures were also observed on the borders of the simple perforation plates are indicated by + when of common occurrence and by (+) when observed rarely.

Loganiaceae
  Geniostoma ligustrifolium A. Cunn.   —
Myrtaceae
  Leptospermum ericoides A. Rich.   +
  Leptospermum scoparium J.R. & G.Forst.   —
  Lophomyrtus bullata (Sol.ex A.Cunn.) Burr.   —
  Metrosideros excelsa Sol. ex Gaertn.   +
  Metrosideros fulgens Sol. ex Gaertn.   +
  Metrosideros parkinsonii Buchan.   —
  Metrosideros perforata (J.R.& G.Forst.)
    A. Rich.   —
  Metrosideros robusta A. Cunn.   +
  Metrosideros umbellata Cav.   +
Onagraceae
  Fuchsia excorticata (J.R.& G.Forst.) L.f.   (+)
Papilionaceae
  Carmichaelia angustata Kirk.   —
  Carmichaelia grandiflora (Benth.) Hook.f.   —
  Sophora microphylla Ait.   —
Polygonaceae
  Muehlenbeckia complexa (A.Cunn.) Meissn.   —
Proteaceae
  Persoonia toru A. Cunn.   —
Rubiaceae
  Coprosma acerosa A. Cunn.   —
  Coprosma australis (A. Rich.) Robinson   —
  Coprosma ciliata Hook. f.   (+)
  Coprosma foetidissima J.R. & G. Forst.   —
  Coprosma lucida J.R. & G. Forst.   —
  Coprosma parviflora Hook. f.   —
  Coprosma propinqua A. Cunn.   —
  Coprosma repens A. Rich.   (+)
  Coprosma rhamnoides A.Cunn.   —
  Coprosma robusta Raoul.   —
  Coprosma rotundifolia A. Cunn.   (+)
  Coprosma serrulata Hook. f. ex Buchan.   —
  Coprosma tenuicaulis Hook. f.   —

Figure 1. Vestures lining both borders of a simple perforation plate in *Coprosma repens* A. Rich. x 4,700.

Figure 2. Branched vestures lining one border in a simple perforation plate in *Coprosma repens*. x 5,000.

Figure 3. Vestures lining both borders of a simple perforation plate in *Leptospermum ericoides* A. Rich. Note that the depression between the perforation plate borders is free from both warts and vestures. x 4,000.
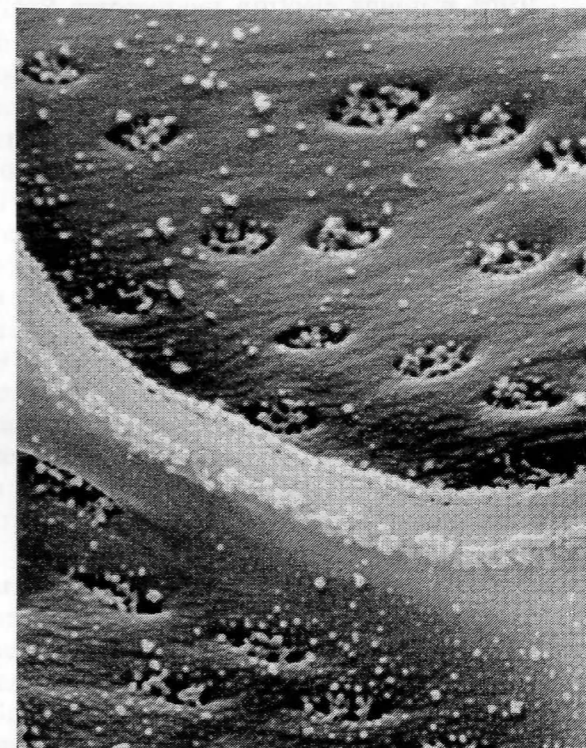
Figure 4. Vestures lining the simple opening in a simple to scalariform combination perforation plate in *Coprosma rotundifolia* A. Cunn. x 5,100.
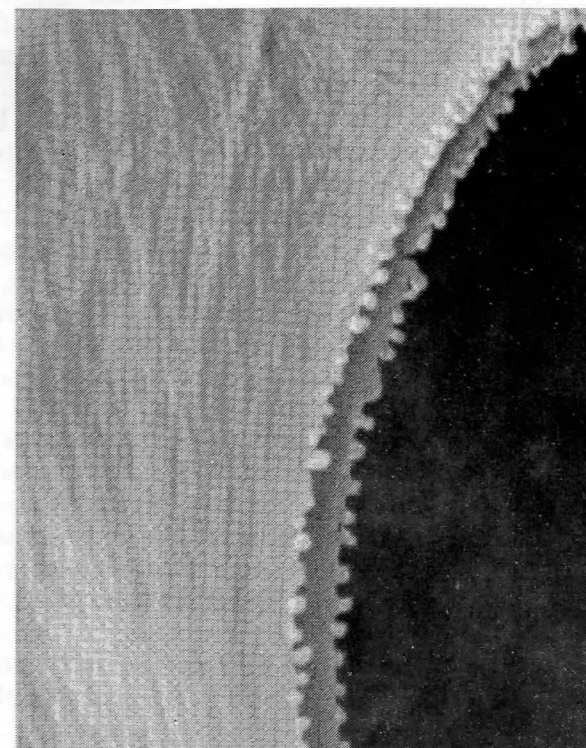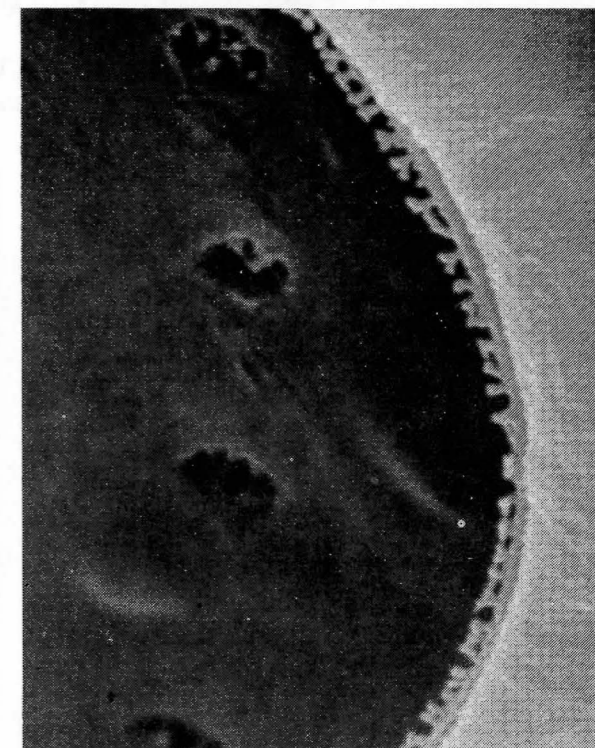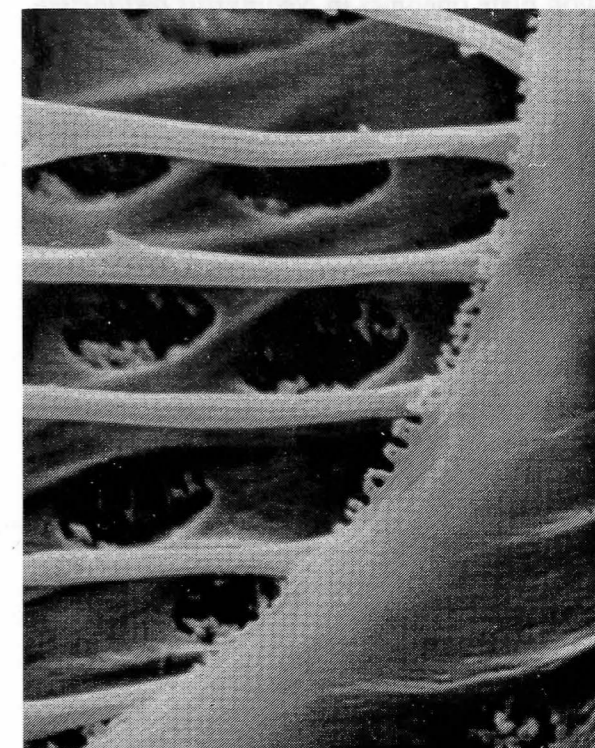
Liese (1965). Similarly, Scurfield and Silva (1970) were unable to distinguish between these features on either morphological or chemical grounds. Schmid and Machado (1964), however, have proposed that vestures are deposited directly on the cell wall outside the plasmalemma by a living protoplast whereas warts are the deposited remnants of a dead protoplast. This present observation of vestured perforation plates suggests that vestures are indeed deposited prior to the death of the protoplast but does not reveal any further information on their relation to warts.

