IAWA BULLETIN

Contents

Front cover: Scanning electron micrograph of the wood of *Eugenia maire* A. Cunn. (Myrtaceae), one of the numerous New Zealand Woods pictured and described by B.A. Meylan and B.G. Butterfield in their 'Structure of New Zealand Wood', N.Z. Government Printer, Wellington, 1978. Courtesy B.A. Meylan and B.G. Butterfield, Lower Hutt and Christchurch.

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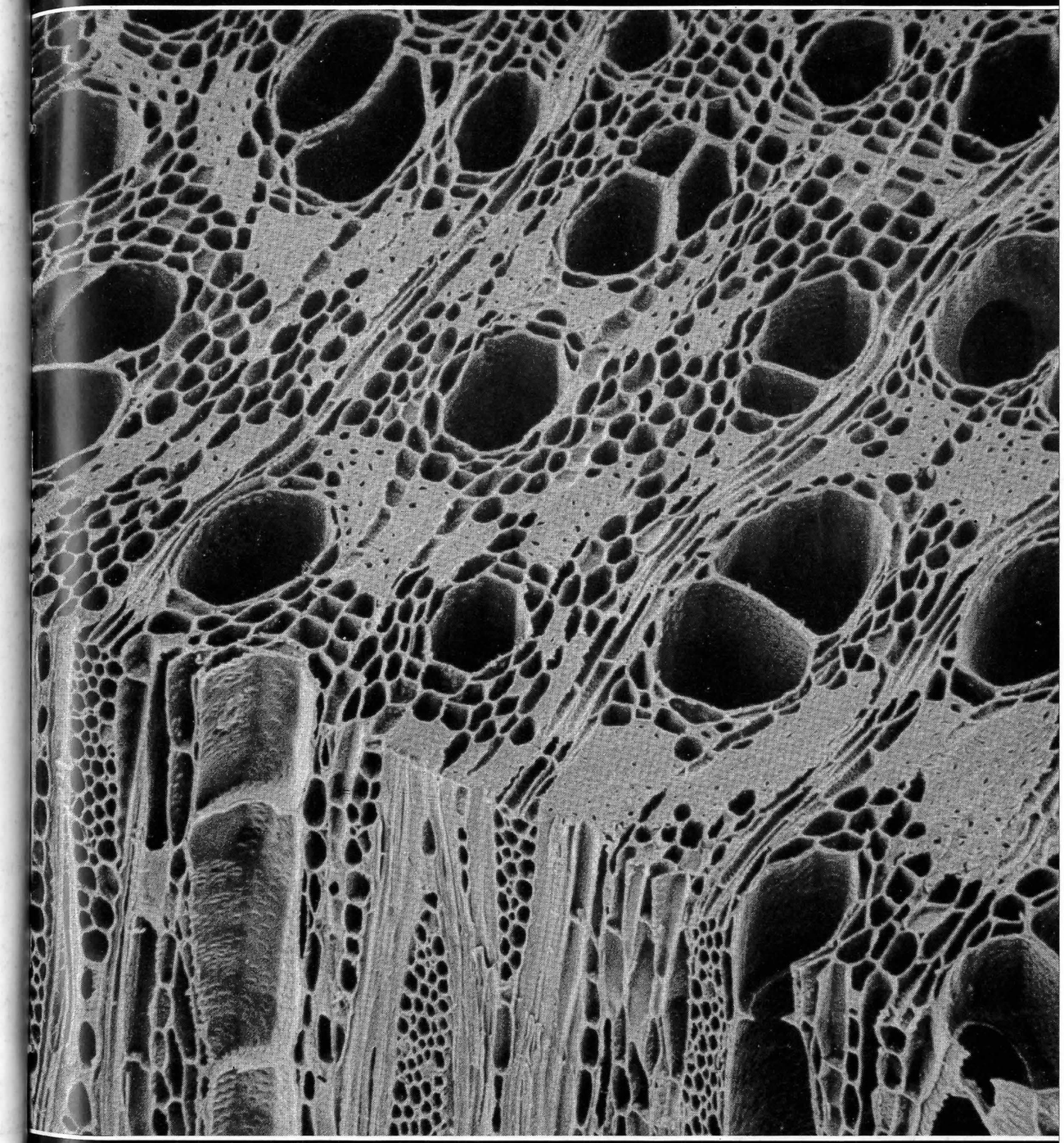

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EDITORIAL

Two topics deserve some comment in this editorial. The first is of a technical nature but has a more fundamental background. This IAWA Bulletin is more voluminous than usual, but it combines issues 2 and 3 for the 1978 volume. This postage saving measure was not taken for mercenary reasons but out of sheer necessity because of a temporary lack of copy which lead to serious delays of what normally should have become issue 1978/2. Again we are in bad need of manuscripts for future IAWA issues. Please help! Constant urges for copy should not be taken as a licence to publish mediocre scientific contributions. We hope you agree with us that the standard maintained in the IAWA Bulletin is a sufficiently high one. In order to safeguard this standard we regularly submit manuscripts which we do not feel confident about ourselves to independent referees who are more knowledgeable than we are in certain fields of specialization.

The other topic concerns a milestone in the history of wood anatomy. Together with this issue we enclose a copy of the second, completely revised edition of *Index Xylariorum*. Once more, our Member Professor Dr. William Louis Stern has been of invaluable help to the wood anatomical world by compiling this indispensable catalogue of the wood collections of the world. The Constitution of the International Association of Wood Anatomists reads in Article IV, 3: *The activities of the Association shall be to facilitate the collection, storage, and exchange of research materials.* One can hardly think of any activity which serves this purpose better than the tedious task of compiling a comprehensive *Index Xylariorum* as Dr. Stern now has done for the second time. We are confident that this new edition will stimulate further contacts and exchange between institutional wood collections and individual research workers. When in 1976 Dr. Stern embarked on collecting new data for the revised Index, the IAWA did not have sufficient financial means to support or completely sponsor its production. We hope that this can be remedied by the distribution free of charge to all our members. Meanwhile we are not only immensely grateful to Dr. Stern, but also indebted to the International Association of Plant Taxonomists (IAPT) for publishing the new *Index Xylariorum* in their journal *Taxon*.

Pieter Baas
Peter B. Laming

TILE CELLS AND THEIR OCCURRENCE IN MALVALEAN FOSSIL WOODS

by

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Summary

Two fossil woods are described which represent the oldest record of tile cells. Analysis of these and other fossils and a reinvestigation of extant genera of the Malvales indicate that the definition of tile cells given by the Committee on Nomenclature, IAWA (1964) is too narrow in scope and requires revision to include the type of tile cell found in *Pterospermum*. The occurrence of tile cells in the Eocene fossil record indicates that tile cells evolved early in the diversification of the Malvales. Several lines of evidence suggest that the *Pterospermum* type of tile cell has evolved from the *Durio* type.

Introduction

Certain members of the Malvales have a peculiar ray composition in which upright cells are interspersed among procumbent cells in the body of the ray. These interspersed upright cells were originally described by Moll & Janssonius (1906), who used the term 'ziegelsteinformig' or 'tile-shaped' in reference to their resemblance to tile work when viewed in radial section (figs. 1–3). Since then, there has been disagreement over how narrowly to define tile cells. This disagreement has resulted mostly from a lack of knowledge of the relationships between different shapes and sizes of the interspersed upright cells. In the present paper, we propose that the definition cited by the Committee on Nomenclature, IAWA (1964) be revised, based on re-examination of extant genera and on new data from the fossil record.

In the Multilingual Glossary of Terms used in Wood Anatomy, published in 1964, the Committee on Nomenclature, International Association of Wood Anatomists, restricted the definition of the tile cells to 'A special type of apparently empty, upright cells of approximately the same height as the procumbent ray cells and occurring in indeterminate horizontal series usually interspersed among the procumbent cells.' The genus *Durio* (figs. 1, 4, 5) typifies this restrictive definition of tile cells. Only 18 genera in the Sterculiaceae, Bombacaceae, Tiliaceae, and Malvaceae (*Kydia* spp.) are known to have tile cells fitting this definition.

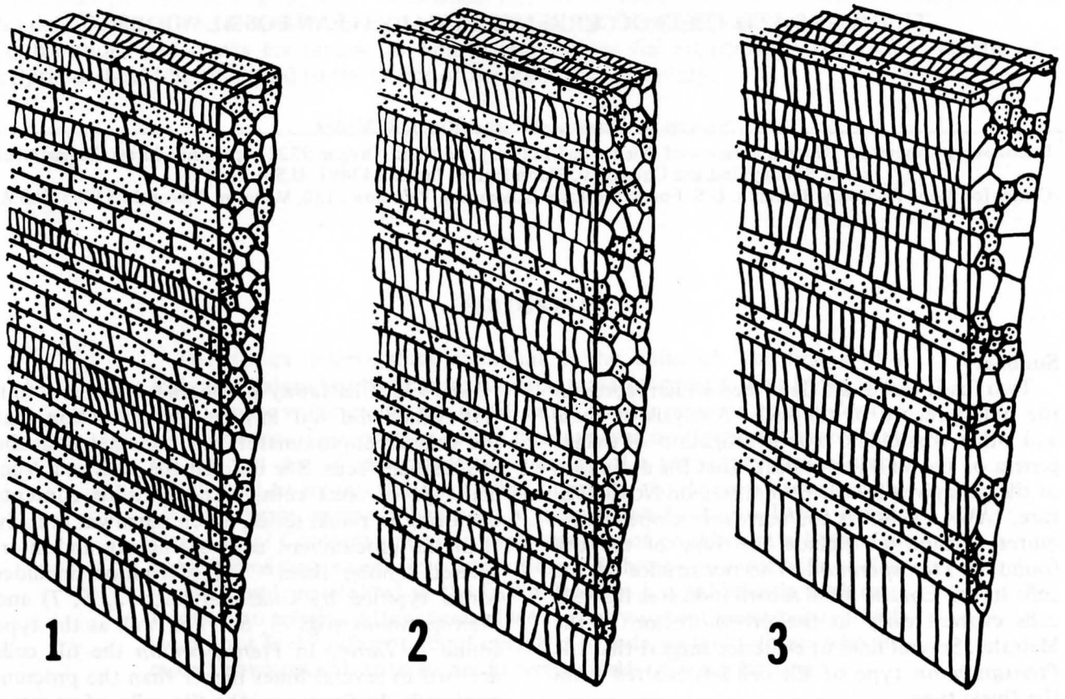
In 1933, Chattaway proposed a broader definition which did not impose the restriction that tile cells be approximately the same height as the procumbent cells. She defined tile cells as a 'special type of erect cells, without visible contents occurring in radial series, much narrower radially than the procumbent cells of the ray and interspersed among them.' This definition includes forms typified by *Guazuma* (figs. 2, 6, 7) and *Pterospermum* (figs. 3, 8, 9) as well as the type found in *Durio*. In *Pterospermum* the tile cells are two to several times higher than the procumbent cells. In *Guazuma*, the tile cells, of an intermediate type, are only slightly higher than the procumbent cells. For 'sake of convenience', Chattaway called the two extreme types of tile cells *Durio* type and *Pterospermum* type. In addition, she recognized at least two intermediate types (*Guazuma* and *Reevesia*) and indicated that there is a gradual transition from one type to the other. Tile cells as defined in this broad sense by Chattaway are found in about 30 genera of the Malvales, including many members of the Malvaceae (Webber, 1934).

As part of a continuing investigation of silicified wood remains from the Eocene Clarno Formation of northcentral Oregon (Manchester, 1977), two new woods with tile cells have been encountered. Extensive comparative work with modern species indicates that the fossils belong to extinct genera of the Malvales. This provides the earliest fossil record of tile cells yet known.

Methods and Materials

Comparative work with modern woods of the Malvales was based on samples and slides in the Samuel James Record (SJRw) and Madison (MADw) wood collections, both of which are housed at the U.S. Forest Products Laboratory in Madison, Wisconsin. Thin sections representing more than 125 genera of the Malvales were examined.

Standard techniques for measurement were employed except in the measurement of vessel element lengths. Since the length of the fossil vessel



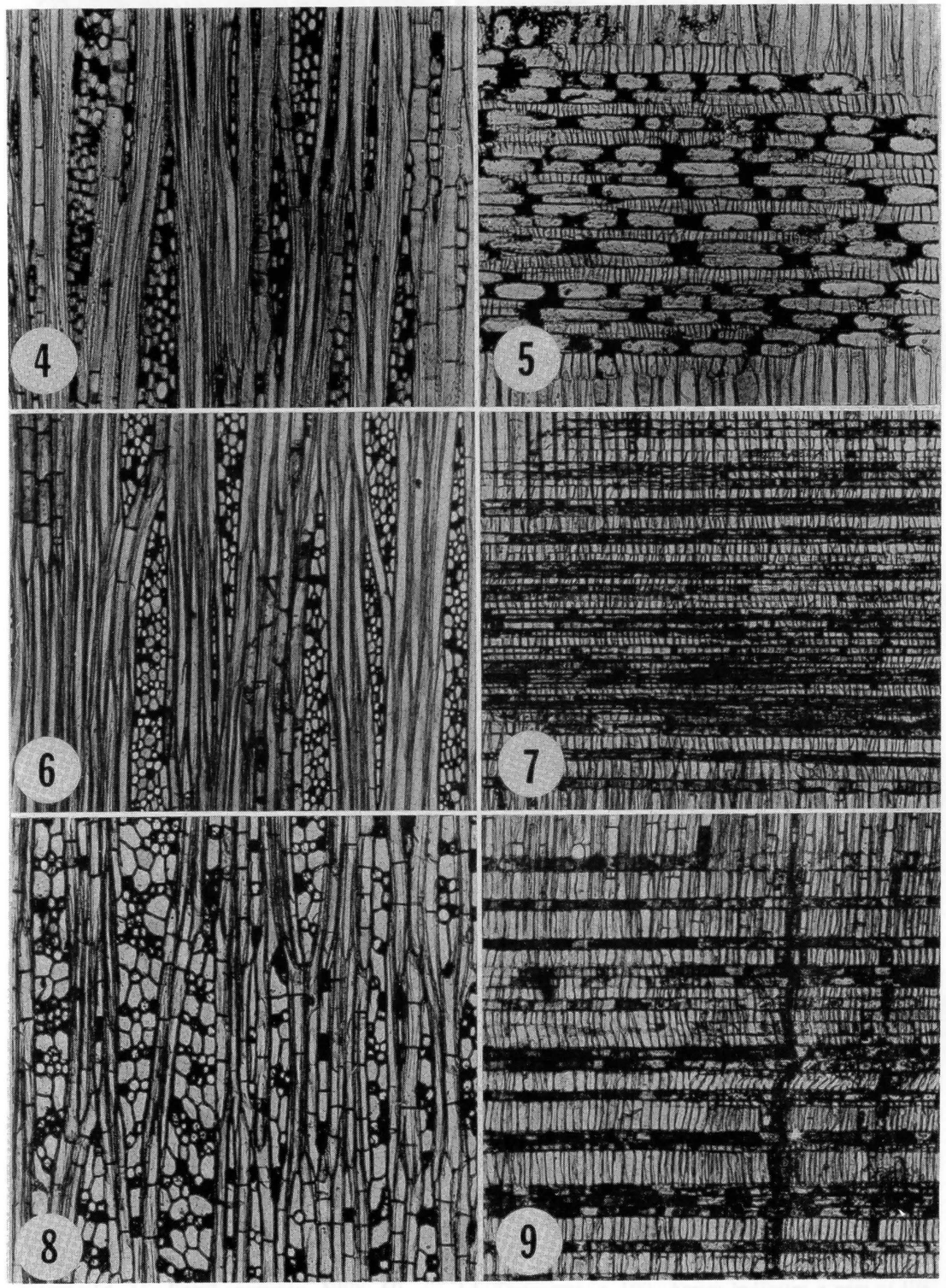
Figures 1–3: Cutaway diagrams of multiseriate rays showing different types of tile cells. Procumbent cells stipled, tile cells not stipled. About x 200. –– 1. *Durio zibethinus* Murr. Tile cells of the *Durio* type, approximately the same height as the procumbent cells; not easily recognized in tangential view. –– 2. *Guazuma crinita* Mart. Tile cells of the intermediate type, slightly higher than the procumbent cells. –– 3. *Pterospermum heterophyllum* Hance. Tile cells of the *Pterospermum* type, two to several times higher than the procumbent cells. Easily distinguished in tangential view.

elements could not be accurately measured from tip to tip, they were measured from midpoint to midpoint of the perforation plate. For comparative purposes, vessel element length for modern species was measured in the same fashion.

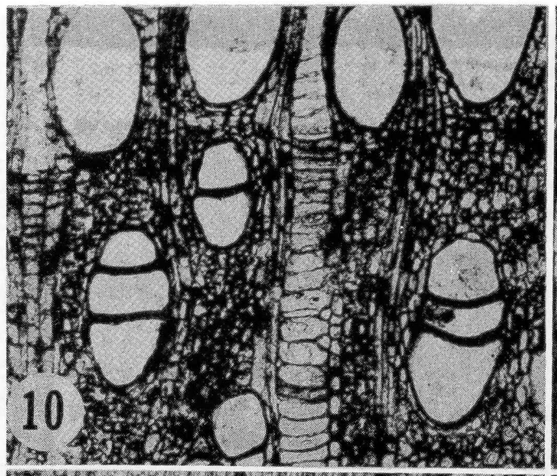
Two fossil wood samples were examined by transmitted light microscopy. Thin sections were prepared by the conventional grinding technique and by the acetate peel method. Type specimens of the fossils are housed in the Natural Sciences Collection of the Oregon Museum of Science and Industry.

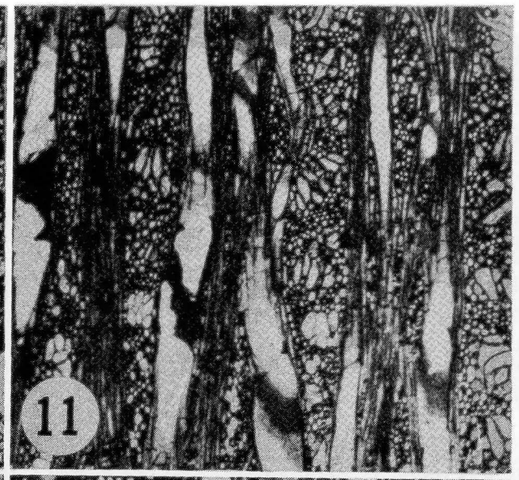
Descriptions

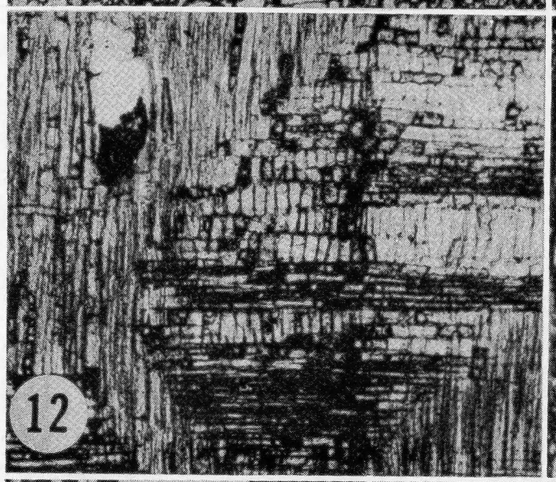
The descriptions which follow summarize the important anatomical characteristics of the fossils. In addition to tile cells, both possess many features, such as reticulate axial parenchyma, storied structure (NBW–50), medium length vessel elements with simple perforation plates and alternate intervascular pitting, which support their assignment to the Malvales. Since the fossils have not yet been formally named, they are referred to herein by their accession numbers (NBW–71 and NBW–50). Diagnoses and more

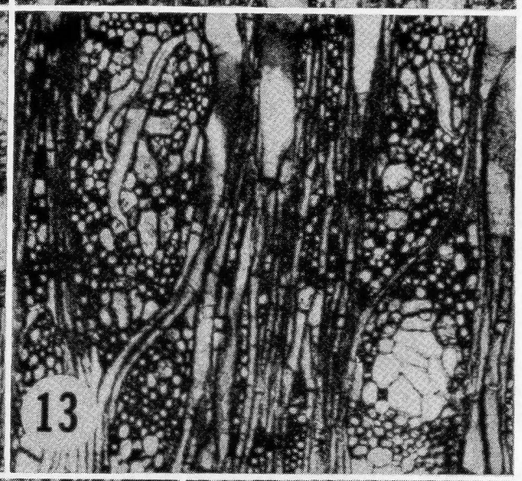


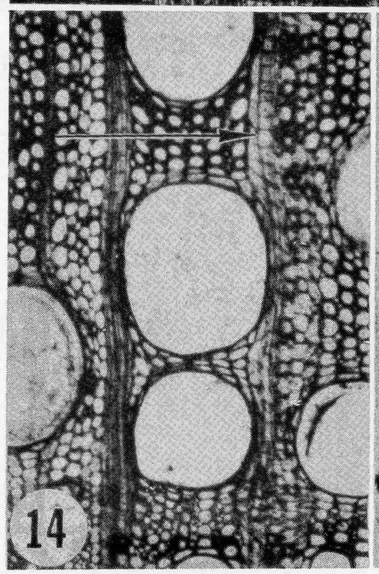
Figures 4–9: Photomicrographs showing different types of tile cells. –– 4, 5. *Durio zibethinus* Murr., SJRw 22318. – 4. Tangential section, x 100. – 5. Radial section, x 100. –– 6, 7. *Guazuma crinita* Mart., MADw 22414. – 6. Tangential section, x 100. – 7. Radial section, x 100. –– 8, 9. *Pterospermum heterophyllum* Hance, SJRw 22040. – 8. Tangential section, x 100. – 9. Radial section, x 100.

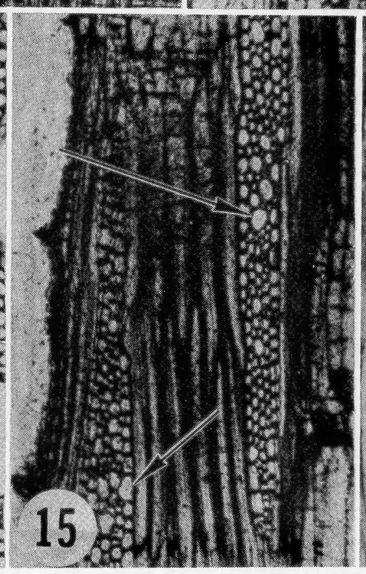


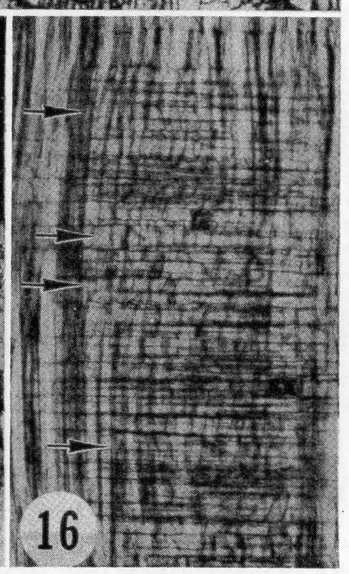












detailed descriptions will follow in subsequent papers (Manchester & Dilcher, in preparation).

Sample NBW–71 (figs. 10–13). Growth rings distinct; wood semi-ring-porous. Pore diameter 20–230, average 125 μm; vessel element length 290–479, average 418 μm; perforation plates simple; intervascular pits alternate, 4–6 μm. Fibres non-septate, not storied. Axial parenchyma reticulate, not notably storied; prismatic crystals common, sometimes in chambered cells, 1–2 per cell aggregating into short chains of 2 to 8. Rays 1–14-seriate, mostly 5–9-seriate; not storied; distinct tile cells of the *Pterospermum* type; tile cells up to five times as high as the procumbent cells and about one-third as long radially. Crystals common, especially in the tile cells.

Sample NBW–50 (figs. 14–16). Growth rings distinct; wood semi-ring-porous. Pore diameter 49–287, average 185 μm; vessel element length 156–470, average 380 μm; perforation plates simple; intervascular pits alternate, 3–5 μm; tyloses common. Fibres non-septate, storied. Axial parenchyma reticulate, storied. Rays 1–10-seriate, mostly 4–6-seriate; not storied; tile cells of intermediate to *Pterospermum* type; tile cells up to 2.5 times as high as the procumbent cells and about one-fifth as long radially. Crystals common, often in the tile cells.

Results and Discussion

The age of the Clarno Formation locality from which the fossils were collected is middle Eocene, or about 48 million years, as indicated by mammal correlations and potassium-argon dates (Hanson, 1973; Hanson, personal comm., 1976). Based on this dating, the above described woods are the oldest known fossils with tile cells. Other confirmed reports of tile cells in the fossil record include: *Grewioxylon intertrappea* from the probable late Tertiary of India (Shallom, 1963), *Reevesia miocenica* from the Miocene of Japan (Watari, 1952) and *Reevesia oligocenica* from the Oligocene of Japan (Suzuki, 1976).

The first of the fossils described above (NBW–71) and *Grewioxylon intertrappea* Shallom display tile cells of the *Pterospermum* type. The second of the fossils described above (NBW–50), and the two fossils assigned to *Reevesia* from Japan have tile cells of the intermediate type. To our knowledge, there have been no reports of woods with *Durio* type tile cells from the fossil record. Thus, the above mentioned fossils possess interspersed upright cells which fit Chattaway's definition of tile cells (1933), but are excluded from the definition given by the Committee on Nomenclature, IAWA (1964).

The term tile cell as presently defined by the Committee on Nomenclature, IAWA (1964) is restricted to include only the *Durio* type. However, the broader definition proposed by Chattaway (1933) has been adopted by Metcalfe & Chalk (1950), Jane (1970), Ayensu & Bentum (1974) and most other workers. The existence of intermediate types and the fact that both the *Durio* and *Pterospermum* types are restricted to the Malvales suggests that there is a definite relationship between the two types. The same position within the rays, and similar general appearance (as viewed in radial and transverse sections, see figs. 1–3), is also significant. In view of the general, but informal, acceptance of Chattaway's definition of tile cells and the apparent relationship between the *Durio* and *Pterospermum* types, we propose that a new definition structured after Chattaway's definition to include the intermediate and *Pterospermum* types as well as the *Durio* type be adopted.