References

Bailey, I.W. 1933. The cambium and its derivative tissues. VIII. Structure, distribution, and diagnostic significance of vestured pits in dicotyledons. J. Arnold Arbor. 14: 259-273.

Butterfield, B.G. & B.A. Meylan. 1974a. Vestured vessel and fibre pits in *Persoonia toru* A.Cunn. (Proteaceae). IAWA Bulletin 1974/1: 10-15.

—— & —— 1974b. Vestured scalariform perforation plate openings in *Neomyrtus pedunculata.* Austr. J. Bot. 22: 425-427.

Côté, W.A. & A.C. Day. 1962. Vestured pits-fine structure and apparent relationship with warts. TAPPI 45: 906-910.

Exley, R.R., B.G. Butterfield & B.A. Meylan. 1974. The preparation of wood samples for the scanning electron microscope. J. Microscopy 101: 21-30.

Liese, W. 1965. The warty layer. *In:* Cellular Ultrastructure of Woody Plants (ed. W.A. Côté). Syracuse University Press, Syracuse, N.Y.

Metcalfe, C.R. & L. Chalk. 1950. Anatomy of the dicotyledons. Vols. 1 and 2. Clarendon Press, Oxford.

Meylan, B.A. & B.G. Butterfield. 1972. Perforation plate development in *Knightia excelsa* R.Br.: A scanning electron microscope study. Austr. J. Bot. 20: 79-86.

—— & —— 1974. Occurrence of vestured pits in the vessels and fibres of New Zealand woods. N.Z. J. Bot. 12: 3-18.

—— & —— 1975. Occurrence of simple, multiple, and combination perforation plates in the vessels of New Zealand woods. N.Z. J. Bot. 13: 1-18.

Schmid, R.& R.D. Machado. 1964. Zur Entstehung und Feinstruktur skulpturierter Hoftupfel bei Leguminosen. Planta 60: 612-626.

Scurfield, G. & S.R. Silva. 1970. The vestured pits of *Eucalyptus regnans* F. Muell.: a study using scanning electron microscopy. Bot. J. Linn. Soc. 63: 313-320.

TRACHEARY ELEMENT SECONDARY WALL PATTERNS AND THE DEFINITION OF PROTOXYLEM AND METAXYLEM

by

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The walls of tracheary elements of the primary xylem develop characteristic secondary thickenings or patterns commonly designated annular, helical (or spiral), scalariform-reticulate, and pitted (Bierhorst, 1960). In vegetative structures the stretchable or extensible annular and helical wall thickenings predominate in the first-formed primary xylem, or protoxylem, whereas the less stretchable or non-extensible reticulate, scalariform-reticulate, and pitted types occur largely in metaxylem, the later-formed xylem differentiating after most or all organ elongation is completed (Esau, 1943, 1965a, b). This is one of the classic correlations between structure and function that has been observed, and it is even noted in most elementary botany textbooks.

Types of secondary wall thickening, however, are invariably discussed in textbooks solely in the context of vegetative structure (see Schmid, 1977, for elaboration), and even the extensive observations by Bierhorst and Zamora (Bierhorst, 1960; Bierhorst and Zamora, 1965; Zamora, 1966) on wall thickenings of primary tracheary elements did not embrace flowers or fruits. No one, to my knowledge, seems to have pointed out that tracheary elements of flowers (including their receptacles) and elongating pedicels usually have secondary wall thickenings of exclusively the extensible annular or especially helical types. As elaborated elsewhere (Schmid, 1976, especially 1977), this is obviously significant since the flower is a transitional structure and since non-extensible reticulate and pitted secondary wall patterns would be a hindrance to the often rapid and drastic expansion characteristic of floral and fruit development.

The tracheary elements of filaments, in particular, seem to be characterized solely by annular or especially helical wall thickenings since many stamens lengthen rapidly (two or three millimeters per minute in some grasses) before and at anthesis (Schmid, 1976, 1977). Petals generally also have tracheary elements with predominantly helical wall thickenings, an obvious adaptation to the great expansibility of these organs at anthesis (Schmid, 1977). I have examined floral parts of some 650 species of angiosperms in about 160 families (*sensu* Airy Shaw, 1973) and have found only a handful of exceptions to these statements, which are based on original data as well as an analysis of the extensive literature of floral anatomy (see Schmid, 1977). A similar emphasis on exclusively annular and especially helical wall patterns in the xylem occurs, it might be noted, in other reproductive and also vegetative structures (e.g., carpels, sensitive styles and stigmas, many leaves, glands of *Drosera*, etc.) capable of rapid expansion and movement. Exceptions involve mainly sepals, receptacles, and mature (post-expansion!) fruits, all of which may have some tracheary elements with non-extensible reticulate and pitted wall patterns (Schmid, 1977).

Awareness of these facts, therefore, completely vindicates the use of the terms protoxylem and metaxylem to indicate the temporal and positional characteristics of the component parts of the primary xylem, as advocated by Esau (1943, 1965a, b, 1969, 1977) and others (see below). In other words, protoxylem (and protophloem) is simply the initial vascular tissue of a system, the character of which is defined by the position of such xylem. Metaxylem (and metaphloem) then simply succeeds the initial tissue.

Protoxylem and metaxylem cannot be morphologically defined on the basis of extensible versus non-extensible types of wall thickening, respectively, since many reproductive structures would be terminologically anomalous indeed in having xylem consisting *entirely* of protoxylem. The converse applies to roots, which may completely lack the extensible annular and helical forms of wall patterns of tracheary elements (Scherer, 1904).

As just implied, the use of morphological criteria to define protoxylem and metaxylem can result in vascular bundles being regarded as consisting entirely of protoxylem or entirely of metaxylem, for example, respectively, in many flowers and roots. Although some anatomists even today describe vascular bundles as being composed in this manner (e.g., Schneider, 1976), there are several reasons why a temporal and positional characterization of protoxylem and metaxylem is preferable (it might be noted, however, that early 'pre-Esau' anatomists stressing development, for example, Bugnon, 1925, Frey-Wyssling, 1940, and Russow, 1872, sometimes also spoke of bundles lacking either protoxylem or metaxylem). The following discussion owes much to the detailed reviews by Bugnon (1925), Frey-Wyssling

(1940), and especially Esau (1943—also 1965a, 1969: 169-171).

(1) As discussed extensively by Esau (1943— also 1969), and earlier by Bugnon (1925) and Frey-Wyssling (1940), the temporal and positional definition of protoxylem and metaxylem is a return to the original definitions of these terms, in particular, Russow's (1872) term protoxylem. Morphological criteria (see below) for protoxylem and metaxylem were subsequently superimposed on the ontogenetic criteria.