Chattaway (1933) observed that tile cells are derived from cambial initials of the same width as those which give rise to procumbent cells and that the formation of tile cells results from post cambial divisions. From a detailed study of ray development in *Guazuma* (intermediate type) she concluded: 'The ultimate shape of the mature cells depends not only on the shape of the cambial initials but also on a physiological factor within the cells which causes some cells (procumbent) to elongate after they are cut off from the cambium and others (tile) to subdivide.' (p. 272). However, the phylogenetic origin and age of tile cells has not been discussed in the literature.

The occurrence of well developed tile cells in extinct genera of the early Tertiary suggests that tile cells originated early in the differentiation of the Malvales, perhaps in the middle or late Cretaceous, and do not represent a recent specialization. Since most modern genera are consistent in

Figures 10–13: Fossil specimen, NBW–71. –– 10. Transverse section, x 100. The ray in the center shows a conspicuous row of tile cells. –– 11. Tangential section, x 60, showing distribution and composition of the rays. –– 12. Radial section, x 100. The rows of tile cells are easily distinguished from those of procumbent cells by their dimensions (higher and narrower) and lack of dark contents. –– 13. Tangential section, x 100, showing conspicuous tile cells of the *Pterospermum* type.
Figures 14–16: Fossil specimen, NBW–50. –– 14. Transverse, x 100. Arrow indicates a row of tile cells. –– 15. Tangential section, x 100, showing tile cells of the intermediate type (arrow). –– 16. Radial section, x 100, showing several files of tile cells (arrows).

the type of tile cells they possess (*Durio* vs *Pterospermum*), it appears likely that the two types of tile cells have evolved independently or diverged early along modern lines.

If tile cells have evolved from normal procumbent cells, then the only step required in the derivation of the *Durio* type would be the regulation of factors promoting post cambial division of ray initials. Intermediate and *Pterospermum* type tile cells differ from the *Durio* type in being higher and wider, as viewed in radial section (figs. 1–3). Webber (1934) noted that the *Pterospermum* type of tile cell differs from normal upright cells, such as sheath cells and tail cells, only by their position within the rays. Development of tile cells of this type would require a dispersion of upright ray initials throughout the ray body, as well as the regulation of factors controlling post cambial division. Such a distribution of upright ray cells could be brought about through unequal divisions of the fusiform initials involved in the formation of ray initials.

If ray bodies composed of procumbent cells are the basic condition in the Malvales, then the *Pterospermum* type tile cell would appear to be more highly specialized than the *Durio* type. Observations of vessel element lengths support this specialization trend.

Vessel element length is a feature classically used to indicate levels of specialization. In a precursory examination of many specimens of extant genera with tile cells, we noted a correlation between vessel element length and type of tile cell. The vessel elements in genera with *Pterospermum* type tile cells (averaging 300–400 μm) are usually significantly shorter and therefore more specialized than those in the genera with *Durio* type cells (averaging 500–600 μm). This correlation between ray structure and vessel element length and the existence of intermediate, possibly transitional types introduces the possibility that *Pterospermum* type tile cells have arisen from the *Durio* type. Certainly the evolution of the *Durio* type from the *Pterospermum* type is less plausible.

Because of the lack of information on *Durio* type tile cells from the fossil record and the incomplete record of *Pterospermum* and intermediate forms, it is not yet possible to substantiate hypotheses concerning the exact mode of origin of the two types of tile cells. If the *Pterospermum* type has arisen from the *Durio* type, as is suggested above, then the occurrence of *Pterospermum* and intermediate types in the middle Eocene indicates that the two types had diverged or were diverging by the early Tertiary.

Acknowledgements

We would like to thank the following individuals for critically reading the manuscript: Dr. David Dilcher, Department of Biology, Indiana University, Bloomington; Dr. Robert Koeppen and Dr. Francis Kukachka, U.S. Forest Products Laboratory, Madison, Wisconsin; Dr. Elisabeth Wheeler, Department of Wood and Paper Science, North Carolina State University at Raleigh.

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A NOTE ON THE FINE STRUCTURE OF PROTOXYLEM ELEMENTS IN BAMBOO

by

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The protoxylem is defined as the first-formed xylem with tracheary elements characterized by annular or spiral thickenings. As a part of the xylem differentiating in the primary plant body that has not completed growth and differentiation the protoxylem matures among actively elongating tissues and is thus subjected to stress. These primary tracheary elements are provided with a variety of secondary wall thickenings in different plants (Esau, 1965, 1976).

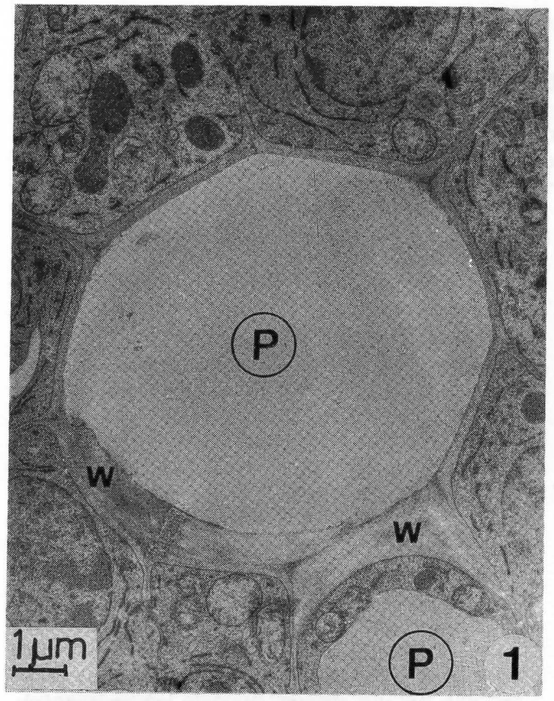
Fine structural studies on primary xylem elements have been concerned mostly with their cytodifferentiation (O'Brien, 1974; Roberts, 1976). Scott *et al.* (1960) investigated the development of annular and spiral vessels in the primary xylem in *Ricinus communis* and described the structure of the wall thickenings.

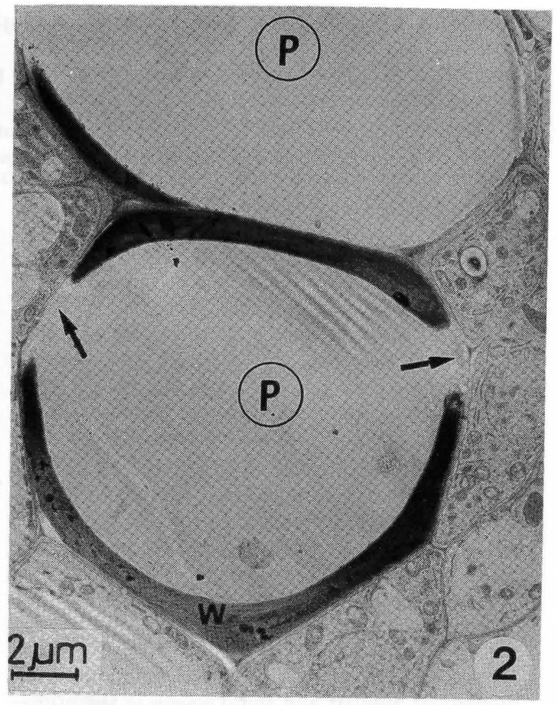
During our studies on the fine structure of bamboo (Parameswaran & Liese, 1976, 1977a, b) some observations were also made on the ultrastructure of protoxylem elements, especially in *Bambusa vulgaris* Schrad. ex Wendl. In most of the bamboo species the protoxylem consists of one or two tracheary elements with annular thickenings (Figs. 1 & 2). They are embedded at the beginning of culm internodal development in living parenchymatous tissue. The annular thickenings are already laid down at a stage where the surrounding cells are still parenchymatous (Figs. 1 & 2). With the further differentiation of the latter tissue, partially into fibres, hydrolysis occurs of the intercellular layer including the primary wall between the protoxylem elements and the surrounding parenchymatous cells (Fig. 3). Such a hydrolysis of the primary wall has been reported for both primary and secondary tissues by O'Brien (1970) and Czaninski (1972). The ring thickenings of the protoxylem elements have generally been termed 'secondary walls' (Esau, 1965). They are as a rule lignified and become deposited in cells undergoing rapid surface growth. The annular thickenings in the bamboo protoxylem must be considered as local zones of stasis accumulating wall material. Structurally they appear to be connected with each other by membranes which become ruptured during the extension growth of the cell and are then seen as remnants (Fig. 4); these membranes could be interpreted as the original primary wall extension. In later stages the rings are completely separated from each other and come to lie loosely in the protoxylem lacuna (Fig. 5). The only common wall separating the protoxylem from the surrounding cells is the hydrolyzed intercellular layer together with the simple pit connections (Figs. 5 & 6).

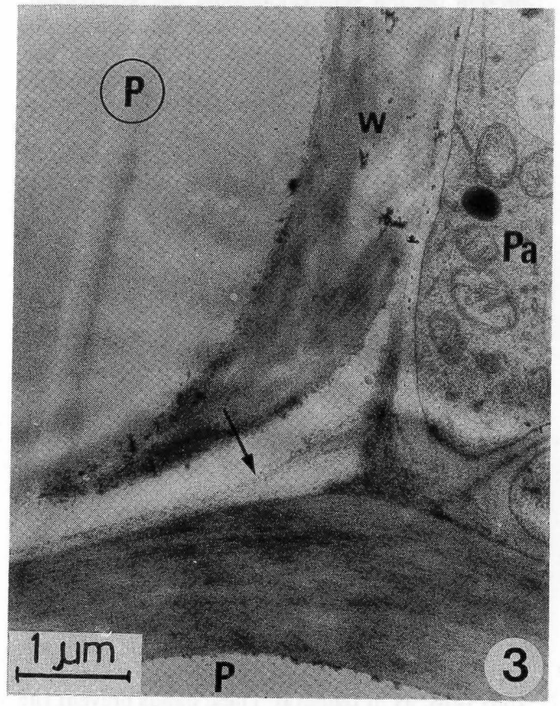
Beginning from the early stages of protoxylem development the ring thickenings are characterized by a more or less parallel microfibrillar orientation, perpendicular to the longitudinal axis of the cell (Fig. 7). The closely woven nature of microfibrils observed by Scott *et al.* (1960) for the primary tracheary elements of *Ricinus* is also present in the ring thickenings of protoxylem. However, the stratification observed by them in the spiral thickenings is missing in bamboo. Lignin skeletons revealed an equally parallel orientation of lignin substances, which seem to follow the cellulose fibrils (Fig. 8).

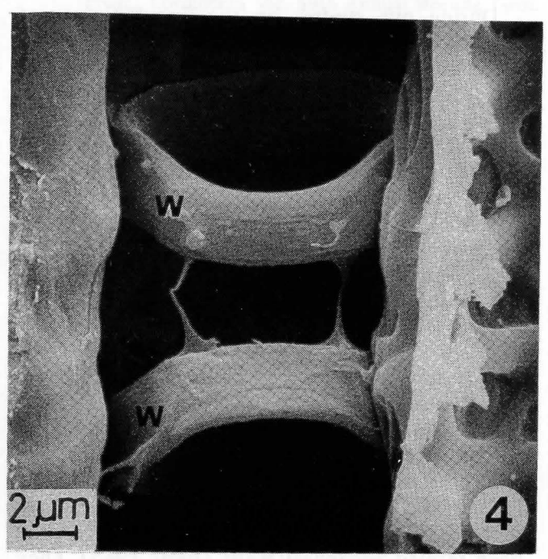
Scott *et al.* (1960) describe a suberization of the vessel wall in *Ricinus* after the death of the protoplast, termed as lipid lining. The annular and spiral thickenings are said to arise as cellulose bands and to become lignified when the vessel has attained maximum diameter.

O'Brien (1974) has elaborated on the adaptiveness of wall hydrolysis in the tracheary element with annular thickenings. He concludes that in a rapidly elongating organ the non-cellulosic polysaccharides are removed from the primary wall between the bands of lignified thickenings at the death of the protoxylem; this is supposedly effected by hydrolases liberated during the autolysis of the protoplast. Thus the cellulose fibrils become liable to passive stretching without the resistance offered by other matrix components. The lignified bands of thickening are either connected to similar bands in neighbouring protoxylem elements after the hydrolysis of the intermediate wall or to the walls of living parenchymatous cells, as in bamboo. These bands prevent the collapse of the passively stretching elements. The stretching process in the primary tracheary elements has been described by Frey-Wyssling (1940). In the case of bamboo with an extreme elongation of the internodes, the rings are stretched apart with a rupture of the connecting mem-









branes and partly also tilted. Here the process of elongation must be considered in terms of extreme values, since in certain bamboo species more than 45 cm elongation growth per day has been recorded. The protoxylem structure can thus be considered as a measure of the elongation phenomenon of the bamboo culm, reflecting both functional and structural consequences.

Thanks are due to Mrs. R. Schultze for technical assistance.

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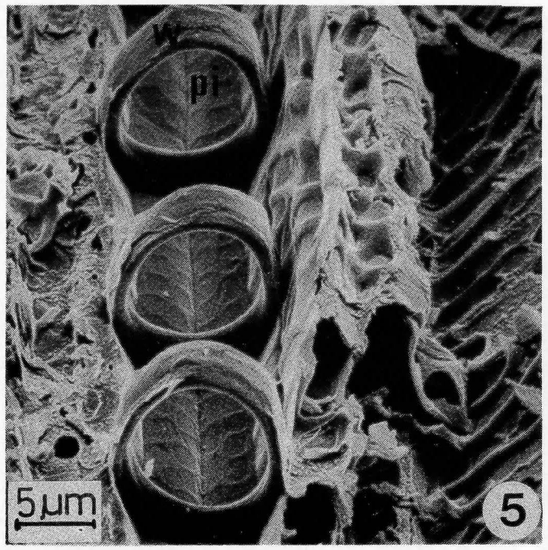
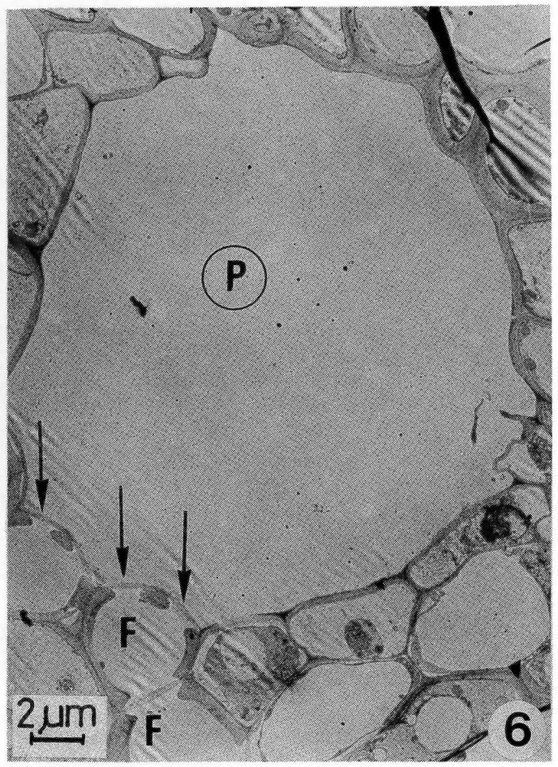
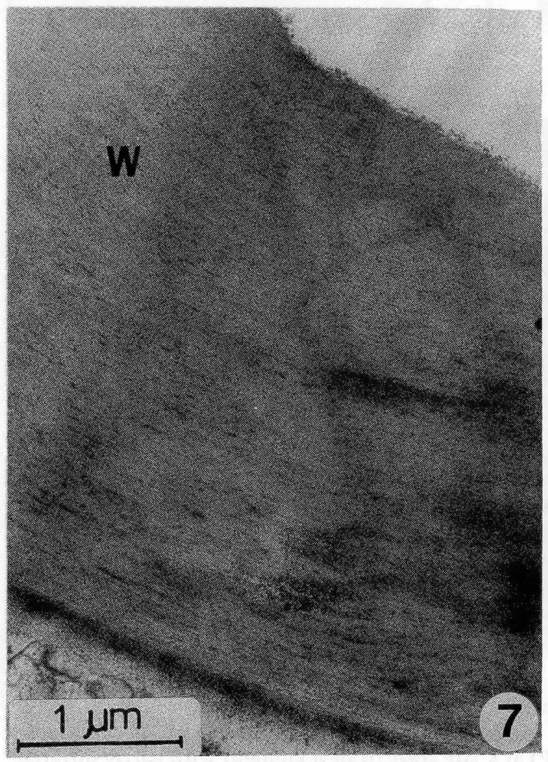
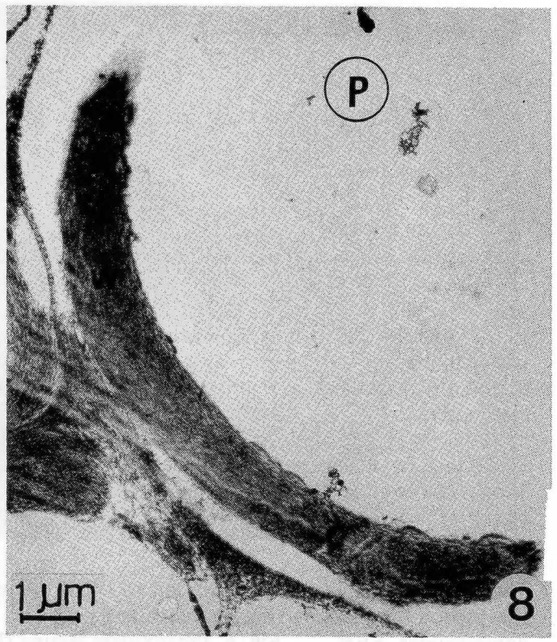
Fig. 1. Cross section showing young protoxylem elements (P) with wall thickenings (w); the surrounding parenchymatous cells still in an early stage with living protoplasts. *Bambusa vulgaris.* TEM. –– Fig. 2. Slightly advanced stage of protoxylem development (P) with ring thickenings (w) cut obliquely and pit connections (arrows). *Bambusa vulgaris.* TEM. –– Fig. 3. Hydrolysis of walls (arrow) between protoxylem elements (P) and surrounding parenchymatous cells (Pa). *Bambusa vulgaris.* TEM. –– Fig. 4. Remnants of membranes between two ring thickenings (w); note attachment to the adjacent cells. *Melocanna bambusoides.* SEM.

Fig. 5. Highly tilted protoxylem cell to show the arrangement of individual isolated ring thickenings in the protoxylem lacuna together with the pit fields (pi) to adjacent cells in the background. *Melocanna bambusoides.* SEM. –– Fig. 6. Protoxylem lacuna (P) at a late stage of development with partly differentiated fibres (F) in the surrounding tissues; pit connections (arrows) between protoxylem and fibres. *Bambusa vulgaris.* TEM. –– Fig. 7. Cross section of the wall thickening (w) of protoxylem element evidencing parallel arrangement of microfibrils. *Bambusa vulgaris.* TEM. –– Fig. 8. Lignin skeleton of protoxylem wall thickening (w) showing arrangement of lignin substances. *Melocanna bambusoides.* TEM.









A RETROSPECTIVE VIEW OF COMPARATIVE ANATOMY, PHYLOGENY, AND PLANT TAXONOMY[1]

by

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Comparative anatomy is so much a part of plant taxonomy today that we are likely to forget this was not always so. Although the practice of traditional plant taxonomy usually requires little more than the accouterments of a good eye and a hand lens, the pursuit of plant anatomy always requires a microscope. And so, while plant taxonomy was the first botanical science, plant anatomy had to wait for its development until after the invention of the microscope in the sixteenth century. But even then, it was not until Robert Hooke in 1665 and the fathers of plant anatomy, Marcello Malpighi and Nehemiah Grew, in the last part of the 1600s published their contributions to the microscopic structure of plant cells and tissues that there was even rudimentary comprehension of the minute parts of plants. Hooke, Grew, and Malpighi trained no students and many decades were to elapse before further significant contributions were to be made to plant anatomy and these by the versatile and controversial Sir John Hill (1759, 1770).

The first compendium of the anatomical structure of vascular plants probably dates to that many-sided botanist Anton de Bary (1877, English translation from the German, 1884), and it is with him we may safely say that the discipline of comparative plant anatomy had its genesis. A few years later (1885) Hans Solereder introduced the idea that wood anatomy might indeed be useful to the plant taxonomist in his considerations of systems of classification and relationships among dicotyledons.

The monumental taxonomic series of Adolf Engler and Karl Prantl (begun in 1889) incorporated anatomical observations into discussions of plant families. Solereder brought together his encyclopedic anatomy of the dicotyledons in 1899. Between 1928 and 1933 (Solereder had died in 1920), four contributions to an anatomy of the monocotyledons appeared in print under the authorship of Solereder and Fritz Meyer. In 1921 a series of anatomical monographs was initiated, originally under the editorship of Karl Linsbauer, and publication of new monographs in this sequence continues to the present. Solereder's work on the dicots was followed in 1950 by the two comprehensive volumes of C. Russell Metcalfe and Laurence Chalk which accounted for dicot anatomical research in the time since the appearance of Solereder's book and its translation from German into English in 1908 (revised and significantly enlarged by D. H. Scott). It ought to be noted in passing, that intensive studies of plant anatomy had been carried on in England since the 1890s, largely at Kew's Jodrell Laboratory of which Metcalfe became a prime mover and eventually Keeper (Metcalfe, 1976). Metcalfe assumed the production of another series of anatomical works on the monocotyledons, the first volume of which appeared in 1960 under his authorship. It is inspiring to contemplate that now, the indefatigable Metcalfe and Chalk, almost 30 years later, have embarked on an ambitious project to rewrite their 1950 anatomy of the dicotyledons. As I write this, the first volume of what is to be a multi-volume series is with the printer being set into type!

The publication of de Bary's work in 1877 can confidently be said to have ushered into botanical science the era of comparative anatomy, but it was probably Engler, among others, who foresaw clearly the growing importance of anatomical data in their relationship and application to a more complete understanding of plant classification. Since the time of these and earlier pioneers, we have progressed in understanding the anatomical structures of plants, the ontogeny of these structures, and the relevance of plant anatomy to the solution of botanical problems, particularly those of taxonomy. There is, however, a great distance yet to travel before the anatomy of all groups of plants, vascular and non-vascular, is known and until developmental and evolutionary studies show us the ways in which this anatomy has come about. The association between ecology and the evolution of anatomical structure is only now being approached systematically (Baas, 1976; Carlquist, 1975) and the relationships among plant anatomy, climate, physiology, and geography are coming under increasing scrutiny (Baas, 1973; Braun, 1970; Carlquist, 1975; van der

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Graaff and Baas, 1974; den Outer and van Veenendaal, 1976; Zimmermann, Brown, and Tyree, 1971).

Giant steps along the path of anatomical comprehension were taken early in this century by Professor Irving W. Bailey of Harvard University, his students and colleagues, and by their students. This group of botanists attempted to use information from the fossil record and from the wood anatomy of seed plants to define and explain certain trends of evolution in a manner not predisposed nor biased by existing systems of plant classification. From their intensive work, and especially that of Professor Bailey over more than 50 years (!), a body of concepts and generalizations on the evolution of anatomy in seed plants has been laid out (Howard, 1968; Wetmore *et al.*, 1974). This foundation has provided the comparative anatomist, taxonomist, and evolutionist with measuring devices for gauging the relative extent of evolutionary progress among the spermatophytes, and especially among the dicotyledons. It has helped and will continue to help botanists in their efforts to establish genetically sound systems of classification.

Bases of the Baileyan Concepts

Development of the Baileyan concepts was preceded by an extensive reconnaissance examination of xylem from a broad spectrum of plants: from vascular cryptogams, from gymnosperms, and from angiosperms (Bailey and Tupper, 1918). Data from the fossil record were utilized wherever possible. All observations and measurements were based on large numbers of diverse kinds of plants so that the resulting interpretations and generalizations could have whatever security is vested in statistically relevant samples. From Bailey's own studies and from those of others, it became clear that among the vascular plants as a whole, the earliest kind of tracheary cell to be found in the fossil record was the *tracheid* – a cell type which is dead when functionally mature, which is elongated and strongly tapered at either end (i.e., is fusiform), which has pitted lateral walls, which is imperforate, which is relatively narrow, and in which the trans-sectional outline is angular. Furthermore, Bailey observed that in general, tracheids present in more recent vascular plants are shorter than those in their forebears. These conductive cells are present in the xylem of every single major group of extinct and extant vascular plants.

The other kind of tracheary cell which occurs in vascular plants is the *vessel element* or *vessel cell*, an elongated cell type which has perforations at either end, pitted lateral walls, and which, like the tracheid, is dead when functionally mature. These cells have evolved in several groups of plants: among the vascular cryptogams, in *Selaginella, Equisetum,* and in a few genera of true ferns (e.g., *Pteridium, Marsilea*); within three genera of gymnosperms (*Gnetum, Ephedra, Welwitschia*); and in the angiosperms. They are characteristic, however, only among the angiosperms, where, associated with the phenomenon of double fertilization, they serve to define the group.

That vessel elements in angiosperms have arisen phylogenetically from tracheids by the palingenetic dissolution of pit membranes and the formation of true perforations through which adjacent superposed cells are uninterruptedly connected, seems to be certain. The morphological transitions between tracheids and vessel elements are so very gradual that, were it not for the lack of pit membranes, some forms of the latter cells would be impossible to distinguish from tracheids on other structural or physiological bases.

Regardless of the fossil plant group from which one attempts to derive the angiosperms, one finds that the only conductive cells present (with some exceptions noted above) are tracheids. Therefore, the tracheid is the sole tracheary cell from which the vessel element could have been derived phylogenetically:

1) Only tracheids occur in fossil and in most of the modern vascular cryptogams.
2) If it is assumed, as is frequently argued, that the angiosperms arose from an ancestor bearing fern-like foliage and naked seeds (i.e., from among the Pteridospermae), the fossil record shows that these early seed plants all had exclusively tracheids; only tracheids are found in most of the modern gymnosperms.
3) Physiologically tracheids and vessel elements are both conductive cells.
4) Ontogenetically, tracheids and vessel elements are homologous, because in secondary xylem they both owe their origins to the vascular cambium, and in primary xylem each arises by differentiation from cells of the procambium.

Thus, phylogenetically, tracheids and vessel elements form an unbroken sequence of development and can be said to be genetically related to one another through time.

Given the fact that tracheids represent the most primitive kind of tracheary cell because they appear first in the fossil record, long before vessel elements do, and the strong presumption that vessel elements are lineal descendants of tracheids, it is logical to conclude that vessel elements which most closely resemble tracheids will be more primitive than vessel elements which depart greatly from the appearance of tracheids (Frost, 1930a). It ought to be emphasized here that the vessel element is chiefly distinguished from the tracheid by the presence of end walls specifically distinct from the lateral walls, and by the presence of perforations which usually occur in those end walls. Also, it must be noted, in contrast with tracheids, vessel elements are united into tubes, one cell above the other, to form structures called *vessels*. Movement of water in a vessel is through the perforations in the upper and lower adjacent end walls of contiguous vessel elements.