(2) Protoxylem, defined on an ontogenetic basis, always has a definite starting point, as recognized by Russow (1872). Admittedly, no sharp distinctions may exist between protoxylem and metaxylem, on the one hand, or between primary xylem and secondary xylem, on the other. In organs lacking secondary xylem, however, metaxylem as an end point is, of course, immediately recognizable. In contrast, the use of morphological criteria for protoxylem and metaxylem is even more arbitrary than the use of ontogenetic criteria. The exceptions involving flowers and roots have been noted above. In addition, in some plants metaxylem elements may have the gamut of wall patterns from helical to pitted, whereas in non-elongating nodal regions the protoxylem elements may have reticulate and scalariform-reticulate wall types. Finally, as also noted by Bugnon (1925) and by Esau (1943) citing him, morphological criteria other than size are of no use in many primitive fossil vascular plants (e.g., *Cooksonia, Rhynia, Psiloxylon*, etc.), which have xylem consisting of tracheids with only annular and/or helical secondary wall thickenings. Clearly, ontogenetic criteria cannot be directly applied to fossils although the common usage of the terms exarch, endarch, mesarch, and centrarch by paleobotanists (e.g., Banks, 1970—see glossary therein) to refer to direction of xylem maturation must, of necessity, employ size criteria (modern definitions of exarch, mesarch, and endarch— e.g., Banks, 1970; Esau, 1965a, b, 1977; Fahn, 1974; Schmid, 1977—correctly define these terms not on the basis of diameter of elements but rather on the basis of the location of protoxylem in the bundle). Size criteria, however, often cannot be used to separate protoxylem from metaxylem. For example, floral vascular bundles frequently have little xylem, all tracheary elements of which may be the same diameter in transection (Schmid, 1977).

(3) Protoxylem and metaxylem not only can be defined ontogenetically, they also can be defined dynamically in relation to the development of the organ as a whole. That is, protoxylem generally matures before (or while) organs undergo intensive elongation whereas metaxylem matures after most or all of this elongation is completed.

(4) A developmental definition of protoxylem and metaxylem permits direct analogy with protophloem and metaphloem, for which morphological criteria other than size are not readily possible (see especially Esau, 1969). Clearly, any consistency in terminology of vascular tissues is desirable. Like protoxylem, protophloem was initially applied by Russow (1872) to the first-formed phloem corresponding to protoxylem, the first-formed xylem. Since morphological criteria separating protophloem and metaphloem are even less well defined than those for protoxylem and metaxylem, botanists generally have not bothered to use the former terms for the phloem, although generally employing the latter for the xylem. The terms exarch, mesarch, and endarch, incidentally, apply only to xylem maturation and not to phloem maturation, the latter being uniformly centripetal in all organs and plant groups (the centrifugal phloem development of internal phloem is an exception). Eventually with the increased emphasis on developmental anatomy, developmental criteria of the first-formed phloem being protophloem and the later-formed phloem being metaphloem became prevalent. In addition, like protoxylem and metaxylem, protophloem generally matures before (or while) organs undergo intensive elongation whereas metaphloem matures after this elongation is concluded.

(5) Largely as a result of Esau's efforts in her 1943 review and especially in her textbooks (1965a, b, 1969, and the 1960 first edition of the 1977 book), an ontogenetic definition of not only protoxylem and metaxylem, but also protophloem and metaphloem, is now the standard in anatomy textbooks (e.g., Fahn, 1974) and much anatomical research.

A related point of the preceding controversy also bears brief discussion. As is well known, shoots of *Equisetum*, many monocotyledons, and certain dicotyledons (e.g., Nymphaeaceae—Schneider, 1976) contain protoxylem lacunae formed as a result of the destruction of the tracheary elements during the extension of the axis. The designation 'protoxylem lacunae' may in many cases be based on a morphological rather than an ontogenetic definition of protoxylem (e.g., by Schneider, 1976). When organs have tracheary elements with only annular and/or helical wall patterns, however, formation of the lacuna may involve at least part of the metaxylem, and in many cases all of it, especially in stamen bundles (see Schmid, 1976, 1977). Consequently, since such lacunae may involve most or all of the xylem of a bundle, a more accurate and less committal expression, particularly in lieu of developmental evidence, would be 'xylem lacuna' rather than 'protoxylem lacuna' (or 'protoxylary lacuna'). Finally, in those cases where some phloem is involved in the formation of the lacuna (e.g., the endocarp of coconut—see Schmid, 1977), the proper designation would be 'xylic-phloic lacuna' or 'vascular lacuna'.

The relevance of the above discussion to wood anatomy is that in the 'Multilingual glossary of terms used in wood anatomy' the Committee on Nomenclature (1964, also the previous 1933 and 1957 versions) defines protoxylem versus metaxylem as follows, respectively (emphasis mine): 'first-formed primary xylem, *with tracheary elements characterized by annular or spiral thickenings*' versus 'later-formed primary xylem, *with pitted tracheary elements*'. I suggest that future editions of the 'glossary' delete the italicized portions of the preceding definitions to bring them in line with the definitions of protoxylem and metaxylem in glossaries of such well-known textbooks as those by Esau (1977, first edition 1960) and Fahn (1974, first edition 1967). If it is indeed felt that mention of wall thickenings is useful, then in *each* definition the following qualifier should be added after the words emphasized above: '(in stems)'. In addition, the last part of the definition for metaxylem should be changed to the following, a correction Esau (1943) noted long ago: 'with scalariform, scalariform-reticulate, or pitted wall thickenings.'

References

Banks, H.P. 1970. Evolution and plants of the past. Belmont, California: Wadsworth Publishing Co.

Bierhorst, D.W. 1960. Observations on tracheary elements. Phytomorphology 10: 249-305.

—— & P.M. Zamora. 1965. Primary xylem elements and element associations of angiosperms. Amer. J. Bot. 52: 657-710.

Bugnon, P. 1925. Origine, évolution et valeur des concepts de protoxylème et de metaxylème. Bull. Soc. Linn. Normandie, Sér. 7, 7 (Année 1924): 123-151.

Committee on Nomenclature, International Association of Wood Anatomists. 1964. Multilingual glossary of terms used in wood anatomy. (Also published *in* Schweiz. Anst.

Forstl. Versuchswesen Mitt. 40: 1-186. 1964.)

Esau, K. 1943. Origin and development of primary vascular tissues in seed plants. Bot. Rev. 9: 125-206.

—— 1965a. Plant anatomy. 2nd ed. New York: John Wiley & Sons.

—— 1965b. Vascular differentiation in plants. New York: Holt, Rinehart and Winston.

—— 1969. The phloem. Bd. 5, Tl. 2 *in* K. Linsbauer's Handbuch der Pflanzenanatomie. 2. Aufl. Berlin: Gebrüder Borntraeger.

—— 1977. Anatomy of seed plants. 2nd ed. New York: John Wiley & Sons. (In press.)

Fahn, A. 1974. Plant anatomy. 2nd ed. Oxford: Pergamon Press.

Frey-Wyssling. A. 1940. Zur Ontogenie des Xylems in Stengeln mit sekundärem Dickenwachstum. Ber. dt. bot. Ges. 58: 166-181.

Russow, E. 1872. Vergleichende Untersuchungen betreffend die Histologie (Histiographie und Histiogenie) der vegetativen und sporenbildenden Organe und die Entwickelung der Sporen der Leitbündel-Kryptogamen, mit Berücksichtigung der Histiologie der Phanerogamen, ausgehend von der Betrachtung der Marsiliaceen. Mém. Acad. Imp. Sci. St-Pétersbourg, Sér. 7, 19(1): i-x, 1-207.

Scherer, P.E. 1904. Studien über Gefässbündeltypen und Gefässformen. Beih. Bot. Centralbl. 16: 67-110.

Schmid, R. 1976. Filament histology and anther dehiscence. Bot. J. Linn. Soc. 73: (In press.)

—— 1977. Functional and ecological interpretations of floral and fruit anatomy. Bot. Rev. 43: (In press.)

Schneider, E.L. 1976. The floral anatomy of *Victoria* Schomb. (Nymphaeaceae). Bot. J. Linn. Soc. 72: 115-148.

Shaw, H.K.A. 1973. *In* J.C. Willis, A dictionary of the flowering plants and ferns. 8th ed. Cambridge: University Press.

Zamora, P.M. 1966. Studies on the primary xylem elements in the order Ranales (*sensu lato*): a systematic survey. Philipp. Agric. 50: 391-623.

MODIFIED TRACHEIDS ADJACENT TO WOUND TISSUE IN PSEUDOWINTERA COLORATA
(WINTERACEAE)

by

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In a previous paper (Kučera and Philipson, 1977) the growth eccentricity and reaction anatomy of inclined branches of *Pseudowintera colorata* (Raoul) Dandy was investigated. The material was collected from adult trees growing naturally in lowland and lower montane forests in the South Island of New Zealand. During this investigation some areas with injuries and resulting wound tissue were observed. These circular areas were 1-10 mm in diameter (as seen in tangential longitudinal section) and 10-20 cell rows deep. They were randomly distributed, and probably the result of superficial injuries.

Transverse and tangential longitudinal sections of areas containing wound tissue of 10-12 μm thickness were stained with safranin and fast green according to Gurr (1965) and examined under light and polarizing microscopes. Wound tissue in this species has previously been reported by Jeffrey and Cole (1916) and Patel (1974). However, during the current investigation a modification to the cell wall of some tracheids not reported by these authors was observed. This modification was confined to the tracheids derived before the injury and was therefore endarch to the wound tissue area. Figure 1 shows a part of a wound tissue area. The modification consisted of an additional cell wall layer adjacent to the cell lumen. Figure 2-4 show some tracheids with this additional cell wall layer (arrows). Modified tracheids were distributed either solitary or in radial multiples of up to 10 cells. Höster (1970) found a similar arrangement of gelatinous tracheids in *Larix leptolepis* (S. & Z.) Gord. The additional layer is heterogeneous as observed in polarized light consisting of a wider outer portion with low birefringence and a narrow inner portion with high birefringence. This layer would appear to be a repetition of the secondary wall S_2 and S_3 layer formation. The employed staining did not indi-

cate major changes in the chemical composition of this additional layer.

This feature apparently results from the reactivation of the cell wall deposition process in fully differentiated but still living tracheids close to the injury. It may be induced by a stimulus connected with injury and/or be a result of the subsequent wound tissue formation. The stimulus could be an increase in the indole acetic acid level in the tissue caused by the autolytical production of IAA in injured cells and its distribution towards pith. An observation similar to the present in circumstances and features was made on wound tissue of yew (*Taxus baccata* L.) by Kučera (1971).

References

Gurr, E. 1965. The rational use of dyes in biology. Leonard Hill, London.

Höster, H.R. 1970. Gelatinöse Tracheiden im sekundären Xylem von *Larix leptolepis* (S. & Z.) Gord. Holzforschung 24: 4-6.

Jeffrey, E.C. & R.D. Cole. 1916. Experimental investigations on the genus *Drimys*. Ann. Bot. 30: 359-368.

Kučera, L.J. 1971. Wundgewebe in der Eibe (*Taxus baccata* L.). Vjschr. naturf. Ges. Zürich 116: 445-470.

—— & W.R. Philipson. 1977. Growth eccentricity and reaction anatomy in branchwood of *Pseudowintera colorata*. In press.

Patel, R.N. 1974. Wood anatomy of the dicotyledons indigenous to New Zealand. 4. Winteraceae. N.Z. J. Bot. 12: 19-32.
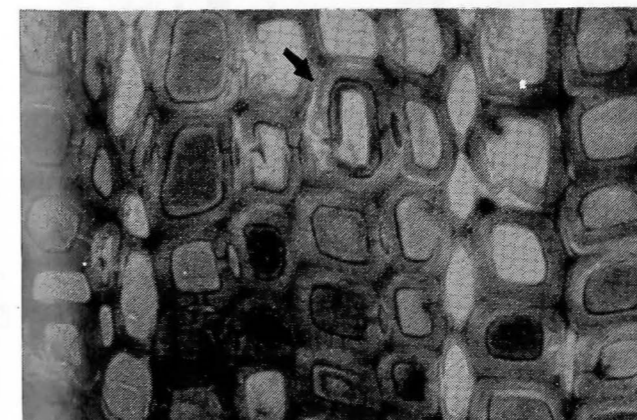
Figure 1. Transverse section. Wound tissue across the centre. x 140.