If we define the features which characterize tracheids as a whole we can establish a model against which to compare vessel elements as a whole. Frederick Frost, who studied in Bailey's Harvard laboratory in the late 1920s and early 1930s, noted these tracheidal features as:

1) great length,
2) small trans-sectional area,
3) angularity of the cell in transverse section,
4) thin walls of constant thickness, and
5) the absence or very slight development of an end wall.

If we had a tracheary cell which conformed to each of these features, yet had perforations in its slightly developed end walls, we would have a vessel element of the most primitive kind. If, at the other extreme, we had a tracheary element which was very short and broad, circular in transverse section, with unevenly thickened cell walls, and pronounced horizontal end walls bearing perforations, we would have a vessel element of an advanced type since it would diverge greatly from the tracheidal type of construction. Thus, we can conclude that not only are tracheids more primitive than vessel elements, but vessel elements which resemble tracheids are more primitive than vessel elements which diverge more or less from the tracheidal type.

The perforations in the end walls of vessel elements are basically of two kinds – *scalariform* (a type of multiple perforation), in which there are many to few small openings in the end wall separated by thin strands of cell wall material arranged like the rungs of a ladder, and *simple*, in which there is only one opening unobstructed by strands of cell wall material. The lateral walls of vessel elements are pitted in much the same way as they are in tracheids. The organization of pits, that is their wall pattern or pitting, falls into a few main categories: scalariform, opposite, and alternate. Bailey (Bailey and Tupper, 1918) was able to correlate the kinds of perforations in vessel elements with the organization of the pits in the lateral walls of these cells. He demonstrated that, generally, vessel elements with scalariform perforations had scalariform lateral wall pitting, that vessel elements with both scalariform and simple perforations (i.e., the intermediate condition), had lateral wall pitting which was scalariform and opposite (i.e., the intermediate condition), and that vessel elements in which the perforations were exclusively simple had lateral wall pitting which was almost entirely alternate (Table 1).

Table 1. Correlations of perforations and lateral wall pitting among dicotyledons*

Perforations	Lateral wall pitting	%
Prevailingly scalariform	Scalariform and opposite	86
	Opposite and alternate or alternate	14
Intermediate, scalariform/simple	Scalariform and opposite	80
	Opposite and alternate or alternate	20
Simple; vessel element end walls tapering	Scalariform and opposite	11
	Opposite and alternate or alternate	89
Simple; vessel element end walls horizontal	Scalariform and opposite	6
	Opposite and alternate or alternate	94

* Modified from Bailey and Tupper (1918).

In this same study, Bailey showed that imperforate tracheary elements (i.e., 'fibers') with large, distinctly bordered pits were correlated with vessel elements having scalariform perforations and scalariform lateral wall pitting, whereas imperforate tracheary elements with tiny, vestigially bordered pits or unbordered pits predominated in xylem where there were vessel elements with simple perforations and alternate lateral wall pitting.

Both Bailey and Frost (1930b, 1931) were able to make further correlations which tended to show that vessel elements with scalariform perforations and scalariform lateral wall pitting were long, narrow, angular in trans-sectional outline, had evenly thickened cell walls, and were markedly tapered at the ends. That is, *these kinds of vessel elements closely resembled tracheids.* On the other hand, they showed that vessel elements with exclusively simple perforations and alternate lateral wall pitting were relatively short, wide, circular in trans-sectional outline, had unevenly thickened cell walls, and horizontal end walls. *Such cells deviated greatly in appearance from tracheids.* Between these two extremes there were all intermediate levels of modification. With these generalizations set forth, it became possible to associate the scalariform configurations of the vessel element end wall and lateral wall pitting with a degree of primitiveness, and the simple perforation plate and alternate lateral wall pitting with a degree of evolutionary advancement.

Establishment of these guideposts permitted correlations of other features of the secondary xylem which could now be placed on a relative scale of evolution. David Kribs (1935), using a modification of Bailey's vessel element types (Table 1; Bailey and Tupper, 1918), was able to demonstrate that vascular rays in which the cells were both upright and procumbent (heterogeneous) correlated with the primitive condition of

vessel elements, whereas vascular rays in which the cells were all procumbent (homogeneous) correlated with vessel elements of a more advanced configuration. He was also able to correlate the pattern of axial xylem parenchyma strands as seen on the transverse section with the condition of vessel elements and from these studies (1937) he concluded that *apotracheal parenchyma* (i.e., parenchyma strands unrelated to vessels) was the ancestral condition and that *paratracheal parenchyma* (i.e., parenchyma strands related to vessels) was the derived condition.

In all of these correlations and their applications caution must be exercised when drawing wide-ranging conclusions and it is always necessary to account for the fact that different cells and tissues of the plant have evolved at different rates and it is entirely possible in modern plants to discover relatively primitive traits side by side with others which are more advanced. But with the judicious application of these general trends, it is possible to evaluate the relative advancement of the secondary xylem in any dicotyledon and to apply this information to the solution of certain taxonomic questions, especially those of plant classification, for the trends noted above were derived completely independently of any established system of classification. Thus, in situations of questionable derivation of one plant group from another, it would be impossible to derive plants having a preponderance of primitive features in the xylem from plants carrying a preponderance of advanced features. The application of concepts from phylogenetic wood anatomy, then, is most useful in negating already existing or proposed relationships among groups of plants.

An application of the Baileyan Concepts

As the Baileyan concepts of evolution in xylem became better known, the ideas embodied in them were applied to the solution of taxonomic questions. Among these was one of enduring importance concerning which families of living angiosperms were closest to the ancestral complex from which modern flowering plants arose. On the one hand was the system of Adolf Engler and on the other hand that of Charles E. Bessey.

Toward the end of the 19th century and well into the 20th century, the system of classification of spermatophytes established by Adolf Engler, his students, and adherents held sway over most of European and American taxonomic botany (reviewed in detail in Stern, 1973). In England, the classification of George Bentham and Joseph Hooker (1862–1883) was the foundation for the taxonomic system employed in that country and its dominions. The Englerian system had a profound effect on American botany, to such an extent that all the major herbaria in the United States of America are still arranged according to the system of Engler with minor modifications. As a filing system for plants, the method is admirable; as a classification purporting to show relationships among spermatophytes, it has several serious drawbacks although over all it has considerable merit even today (Melchior, 1964).

Also toward the end of the 19th century and into the 20th century, another system of classification was supported by Charles E. Bessey (1915; Kiger, 1971), Professor of Botany at the University of Nebraska in the United States of America. Although Bessey's system was not nearly as complete nor well developed as was that of Engler, nevertheless, there were followers both in the United States and abroad, e.g., Hans Hallier (1903, 1912) in Germany and Holland, and John Hutchinson (in much earlier works, but culminating in his final treatise of 1973) in England. Presently, Cronquist (1968), Takhtajan (1966, 1969), and Thorne (1976) support the basic tenets of the Besseyan system.

The two systems differ essentially in the selection of primitive groups among the angiosperms and in the establishment of primitive features. In the Englerian system, the amentiferous or catkin-bearing plants (the early families of his Archichlamydeae) were chosen as the primitive group. Engler pointed to the similarity between the catkins and wind pollination of the gymnosperms and these same conditions in Fagaceae, Betulaceae, Juglandaceae, Myricaceae, Casuarinaceae, etc. In contrast, the Besseyan primitive groups were chosen from among plants he included in Ranales, that is, plants with large, conspicuous flowers borne in a solitary manner and pollinated by insects, e.g., Magnoliaceae, Annonaceae, and Dilleniaceae. Some of the basic differences between the primitive groups of the Englerian and Besseyan hypotheses are listed in Table 2.

Table 2. Comparison between amentiferous and ranalean families

Englerian amentiferous families	Besseyan ranalean families
1. Flowers in catkins; tiny	Flowers solitary; large
2. Flowers apetalous	Flowers petalous
3. Anemophily	Entomophily
4. Flowers unisexual	Flowers bisexual
5. Syncarpy	Apocarpy

Because, as I have shown above, the evolutionary trends in the anatomy of the secondary xylem have been established without recourse to existing systems of plant classification, they should provide an objective test of these two hypotheses. Below (Table 3) is a comparison of certain features of the secondary xylem of amentiferous and ranalean families.

Table 3. Comparison of anatomical characters of the xylem in amentiferous and ranalean families

Englerian amentiferous families	Besseyan ranalean families
1. Perforations tending toward simple or simple and scalariform	Perforations predominantly scalariform
2. Vessel elements relatively short	Vessel elements relatively long
3. Lateral wall pitting opposite to alternate	Lateral wall pitting commonly scalariform and opposite
4. Vessels broad and rounded in trans-section	Vessels narrow and angular in trans-section
5. Axial xylem parenchyma both apotracheal and paratracheal	Axial xylem parenchyma usually apotracheal
6. Vascular rays tending toward homogeneous	Vascular rays basically heterogeneous
7. Imperforate tracheary elements often with minutely bordered or unbordered pits	Imperforate tracheary elements often with conspicuously bordered pits

The anatomical generalizations in Table 3 indicate that, while the first archichlamydeous families of Engler's classification are by no means primitive, yet neither are they anatomically very highly modified. Following his broad survey, Moseley (1973) asserted that the secondary xylem of the amentiferous families is indicative 'of a moderately advanced level of evolution. One can observe .... that in most families roughly half of the characters are primitive and half are advanced. In the parlance of the phylogenist, this indicates, generally, that each family is moderately advanced and certainly not primitive.' On the other hand, there is to be found among extant ranalean families all or most of the features of the secondary xylem regarded as primitive. In addition, among the ranalean families are counted Winteraceae, Trochodendraceae, Tetracentraceae, and Amborellaceae in which the secondary xylem is completely devoid of vessel elements. These plants are considered to be ancestrally vessel-less, that is, evolutionarily speaking, they never developed vessels and exist in the primitive condition today, at least in this respect.

I do not mean to give the impression that the only valid explanation of the evolution of the angiosperms and the relationships among the various groups of flowering plants rests solely on an application of the Baileyan concepts. These tenets have been derived largely from a study of the secondary xylem, and this tissue is only one part of the plant. Interpretations of phylogeny and evolution based upon it are thus limited. Not only have all tissues of plants changed during the course of evolution, but many of the basic physiological and chemical processes have undergone changes as well. Plants have migrated, occupied differing ecological niches, come into existence, and passed out of existence, and these phenomena continue into the present and will continue into the future.

It would be spurious and misleading, and certainly unscientific, if in our investigations we ignored information and data from other tissues and from other botanical disciplines in fanatic attempts to value wood anatomy above evidence which might be contributed from other areas of botanical enterprise. Bailey (1949) himself never intended this and he entreated us, saying, 'Each botanical discipline, Taxonomy, Paleobotany, Phytogeography, Cytology, Embryology, Anatomy, Developmental Morphology, Genetics, etc., has important contributions to make in the ultimate solution of various aspects of the great central mysteries (those involved in the origin of the angiosperms), but the limitations of each field of research in the solution of specific problems of phylogeny and relationship should be clearly visualized and freely admitted.' It is, therefore, incumbent upon us to use all the resources at our disposal in our attempts to discover the mechanisms involved in the evolution of plants, to define the effects of these mechanisms on the changing structure and pattern of plants, and to interpret the direction of that evolution.

An application of Comparative Anatomy

Let us turn our attention now to a different aspect of anatomy, one which bears more directly on the solution of practical problems, and where comparative anatomy finds one of its applications. Comparative plant anatomy seeks to measure differences and similarities of structure between and among plants in an attempt, thereby, to reckon the degree of genetic relationship of those plants. The approach is evolutionary and rests on the premise that similar structures will have evolved in organisms if they are genetically related to one another. The more numerous the similar structures, the closer the relationship of the organisms; the fewer the similarities, the more distant the relationship. Thus we assume homology (common derivation) among similar structures, but extreme caution is necessary to separate homologous structures and homologous development from those which are merely analogous and are not lineally derived.

An exception to homology is illustrated by the phenomenon of *convergence*, or the development of similar characters in unrelated organisms, especially those growing in similar environments, presumably in response to similar selection pressures. Examples of convergence are the sclerophyllous Zygophyllaceae (e.g., *Larrea, Bulnesia*) of American deserts which resemble certain Rutaceae and Proteaceae of Australia, and New World cacti which are almost indistinguishable vegetatively from certain African species of *Euphorbia* (Steb-

bins, 1974). The hard-leaved Zygophyllaceae, Rutaceae, and Proteaceae, and the fleshy-stemmed, leafless Cactaceae and euphorbias are examples of analogous development, for the flowers of these plants betray their analogous similarities. Convergent evolution may affect habit, function, and structure, and thus it may be reflected in the cells and tissues of plants.

In a recent study of the comparative anatomy and systematics of *Hydrangea* (Stern, in press) there appeared to be overwhelming evidence to support the view that this genus ought to be divided into two genera. The circumscription of *Hydrangea* is based on Linnaeus's 1753 adoption of Gronovius's 1739 name for an unknown plant bearing small white flowers in a broad umbel which became *H. arborescens*, a plant of eastern North America, in the *Species Plantarum*. In 1794 Ruiz & Pavón dedicated the name of a new tree, *Cornidia*, to Joseph Cornide, naturalist, and *C. umbellata* Ruiz & Pavón, now referred to *Hydrangea preslii* Briquet (McClintock, 1957), became the first species in that genus. Engler (1891) submerged *Cornidia* within *Hydrangea* as a section, and there it has lain these many years (except for John Small, in Small and Rydberg, 1905, who continued to consider *Cornidia* a useful category). *Hydrangea, sensu lato*, has a rather unusual geographic distribution. Species of section Hydrangea grow in eastern North America and eastern Asia, a not uncommon pattern, but species of section Cornidia (with a single exception) occur in tropical America.

Evidence from the morphology and anatomy of leaves, especially those features enumerated in Table 4, is strongly favorable to the continued support of two generic entities, *Hydrangea* L. and *Cornidia* Ruiz & Pavón.

Even certain features of the xylem argue persuasively for this position: Xylem rays in section Hydrangea are homogeneous, i.e., homocellular (with certain exceptions), whereas xylem rays in section Cornidia are both homo- and heterogeneous, i.e., homo- and heterocellular; the pattern of ray cell to vessel element pitting parallels lateral wall pitting in section Hydrangea (basically scalariform), but it is gash-like, fenestriform, and random in section Cornidia; xylem ray cells lack crystals in section Hydrangea, whereas ray cells of section Cornidia are crystalliferous; vessel elements in section Hydrangea lack spiral thickenings, though they do occur in some members of section Cornidia; and perforated ray cells were noted only in species of section Hydrangea.

That *Cornidia*, as a genus, has continued to be subordinated to *Hydrangea*, despite the constellation of vegetative differences between the two entities, is tribute to the reserve of some botanists who seem always to place greater weight on reproductive over vegetative features in making

Table 4. Comparison of some morphological and anatomical features in mature leaves of *Hydrangea*

Section Hydrangea	Section Cornidia
1. Basic leaf outline ovate	Basic leaf outline oblong to elliptic
2. Secondary veins tend to be crowded toward leaf base	Secondary veins about evenly spaced
3. Secondary veins tend to be decurrent	Secondary veins usually not decurrent
4. Margins prominently toothed	Margins entire or denticulate
5. Blades chartaceous, thin	Blades coriaceous, thick
6. Palisade mesophyll uniseriate	Palisade mesophyll bi- to triseriate
7. Vascular bundle sclerenchyma poorly developed	Vascular bundle sclerenchyma well developed consisting of septate fibers
8. Bundle sheath cells lack prismatic crystals	Bundle sheath cells contain prismatic crystals
9. Upper epidermis uniseriate	Upper epidermis bi- to triseriate
10. Epidermal cell walls thin	Epidermal cell walls moderately to much thickened
11. Unicellular, unbranched trichomes*	Multicellular, stellate trichomes
12. Blades eglandular	Blades glandular
13. Hydathodes prominent	Hydathodes weakly developed

**Hydrangea quercifolia* has both unicellular and stellate trichomes.

taxonomic decisions, and who stubbornly refuse to recognize the validity of data other than those from their own disciplines. Though, as McClintock (1957) states, there is 'not a single floral structure .... to separate them (i.e., sections Hydrangea and Cornidia),' there is an impressive list of contrasting features, mostly of easily seen morphological characters coupled with more recondite, but nonetheless valid, anatomical features, by which *Hydrangea* differs from *Cornidia.* We have in *Hydrangea*, then, a group of floral and related reproductive characters which tie it together into a homologous whole. In addition, there are two other sets of characters, vegetative in nature, which provide strong evidence to show that the genus, *sensu lato*, evolved along two branches. Furthermore, these two branches of development have a geographical base which is very persuasive in support of the division of *Hydrangea* into two separately evolved entities – *Hydrangea*, of eastern North America and eastern Asia, and *Cornidia*, of tropical America. At this stage, however, the original center of origin and divergence of these two units remains obscure.

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SEM OBSERVATION OF COLLAPSE IN WOOD

by

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Abstract

Both earlywood and latewood tracheids in redwood and fibers in tanoak and chinkapin wood were found to be prone to collapse. The majority of the earlywood tracheids and fibers collapsed at an angle between the radial and tangential planes of the stem resulting in a distortion of the regular filing of cells and the growth ring pattern. Latewood tracheids and fibers, on the other hand, collapsed mainly in the radial direction. No collapse of white fir latewood tracheids was observed. White fir earlywood tracheids collapsed in the tangential direction causing wood separation and formation of honeycomb fissures. Vessels and the axial parenchyma cells were free from collapse. The ray parenchyma cells in redwood, white fir, and chinkapin did not collapse but ray cells in tanoak collapsed, especially those in the broad rays. It was impossible to determine the anatomy of collapse in the longitudinal direction.

Introduction

Collapse of wood as a result of drying is a very severe and common problem, often leading to appreciable degrade in material. It occurs during the early stage of drying when wood has a very high moisture content. It is frequently accompanied by internal checking or splitting (honeycombing) as a result of localized and abnormal shrinkage and stress development. The cause of collapse may involve capillary tension and compressive stresses developed during drying (Tiemann, 1941; Kauman, 1958). The mechanism of collapse involving capillary tension has been given in detail by Siau (1971). According to this theory, cell cavities must be completely filled with liquid water and the radii of the pit openings must be smaller than 0.041 μm for collapse to occur. The processes of pit aspiration and pit membrane encrustation during the formation of heartwood reduce the size of pit openings and sometimes render the pit membranes completely impermeable. Such morphological changes undoubtedly increase the tendency for wood to collapse. Meyer and Barton (1971) found that collapse of western redcedar wood was related to high extractive content and the pit chambers and membranes of heartwood tracheids were heavily deposited with extractives. Certain woods, such as redwood, western redcedar, oaks, redgum, and eucalyptus species, are more susceptible to collapse than other woods (Panshin and deZeeuw, 1970).

The microscopic nature of collapsed wood has not been extensively studied mainly because of difficulty in preparing specimens for observation. Collapsed material is usually very dense so that microscopic sections are difficult to obtain without softening and embedding procedures. However, the usual methods of softening and embedding of samples involve swelling agents which would certainly change the configuration of collapsed cells by swelling. With a special method, Tiemann (1941) was able to prepare smooth transverse surfaces of collapsed wood for microscopic observation using vertical illumination. Micrographs provided by Tiemann show the general outline of collapse in wood but lack detailed information at the cellular level. The present study was undertaken to elucidate the structural changes occurring in the different cell types in wood as a result of collapse and to determine if different species are similar in this respect.

Materials and Methods

Two softwoods and two hardwoods were selected for study. Boards exhibiting collapse were obtained for redwood (*Sequoia sempervirens* (D. Don) Endl.), white fir (*Abies concolor* (Gord. & Glend.) Lindl.), tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.), and chinkapin (*Castanopsis chrysophylla* (Dougl.) A. DC.). Only the white fir sample showed extensive honeycombing. Small sticks about 25 mm long and 9 mm square in cross section were first made from collapsed areas. The transverse surfaces of these small sticks were prepared by a procedure described by Exley *et al.* (1974) using a hand-held single edge razor blade. Cutting was performed under a light stereoscope so as to ease the cutting operation, and at the same time, to inspect the quality of surfaces. Small cubical specimens containing the razor blade-cut transverse surface were then carefully cut off from the sample sticks and mounted on stubs. These specimens were then coated with 60:40 gold-palladium and examined with a Coates & Welter scanning electron microscope.

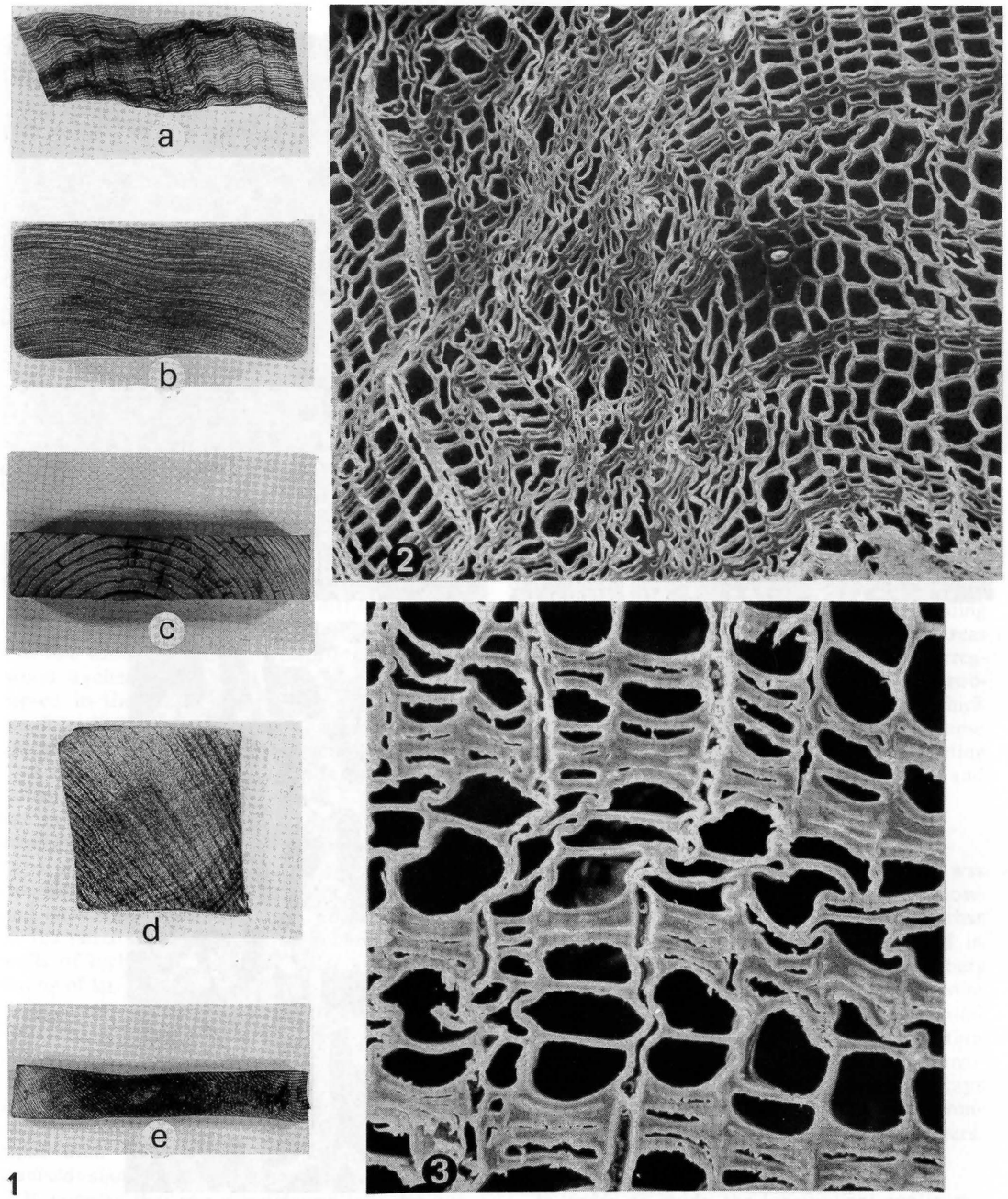
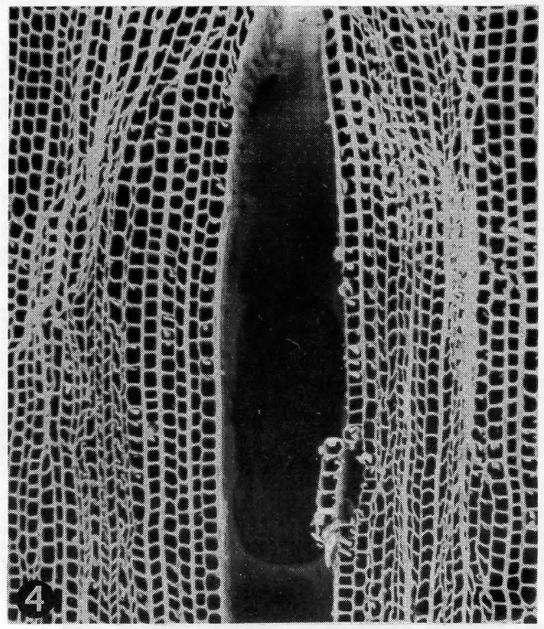
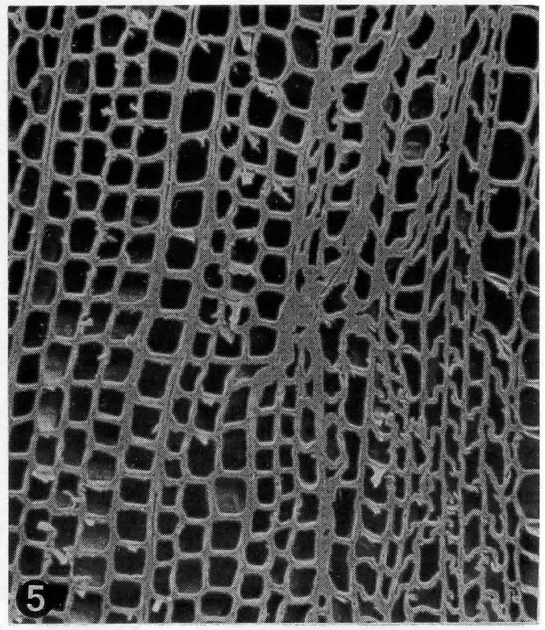


Fig. 1. Cross section views of the wood samples studied: a. **Redwood, collapsed heartwood sample.** Note the wavy distortion of the piece and wavy pattern of the growth rings. b. Redwood, heartwood sample with a mild collapse condition. Note the abnormal radial shrinkage. c. White fir, showing honeycombs initiated in the earlywood region. d. Tanoak sample showing collapse at the left side bottom corner. e. Chinkapin, collapsed wood. The sapwood portion at the left did not collapse. —— Fig. 2. SEM micrograph of collapsed area of the sample shown in Fig. 1a. Earlywood tracheids collapsed obliquely while the axial parenchyma cells did not collapse. x 66. —— Fig. 3. SEM micrograph of specimen taken from the mildly collapsed redwood sample (Fig. 1b). Both earlywood and latewood tracheids collapsed radially. x 170.