Figure 2-3. Transverse section. Tracheids with additional cell wall layer marked with arrows. x 700 (2) and x 550 (3).
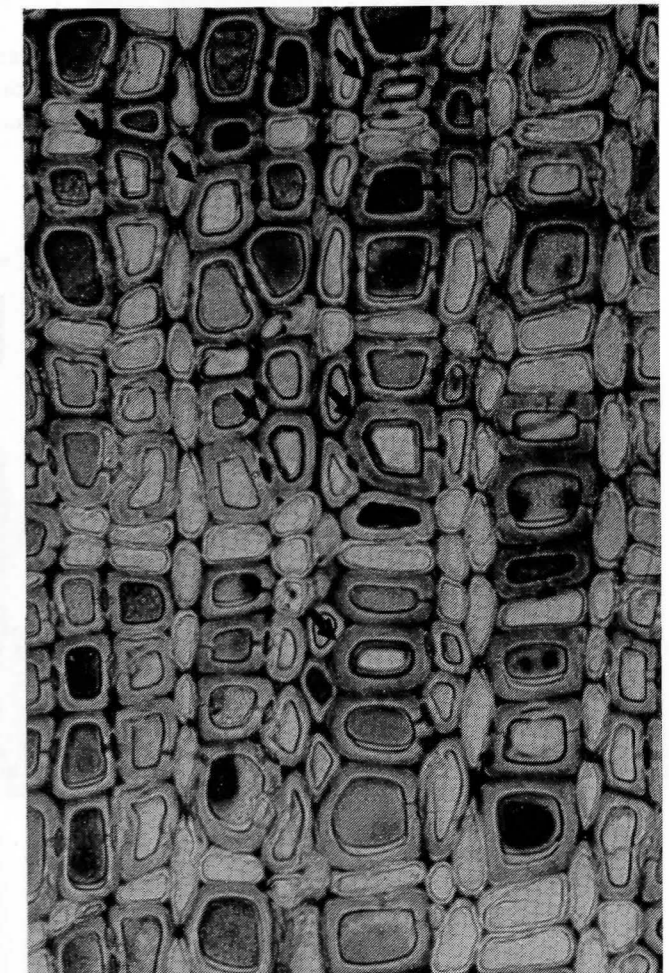
Figure 4. Transverse section. Radial multiple of tracheids with additional cell wall layer marked with arrows. x 350.
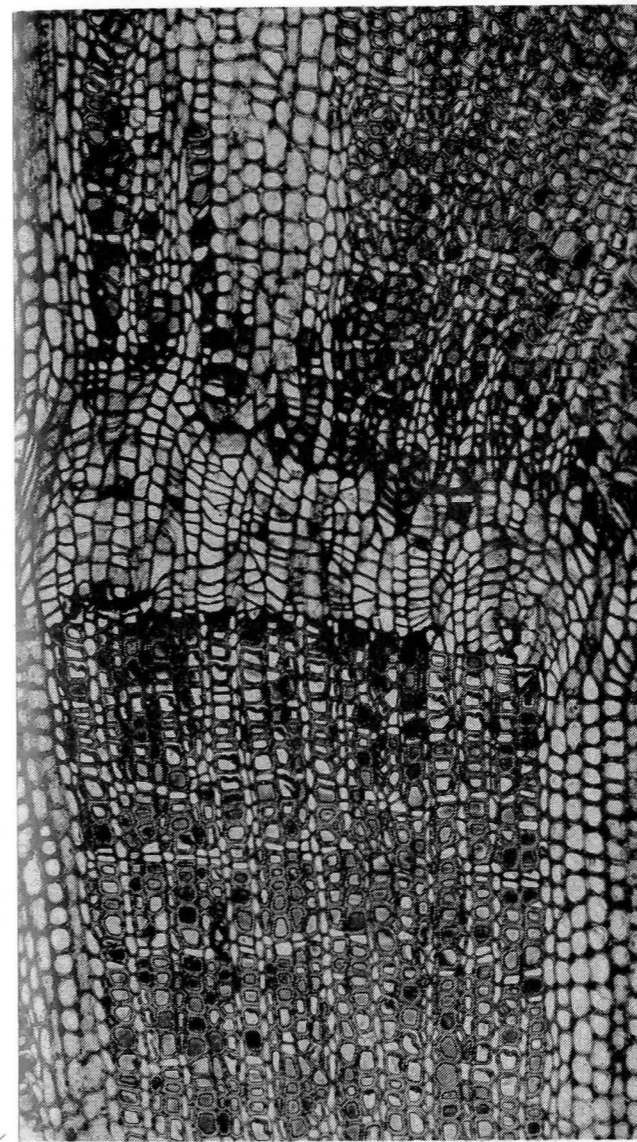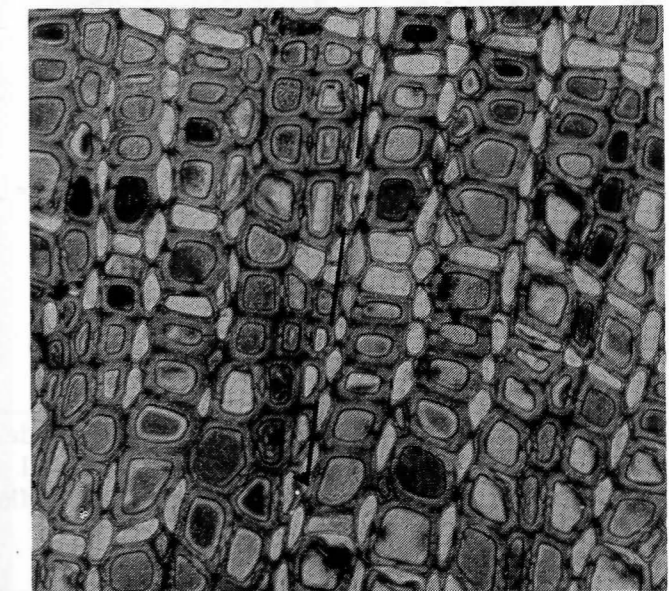
OBSERVATIONS ON THE SECTIONING CHARACTERISTICS OF NORMAL AND GAMMA-IRRADIATED CONIFER WOOD

by

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Summary

Thin longitudinal sections of plastic-embedded coniferous wood frequently show characteristic fractures in the walls of the axial tracheids. The fracturing pattern suggests that it is related to the orientation of the microfibrils of the middle secondary wall.

Exposure of the wood to high levels of gamma radiation before embedding eliminates fracturing but causes loss of parenchyma cell walls, pit membranes and certain cytoplasmic material. The walls of the axial tracheids are also reduced in thickness.

Introduction

It has been found in this laboratory that sectioning of epoxy-embedded wood with glass knives at thicknesses of c. 70 nm is difficult and rarely more than one or two sections can be cut before the block face becomes wet and cutting ceases. The difficulty appears to be due to the rapid loss of the cutting edge of the knife during sectioning. This rapid loss of the cutting edge does not appear to be due simply to the gross hardness of wood as hard plastics such as Spurr's epoxy are readily sectioned with glass knives.

Antoine *et al.* (1971) found that the preparation of wood for scanning electron microscopy was improved by exposure to high levels of gamma radiation. This made the wood very brittle and enabled surfaces to be prepared by breaking with little apparent loss of structural detail.

In the following experiments some of the sectioning characteristics of both normal and irradiated wood have been examined in order to gain some understanding of the basic problems of sectioning with glass knives and to determine whether gamma irradiation would enable wood to be sectioned satisfactorily with glass knives.

Materials and Methods

Green sapwood of *Araucaria cunninghamii* D. Don and *Pinus pseudostrobus* Lindl. was fixed overnight in a standard formaldehyde, acetic acid, ethanol mixture and then thoroughly washed with distilled water. The wood was divided with a sharp razor blade into cubes about 2 mm³ and then prepared with one of the following treatments: (a) irradiation with 343 Mrads of gamma radiation in water; (b) dehydration in a graded series of ethanol, the ethanol replaced with solvent ether and the blocks allowed to dry in air before being irradiated as in (a); (c) control, untreated. Blocks in treatments (a) and (c) were dehydrated in a graded series of ethanol; the ethanol replaced with propylene oxide and then embedded with either Araldite or Spurr's epoxy resin (Glauert, 1975). Blocks in treatment (b) were infiltrated with propylene oxide after irradiation and then embedded as above.

Tangential longitudinal sections of material from each treatment were cut with glass knives on an LKB Ultrotome 3 at thicknesses of approximately 2 μm and 70 nm. The 2 μm sections were dried onto microscope slides and stained with toluidine blue 0 and examined with a light microscope. The 70 nm sections were picked up on copper grids, stained with uranyl acetate and lead citrate and examined in a transmission electron microscope.

Figure 2. Longitudinal section of portion of the side wall of two adjacent tracheids of *Araucaria cunninghamii* sapwood. Regular fractures (F) in the wall of the right hand cell but absent from the left hand wall. The fractured zone appears to be the middle secondary wall (S₂). Transmission electron micrograph, x 3100.

Figure 3-5. Tangential longitudinal sections of the sapwood of *Pinus pseudostrobus* embedded in Araldite showing the effect of the direction of knife cut on the characteristics of the section. The knife direction is shown by arrows. Phase contrast, x 460. — 3: The right hand walls of the axial tracheids are fractured; 4: Walls of the axial tracheids are not fractured; 5: The left hand walls of the axial tracheids are fractured.

tracheid wall

orientation of microfibrils
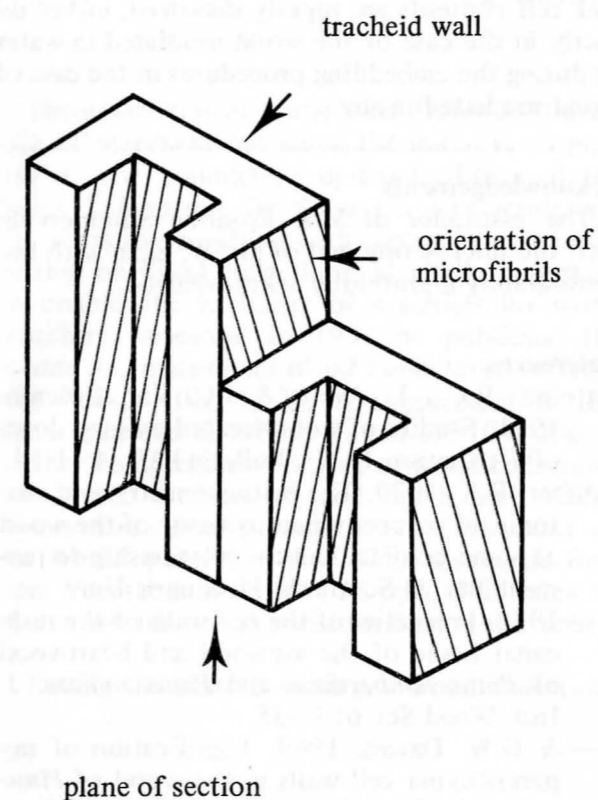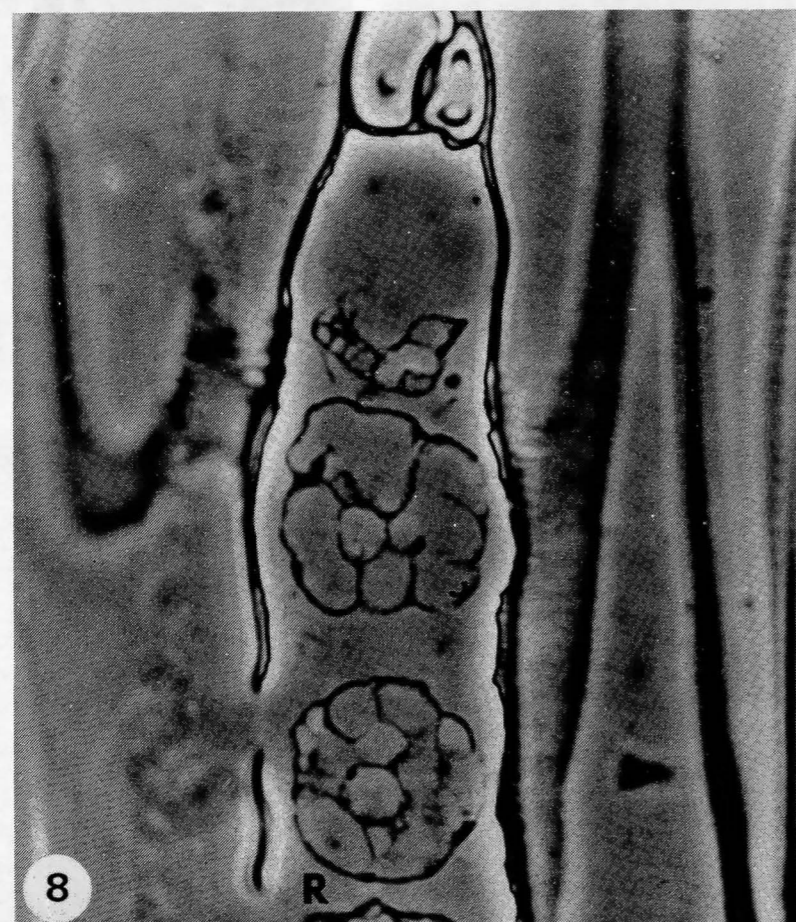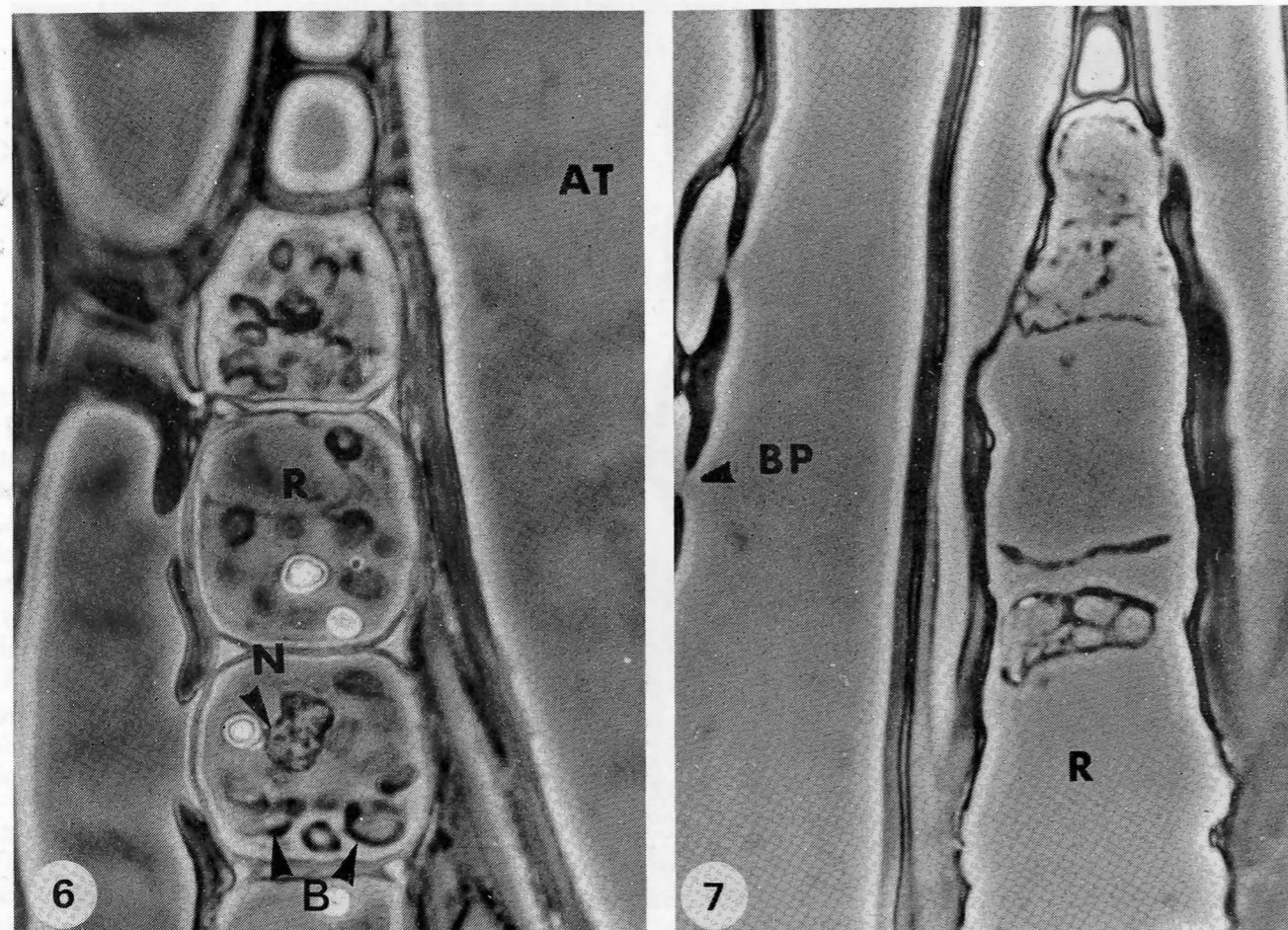
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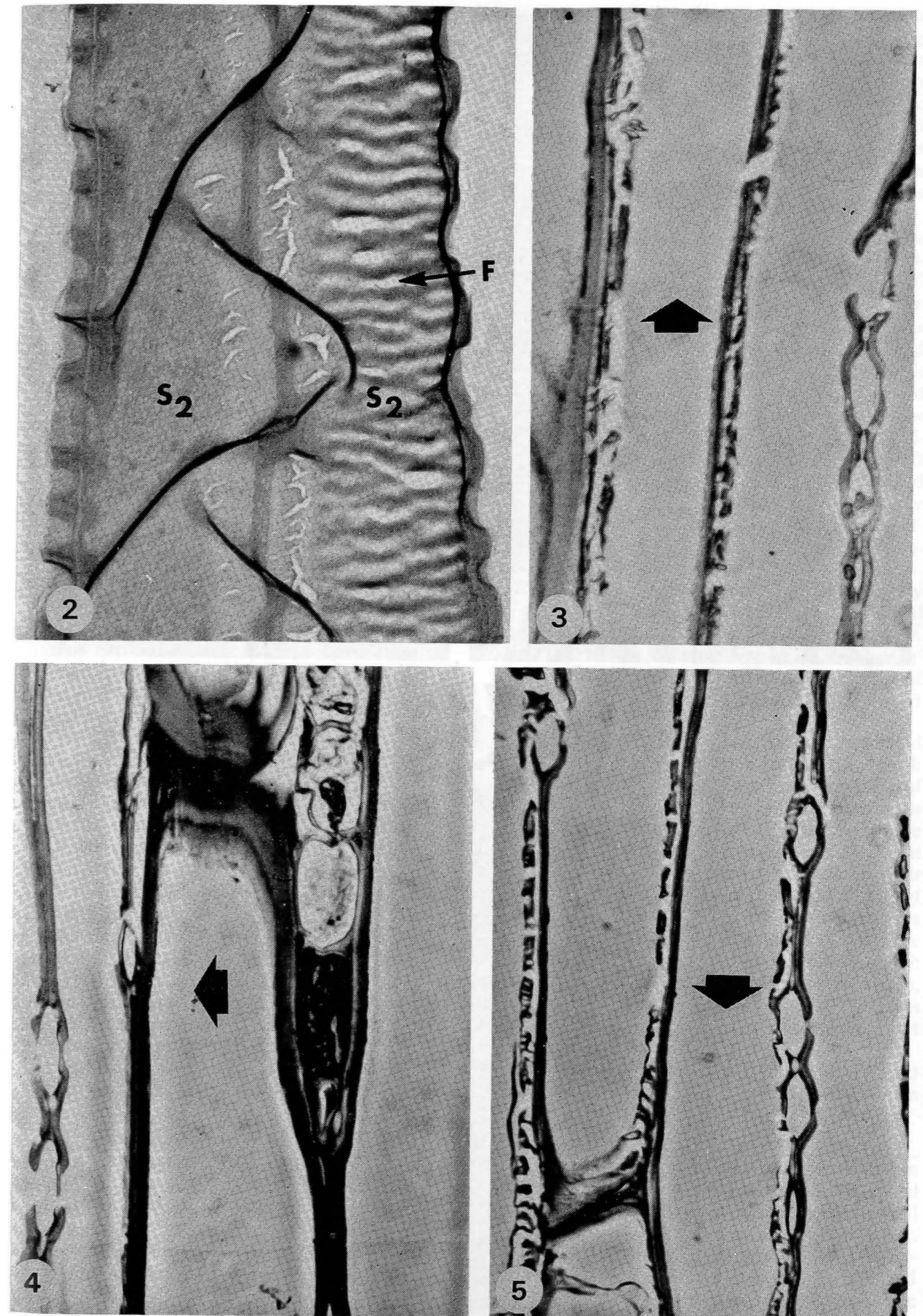
Figure 1. Simplified diagram of portion of the walls of two axial tracheids. The orientation of the microfibrils of the middle secondary wall are shown in relation to a sectioning plane parallel to the longitudinal axes of the tracheids.