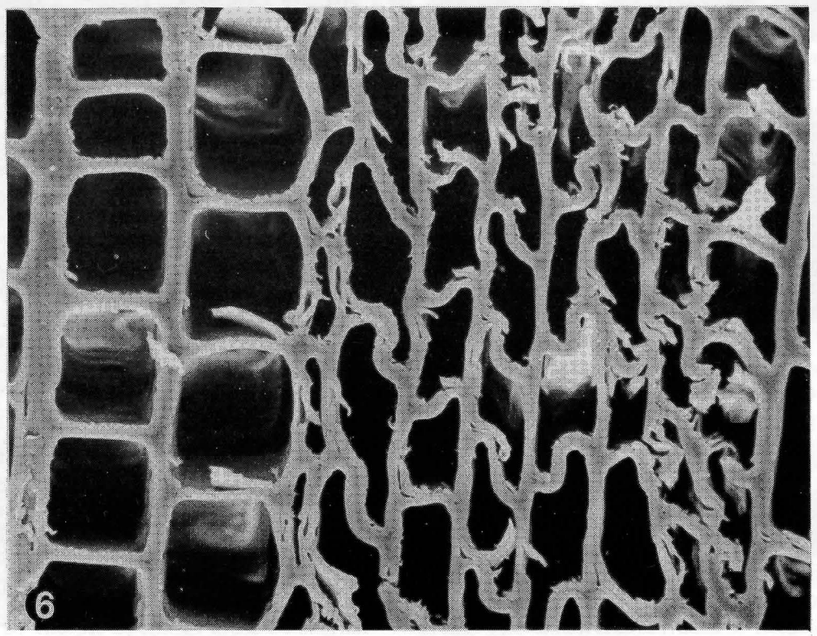


Fig. 4. SEM micrograph of a white fir honeycomb, showing collapse of earlywood tracheids on both sides of the honeycomb fissure. x 33. — Fig. 5. SEM micrograph of collapsed tracheids at the left side of the honeycomb fissure shown in Fig. 4. Earlywood tracheids collapsed tangentially. x 66. — Fig. 6. Similar to Fig. 5 at a higher magnification, showing buckling of tangential walls of earlywood tracheids as a result of tangential collapse. x 230.

Results and Discussion

Most of the samples used in this study were from moderately collapsed material. The razor blade cutting method was quite successful in preparing clean and smooth transverse surfaces from these samples for SEM observations. This method, however, could not obtain satisfactory specimens from severely collapsed wood samples.

Redwood

Two old-growth redwood heartwood samples showing different degrees of collapse were examined. A sample displaying severe collapse as indicated by a greater external cross sectional dimension distortion was examined first (Fig. 1a). It was noted that the distortion caused by collapse in this sample generally followed the wavy pattern of the growth rings. This wavy pattern in the growth rings in turn was apparently due to collapse of groups of tracheids (Fig. 2). The majority of earlywood tracheids collapsed at an angle between the radial and tangential planes resulting in excessive shrinkage in this direction and distortion of the normal growth ring pattern. Earlywood tracheids collapsed into different shapes but their lumina were rarely completely closed due to a strong resistance at the cell corners. Latewood tracheids, on the other hand, usually collapsed in the radial direction. Because of their small radial lumen diameters, many latewood tracheid cavities were completely closed.

A redwood heartwood sample showing mild collapse is illustrated in Fig. 1b. Abnormal shrinkage in the radial direction is clearly shown. SEM examination of this sample indicated that this type of abnormal shrinkage was caused by a reduction in the radial diameter of both earlywood and latewood tracheids (Fig. 3). Collapse of cells in the radial direction caused buckling of radial walls of earlywood tracheids and complete flattening of latewood tracheids.

Pit membranes of earlywood tracheids in the collapsed areas were encrusted with extractives indicating a highly impermeable condition, but latewood tracheid pit membranes were even more heavily encrusted (Kuo, 1977). This may explain why both earlywood and latewood tracheids collapse even though the thick-walled latewood tracheids should be more resistant to collapse.

It appears that ray parenchyma cells did not collapse by themselves but were buckled or compressed when the adjacent tracheids collapsed (Fig. 2). Axial parenchyma cells were also distorted into different shapes by the surrounding collapsed tracheids (Fig. 2).

White Fir

The white fir sample used showed extensive honeycombing (Fig. 1c). Macroscopically, these fissures initiated in the earlywood region, and except for a few cases the wood separation was usually confined to individual growth increments. SEM observation of many areas in this sample showed an absence of collapse of latewood tracheids. Earlywood tracheids collapsed mainly in the tangential direction (Fig. 4 and 5). As a result of this type of collapse, tangential walls of earlywood tracheids were severely buckled while radial walls were relatively unchanged (Fig. 6). Honeycomb fissures developed when the stresses caused by excessive tangential shrinkage exceeded the strength of wood, with separation of the wood occurring along the rays.

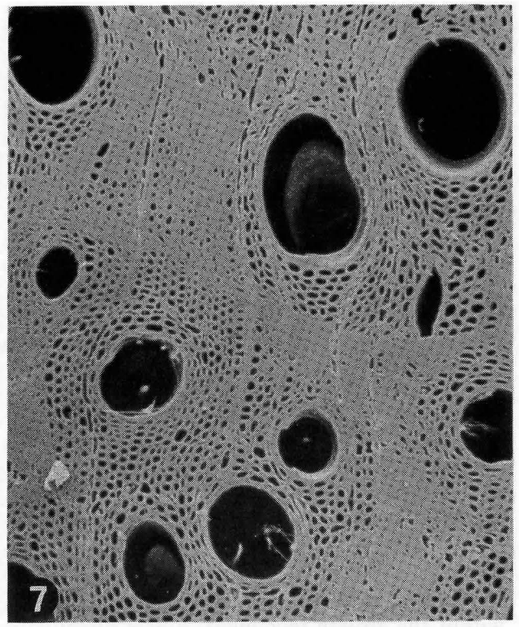
Tanoak

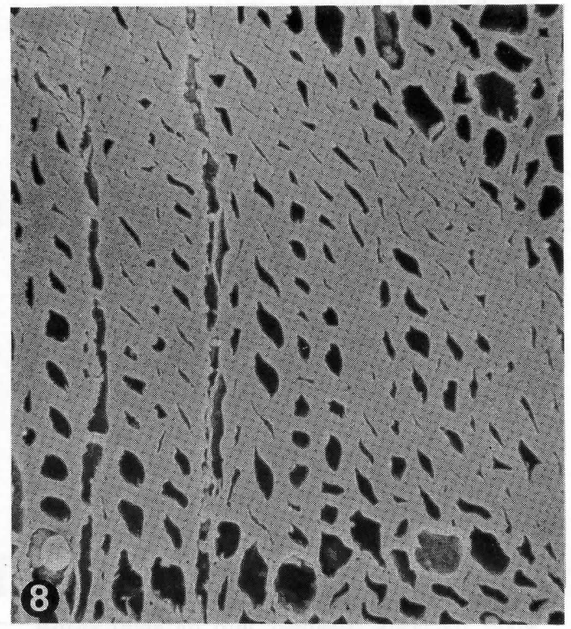
As shown in Fig. 1d, in addition to diamonding, a drying defect due to differences in the growth ring orientation in the piece, the tanoak sample also exhibited collapse. Normal growth ring patterns and regular filing of the fibers were somewhat distorted as a result of the collapse (Fig. 7). There was no preferential location of collapse within the growth increment. Fibers surrounding vessels tend to collapse obliquely (Fig. 8). In areas mainly composed of fibers, fibers collapsed irregularly. Vessels were not seriously distorted probably because of the mild collapse and their thick walls. Axial parenchyma cells did not collapse but were severely distorted by the surrounding collapsed fibers (Fig. 8). Some rays collapsed and especially the broad rays (Fig. 9).

Chinkapin

The sapwood portion of the sample used was not collapsed while the heartwood portion showed severe collapse (Fig. 1e). It was found that collapse in this sample frequently occurred in areas composed mainly of fibers (Fig. 10). Fibers among the flame shape distributed vessels were relatively free from collapse (Fig. 11). Latewood fibers collapsed mainly in the radial direction (Fig. 12) while fibers in the earlywood and transitional regions collapsed irregularly (Fig. 13). Rays did not collapse but they were frequently compressed and buckled by adjacent collapsed fibers.

In order to study the longitudinal configuration of collapse, radial and tangential surfaces were prepared using the same preparative methods and these were also examined by SEM. Micrographs obtained from longitudinal surfaces were very difficult to interpret. In addition, it was impossible to trace any single tracheid or fiber cavity over an appreciable distance since collapse severely distorted the normal alignment of cells in both the transverse and longitudinal planes.





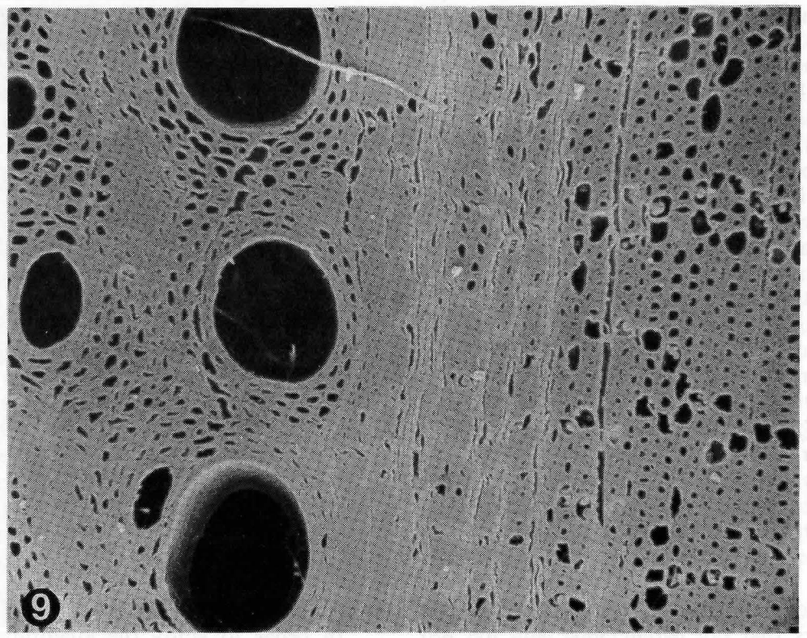
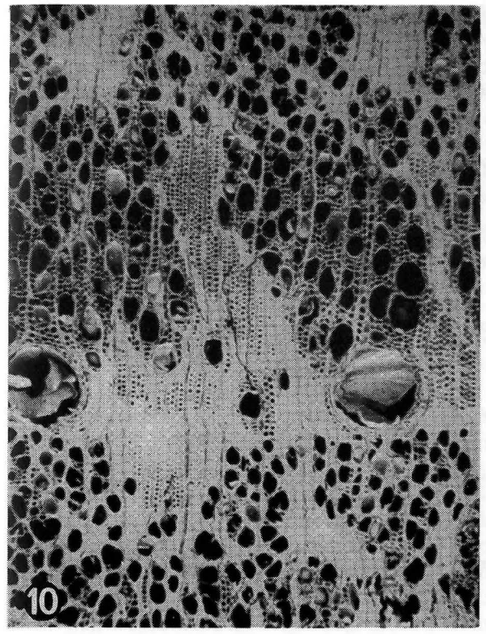
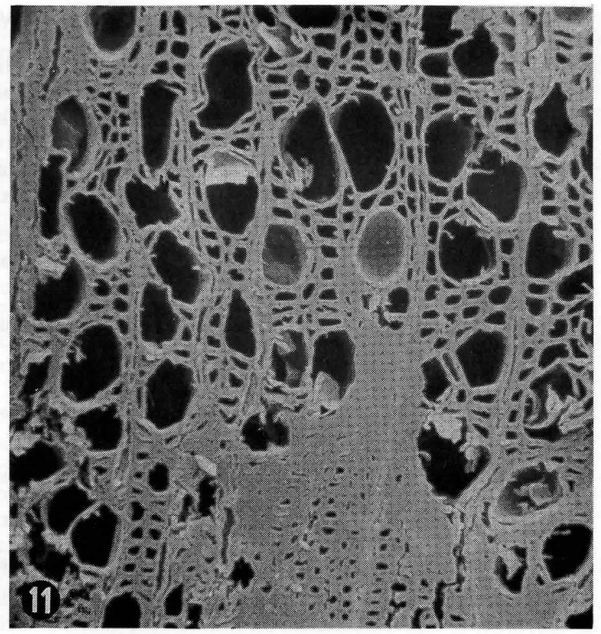
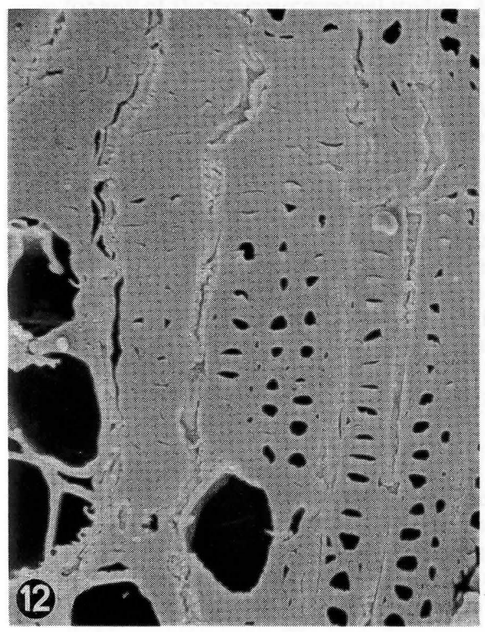


Fig. 7. SEM micrograph of collapsed tanoak wood. Collapse of fibers resulted in distortion of the growth ring and the radial filing of cells. x 33. — Fig. 8. SEM micrograph of collapsed tanoak fibers in the vicinity of vessels. Earlywood fibers collapsed obliquely while the ray and parenchyma cells did not collapse. x 230. — Fig. 9. SEM micrograph of tanoak wood, showing collapse of the broad rays. x 170.







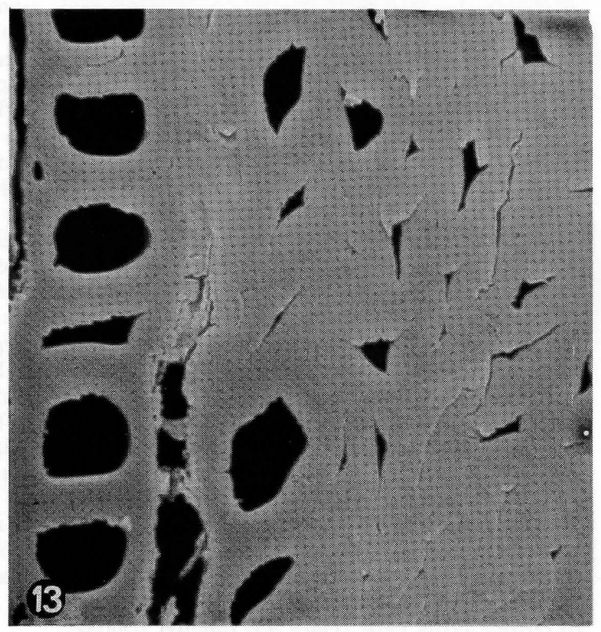


Fig. 10. SEM micrograph of collapsed chinkapin heartwood, showing collapse concentrated in the areas composed mainly of fibers. x 33. — Fig. 11. SEM micrograph of collapsed chinkapin with fibers between small vessels relatively free from collapse. x 100. — Fig. 12. SEM micrograph of chinkapin with fibers both in the earlywood and latewood zones severely collapsed. x 170. — Fig. 13. Similar to Fig. 12, showing irregularity of collapsed fibers in the earlywood zone. x 600.

Conclusions

Tracheids in softwoods and fibers in hardwoods were found to be the cell types most responsible for collapse of wood. Vessels and axial parenchyma cells were not prone to collapse. Ray cells, except for those in tanoak, were also free from collapse but their alignment was usually distorted by the collapse of adjacent cells.

Earlywood tracheids in redwood and fibers in tanoak and chinkapin usually collapsed at an angle between the radial and tangential planes of the stem resulting in excessive shrinkage in this direction and distortion of the normal growth ring pattern. Latewood tracheids and fibers in these three species collapsed mainly in the radial direction apparently because of their small radial diameters. In the white fir sample studied, no collapse of latewood tracheids was observed. White fir earlywood tracheids collapsed in the tangential direction causing excessive shrinkage in this direction. Honeycomb fissures develop when the stresses caused by excessive tangential shrinkage exceed the strength of wood.

Acknowledgement

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PROCEEDINGS OF THE JOINT MEETING OF THE STRUCTURAL SECTION OF THE BOTANICAL SOCIETY OF AMERICA AND THE PAN AMERICAN REGIONAL GROUP OF THE INTERNATIONAL ASSOCIATION OF WOOD ANATOMISTS

Virginia Polytechnic Institute & State University, Blacksburg, Virginia, U.S.A., June 26, 1978
Chairman Dr. W.A. Côté

RICHARD L. GRAY, ITT Rayonier Incorporated, Olympic Research Division, Shelton, Washington 98584 and CARL H. deZEEUW, Wood Products Engineering Department, S.U.N.Y. College of Environmental Science and Forestry, Syracuse, New York 13210. – **Anatomical studies in the genus Vitex.**

The secondary xylem anatomy of the genus *Vitex* has been studied comparatively to prepare a more precise definition of the structural variation within the genus, to find possible relationships of anatomical structure to geographical regions, and to determine the possible cause or causes of the reported slow air-drying of the wood of several species in this genus. The material examined was world-wide in origin and more extensive than for any of the previous regional studies. Anatomical evidence obtained from this investigation corroborates existing data that the wood structure of *Vitex* is essentially homogeneous. The only exception is a slight trend for segregating African species by the more common presence of multiperforate perforation plates as well as low density and generally pale colored wood. Multiperforate and scalariform perforation plates in vessel elements were observed in many species, in contrast to previous reports which indicated that these specialized perforations were very rare in *Vitex*. The presence of multiple calcium crystals per parenchyma cell in a majority of species studied is a possible diagnostic character for the genus, while the presence of silica sand and specialized cell wall sculpturing can be used for diagnostic features for certain species within the genus. Unusual amounts of starch deposits observed in the septate fibers of the heartwood in over half the species studied is suggested as a diagnostic character for the genus and as a possible cause for the reported slow drying characteristics for these species.

C.T. KEITH, S.E. GODKIN, G.A. GROZDITS, and G. CHAURET, Eastern Forest Products Laboratory, 800 Montreal Road, Ottawa, Ontario, Canada. K1G 3Z5. – **Further observations on the anatomy and fine structure of the trabeculae of Sanio.**

Descriptions are given of unusually – and normally – shaped trabeculae occurring singly, as single strands, or as multiple strands in the bark, cambium and wood of conifers. Evidence obtained by chemical extraction and histochemical staining procedures combined with light microscopy and transmission and scanning electron microscopy verifies the confluency of cell wall and trabecula. The core of the trabecula is structurally confluent with and histochemically indistinguishable from the compound middle lamella. The trabecula wall is confluent with the primary walls in cambial cells and with the secondary walls in mature tracheids and sieve cells. It has the same lamellar and histochemical characteristics as the contiguous cell walls. Microfibrillar orientation is usually nearly parallel to the long axis of the trabecula. Additional cell wall elaborations such as warts or helical thickenings are also present in trabeculae.

J.G. ISEBRANDS, Institute of Forest Genetics, USFS, P.O. Box 898, Rhinelander, WI 54501 and R.A. PARHAM, Institute of Paper Chemistry, Appleton, WI 54911. – **On the nature of surface dislocations on Populus tension wood fibers.**

Historically, tension wood (TW) fibers have been shown to exhibit numerous cell wall deformations (CWD) known as 'slip planes and minute compression failures' (SP and MCF). These deformations are characterized under polarized light as single and double folds in the cell wall, respectively. *Populus* TW fibers also exhibit a third type of CWD when viewed under polarized light that allows them to be distinguished from normal wood fibers. An investigation of glutaraldehyde fixed, kraft-pulped, and acid-treated TW fibers with polarized light microscopy, and transmission and scanning electron microscopy revealed that the CWD were not true SP and MCF as previously suggested. Thus, terminology used in the literature for describing the CWD we have observed in *Populus* TW is confusing and possibly even inaccurate. Deformations on both fixed and kraft-pulped *Populus* TW fibers were characterized by regularly spaced 'surface dislocations' on the exterior of S_1 and S_2 layers of the cell wall. In no case did they extend across the middle lamella and primary wall of adjacent fibers, or give the characteristic birefringence of SP and MCF. Moreover, after acid treatment, the TW fibers did not break up as fibers normally do when true SP and MCF are present. These observations all suggest that the wall deformations in *Populus* TW were truly only surface dislocations and not SP and MCF.

J. THOMAS QUIRK, Center for Wood Anatomy Research, U.S. Forest Products Laboratory, Madison, WI 53705. – **Shrinkage and related properties of cell walls of Douglas-fir.**

The differences in shrinkage between earlywood and latewood is of more than academic interest, since it causes checking, the shelling failures in flat sawn boards and also, the buckling of veneers can frequently be traced to the presence of earlywood on one face and latewood on the other. Two optometric measuring techniques were utilized for anatomical measurements of intact-extractive-free-wood of isolated earlywood and latewood from the same annual ring. Measurements were made in both the green and ovendry conditions on all specimens and shrinkages computed. The percent shrinkage expressed as a percent of cell area was 26.5% for latewood and 7.1% for earlywood. By either measuring technique it was found that the lumen of the earlywood tracheids expanded with drying whereas the lumen of latewood cells shrank, indicating a greater influence of the secondary wall over the restraining lignified middle lamella in latewood. The ratio of tangential to radial cell diameters (T/R) was 1.315 for green latewood and 1.312 for ovendry latewood indicating cellular integrity upon drying. Latewood shrank 14.4% tangentially and 14.2% radially. In earlywood the T/R green was 0.725 but only 0.681 upon drying. The shrinkage mechanism in earlywood is unequal and different from that of latewood. The tangential and radial shrinkage of whole wood lies between the extremes of shrinkage found in earlywood or latewood.

N. D. NELSON, J. G. ISEBRANDS, Institute of Forest Genetics, USFS, Box 898, Rhinelander, WI 54501 and W. E. HILLIS, CSIRO Division of Building Research, Graham Road, Highett, Victoria, 3190 Australia. – **Some effects of ethylene on the morphology and anatomy of Eucalyptus and Populus seedlings.**

Eucalyptus gomphocephala A. DC. seedlings grown horizontally for 103 days in a greenhouse had higher internal and emanated ethylene levels in the basal portion of the stem than seedlings grown vertically under otherwise identical conditions. Upper halves of the basal portion of the stem of horizontal seedlings had greater amounts of internal and emanated ethylene than lower halves. Upper halves of horizontal seedlings contained 60–80% tension wood by volume, lower halves 0–10%. Vertical seedlings contained negligible tension wood. The data suggest an association between increased ethylene levels and tension wood formation. This association was further supported by an experiment in which leaves from 16-leaf growth room-grown *Populus deltoides* Bartr. seedlings were treated with an ethylene releasing compound. Groups of leaves were sprayed to saturation with a 10^{-2}M solution of 2-chloroethylphosphonic acid (CEPA), and the seedlings were returned to the growth room for 35 days. Specific effects of CEPA varied with developmental stage of leaves treated. All CEPA treatments resulted in abnormal leaf shape, and reduced radial increment and shoot elongation. A common treatment effect at the LPI 4 internode was a gradient of cell types from the pith to the cambium. The first xylem produced had thinner secondary walls (low birefringence) and fewer and smaller diameter vessels than normal wood; next was a zone of gelatinous fibers, followed by normal wood.

JOHN PHELPS, E.A. McGINNES, Jr., School of F.F.W., University of MO, Columbia, 65201, M. SANIEWSKI, J. PIENIAZEK, Inst. of Pomology, Skierniewice, Poland and M. SMOLINSKI, Inst. of Physiology and Cytology, University of Lódź, Poland. – **Some anatomical observations on the effect of morphactin IT 3456 and ethrel on wood formation in Salix fragilis L.**

Two-year old shoots of *Salix fragilis* L. were treated with morphactin and ethrel to observe the influence of these compounds on xylem differentiation. Three treatments were used, two shoots per treatment: (1) morphactin IT 3456 was applied on 23 May 1976; (2) ethrel on 23 May 1976; and (3) ethrel on 20 June 1976. Each compound was applied in a lanolin paste as a ring around the shoot. The samples were collected at the end of the growing season. Each treatment caused a pronounced swelling around the place of treatment. Both xylem and phloem were markedly influenced by the treatments. Anatomical analyses of xylem revealed: a disorientation of cell types in all samples, the formation of tyloses in all samples (with unusual nucleated bud-type in treatment 3), a general lack of vessels in treatment 1, the occurrence of crystals in longitudinal members and highly lignified fibers immediately following treatment in treatments 2 and 3, and the occurrence of areas of low birefringence immediately following treatment in treatment 3. These observations indicate the influence that the treatments have on xylem differentiation, primarily through an interference with endogenous hormones.

JOAO P. CHIMELO, Instituto de Pesquisas Tecnologicas, Sao Paulo, S.P., Brasil and GEZA IFJU, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061. – **A quantitative approach to wood anatomy.**

The techniques of stereology were applied to the transverse and tangential sections of 22 diffuse porous tropical deciduous woods. Simple point fractions, feature counts and intersection counts were converted to cell distribution parameters such as mean tangential and radial cell diameter, mean cord intercept and mean free distance values. In addition, area percentages, number of anatomical elements per unit area and two moments of cell diameter distribution were calculated. Ray size and shape parameters were obtained from simple counts done on tangential sections. The results indicated large differences among the species studied in practically all quantitative parameters calculated. Some of the differences appeared to be large enough to suggest strong species specificity. No strong similarity occurred among species of the same family. It was suggested that a stereological data bank of many species be established, against which unknown woods may be tested for purposes of identification and characterization.