Results and Discussion

The walls of the axial tracheids of the control specimens were frequently found to be fractured. The fractures took the form of regular breaks at right angles to the long axis of the tracheids (Fig. 2). From the location of the fractured area it appears that the fractures are in the middle secondary wall (S_2). In addition the fractured zone was confined to the wall on one side of the tracheid (Fig. 2). The occurrence of the fractures on one side only suggested that the fracturing was related to the microfibrillar orientation in the wall. The principal layer of the wall, and the one which most influences wood properties, is the middle secondary wall (S_2) in which the microfibrils are

oriented at a small angle to the cell axis (Kerr and Bailey, 1933; Wardrop and Bland, 1959). In Fig. 1 it can be seen that, because of the steep helix described by the microfibrils in the S_2 layer, a section taken through the side walls of a tracheid will have microfibrils inclined towards the knife edge on one side but away from the knife edge on the other side. Thus the knife in terms of microfibrillar orientation cuts 'against the grain' on one side and 'with the grain' on the other.

This hypothesis was tested by cutting sections in three directions, that is, with the block oriented so that the axial tracheids were (a) 0°, (b) 90° and (c) 180° respectively to the cutting direction. It can be observed from Figs. 3-5 that where the tracheids are oriented at 0° (Fig. 3) the left hand walls are fractured, at 90° (Fig. 4) neither walls are fractured and at 180° (Fig. 5) the right hand walls are fractured. These results support the above hypothesis as the microfibrils are considered to slope towards the knife edge in the left hand walls in Fig. 3 and towards the right hand walls in Fig. 5. In Fig. 4 the microfibrils are oriented sideways to the cutting edge so that differences between left and right hand walls in respect to microfibril orientation are neutralised.

A similar effect has been reported by Exley et al. (1974) in the preparation of longitudinal wood surfaces for scanning electron microscopy. They found that a slight fraying or 'brooming' sometimes occurred on one wall of each cell and attributed this to cutting "against the grain' of the microfibrils'.

The walls of the tracheids of the irradiated wood did not show fractures in the 2 μm thick sections. However, while the general structure of the irradiated wood was unchanged, both walls and cytoplasm were affected (Figs. 6, 7, 8): the walls of the tracheids being reduced in thickness particularly in the specimens irradiated in water (Fig. 7); tori and margo from the bordered pits of the tracheids and the walls of the parenchyma cells being either severely degraded or lost; the cytoplasm either lost or shrunken; and the starch and lipid bodies lost. Nuclei, although shrunken, were observed in the parenchyma cells. The walls of the tracheids of the irradiated wood were not birefringent.

The irradiated material sectioned and ribboned easily at a thickness of 70 nm. However, when

Figure 6-8. Tangential longitudinal sections of the green sapwood of *Pinus pseudostrobus* embedded in Araldite showing portion of a ray (R) and adjacent axial tracheids (AT). RP, ray parenchyma; RT, radial tracheid. Phase contrast, x 770. — 6: Untreated. The ray parenchyma cells contain storage bodies (B) and nucleus (N); 7: Exposed to 343 Mrad dry. The walls of the ray parenchyma are almost entirely lost. The cytoplasm is shrunken and storage bodies, tori and margo are not visible. BP, bordered pit; 8: Exposed to 343 Mrads in water. As in Fig. 4 the ray parenchyma cell walls are almost entirely lost and storage bodies are not visible. The walls of the axial tracheids appear to be reduced in thickness. The cytoplasm is shrunken.

examined in the transmission electron microscope the irradiated material was found to be severely fragmented and structural details of the walls and cytoplasm were not visible.

The basic structural units of the microfibrils are cellulose crystallites (Frey-Wyssling and Mühlethaler, 1965) so that it could be reasoned that a reduction in the crystalline properties of the wall would reduce the influence of the microfibrillar orientation on the sectioning characteristics and perhaps make sectioning easier. It has been shown that high levels of gamma radiation break down the cellulose in wood (Seifert, 1964). This is supported by the observation referred to earlier that birefringence was lacking in the tracheid walls of irradiated wood.

The improvement in the ease of sectioning effected by the irradiation suggests that the principal difficulty in sectioning wood is the presence of highly organised crystalline material. Because diamond knives section wood with relative ease it would appear that the glass edge is not strong enough to sever the microfibrillar chains; the force required to sever the microfibrils being greater than the force required to fracture the glass edge. It could well be that the crystalline components of the wall are much harder than the generally accepted (gross) hardness values for wood. It should be remembered that wood is a composite material and that the properties of the other (softer?) components probably have a strong influence on the gross properties.