BARRETT N. ROCK, Division of Biological Sciences, Alfred University, Alfred, New York 14802. – **Wood anatomy of members of the subtribe Espeletiinae (Compositae).**

The wood anatomy of the seven genera comprising the Espeletiinae of the tribe Heliantheae is described. Members of the subtribe are endemic to the paramos of the Andes of Colombia, Venezuela, and a portion of northern Ecuador. They occupy a variety of altitudinal niches and range in habit from true arborescent to caulirosulan (megaphytic) to rosulan. This investigation indicates that the members of the subtribe are anatomically homogeneous with regard to their wood. Xylem features of both arborescent and caulirosulan species are very similar, while the xylem features characteristic of the rosulan species are essentially features of juvenile wood. Woods of the Espeletiinae possess relatively unspecialized features for Compositae; the woods of the arborescent members exhibit the least specialized features. The anatomy of a number of other woody Compositae considered to be closely related to the subtribe were studied, and of these, the wood anatomy of the Espeletiinae most closely resembles that of *Polymnia pyramidalis*.

BILLY G. CUMBIE, Division of Biological Sciences, University of Missouri, Columbia, MO 65201. –– **Developmental changes in the xylem of Bocconia vulcanica (Papaveraceae).**

Developmental changes in the xylem were studied in a stem of *Bocconia vulcanica* Donn. Smith with a xylem radius of 30–50 mm. Growth rings are absent. The vascular cambium is non-storied. There is a marked decrease in length of vessel elements and fibres at the beginning of secondary growth. Subsequently, vessel element length remains constant at about 300 μm and fibre length remains fairly constant at about 600 μm. The vessel elements are specialized with oblique end walls, simple perforations, and alternate intervascular pitting. Vessels are relatively uniform in diameter (125 μm) and distribution (mainly clusters and solitary) throughout secondary growth. Axial parenchyma is similar in distribution (paratracheal-scanty to vasicentric) and cells (fusiform, few strands of 2 cells) throughout xylem production. At the beginning of cambial activity, the rays are 2–3 cells wide and nearly all extend the entire height of the sections of about 10 mm. They consist of erect cells. During the production of approximately 5 mm of xylem, the rays are broken up into shorter rays (average height 1300 μm) and increase in average width to 4.5 cells. Subsequently, ray height remains the same while ray width increases to an average of 12 cells in the outermost secondary xylem. New multiseriate rays originate during secondary growth and reach average size during the production of a few mm of xylem. The rays are heterocellular throughout secondary growth. In most respects, the developmental changes in the xylem of *Bocconia vulcanica* appear to be more similar to those which characterize herbaceous dicotyledons than to those commonly occurring in woody dicotyledons.

ROBERT C. KOEPPEN, Center for Wood Anatomy Research, U.S. Forest Products Laboratory, Madison, Wisconsin 53705. – **Similarities of Apuleia and Distemonanthus.**

Taxonomic studies almost traditionally ignore wood structure. Yet, the wood anatomy may contain features having significant taxonomic implications. The South American genus *Apuleia* and the West African genus *Distemonanthus* are a good example since they display striking anatomical similarities. During an investigation of the woods of the Leguminosae, the presence of silica in both these genera was noted. While the presence of silica bodies in the wood structure of this large family is comparatively rare, it is a constant feature of both *Apuleia* and *Distemonanthus*. The armorphous silica bodies can be readily detected under a light microscope. They are deposited in the same basic pattern in both genera, being located in the axial parenchyma cells and upright marginal ray cells, but not in the procumbent ray cells. This anatomical distribution also indicates a similar system of physiology. Other structural similarities are: the irregular (clinkerlike) shape of the silica bodies, the presence of rhombic crystals in the axial parenchyma, rays being both heterocellular and storied, parenchyma patterns aliform to confluent, and the heartwood having a yellowish hue. Morphological similarities are also found in the leaves, type of inflorescence, flowers and fruits. In view of the many anatomical and morphological similarities, a close natural relationship is clearly indicated for these two genera.

REGIS B. MILLER, Center for Wood Anatomy Research, U.S. Forest Products Laboratory, Madison, WI 53705. – **Potassium calcium sulfate crystals in the secondary xylem of Capparis.**

Crystals in procumbent ray cells of secondary xylem of *Capparis* were identified under a polarized light microscope as being different from typical calcium oxalate crystals. Thirty-one of the forty-three species examined contained crystals. Often these crystals occurred abundantly; often there was more than one crystal per cell. Viewed with a light microscope without polarized light, the shape and the general appearance are similar to typical crystals. With polarized light, each calcium oxalate crystal shows hues of reds, blues, yellows, and greens; the crystals of *Capparis*, however, are whitish and no color is evident. Further investigation revealed the crystals in *Capparis* were soluble in water. Radial sections containing crystals were mounted for SEM examination and for electron microprobe analysis of the crystals *in situ*. The peaks on a microprobe spectrum were clearly potassium, calcium, and sulfur. A fine white precipitate formed by uniting one drop of water containing a few dissolved crystals of *Capparis* and a drop of $BaCl_2$ confirmed the presence of the sulfate ion. Five crystals were handpicked from sections of *Capparis pringlei* (SJRw 47204) and analyzed with the electron microprobe. All five of the crystals and the crystals *in situ* had identical EDXRA spectra. The estimated elemental composition was calcium 20–25%, potassium 10–15%, and sulfur 15–20%. The same five crystals produced an x-ray diffraction pattern that could not be matched with any from standard sources. Thus, the potassium calcium sulfate crystals in the wood of *Capparis* are not only a new kind of crystal in wood, but also a crystalline compound that has not been described.

JOSEPH ARMSTRONG, School of Forestry, Fisheries, and Wildlife, University of Missouri, Columbia, MO 65201. – **Genotypic variation of the wood anatomy of Fraxinus americana L.**

The wood of two-year-old, nursery-grown, white ash seedlings was anatomically examined to determine the amount of genotypic variation between seven populations collected in New Brunswick, Vermont, New York, Ohio, Indiana, Illinois, and Arkansas. Going from north to south the expected clinal increase in cambial initial lengths, as expressed by the lengths of vessel elements, was not found. The vessel element lengths of the four northern-most populations were short and very uniform. The three southern-most populations had longer vessel elements, although some seedlings had vessel elements similar in length to those of northern populations. This variation of vessel element lengths seems to correlate with the ploidy levels of the populations; diploid in the four northern-most populations and, mixed hexaploid-diploid in the three southern-most populations. Generally the fiber-tracheids varied similarly in length to the vessel elements. Vessel element diameters were somewhat larger in the three southern-most populations but, greater diameters did not statistically correlate with greater vessel element lengths. Ring-porous vessel organization was most common in the northern populations; all but one seedling from the four southern-most populations were diffuse-porous. The amount of secondary xylem produced varied widely and did not correlate with the other anatomical features examined.

GER J.C.M. VAN VLIET, Rijksherbarium, Leiden, The Netherlands. – **Wood anatomy of Combretaceae and related families with special reference to the structure of vestured pits.**

In Combretaceae two major types of vesturing are recognized: type A, in which vestures are attached to all parts of the roof of the pit chamber and branch into a mass of vestures of equal thickness; and type B, in which trunk-like vestures are attached to the roof of the pit chamber nearby the pit canal and branch to various extents into gradually thinner vestures. Based on the degree of branching three forms can be recognized within type B. The systematic and diagnostic value of these three forms is limited within Combretaceae because of the occurrence of intermediate types and the fact that within the single genus *Terminalia* two forms and their intermediates occur. The distribution of the major types A and B coincides with a subdivision of the Combretaceae into two subfamilies. The occurrence of structures intermediate in form and distribution between warts and vestures has been noted and is interpreted in support of a homology of these two (a comprehensive account will be published in Acta Botanica Neerlandica 27, issue 5/6).

Wood Science and Technology
Journal of the International Academy of Wood Science

(Note from the Editors of Wood Science and Technology, who have agreed to publish a similar note on the IAWA Bulletin in their Journal)

The constitution of the International Academy of Wood Science, which was founded in 1966, states that the Academy shall:

1. Promote the highest standard of research in the science and technology of wood.
2. Call attention at all appropriate levels not only to research and development accomplishments, but to research needs which must be met, if wood is to achieve its full potential in human life and world economy.
3. Recognize outstanding work and accomplishments of wood scientists throughout the world.

To realize these objectives, F.F.P. Kollmann in 1967 founded the journal Wood Science and Technology in cooperation with Springer-Verlag, a publisher of scientific books and journals with offices in New York, Heidelberg, and Berlin. The journal covers the entire field of the science and technology of wood, such as tree physiology, the formation and structure of xylem and phloem, the microbiological degradation of wood, the chemistry of all wood and bark constituents, and the physical properties of wood. Problems related to wood technology include combustion, drying, and impregnation of wood, its machining, gluing, and finishing, timber mechanics and rheology, and the conversion of wood into pulp.

Since 1977, Wood Science and Technology is edited by W. Liese (Hamburg), H. Schulz (München), and T.E. Timell (Syracuse, N.Y.). K.A. Sorg is in charge of the editorial office in München. The editors are assisted by an Editorial Board, at present consisting of F.E. Dickinson (Richmond, Cal.), W.E. Hillis (Melbourne), R. Kennedy (Vancouver, B.C.), K. Kratzl (Wien), J.F. Levy (London), and D. Noack (Hamburg). The journal appears in March, June, September, and December of each year, with about 80 pages constituting one issue. A total of 293 scientific papers have been published in the twelve volumes that have appeared so far. In addition to articles, the journal also contains book reviews, reports of scientific meetings, and news about the Academy.

The IAWA Bulletin and Wood Science and Technology both publish papers dealing with wood anatomy and ultrastructure. Approximately one quarter of the publications in the latter journal are concerned with biological topics. The content of Volume 12 (1978) of Wood Science and Technology is listed below in chronological order.

No. 1/1978
Timell, T.E. – Helical thickening and helical cavities in normal and compression woods of Taxus baccata
Seth, M.K. & K.K. Jain – Percentage of compression wood and specific gravity in blue pine (Pinus wallichiana A.B. Jackson)
Boyd, J.D. – Significance of laricinan in compression wood tracheids
Bolton, A.J. & J.A. Petty – A model describing axial flow of liquids through conifer wood
Dunlop, J.I. - Damping loss in wood at mid kilohertz frequencies
Nyguen, T. & E. Johns – Polar and dispersion force contributions to the total surface free energy of wood
Cave, I.D. – Modelling moisture-related mechanical properties of wood – Part I: Properties of the wood constituents
Book reviews

No. 2/1978
Bolton, A.J. & J.A. Petty – The relationship between the axial permeability of wood to dry air and to a non-polar solvent
Cave, I.D. – Modelling moisture-related mechanical properties of wood – Part II: Computation of properties of a model of wood and comparison with experimental data
Fengel, D., M. Stoll & G. Wegener – Studies on milled wood lignin from spruce – Part 2: Electron microscope observations on the milled wood
Polcin, J. & B. Bezuch – Enzymic isolation of lignin from wood and pulps
Timell, T.E. – Ultrastructure of compression wood in Ginkgo biloba
Zainal, A.S. – A new explanation for soft rot cavity formation in the S_2 layer of wood cell walls

No. 3/1978
Cousins, W.J. – Young's modulus of hemicelluloses as related to moisture content
Fairbridge, C. & R.A. Ross – The thermal reactivity of wood waste systems
Polge, H. – Fifteen years of wood radiation densitometry
Stamm, A.J. – Cross sectional dimensions of wood pulp fibers from softwood fiber counts
Chafe, S.C. – On the mechanisms of cell wall microfibrillar orientation
Meylan, B.A. & B.G. Butterfield – Helical orientation of the microfibrils in tracheids, fibers and vessels
Goto, T., H. Harada & H. Saiki – Fine structure of cellulose microfibrils in poplar gelatinous layer and Valonia
Letters to the Editor: IAWA-Bulletin

No. 4/1978
van Zyl, J.D. – Notes on the spectrophotometric determination of lignin in wood samples
Kutscha, N.P., J.T. Lomerson & M. Viik Dyer – Separation of eastern spruce and balsam fir by chemical methods

Arganbright, D.G., H. Resch & J.R. Olson – Heat transfer from impinging slot jets of air – Part 1: Aerodynamic characteristics of free jets

Dinwoodie, J.M. – Failure in timber – Part III: The effect of longitudinal compression on some mechanical properties

Fengel, D. & M. Stoll – Studies on holocellulose and alpha-cellulose from spruce wood using cryo-ultramicrotomy – Part 2: The influence of heavy metal salt impregnation and the dimensions of delignified cell wall layers

Nelson, N.D. & W.E. Hillis – Ethylene and tension wood formation in Eucalyptus gomphocephala

Ruel, K., F. Barnoud & D.A.I. Goring – Lamellation in the S_2 layer of softwood tracheids as demonstrated by scanning electron microscopy

Requests for wood samples for sectioning

In order to complement the collection of microscope slides, authenticated wood samples of the following woody species growing in South Europe and the Middle East are requested by Dr. Dietger Grosser, Institut für Holzforschung, Universität München, Winzerestrasse 45, D-8000 München 40, West Germany. Duplicate slides will be sent to all institutes or persons giving their assistance.

In addition to the woods listed, Dr. Grosser also requests authentic wood specimens of Caprifoliaceae from all over the world for a comparative study and sectioning blocks of *Ficus sycomorus* L. (Moraceae) in order to determine the range of structural variation within this species. The latter is essential for the identification of woods used for Egyptian antiquities, especially coffins. The results of these studies will be published in a future issue of the IAWA Bulletin.

Acacia cyanophylla Lindl.; A. dealbata Link; A. farnesiana Willd.; A. tortilis (Forsk.) Hayne ssp. raddiana (Savi) Brenan (A. raddiana Savi); A. tortilis (Forsk.) Hayne ssp. spirocarpa (Hochst. ex A. Rich.) Brenan (A. spirocarpa Hochst. ex A. Rich.; A. tortilis (Forsk.) Hayne) – Acer heldreichii Orph.; A. lobelii Ten.; A. monspessulanum L.; A. opalus Mill. (A. italum Lauth); A. opalus var. obtusatum (Willd.) Henry (A. obtusatum) – Adenocarpus decorticans Boiss. – Albizzia julibrissin Durazz.; A. lebbeck (L.) Benth. – Alnus cordata (Loisel.) Desf. (A. cordifolia Ten.); A. orientalis Dcne. – Amelanchier ovalis Med. (A. vulgaris Moench) – Anagyris foetida L. – Anthyllis barba-jovis L. – Arbutus unedo L. – Atriplex halimus L.

Berberis nummularia Bge. – Broussonetia papyrifera (L.) L'Hér. – Bupleurum fruticosum L. – Buxus balearica Lam.; B. longifolia.

Calicotome spinosa (L.) Link; C. villosa (Poir.) Link – Carpinus orientalis Mill. – Castanea sativa Mill. – Celtis australis L.; C. tournefortii Lam. – Chamaerops humilis L. – Cistus ladanifer L. – Citrus limon (L.) Burm.; C. medica L.; C. sinensis (L.) Pers. – Clematis flammula L.; C. viticella L. – Colutea arborescens L. – Cordyline australis Hook. – Coriaria myrtifolia L. – Corylus colurna L.; C. maxima Mill. – Cotinus coggygria Scop. (Rhus cotinus L.) – Cotoneaster insignis Pojark; C. nebrodensis (Guss.) K. Koch (C. tomentosus (Ait.) Lindl.) – Crataegus orientalis Pall. (C. laciniata Urcia) – Cydonia oblonga Mill. – Cytisus monspessulanus L. (Genista candicans L.; Teline monspessulanus); C. multiflorus (Ait.) Sweet.

Diospyros kaki L.; D. lotus L. – Dracaena draco L.

Erica lusitanica Rud.; E. multiflora L.; E. scoparia L. – Eucalyptus globulus Labill.; E. gomphocephala DC. – Euphorbia dendroides L. – Evonymus latifolius (L.) Mill.

Ficus sycomorus L. – Fraxinus angustifolia Vahl (F. oxyphylla Bieb.: F. oxycarpa Willd.); F. ornus L.

Genista cinera (Vill.) DC.; G. sphaerocarpa (L.) Lam. (Retama sphaerocarpa (L.) Boiss.; Lygos sphaerocarpa).

Haloxylon persicum Bge. – Hedera colchica K. Koch – Hibiscus syriacus L.

Jacaranda mimosifolia D. Don

Laburnum alpinum (Mill.) Bercht. & Presl (Cytisus alpinus Mill.) – Lagerstroemia indica L. – Ligustrum japonicum Thunb.; L. lucidum Ait. f. – Lonicera arborea Boiss.; L. etrusca Santi; L. implexa Sol. – Lycium europaeum L. (L. mediterraneum Dun.).

Magnolia grandiflora L. – Malus trilobata (Labill.) Schneid. (Eriolobus trilobata Roem.) – Medicago arborea L. – Moringa peregrina (M. arabica) – Morus nigra L. – Myrtus communis L.

Nerium odorum Soland. – Nicotiana glauca Graham.

Opuntia ficus-indica (L.) Mill. – Ostrya carpinifolia Scop. (O. vulgaris Willd.).

Paliurus spina-christi Mill. – Periploca graeca L. – Philadelphus coronarius L. (P. pallidus Hayek) – Phillyrea angustifolia L.; P. latifolia L. – Phoenix canariensis Chabaud.; P. dactylifera L. – Pistacia atlantica; P. lentiscus L.; P. terebinthus L.; P. vera L. – Pittosporum tobira Ait. – Populus caspica; P. euphratica Oliv.; P. nigra L.; P. nigra L. 'Italica' – Prunus persica (L.) Batsch (Amygdalus persica); P. tenella (P. nana) – Pterocarya fraxinifolia (Lam.) Spach – Punica granatum L. – Pyracantha coccinea M.J. Roem. (Cotoneaster pyracantha) – Pyrus amygdaliformis Vill.

Quercus coccifera L.; Q. frainetto Ten. (Q. conferta Kit.); Q. pubescens Willd.; Q. pyrenaica Willd. (Q. toza Bosc.); Q. suber L.

Rhamnus alaternus L.; R. alpinus L. – Rhododendron luteum Sweet; R. ponticum L. – Rhus coriaria L. – Ricinus communis L. – Rosmarinus officinalis L.

Salix subserrata Willd. (S. safsaf) – Schinus molle – Smilax aspera L. – Solanum sodomeum L. – Sorbus umbellata (Desf.) Fritsch; S. umbellata var. cretica (Lindl.) Schneid. (S. graeca (Spach) Hedl.) – Styrax officinalis L. – Suaeda monoica Forsk.

Tamarix africana Por.; T. gallica L.; T. nilotica Ehrbg.; T. palaestina; T. stricta Bge – Teucrium fruticans L. – Tilia petiolaris DC.

Viburnum orientale Pall.; V. tinus L.

Zelkova abelicea (Lam.) Boiss. (Z. cretica (Sm.) Spach); Z. carpinifolia (Pall.) K. Koch (Z. crenata Spach) – Zizyphus jujuba Mill. (Z. vulgaris Lam.; Z. sativa); Z. lotus (L.) Lam.; Z. spina-christi (L.) Willd.

Exchange of wood samples requested

The wood anatomy section of the Forest Products Research Institute of Ghana has established a collection of authenticated wood samples from all over the world. Mr. Oteng-Amoaka, Head of the Anatomy section, has written to us to solicit the cooperation from curators of wood collections to enlarge this new collection. Samples of indigenous Ghanaian woods can be offered in exchange. All parties interested should write directly to Mr. A. Oteng-Amoaka, Forest Products Research Institute (CSIR), University, P.O. Box 63, Kumasi, Ghana.

Structure and function of root wood

Wood anatomists are well aware of the fact that the structure of the wood of roots may be very different from that of the stem and branches of a tree. For example, deciduous oaks are known for their wide rays in the stem wood. Certain roots of oak, however, have aggregate rays and others have no wide rays at all. There is very little literature available on this topic, one of the few publications is a paper by Helmut Riedl, entitled 'Bau und Leistungen des Wurzelholzes' in Jahrb. wiss. Bot. 85: 1–75. 1937. It is a Ph.D. thesis made under the direction of the late Bruno Huber, then in Tharandt, Germany. The paper discusses root structure in detail, gives a key to the anatomy of root wood of major European forest tree species, and reports on experiments on storage in, water conduction through, and mechanical properties of roots. In order to have this paper accessible to students, I translated it into English. A copy of the translation has been deposited in the National Translation Center, 35 West 33rd Street, Chicago, Illinois 60616, U.S.A. Xerox copies are available from them.

Martin H. Zimmermann
Harvard University
Harvard Forest

Successful Conference on Utilization of Tropical Forests

A 5-day International Conference on Improved Utilization of Tropical Forests was held at the U.S. Forest Products Laboratory, Madison, Wisconsin in May 1978. Several papers were devoted to the problems ensuing from mismanagement and the vital necessity to preserve the tropical forest environment. Possibilities were indicated for a more efficient use of the diverse rain forest species and at the same time to protect the tropical environment through plantation and better land management.

ASSOCIATION AFFAIRS

Report from the Blacksburg meeting

The joint session of the Structural Section of the Botanical Society of America (BSA) and the Pan-American Regional Group of IAWA on Monday, June 26, in Blacksburg, forming part of the program of the annual meetings of the BSA and certain affiliated groups has been very successful. Numerous IAWA members and others interested enjoyed the many papers covering a wide diversity of subjects and specializations.

In his introduction Chairman Dr. W.A. Côté commented on the historical significance of this first regional group meeting of IAWA and on the successful course Association affairs had taken over the passed decade.

It was a great pleasure and privilege for me to chair the IAWA business meeting following the stimulating scientific program. Motions were passed to thank Dr. Côté for his work for IAWA in the past and on this occasion, and to express the appreciation to the Regional Committee members and organizers of this meeting, Dr. Judson G. Isebrands and Dr. William C. Dickison, and to the officers of the BSA especially of the Structural Section for their active help in enabling this meeting to be organized. A motion was also passed to thank Dr. William Louis Stern (present at the meeting) for his significant contribution to wood anatomical research by compiling a second, revised and much enlarged version of the *Index Xylariorum*.

Regional Group affairs were discussed at some length. It was unanimously agreed that Drs Dickison and Isebrands should continue their Regional Committee work and explore further possibilities of joint meetings of the Pan-American Regional Group with BSA and other organizations. American members from outside the USA present at the meeting, Mr. J.P. Chimelo from Brasil and Dr. C.T. Keith from Canada, were appointed as correspondents to the Regional Committee.

General IAWA topics discussed during the business meeting concerned the IAWA Bulletin, financial affairs and future meetings in Amsterdam (1979) and Sydney (1981). It was agreed that, although some members might prefer the informal news letter character to the present format of the IAWA Bulletin, it remains essential to aim at a sufficient numbers of high quality scientific pa-

pers in order to ensure that the Association remains attractive for its numerous new members. The necessity to increase the number of library subscriptions of the IAWA Bulletin was also felt generally.

The possible role of IAWA in stimulating certain fields of research and to improve or expand wood anatomical terminology was briefly discussed. Ideas on this theme still have to be worked out, and the IAWA Bulletin will hopefully contain suggestions from members in the near future. One suggestion to start a column in the Bulletin with formal proposals to give new or amended definitions for wood anatomical terms was unanimously accepted. This procedure was much preferred to the alternative of revising the Multilingual Glossary of Terms in the near future.

The business meeting was followed by a social hour and an informal banquet organized by Dr. Geza Ifju who acted as local host. The attending members are much indebted to Dr. Ifju for providing this means of contact and they will long remember the splendid atmosphere of this long evening in Blacksburg, Virginia.

Pieter Baas

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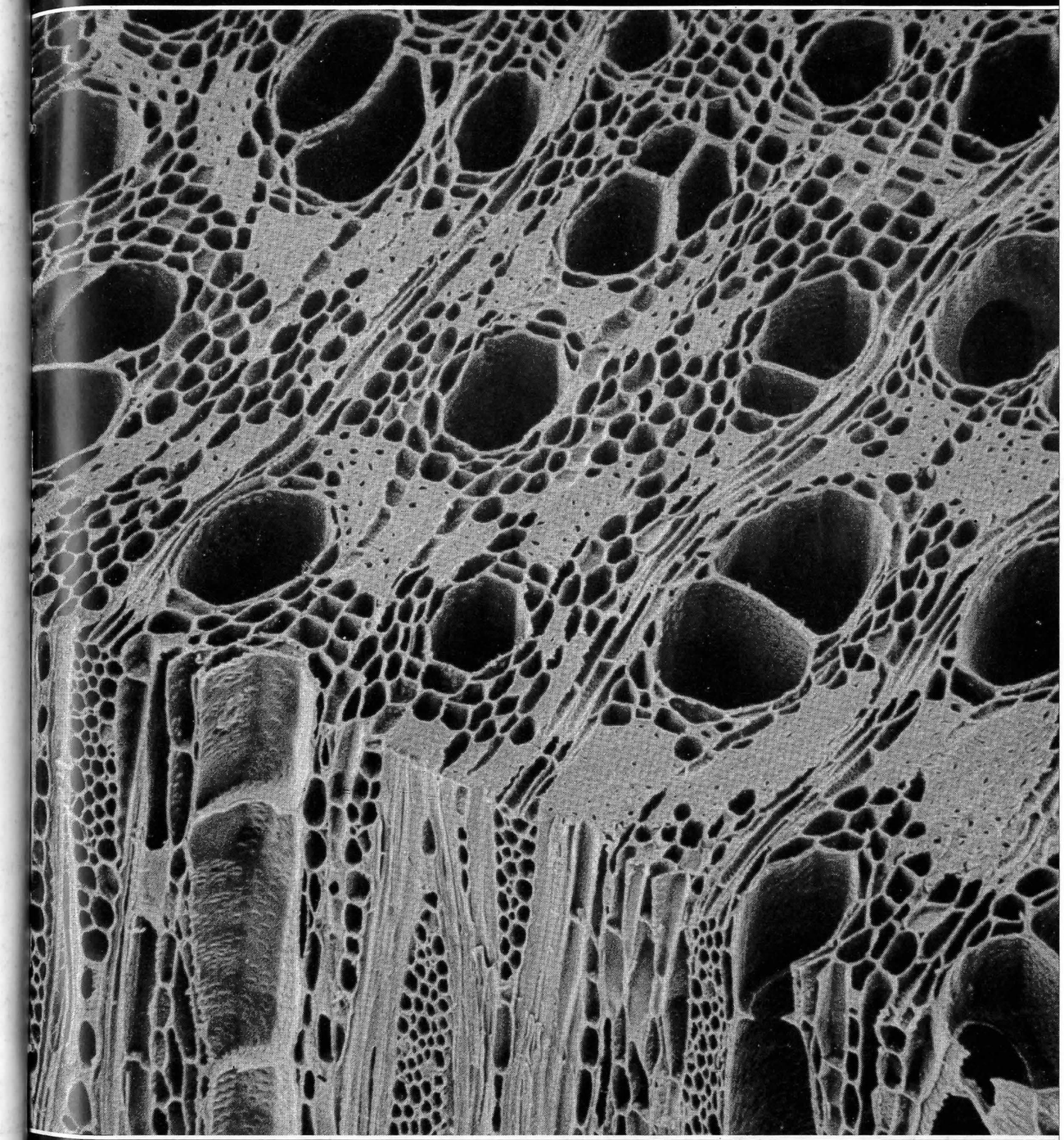
IAWA BULLETIN

Contents

Front cover: Scanning electron micrograph of the wood of *Eugenia maire* A. Cunn. (Myrtaceae), one of the numerous New Zealand Woods pictured and described by B.A. Meylan and B.G. Butterfield in their 'Structure of New Zealand Wood', N.Z. Government Printer, Wellington, 1978. Courtesy B.A. Meylan and B.G. Butterfield, Lower Hutt and Christchurch.