Lignin is resistant to high levels of gamma radiation whereas cellulose is rapidly broken down (Seifert, 1964). The presence of lignin in the secondary walls of the tracheids therefore ensures that the general form of these cells is retained. The parenchyma cell walls of the sapwood in both of the species tested are not lignified (Bamber and Davies, 1969; Bamber, 1970, 1972) so that with the destruction of the cellulose the parenchyma cell walls were lost. The storage materials in the cells, for example starch, were also readily lost.

The scanning electronmicrographs of irradiated wood obtained by Antoine et al. (1971) show better retention of structure than was observed in the sectioned embedded-wood (Figs 4, 5). It is likely that the irradiation products of the cell wall and cell contents are rapidly dissolved, either directly in the case of the wood irradiated in water or during the embedding procedures in the case of wood irradiated in air.

Acknowledgements

The assistance of Mrs. Rosanne Summerville with the microscopy and of Mr. W. Egan with the photography is gratefully acknowledged.

References

Antoine, R.C., T. Avella & J.C. Van Eyseren. 1971. Studies of wood treated by high doses of Y-radiation. IAWA Bulletin 1971/4:11-14.

Bamber, R.K. 1970. The histochemistry and anatomy of parenchymatous tissue of the wood of some conifers and the relationship to permeability. M.Sc. thesis. Macquarie Univ.

------ 1972. Properties of the cell walls of the resin canal tissue of the sapwood and heartwood of *Pinus lambertiana* and *Pinus radiata*. J. Inst. Wood Sci. 6: 32-35.

------ & G.W. Davies. 1969. Lignification of ray parenchyma cell walls in the wood of *Pinus radiata* D. Don. Holzforschung 23: 83-84.

Exley, R.R., B.G. Butterfield & B.A. Meylan. 1974. Preparation of wood specimens for the scanning electron microscope. J. Microscopy 101: 21-30.

Frey-Wyssling, A. & K. Mühlethaler. 1965. Ultrastructural Plant Cytology. Elsevier, New York.

Glauert, A.M. 1975. Fixation, dehydration and embedding of biological specimens. *In:* Practical Methods in Electron Microscopy (ed. A.M. Glauert). North-Holland/American Elsevier. Amsterdam.

Kerr, T. & I.W. Bailey. 1933. The cambium and its derivative tissues. X. J. Arnold Arbor. 15: 327-349.

Seifert, K. 1964. Zur chemie gammabestrahlten Holzes. Holz als Roh- und Werkstoff 22: 267-275.

Wardrop, A.B. & D.E. Bland. 1959. The process of lignification in woody plants. Proc. 4th Int. Congress of Biochem. Vol. II.

NEW INDEX XYLARIORUM

Professor William Louis Stern from the University of Maryland has taken the initiative to publish a new completely updated edition of the *Index Xylariorum*. Dr. Stern has been active over the years to provide us with comprehensive information on wood collections, so vitally important to enable the exchange of materials for wood structural research. In 1957 he published the '*Guide to Institutional Wood Collections*' in Tropical Woods 106: 1–29. A supplement to this guide appeared in 1962 in Taxon 11: 104–106. A further comprehensive listing of wood collections led to the well-known and much used '*Index Xylariorum: Institutional Wood Collections of the World*' published in 1967 as a separate Regnum Vegetabile issue (49: 36 pp.). This index included details on 113 institutional wood collections.

During the past 10 years new wood collections have been established; others have been disbanded and for the majority there have been changes in staff and associated research programs. This fully justifies the effort to prepare a new edition of the Index.

The International Association of Wood Anatomists warmly supports this initiative, and the Council has agreed to give this project official IAWA status. Many members of IAWA will have received a questionnaire from Dr. Stern. Those members who did not receive a questionnaire but who are in charge of an institutional wood collection are requested to write to Dr. W.L. Stern, Professor of Botany, University of Maryland, College Park 20742, Maryland, U.S.A. at their earliest convenience.

We urge all of you, to cooperate actively to complete this valuable project as comprehensively and efficiently as possible.

WOOD ANATOMY ACTIVITIES AROUND THE WORLD

Request for Wood and Bark samples of Lauraceae

Mr. Hans Georg Richter from Hamburg has embarked on a comprehensive study of wood and bark anatomy of the large family of the Lauraceae. To this end he has already directed requests to several institutional wood collections for wood and bark samples. Mr. Richter writes us that, although the 'laurel-family' itself is well-defined anatomically, intra-family relationships are quite confused and generic boundaries seem unclear in many cases. Early experience has shown that much of the possible success of the project will depend on the availability of abundant authenticated material, allowing a certain degree of confidence in specific and generic identification.

About 600 Lauraceous species are already available for wood and bark anatomical study, but some genera and geographic regions are poorly or not at all represented in Mr. Richter's research materials. Curators of wood and bark collections are kindly requested to prepare a list of available authenticated specimens of Lauraceae, and send this to Mr. Richter. He will then check the list and restrict his actual request to the samples which are necessary to fill the voids. Your cooperation will be highly appreciated. Please write directly to: Hans Georg Richter, Institut für Holzbiologie und Holzschutz der BFH, 205 Hamburg 80, Leuschnerstrasse 91d, West Germany.

ASSOCIATION AFFAIRS

Professor Côté elected an Honorary Member

The IAWA Council has elected Professor W.A. Côté an Honorary Member of our Association. The merits of Dr. Côté for IAWA were outlined in a previous editorial (IAWA Bulletin 1976/3: 34). We congratulate Dr. Côté most sincerely with this honour, which has only been bestowed on those who have rendered notable service to the advancement of the knowledge of wood anatomy. We are confident that in his new capacity he will continue to be an active member of our Association, which owes so much to him.

Reminder I. The New Directory

Dr. R.K. Bamber who is actively engaged in producing the New IAWA Membership Directory writes us that not all members have yet returned their completed questionnaire. It is absolutely essential that data on research projects of all of our members become available, in order to make this new type of directory a useful project. Those of you who did not yet return the questionnaire are most urgently requested to do so at your earliest convenience (by air-mail) to Dr. R.K. Bamber, Forestry Commission of N.S.W., Wood Technology Division, P.O. Box 100, Beecroft, New South Wales 2119, Australia.

Reminder II. Ballot on Amended Constitution

Ballot forms with proposals for necessary amendments of the Constitution of our Association were sent to you in November 1976. A majority of our members did not yet return these ballot forms with their verdict. Since our Constitution prescribes a two-third majority for changes in the Constitution you are all requested to fulfill your democratic 'duties' at your earliest convenience, in order to prevent that your Executive Secretary has to carry out most of his activities in conflict with the constitutional rules!

Reminder III. Annual Dues

Those members who did not yet pay their 1977 or earlier dues are kindly reminded to do so. Please pay in Dutch Guilders and use an International Postal Money Order. This is possible for all countries which maintain postal giro contacts with the Netherlands. Payment by cheque invariably leads to heavy banking costs for our Association (Dfl. 5.00). If either out of necessity or for reasons of convenience you make use of cheques, an extra addition of 5 guilders to the normal dues (Dfl. 30.00), on a voluntary basis, will be highly appreciated.

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IAWA BULLETIN

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Front cover: Scanning electron micrograph of vestured intervessel pits (pit floors removed) in *Anogeissus acuminata* (Roxb. ex DC.) Wall. (Combretaceae). Courtesy G.J.C.M. van Vliet, Leiden.

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