IAWA BULLETIN 1978/4



International Association of Wood Anatomists

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Contributions and books for review, as well as applications for membership, and IAWA Bulletin subscriptions should be addressed to the Office of the Executive Secretary.

ASSOCIATION AFFAIRS

News on the Afro-European Wood Anatomy Congress August 1979

When this Bulletin issue reaches your desk, all IAWA members in Africa and Europe should have received a final registration form for the Wood Anatomy Congress to be held from August 26 through August 30, 1979, in the Royal Tropical Institute, Amsterdam, The Netherlands. This Congress, organized by the Afro-European Regional Committee of IAWA in close collaboration with the Wood Quality Subject Group of IUFRO Division V and with the Anatomy and Morphology Section of the Royal Dutch Botanical Society, will be attended by ca. 80 participants from numerous countries (also from outside Africa and Europe). Based on the reactions to the first questionnaire the following preliminary program has been composed:

Sunday evening 26 August: Registration and informal social hour.

Monday 27 August: Full day program with papers on comparative wood anatomy as related to other botanical disciplines (systematics, phylogeny, ecology) and to wood identification. Congress dinner.

Tuesday 28 August: Full day program on ultrastructural, ontogenetic, and physiological aspects of wood anatomy.

Wednesday 29 August: Half day program on the anatomy of bamboo and bark and its significance for the utilization of 'minor products'. Excursion to the Forest Products Institute TNO, at Delft. Informal dinner.

Thursday 30 August: Full day program on various aspects of wood anatomy in relation to technological and other aspects of timber utilization.

IAWA members outside Europe and Africa who wish to participate in the congress should write to the Executive Secretary, Schelpenkade 6, Leiden, The Netherlands, and register before January 15, 1979! African and European members are also urged to register at their earliest convenience and not later than this date. Please note that there is a slight change in dates for the congress as compared with earlier notices.

The organizing committee includes the following members: P. Baas (Leiden), P.B. Laming (Delft), G.J.C.M. van Vliet (Groningen), B.J.H. ter Welle (Utrecht), and S.I. Wiselius (Amsterdam).

Dr. William Louis Stern elected an Honorary Member

The IAWA Council has elected Professor Dr. William Louis Stern an Honorary Member of our Association. Dr. Stern has rendered notable service to the advancement of knowledge of wood anatomy through his many activities in this field over the years. For all wood anatomists making use of materials stored in institutional wood collections he has enormously facilitated exchange and communication through his 'Guide to the Institutional Wood Collections' published in Tropical Woods 106 in 1957 and the two editions of the 'Index Xylariorum' published as Regnum Vegetabile issue 49 in 1967, and in Taxon 27 of this year respectively. Besides all merits of Dr. Stern for the botanical and wood anatomical world at large, he has always been actively interested in our Association affairs, and he has served the IAWA as a Council Member for a number of years.

We warmly congratulate Dr. Stern with this honourable distinction.

ELECTRON MICROSCOPY OF THE ACTIVE CAMBIAL ZONE OF FRAXINUS EXCELSIOR L.

by

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Summary

Actively dividing cells in the cambial zone of woody plants have resisted ultrastructural investigations because of difficulties encountered during their isolation from the tree, preparation for electron microscopy and orientation for ultrathin sectioning in a pre-defined plane. This paper describes techniques to obtain well-preserved active cambial zones permitting ultrastructural research of sections in transverse, radial, and tangential planes.

Introduction

The actively dividing cambial zone has seldom been studied with the electron microscope (for a review see Catesson, 1974). The dormant cambial zone was investigated more frequently. However, almost all studies concerned transverse sections. Since nearly all fusiform cambial cells have a very elongated shape, transverse sections are rather inappropriate material to study, for instance, the ultrastructure of cambial cells during nuclear and cellular division. Up to now, there are no electron micrographs showing the phragmoplasts during the formation of the new tangential cell walls in these elongated, cambial cells. The rareness of ultrastructural studies of the active cambial zone is mainly due to the various difficulties encountered during the successive stages of obtaining the desired material:

1. Isolation of the active cambial zone from the living tree is difficult. The cambial zone is of a soft and jelly-like consistency between wood and bark. Tensions in the bark can cause the cells, in an isolated sample of the zone, to collapse and the cell rows to become skew. Moreover, each small pressure sideways or outwards against the sample during or after isolation results in tearing loose the bark off the young wood, which destroys the cambial zone. This is especially likely in *Fraxinus excelsior*, European ash, when early in spring (April and May) the very wide vessels are formed that eventually give rise to the ring-porous wood.
2. Preparation of the isolates for electron microscopy poses special difficulties because the fusiform cells are highly vacuolated. Thus, fixation, dehydration and penetration of the material by the embedding medium can easily cause damage to the tonoplast and to the large vacuoles. This may result in the appearance of confusing membranous structures inside the vacuoles.
3. The orientation of the elongated, but often somewhat curved cambial cells is rather difficult to determine within the prepared isolates. Therefore, it is very difficult to obtain, for instance, longitudinal sections through the whole length of these cells.

This paper describes some techniques by which the above difficulties can be largely resolved. It also presents some preliminary observations on the active cambial zone of *Fraxinus excelsior* from shoots on old stumps growing in the Royal Domains 'De Horsten' at Voorschoten, The Netherlands.

Results

1. Isolation of the samples occurred by using the method described by Newman (1956) which has apparently largely been forgotten but was recently used for ash by Burggraaf (1973). After removal of part of the bark, two razor blades kept together in vertical direction by a special holder are hammered simultaneously into the shoot. Meanwhile the site of isolation is kept wet. After making horizontal incisions at the upper and lower part of the sample, with a narrow chisel, the piece of stem between the two razor blades is removed by use of this chisel. The critical point that prevents collapsing of the cells in the cambial zone is that the large vertical incisions are made simultaneously and prior to the horizontal incisions (Newman, 1956). Besides, the piece of stem must contain sufficient mature wood to prevent bending of the sample during removal. In the present study samples taken from the middle of the oldest part of nine-year-old shoots, are 40 mm in length, 4 mm in width, and 4 mm in depth. The samples were immediately immersed in fixing fluid and then transported to the laboratory. The wounded tree was treated with Lac Balsam (Scheidler KG, 495 Minden i.W., West-Germany; internat. nr. 336.788).

2. The preparation of the samples for electron microscopy was carried out as described below. In the laboratory the samples are cut in 4 pieces (10 mm, 4 mm, 4 mm), immersed in the fixative, and placed in a vacuum desiccator for at least one

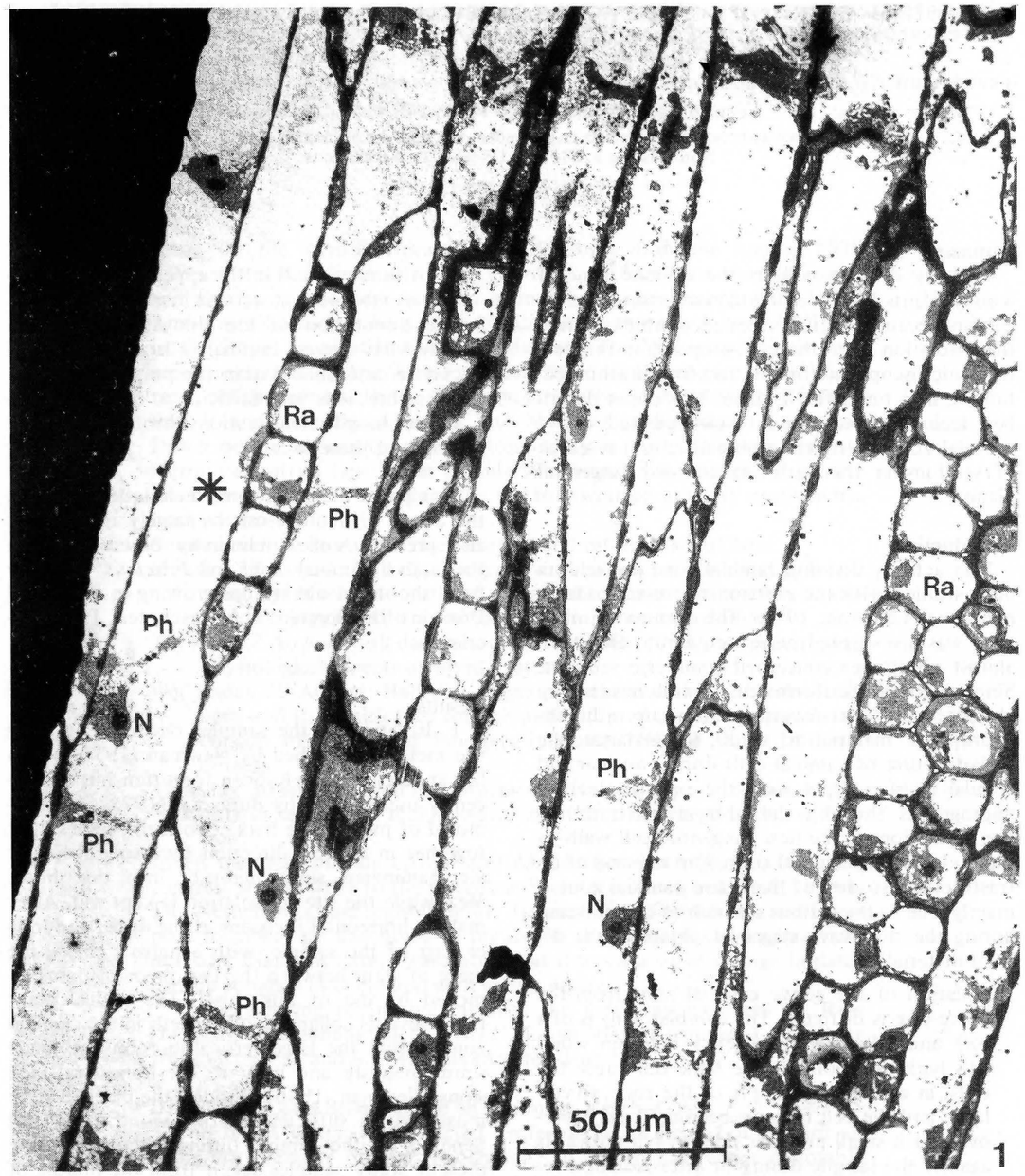


Fig. 1. *Fraxinus excelsior* L. – Tangential view of an active cambial zone isolated in April. The nucleus and one phragmoplast of the cell marked with an asterisk are shown in Figures 2 and 3. –– N: nucleus; Ph: phragmoplast; Ra: ray.

hour. The use of samples of these sizes is rather unusual for electron microscopical purposes. It should be noted that not the whole isolate can be used after fixation. The outside of the pieces is too much oxidized whereas the centre of the pieces is hardly preserved. Only the region between the two areas is suitable for study. The pieces were fixed in 6.5% glutaraldehyde in a 0.1 M sodium cacodylate buffer, pH 7.2, for 24 hours at room temperature. This was followed by washing in the same buffer for two hours and post-fixation with 1% osmium tetroxide in the same buffer, for 24 hours at room temperature. After osmium tetroxide post-fixation the pieces were rinsed in distilled water for one hour and partially dehydrated with an ethanol series, each step lasting at least one hour (20%, 30%, 40%, and 50%).

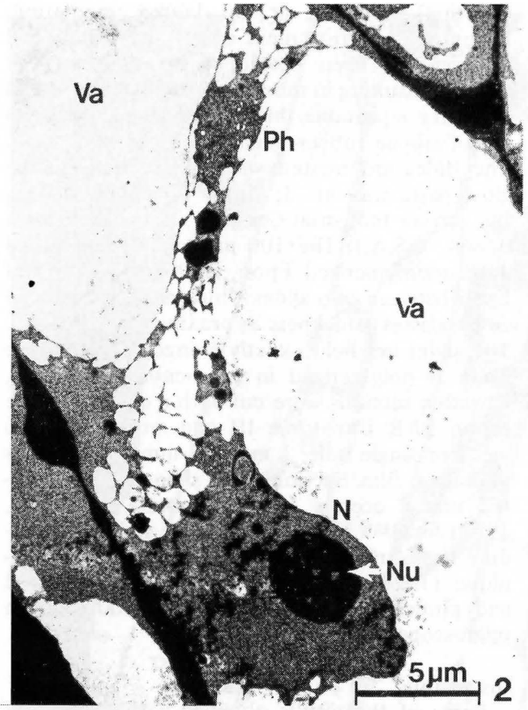
3. The intended orientation of the cells for ultrathin sectioning can be obtained by cutting thick sections (100 µm) in the desired orientation from the material, still in ethanol 50%, by using a bench microtome (for details see Burggraaf, 1973). These sections are then further dehydrated and embedded in Epon. The penetration by Epon of the thick sections does not give problems. In our study the sections were dehydrated in ethanol (70%, 80%, 96%, and 100%) followed by propylene oxide, each step taking at least one hour. Then the thick sections were successively immersed in mixtures of propylene oxide and Epon with the ratios 2:1, 1:1, and 1:2, respectively, each time for one hour or longer. Afterwards, the sections were put in pure Epon for 12 hours or longer. Subsequently the 100-µm sections were embedded in some drops of Epon which are contained between two slices of smooth silicon rubber (the back of flat silicon rubber molds). The Epon was polymerized for 48 hours at 60°C. After removal of the silicon rubber, the sheet of polymerized Epon containing the sections had a thickness of about 200 µm. Because the Epon sheets are transparent, parts of the cambial zone with adjacent bark and wood are easily discernible under a light microscope. The wanted parts can be cut from the Epon-embedded sections. The excised parts (to a maximum size of approximately 2.0 x 1.5 mm) are glued to Epon blocks by a drop of fresh Epon which is then polymerized for 48 hours at 60°C, so that the appropriate material is available for ultrathin sectioning in the desired orientation. Recently an improvement of the above described method has been developed by Weeda (pers. comm.) resulting in more transparent Epon sheets of better repeatable thickness. Instead of the slices of silicon rubber, microscope slides are used. The slides are treated with silicon wax (Fernagloss paste wax nr. 3; Mirror Bright Polish Co., Inc., Irvine Industrial Complex, Irvine, California 02664, U.S.A.). The 100 µm sections infiltrated with unpolymerized Epon, are kept in a drop of Epon between two slides which are held apart by cover glasses (thickness approximately 150 µm). The slides are held exactly horizontal when the Epon is polymerized in an incubator at 60°C. Ultrathin sections were cut with a diamond knife on an LKB Ultrotome III and mounted on 50 mesh or single hole, 1 mm x 2 mm, grids with a pioloform film. Sections were stained with saturated uranyl acetate and lead citrate (Reynolds, 1963) for 3–5 minutes each. The staining procedure was a modification of the Mollenhauer technique (1974, 1975). The sections were viewed and photographed, using a Philips 300 electron microscope.

Discussion

Some of the results obtained with the techniques described above are illustrated in the photographs. They show the active cambial zone, isolated in spring (April), in tangential, transverse, and radial view, as overall pictures (Figs. 1, 4 & 5) and as details (Figs. 2, 3, 6 & 7).

The tangential view of an active cambial zone is given in Figure 1. The cell marked with an asterisk is about 25 µm wide and at least 300 µm long. The cell to the right of this cell is also about 25 µm wide and is 240 µm long. These sizes indicate that those cells are not collapsed and are cut through their whole length. The average length of cambial cells of *Fraxinus excelsior* is 250–300 µm; the width 20–25 µm when measured in material in ethanol 50% under the light microscope (Burggraaf, pers. comm.). Many of the fusiform cambial cells are dividing: phragmoplasts are present. The cell division in the cell marked with an asterisk has just started, the phragmoplasts are still close to the nucleus. The cell division in the cell to the right is more advanced, the phragmoplasts are further separated. Figures 2 and 3 give details of a phragmoplast, with many Golgi vesi-

Fig. 2–4. *Fraxinus excelsior* L. –– 2. Detail of Figure 1. Nucleus with one nucleolus and a phragmoplast. –– 3. Detail of Figure 2. Many Golgi vesicles in the neighbourhood of dictyosomes. Many ribosomes are present. –– 4. Transverse view of an active cambial zone, isolated in April. The bark is present at the top of the photograph, the wood at the bottom of the photograph. There are some folds (straight dark lines) present in the ultrathin section. –– D: dictyosomes; Gv: Golgi vesicle; N: nucleus; Nu: nucleolus; Ph: phragmoplast; R: ribosomes; Ra: ray: Va: vacuole; Ve: vessel.


Va
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Va
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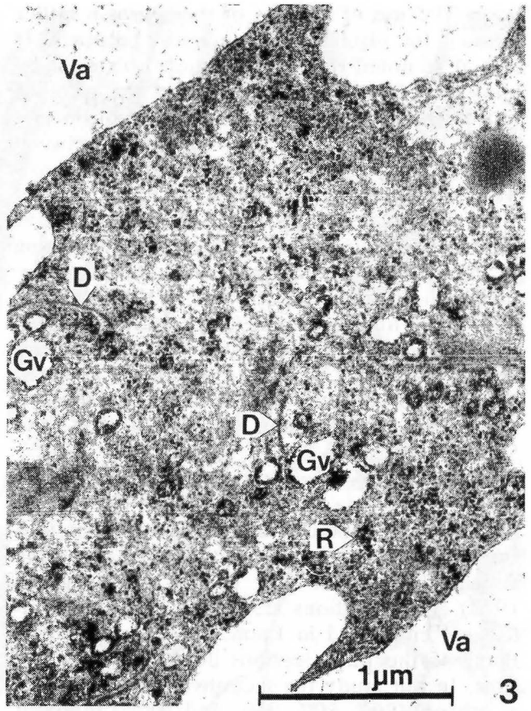
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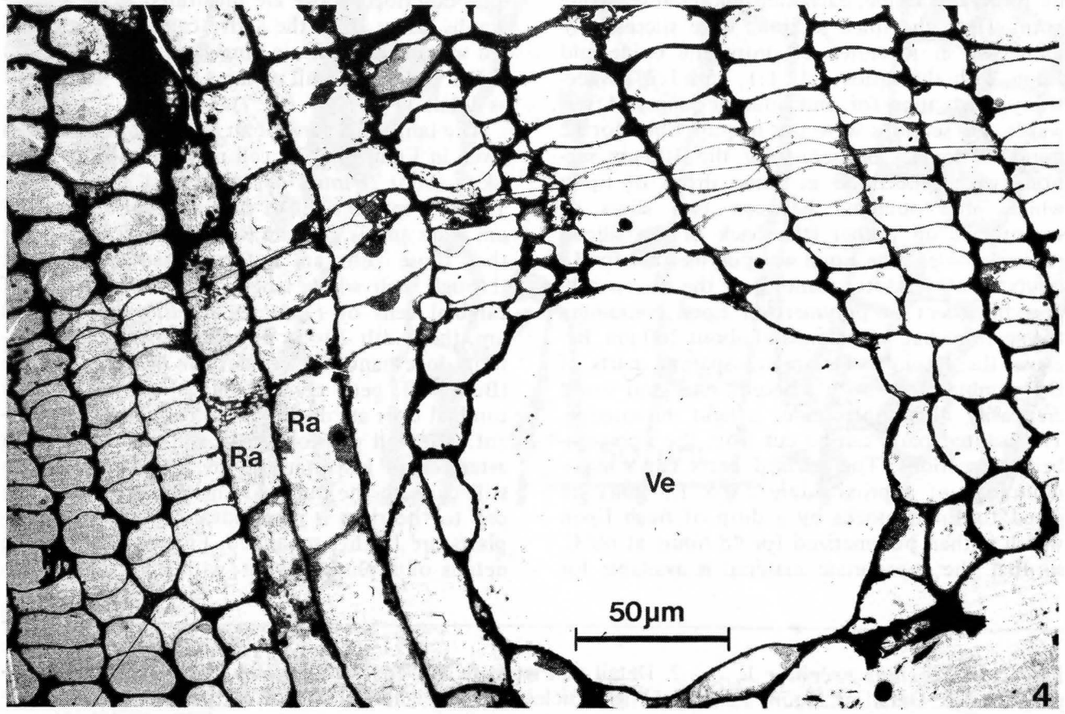
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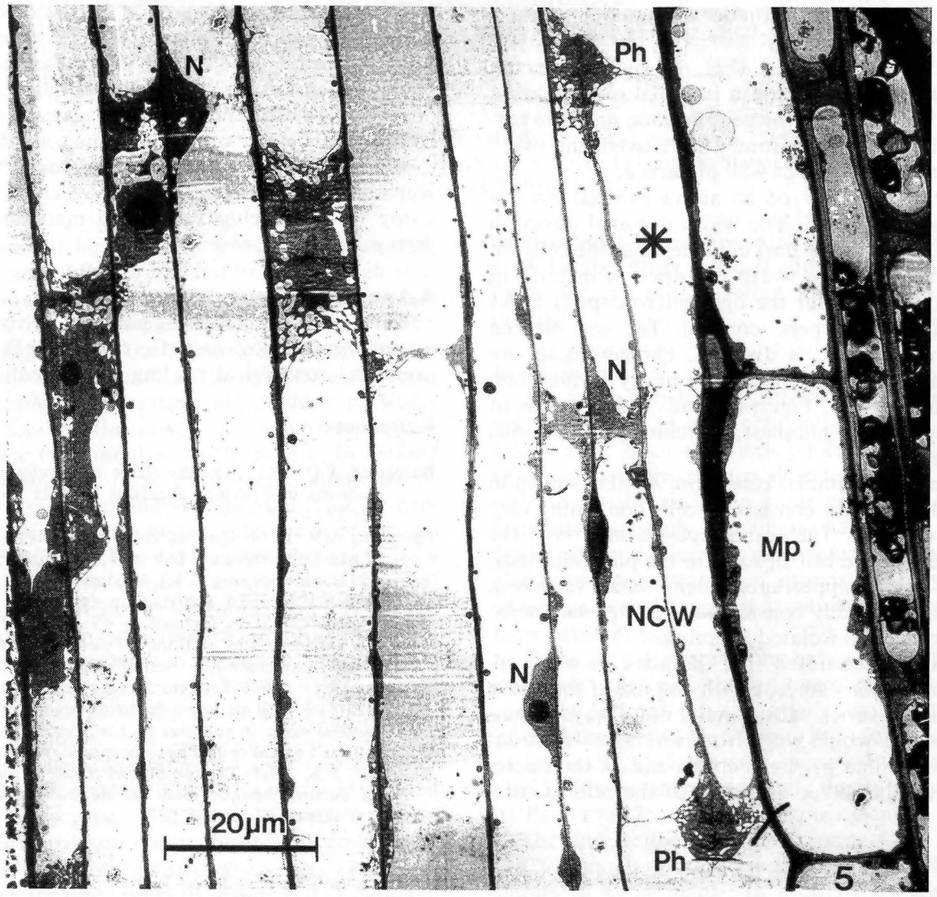
4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Ph
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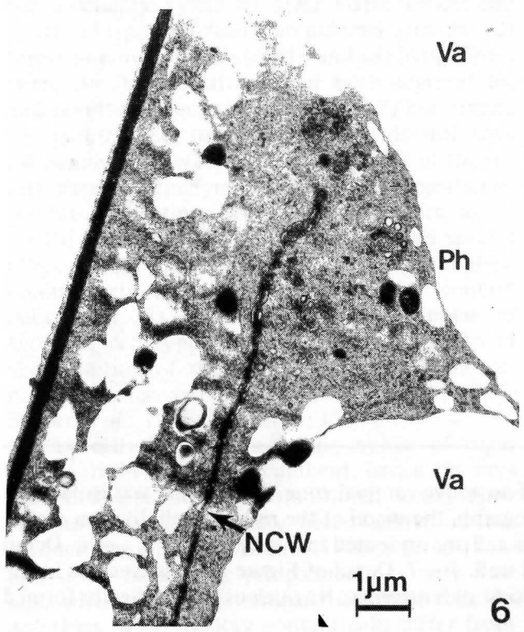
5


Va
Ph
Va
NCW
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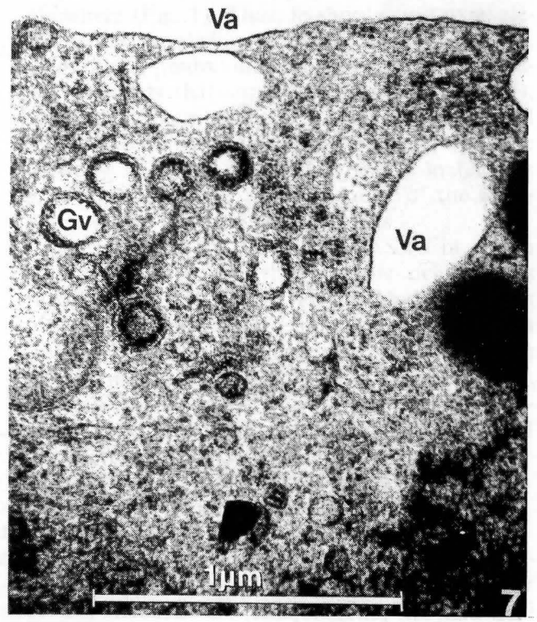
6


Va
Gv
Va
1µm
7

cles containing electron-dense material at their periphery.

The transverse view (Fig. 4) shows that the cambial cells are arranged in radial rows. A wide vessel has just been formed. Because only the tangential cell walls are somewhat curved, the material can be regarded as well preserved.

The radial view of an active cambial zone is shown in Figure 5. The width in radial direction of the cells (6–12 μm) indicates that the cells are not collapsed. The width measured in material in ethanol 50% under the light microscope is 5–15 μm (Burggraaf, pers. comm.). The cell marked with an asterisk is dividing. Phragmoplasts are present at the far ends of the newly formed tangential cell wall. Figures 6 and 7 give details of the upper phragmoplast, containing many Golgi vesicles.

The active cambial zone from April as shown in the photographs consists of cells containing very large vacuoles. The scarce cytoplasm around the nucleus, at the cell tips and in the phragmoplasts, has a foamy appearance (many small vacuoles), which is generally considered as being characteristic for material isolated in spring.

It should be noted that the plane in which ultrathin sections are cut with the use of the above techniques varies within limits not always as narrow as one would wish. However, large deviations are discernible in the sections and in the micrographs, using shape and sizes of the cells as criteria.

The preparation for electron microscopy of the samples as described above, gives acceptable results. All cell organelles are well preserved. Peripheral microtubules and microtubules in the phragmoplasts are present. The plasmalemma is continuous. On the other hand, the tonoplast surrounding the large vacuoles is sometimes broken. Apparently the preparation for electron microscopy of this highly vacuolated material is still susceptible of improvement.

Acknowledgements

We thank Drs. P.D. Burggraaf for 'introducing' us to *Fraxinus excelsior* L., for valuable discussions and for critical reading of the manuscript.

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Fig. 5–7. *Fraxinus excelsior* L. — 5. Radial view of an active cambial zone. The sample was isolated in April. The bark is present at the left side of the photograph, the wood at the right. A cell division can be seen in the cell marked with an asterisk. Details of this cell are presented in Figures 6 and 7. — 6. Detail of Figure 5. Phragmoplast and the newly formed cell wall. — 7. Detail of Figure 6. Golgi vesicles in the phragmoplast. — Gv: Golgi vesicle; Mp: marginal wood parenchyma; N: nucleus; NCW: newly formed cell wall; Ph: phragmoplast; Va: vacuole.

LIVING ELEMENTS OF THE CONDUCTING SECONDARY XYLEM OF SUGAR MAPLE (ACER SACCHARUM MARSH.)

by

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Occasional high positive pressures in late fall, winter, and early spring, and unusually high concentrations of sucrose in vessel sap are well known features of sugar maple xylem. The interconnected protoplasts of the living cells (being components of the symplast) of the xylem are undoubtedly involved in creating the positive pressures and in loading the vessels of the extraprotoplasmic space (the apoplast) with sucrose. In seeking explanations for these phenomena, attributes of both the symplast and the apoplast must be considered. Many characteristics of the apoplast, especially the tracheary elements, are fairly well known in many woody dicotyledons. Those of the symplast are not as well understood. Although there have been numerous reports on the presence and characteristics of living ray and axial elements in *Acer* xylem (Heimsch, 1942; Braun, 1961; Sauter, 1974; Sauter *et al.*, 1973; Parker, 1975; Dumbroff and Elmore, 1976), none has described these elements as a continuous protoplasmic unit, or shown how this unit is integrated with the apoplast. This is an attempt to do so, based primarily on observations of tissue samples prepared for light microscopy.

There are three types of living axial elements in the secondary xylem of sugar maple shoots and roots: (1) paratracheal parenchyma strands; (2) terminal parenchyma strands, and (3) living fibers (Figs. 1–9). The latter occur both adjacent to, and removed from, vessels (Figs. 1, 7) but, unlike the paratracheal parenchyma, they do not have pit connections with vessels. Most cells of the paratracheal parenchyma strands have large-diameter pit connections with vessel members, as reported by Sauter *et al.* (1973) for this species (Figs. 4–6). These axial contact cells and their counterparts in the xylem rays (ray contact cells) (Fig. 8), have characteristics similar to those of cell types that presumably function in the secretion of substances into conducting elements (Sauter and Braun, 1968; Läuchli, 1975; Sauter *et al.*, 1976; Czaninski, 1977).

Ray cells in the conducting xylem of sugar maple are living and procumbent, hence the rays are homocellular in the traditional sense. They are, however, functionally heterocellular in the manner described by Braun (1970): some (contact cells) have large pit connections with vessels, whereas the predominant isolation cells do not (Figs. 4, 5, 8). Ray contact cells differ from axial contact cells only in shape (long axis horizontal rather than vertical) and in origin (derived from ray cell initials rather than from fusiform initials).

Isolation cells

The living noncontact cells of the xylem, both ray and axial, can be functionally grouped as isolation cells, since they lack pit connections with vessels. They are storage sites for reserve material, principally starch in sugar maple. The axial elements, especially the fibers, have thick walls, fewer pits, and relatively narrow lumens, and thus also function in mechanical support. The ray cells, of course, serve as radial conduits for translocatable substances.

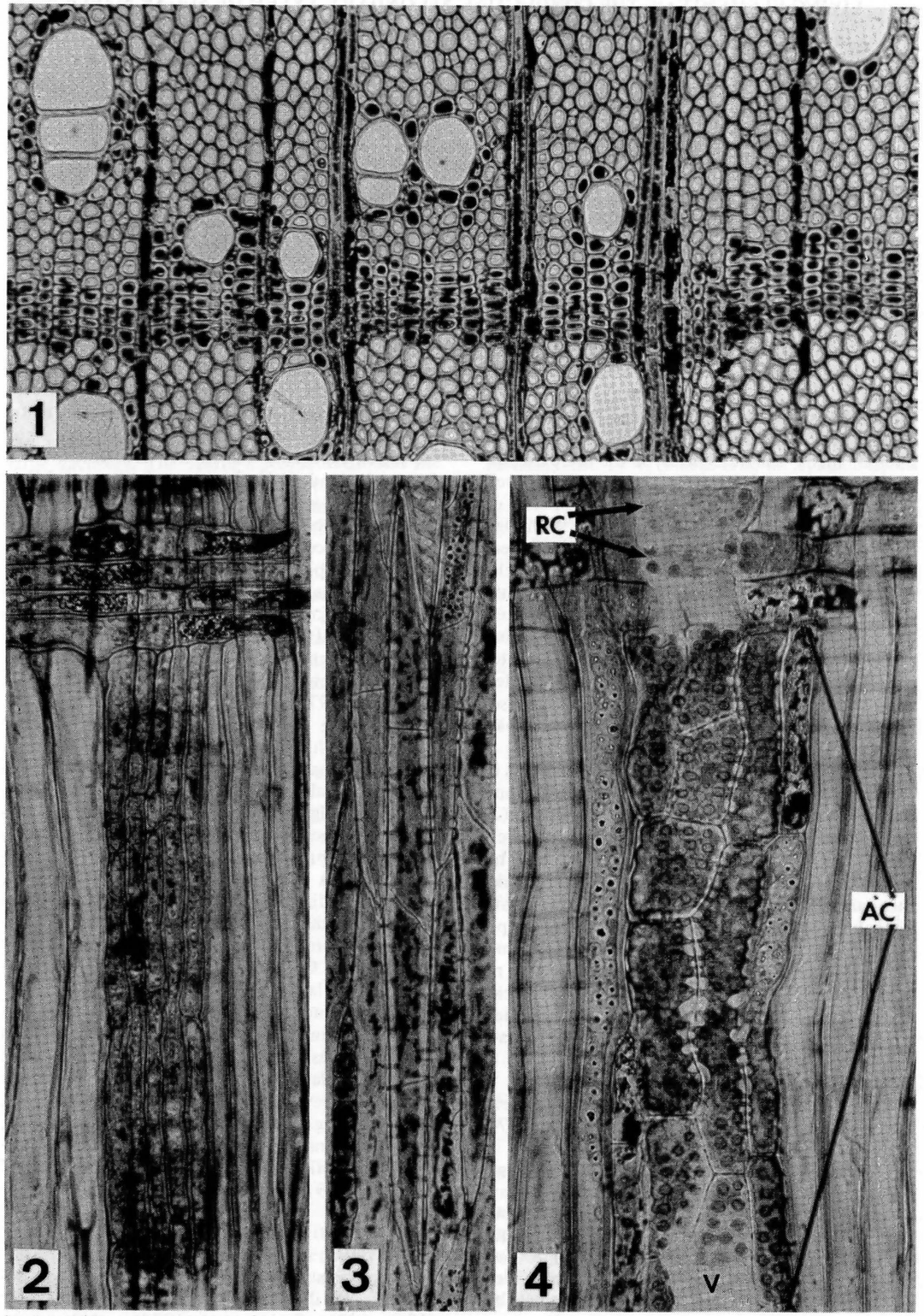
There are pit connections between all of these isolation cells, and the pit membranes are presumably perforated by plasmodesmata, as reported by Schmid and Machado (1968) for the xylem of several leguminous tree species, by Czaninski (1977) for several other woody dicotyledons, and by Parker (1975) for sugar maple xylem.

The living fibers are, as reported by Parker (1975), much more abundant in roots than in shoots of sugar maple. In shoots they are paratracheal, usually occurring next to vessels, seldom elsewhere (Fig. 1). Thus, in shoots most axial elements are nonliving fibers. In roots, however, living fibers predominate; they occur in wide tangential bands that surround the vessels (Fig. 7), hence their distribution is confluent paratracheal (IAWA Committee on Nomenclature, 1964). The capacity of roots for storing reserve material is greater than that of shoots because of the abundance of the latter cell type in roots.

The presence of starch, easily seen in xylem sections stained by the periodic acid-Schiff's reaction (Figs. 1, 7, 9), clearly identifies living elements in late summer and winter. I have been unable, however, to distinguish between living and nonliving fibers on the basis of size, shape, or wall characteristics, including thickness, degree of lignification, or abundance and type of pitting (Fig. 9).

Contact cells

Characteristics of contact cells have been described and illustrated by Braun (1970), Sauter (1966, 1971), Sauter *et al.* (1973), and Czaninski



(1977). In sugar maple, and possibly in other species also, they are the only cells with pit connections to vessels, and these pits are, as described elsewhere, greatly enlarged (Figs. 4–6, 8). Contact cells are connected with other living xylem elements by smaller pit pairs. Anatomical and cytoenzymatic evidence indicates that contact cells are specialized sites for exchange of solutes between the xylem symplast and vessels of the xylem apoplast. In sugar maple, increased respiratory activity in the contact cells during periods when sucrose appears in vessel sap, especially phosphorylation, suggests that movement of sucrose across the plasmalemma of the contact cells is metabolically controlled (Sauter *et al.*, 1973).

Axial contact cells appear to have much more surface area contact with vessels than do ray contact cells (Figs. 5, 6). Presence of the axial elements seems, therefore, to ensure better communication between the symplast and vessels.

The apoplastic part of the solute exchange, across the membrane of the contact pit, seems facilitated by the obvious absence of lignification in this region. Czaninski (1977) noted that in woody dicotyledons the pit membranes of contact cells remain unlignified and do not contain plasmodesmata, whereas those between living xylem elements remain lignified and possess plasmodesmata. In sections of sugar maple xylem stained with safranin and fast green, the contact pit membranes stained green, indicating an absence of lignin in this wall region, in contrast to the remaining wall areas, which stained red. The same staining characteristics for pit membranes and wall areas have been observed in other angiosperms (Bamber, 1961; Schmid and Machado, 1968). This reaction is what one would expect, because incrustation of cell walls with lignin appears to decrease wall permeability greatly (Läuchli, 1976). Hence, the highly lignified cell walls of secondary xylem elements would be considered less permeable than contact pit membranes.

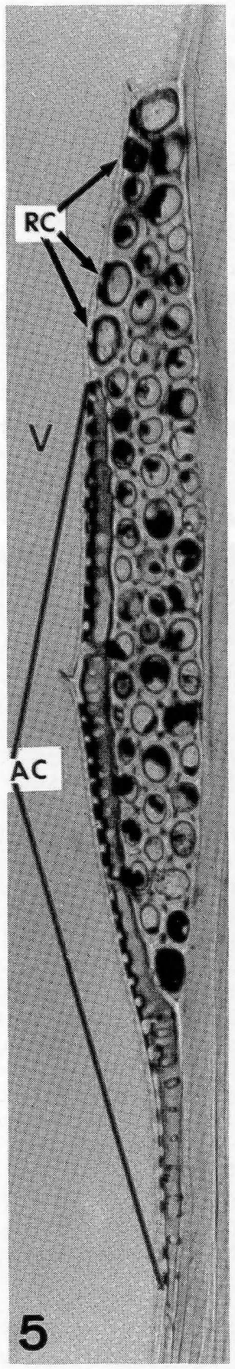
Other cell types that have a significant role in secretion or transport of carbohydrates (Strasburger or albuminous cells of gymnosperm phloem, companion cells, cells of vascular bundle sheaths, Strasburger cells of conifer leaves, and secretory cells of nectaries) also show high phosphatase activity (Sauter and Braun, 1968). Contact cells often have in common with these other cell types unusually large nuclei, dense cytoplasm, numerous ribosomes, many mitochondria, high activity of other respiratory enzymes, and an absence of starch during periods of respiratory activity (Sauter and Braun, 1968; Sauter *et al.*, 1973, 1976; Czaninski, 1977).

Czaninski (1977) notes that the term *contact cell* is not fully descriptive because, in addition to being in contact with vessels, these cells represent a specific category analogous to specialized cells (companion and Strasburger) of the phloem. Hence, the term *associate cells*, or more specifically for the xylem, *vessel-associated cells*, would be more descriptive of their unique physiological function. These cell types of the phloem and xylem are, however, equally unique in another respect. They are apparently the only cells in effective contact with conducting elements of the long-distance transport systems, having either pit connection with vessel members or one-sided sieve areas with sieve elements. Thus, for broad categorization, the terms *contact cell* and *isolation cell* seem equally appropriate.

I refer to the axial contact cells as parenchyma strands because they are derivatives of fusiform initials that have undoubtedly divided transversely during their differentiation. Axial contact cells, however, differ from the common parenchyma strands in other respects. They, like adjacent vessel members, undergo appreciable change in shape during differentiation. Radial width of the mature axial contact cells is often greater than that of fibers and terminal parenchyma strands, and their final configuration suggests that their progenitors sometimes divided longitudinally in the tangential plane during the differentiation and enlargement of neighboring vessel members (Fig. 4). Therefore, in the tangential plane, axial contact cells appear strand-like, and their overall shape resembles that of the fusiform initials from which they were derived (Figs. 5, 6); in radial view, they are not strictly strand-like, because their shape in this plane has undergone considerable change during differentiation (Fig. 4). Not all members of these strands become contact cells. Occasionally, some members do not border vessels and fail to develop large contact pits in their radial walls (Fig. 6).

Overall, one can see that there are considerably more living than dead cell types in the conducting xylem of sugar maple. The living elements function to some extent in mechanical support, as well as in secretion, transport, and storage. Storage capacity of roots is greater than that of shoots per unit volume of xylem, because there are rela-

Fig. 1–4. Sections of *Acer saccharum* stemwood. — 1. Transverse view of terminal and other living axial and ray elements. Sections stained by the periodic acid-Schiff's (PAS) reaction. Living cells have darkly stained starch inclusions; x 246. — 2 & 3. Terminal parenchyma strands as seen in radial (2) and tangential (3) view; 2, x 181; 3, x 502. — 4. Radial view of ray (RC) and axial (AC) contact cells bordering a vessel (V); x 320.



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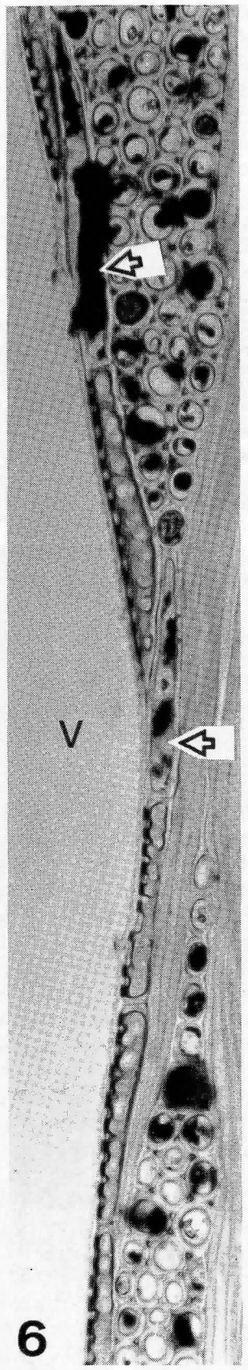

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Fig. 5 & 6. Tangential view of ray (RC) and axial (AC) contact elements; x 770. Note that some cells of the axial contact strands (arrows) do not have pit connections with vessel members (V).

tively more axial isolation cells in roots. Finally, it seems possible that an abundance of axial contact cells may appreciably increase exchange between the symplast and the vessels.

Acknowledgements

I am grateful to Mr. Barry S. Faigel for preparation of Figure 8.

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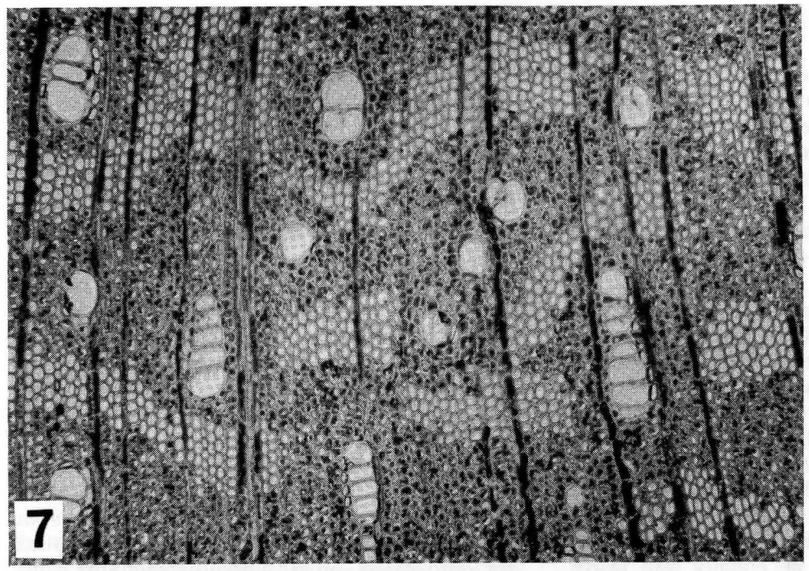

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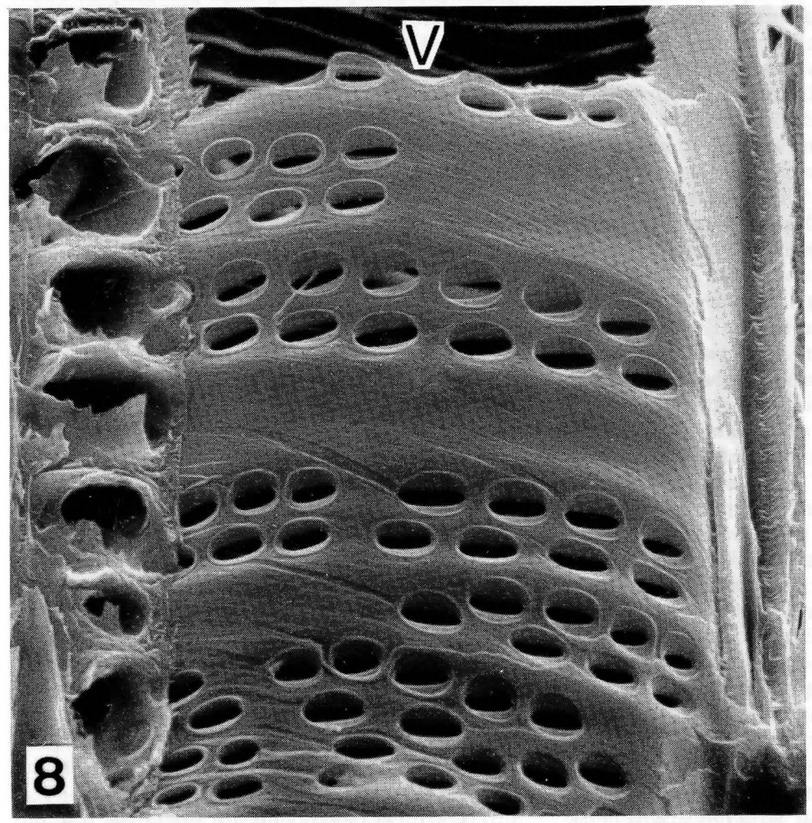

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Fig. 7. Transection of *Acer saccharum* rootwood stained by the PAS reaction; x 118. Note the abundance of living, starch-containing fibers. –– Fig. 8. SEM micrograph illustrating details of pitting between ray contact cells and a vessel member (V); x 1880. –– Fig. 9. Living, starch-containing (left) and dead (right) fibers from macerated rootwood stained by the PAS reaction; x 550.

BOOK REVIEW

Mikroskopische Holzanatomie – Anatomie microscopique du bois – Microscopic wood anatomy: Structural variability of stems and twigs in recent and subfossil woods from Central Europe. F.H. Schweingruber, 226 pp. including 82 plates, text in German, French and English. Swiss Federal Institute of Forestry Research, CH-8903 Birmensdorf and Zürcher AG, CH-6301 Zug, Switzerland, 1978. Price 28 Sw. Fr.

This book is another high quality publication fascilitating the identification and understanding of European woods. The author, Dr. Fritz H. Schweingruber, must have been involved in its composition when Dr. Grosser published his authoritative book 'Die Hölzer Mitteleuropas' (see IAWA Bulletin 1978/1: 11). A comparison between the two books which both deal with largely the same species naturally comes to mind, and it is a pleasant surprise to find that both stand the test admirably well and are equally well worth having as companions for identification work and as sources of anatomical information.

Schweingruber's book starts with an illustrated glossary of the macroscopic and microscopic characters of temperate woods. This is followed by keys to softwoods and hardwoods, somewhat intermediate in lay-out between true analytical keys and tables of characters. The main body of the book consists of concise descriptions of the main qualitative features of approximately 100 species belonging to 55 genera of Central European woods. There are additional notes on their occurrence in prehistoric sites in Switzerland. The plates accompanying the text, do not only show the microscopic histology as seen in transverse, radial and tangential sections but also demonstrate a great deal of infraspecific or infrageneric variability because each taxon is represented by 8 photomicrographs. Drawings of vessel elements copied from Greguss' 'Xylotomie' complete the plates. According to the author the coverage of species is sufficiently comprehensive to identify 99% of woods from recent origin or postglacial deposits.

Following this main section there is a most valuable section on the identification of branch wood: 56 species are pictured in 86 excellent photomicrographs of transverse sections. Again much variability for many species is illustrated but interesting diagnostic features such as pith outline and histology also stand out clearly. There are also brief but well-illustrated sections on root wood, aberrant and special structures, and most interesting texts and plates on the degradation of wood under aerobic and anaerobic conditions, and on lignites and carbonized woods. The book is concluded by a useful guide to prepare recent, subfossil, fossil and carbonized wood for microscopic examination.

Almost all micrographs are of superb quality and it is an aesthetic delight to use this manual. Criticisms mainly concern some unfortunate choices of terminology in the illustrated enumeration of anatomical characters and in some of the descriptions. For instance, the classification of heterogeneous rays, however attractive, runs precisely opposite to the one proposed by Kribs; the 'tyloses with gum deposits' in *Pirus* have nothing to do with tyloses but are gummy vessel contents; the definition of cupressoid pits on page 16 is not in agreement with the accompanying illustration on page 19; the use of *Platanus* for showing the semi-ringporous condition invites debate and will be confusing for the non-initiated.

The keys – like all attempts in this direction – must be used with 'loving care', otherwise one may easily go astray. If one applies the leads too rigidly, e.g. on ray width for *Robinia*, on spirals for *Pirus/Malus*, on tangential parenchyma bands in latewood of *Berberis* these taxa cannot always be keyed out, even if one uses the photomicrographs of Dr. Schweingruber's book to test the keys. However, if one uses several columns in the keys more or less simultaneously, one is not likely to go wrong, and one will be pleasantly surprised to find how quickly the woods can be identified with them. Like Grosser, Schweingruber is realistic in his approach to the problem of separating species from wood anatomically homogeneous or continuously varying genera or groups of genera. There are, however, some interesting differences for specific cases which will make it useful to use both books as complementary tools. Especially for the woody Rosaceae, Schweingruber goes much further than Grosser and indicates possibilities for separating individual genera and sometimes species using their wood anatomy; this is based on his own, extensive research in these groups. It is a pity, however, that for genera of which the species cannot be separated according to the author, no legends are given to the plates stating which species is illustrated. This might become useful at a later stage if differentiating characters were to be found after all.

It must be applauded that the texts are given in three languages. Users of the English text must, however, be warned that many rather vital mistakes and omissions have crept into the English version, which are fortunately absent from the German 'Urtext'.

The critical remarks do not effect the true value of this manual for the understanding and identification of European woods. There can never be a replacement for a reference collection of microscope slides, but Dr. Schweingruber's atlas highlighting structural variation constitutes a very good alternative at low cost.

Pieter Baas

THE FINE STRUCTURE OF PITS IN YELLOW BIRCH (BETULA ALLEGHANIENSIS BRITTON)

by

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Summary

The shape and fine structure of the pits in yellow birch (*Betula alleghaniensis* Britton) were studied in cross sections and tangential sections using transmission electron microscopy. The shape and structure of the pits is highly dependent on the thickness of the cell wall and the type of cell elements joined. The structure of the border of bordered pit-pairs is apparently different from that of coniferous wood. Structural variations in simple pit-pairs, half-bordered pit-pairs and bordered pit-pairs are described and discussed.

Introduction

Because a great variety of cells occurs in hardwoods, the pit structure can vary substantially. The structure of pits in hardwoods has not been as extensively studied as in coniferous woods, especially in cross-sectional view of various cell elements. The surface view of some hardwood pits has been studied by Harada (1954), Liese (1957), and Meylan and Butterfield (1972). The structure of the hardwood pit membranes has also been studied; e.g., *Fagus* (Harada, 1963; Schmid, 1965, and Fengel, 1966), *Tilia* (Côté, 1958), Leguminosae (Machado and Schmid, 1964; Schmid and Machado, 1968), and *Eucalyptus* (Cronshaw, 1960). The primary objective of this study was to provide comprehensive descriptions of yellow birch pits at the ultrastructural level.

Materials and Methods

Three fresh increment cores were collected at breast height from a healthy 51-year-old yellow birch in Dorset, near Toronto, Canada. The specimens were immediately fixed in a 3% phosphate-buffered glutaraldehyde solution. These increment cores included sapwood and heartwood.

The convential technique of O_sO_4 fixation to prepare biological specimens (Spurr, 1969) for transmission electron microscopy was used. Thin tangential and cross sections (600–900 Å) were cut with a diamond knife and mounted on uncoated 200 mesh copper grids. A Philips 300 Transmission Electronic Microscope was used in this study.

Observations

Pits between parenchyma cells

The shape of the pit cavity varies with the thickness of the wall of the parenchyma cells (Figs. 1–6). It was found that the thickness of the cell wall of the ray parenchyma in uniseriate rays is not equal on all sides of the cell, when viewed in the tangential section (Fig. 2). The thickest walls are usually located at the upper and lower part of the cell. In this thickened wall the pit cavity is long and uniform in width. This uniform width of the pit cavity was also observed in the pits between end walls of two axial parenchyma cells (Fig. 6), although the thickness of the wall of axial parenchyma cells is relatively even on all sides. Pits in radial walls between two ray parenchyma cells appear as a 'bordered pit type' (Fig. 1), in which the outer pit cavity is wider than the inner one. Occasionally, so-called 'bilaterally compound pitting' can be observed at the end wall of two ray parenchyma cells (Fig. 4). In the case where the pit-pair connects a ray parenchyma cell and an axial parenchyma cell (Fig. 5), the pit cavity is only enlarged on the side of the thicker-walled axial parenchyma cell, and forms an asymmetric pit-pair.

The pit membrane of the simple pits between two parenchyma cells shows a continuation of the compound middle lamella. No central thickening can be found. The thickness and density of the pit membrane are the same as those of the compound middle lamella. Plasmodesmata are typically present. Occasionally, plasmodesmata were observed in the compound middle lamella of the unpitted area (Fig. 6). They are particularly abundant in the pits which are located in the end walls of the ray parenchyma cells. Plasmodesmata may appear as individual channels (Figs. 2, 5 & 6) or as branched structures (Fig. 4).

Pits between parenchyma cells and vessels

The pits between parenchyma and vessels in yellow birch are half-bordered. The pits on the parenchyma side are about the same width as the pit chambers on the vessel side (Figs. 7, 9 & 11). There are no apparent differences between the parenchyma–earlywood vessel pits and the parenchyma–latewood vessel pits.

It was observed that the S_1 layer of the secondary wall in the vessel element ended at the edge of the pit chamber (Figs. 7, 9 & 11). The texture and density of the S_1 layer in the vessel element are very similar to those of the walls of the parenchyma cells. The pit membrane of the half-bordered pit also shows a continuation of the compound middle lamella. In some pit membranes, as indicated in Figures 7 and 9, the centre of the membrane is slightly swollen or thickened. This part of the pit membrane shows up as a loosened texture, as compared with the adjacent compound middle lamellae. The characteristic feature of the half-bordered pit is the presence of a 'protective layer' which is located between the parenchyma cells and the vessel elements. The thickness of the layer varies considerably. It may be thicker around the pits than elsewhere (Fig. 11).

Pits between parenchyma cells and fibre-tracheids

Pits between parenchyma cells and fibre-tracheids are also half-bordered. Due to the thickness of the cell walls, the parenchyma–fibre-tracheid pits have a long and even pit canal, whereas the parenchyma–vessel pits exhibit a short pit canal. The pits on the axial parenchyma side are slightly narrower than the pit chambers on the fibre-tracheid side (Fig. 8). In ray parenchyma–fibre-tracheid contacts, the pits on the parenchyma side are appreciably narrower than the pit chambers on the fibre-tracheid side (Fig. 10). Occasionally, two simple pits may unite with a bordered pit to result in 'unilaterally compound pitting', as illustrated in Figure 12.

The S_1 layer of the secondary wall in the fibre-tracheid ends at the edge of the pit chamber (Fig. 8). The pit membrane of the half-bordered pit shows a continuation of the compound middle lamella. A protective layer exists between the parenchyma cells and the fibre-tracheids. This layer varies in density and thickness (Figs. 8, 10 & 12).

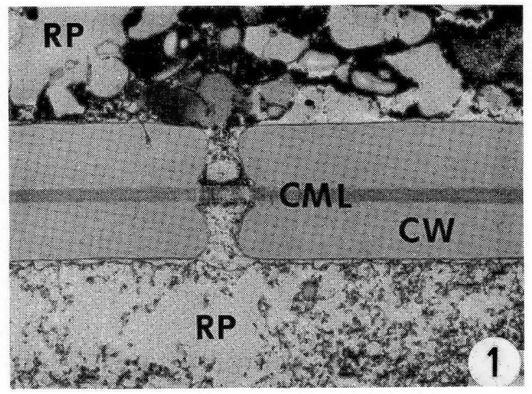
Pits between two fibre-tracheids or between two vessels

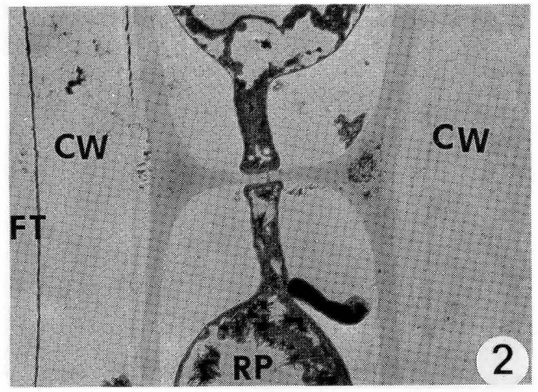
The thickness of fibre-tracheid walls is normally greater than that of vessel walls. Therefore, the shape of the pits is different. The pit canal in fibre-tracheids is long and uniform (Figs. 8, 10, 12 & 13), whereas the pit canal in vessels appears as a short and irregular structure (Figs. 7, 9, 11 & 14–17). The rim of the pit border in fibre-tracheids is angular while rounded in vessels. As a result of different configurations of the pit border and the pit canal, the pit cavity in fibre-tracheids resembles a funnel, while the pit cavity in vessels is dome-shaped. In general, the pit canal and the pit chamber of the vessel elements are not so symmetrically shaped as those of the fibre-tracheids. These asymmetric pit-pairs are quite common in earlywood vessels (Fig. 17).

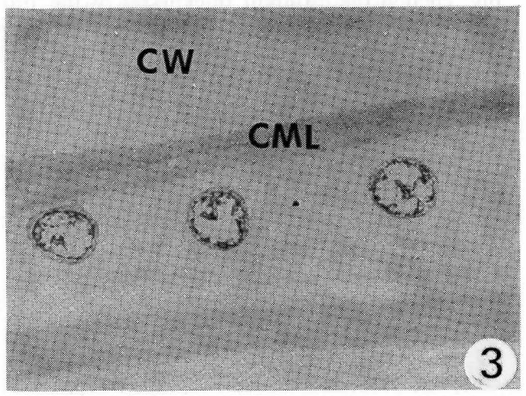
Figure 18 demonstrates a cross-sectional view of a scalariform perforation bar. The compound middle lamella between two bars is absent. There is no overarching border on these bars. A conventional type of bordered pit-pair remains at the rim of the perforation plate. This bordered pit-pair resembles that of earlywood inter-vessel pit-pairs.

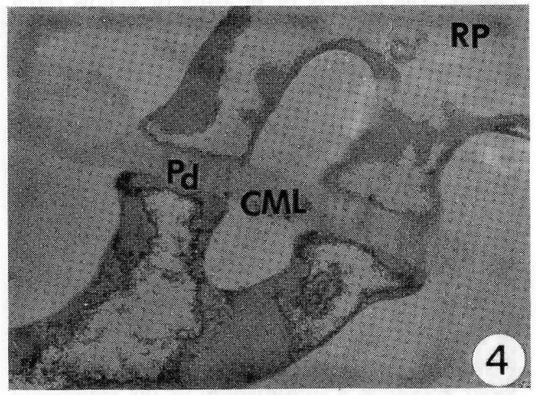
In bordered pit-pairs, the structure of the pit membrane varies considerably. It may have the same density as the compound middle lamella in a fibre-tracheid (Fig. 13) or be distinctly more dense in latewood vessel elements (Figs. 14 & 16). The membrane may also be 'perforated' as indicated in Figures 15 and 17. Nevertheless, no actual openings could be traced. In the perforation plate (Fig. 18), there is of course no pit membrane between the bars. However, the bordered pit-pairs at the rim of the perforation plate still retain intact pit membranes.

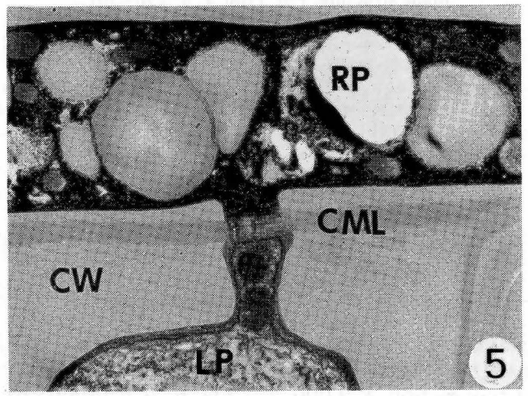
Fig. 1. A 'bordered pit type' pit-pair between two ray parenchyma cells (RP). Note the widened pit apertures. CML (Compound middle lamella). Cross section, x 5,000. — Fig. 2. A simple pit-pair between two ray parenchyma cells (RP). Note the thick wall at upper and lower part of the ray parenchyma cells resulting in a narrow and long pit canal. CW (Secondary wall), FT (Fibre-tracheid). Tangential section, x 5,000. — Fig. 3. Cross-sectional view of three simple pit canals which connect two ray parenchyma cells. CW (Secondary wall), CML (Compound middle lamella). Cross section, x 12,000. — Fig. 4. 'Bilateral compound pitting' at the end walls of two ray parenchyma cells (RP). Note the branched and unbranched plasmodesmata (Pd). CML (Compound middle lamella). Cross section, x 18,000. — Fig. 5. An asymmetric simple pit-pair between a ray parenchyma cell (RP) and an axial parenchyma cell (LP). Note the widened pit aperture. CML (Compound middle lamella). Cross section, x 9,000. — Fig. 6. Three simple pit-pairs (arrows) at the end wall of two axial parenchyma cells (LP). Note the plasmodesmata (Pd) embedded in the compound middle lamella (CML) of the unpitted wall area and in the pit membranes. Tangential section, x 4,800.

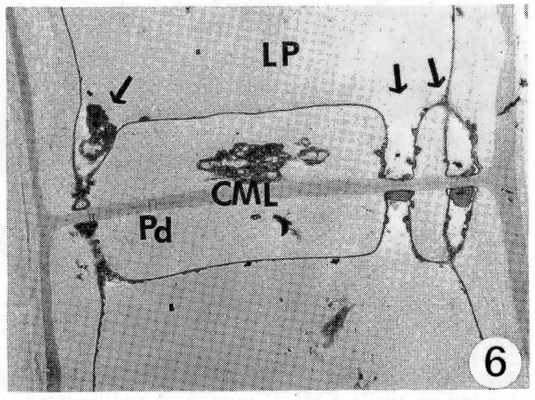












Discussion

A 'bordered pit type' simple pit-pair between two parenchyma cells does not only exist in yellow birch, but has also been reported for white birch (*Betula papyrifera* Marsh.) (Côté and Marton, 1962). This type of pitting is apparently absent in other hardwood ray parenchyma cells (Harada, 1963; Fengel, 1966). The cell walls of fibre-tracheids are thick compared with vessel elements. For white birch and beech (*Fagus grandifolia* Ehrh.), similar observations had been reported (Côté and Marton, 1962; Fengel, 1966). The edge of a pit border in yellow birch fibre-tracheids is rectangular, whereas the edge of a pit border in a vessel element is rounded, like a coniferous pit border. The borders of pit-pairs of yellow birch fibre-tracheids and vessel elements are composed of a secondary wall without an S_1 layer (Figs. 7, 8, 11 & 13). In contrast, the S_1 layer of the secondary wall in coniferous bordered pits is usually extended to the pit border, accompanied by the initial pit border (Wardrop and Davies, 1961; Harada and Côté, 1967; Murmanis and Sachs, 1969). The accompanying pictures (Figs. 6, 7, 8 & 11) demonstrate that the cell walls between axial parenchyma and ray parenchyma are similar to the S_1 layer of vessel elements and fibre-tracheids, in terms of texture and thickness.

The pit membrane of simple pit-pairs, half-bordered pit-pairs and bordered pit-pairs of yellow birch appear as a continuation of the compound middle lamella, as in other hardwoods (Schmid, 1965). However, the pit membrane on a simple pit of parenchyma cells abounds in plasmodesmata, whereas these plasmodesmic canals are lacking in half-bordered pit-pairs and bordered pit-pairs. The variation in density of pit membranes in fibre-tracheids, latewood vessels and earlywood vessels might reflect differences in function and ontogeny of the individual cell elements. The pit membranes of earlywood vessels in yellow birch are quite similar to those in the Leguminosae (Schmid and Machado, 1968).

Half-bordered pit-pairs are always accompanied by a 'protective layer', although it varies in thickness and texture. Similar findings were reported for other hardwoods (Meyer and Côté, 1968; Schmid and Machado, 1968; Chafe, 1974). The different thicknesses of the layer in different cell types might indicate a pressure difference between fibre-tracheids and vessels in the case of yellow birch. Sapwood functions as the water conductor, creating high negative pressures. The diameter of a vessel is larger than a fibre-tracheid and also has an open end to form a continuous tube-like element. These structural differences have, presumably, created the different thicknesses of the 'protective layer'. Therefore, the function of the 'protective layer' seems to be as suggested by Schmid viz. a 'protection' (1965) rather than a translocation function, as advocated by Chafe (1974).

Acknowledgements

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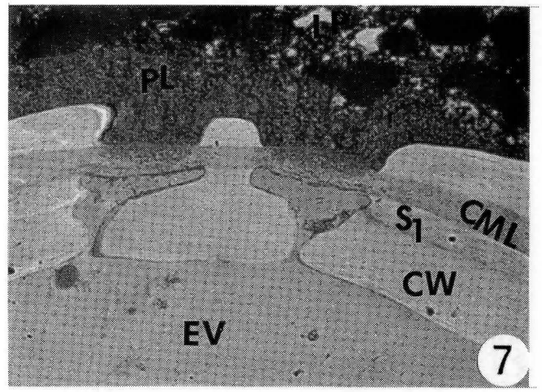
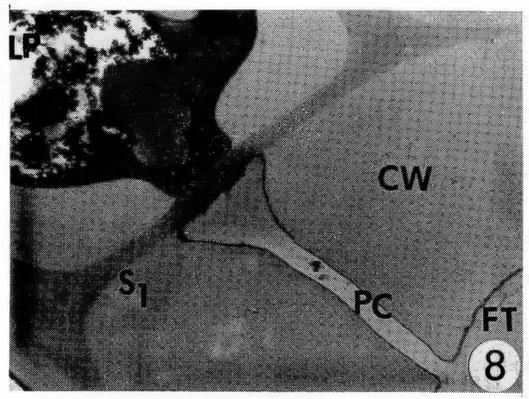
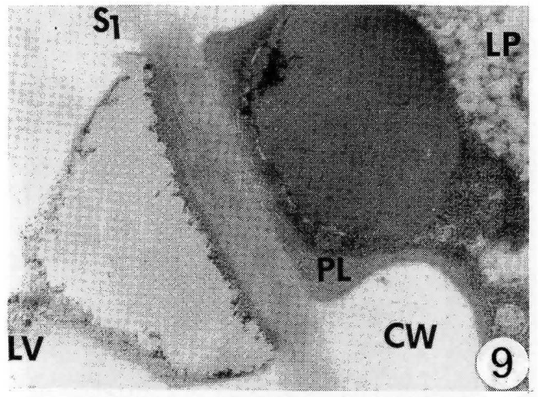
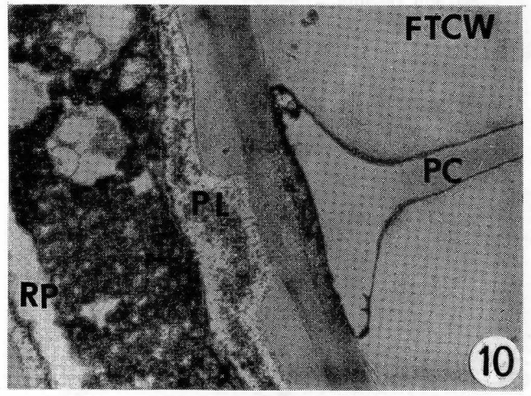
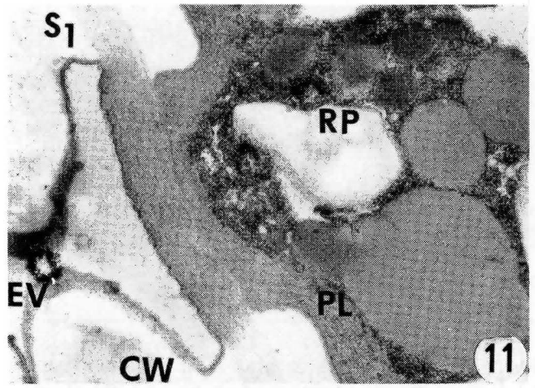
Fig. 7. Two half-bordered pit-pairs between a living axial parenchyma cell (LP) and a dead earlywood vessel (EV). Note the protective layer (PL) between the protoplast and the cell wall. S_1 (S_1 layer of the secondary wall), CML (Compound middle lamella). Cross section, x 9,000. –– Fig. 8. A half-bordered pit-pair between an axial parenchyma cell (LP) and a latewood fibre-tracheid (FT). Note a protective layer (PL) between the protoplast and the cell wall. Note also the S_1 layer of the secondary wall ending at the pit chamber. PC (Pit canal). Cross section, x 13,000. –– Fig. 9. A half-bordered pit-pair between an axial parenchyma cell (LP) and a latewood vessel (LV). PL (Protective layer), S_1 (S_1 layer of the secondary wall), CW (Secondary wall). Cross section, x 13,000. – Fig. 10. A half-bordered pit-pair between a ray parenchyma cell (RP) and an earlywood fibre-tracheid (FT). Note the loose texture of the protective layer (PL). The diameter of the pit chamber of the bordered pit in the fibre-tracheid is larger than that of the opposite pit. FTCW (Cell wall of fibre-tracheid), PC (Pit canal). Cross section, x 13,000. –– Fig. 11. A half-bordered pit-pair between a ray parenchyma cell (RP) and an earlywood vessel (EV). Note the density of the pit membrane which is similar to that of the adjoining protective layer (PL). S_1 (S_1 layer of the secondary wall). Cross section, x 14,500. –– Fig. 12. A half-bordered pit-pair between a ray parenchyma cell (RP) and a fibre-tracheid (FT). Note the two simple pits opposite to a bordered pit. PC (Pit canal), PL (Protective layer). Cross section, x 21,000.











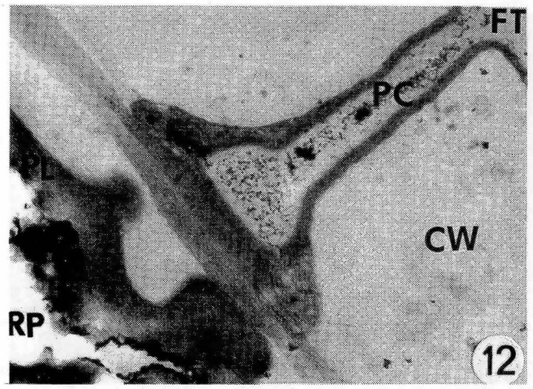


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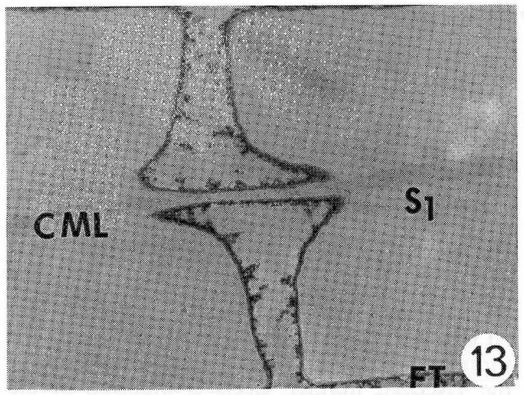
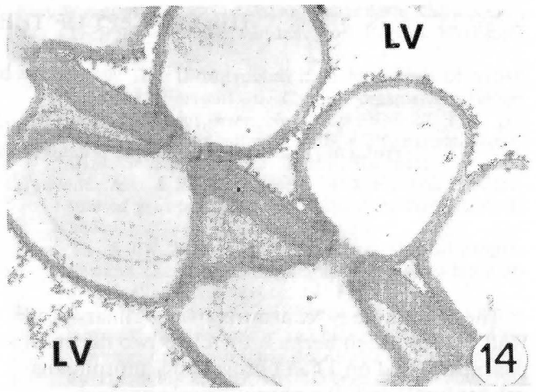
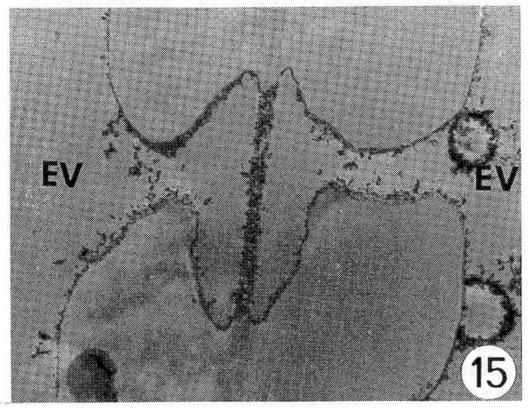
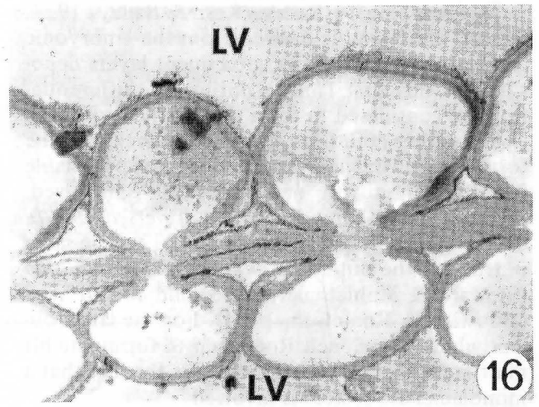
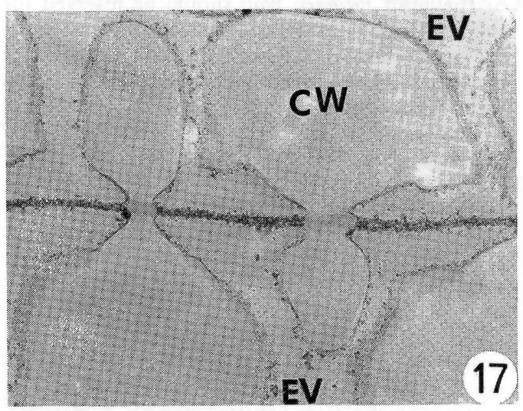
Fig. 13. A bordered pit-pair between two fibre-tracheids (FT). Note the pit membrane showing no visible openings. Note also the S_1 layer of the secondary wall ending at the edge of the pit chamber. CML (Compound middle lamella). Cross section, x 15,000. –– Fig. 14. Three bordered pit-pairs between two latewood vessels (LV) in the heartwood area. Note the deposition of secondary encrustants darkening the pit membrane. Cross section, x 15,000. –– Fig. 15. A bordered pit-pair between two earlywood vessels (EV) in the sapwood area. Note that primary matrix substances have already disappeared from the pit membrane and only the cellulosic microfibrils remain. Cross section, x 15,000. –– Fig. 16. Three bordered pit-pairs between two latewood vessels (LV) in the heartwood area. Note a discontinuity in the middle of the compound middle lamella and the deposition of secondary encrustants in the pit membrane. Cross section, x 15,000. –– Fig. 17. Irregular bordered pit-pairs between two earlywood vessels (EV). Note the two pit cavities joined together forming a single pit canal. Cross section, x 11,000. –– Fig. 18. A scalariform perforation plate between two earlywood vessel elements (EV) in the heartwood area. Note the sectional view of a perforation bar (PB) and a bordered pit-pair (arrow) at the edge of the perforation plate. Cross section, x 4,500.
N o t e : All sections were taken from the sapwood area, except the sections in the Figures 14, 16 and 18.

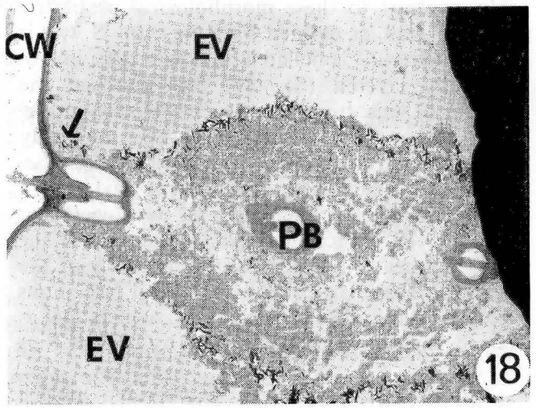












THE CONCEPT OF THE PRIMARY CELL WALL

by

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The terminology concerning the Primary Cell Wall P is confused because there are two different concepts based on 1) an ontogenetic (morphological, textural) and 2) a physiological approach.

1) According to Bailey (Kerr & Bailey, 1934, fig. 1), the P wall is derived from the embryonic cambial wall, and all the subsequent layers deposited on this first lamella during cell differentiation are considered to form the Secondary Wall S.

Since this definition applied originally to the formation of tracheids in Conifers, no appreciable longitudinal growth of the P wall is involved. Electron microscopy disclosed a *dispersed texture* of its cellulose fibrils (Bosshard, 1952). The same is true for the outermost wall lamella of *Valonia* (Steward & Mühlethaler, 1953) and cotton hairs (Houwink & Roelofsen, 1954). For the latter object which occasioned Roelofsen to formulate his multi-net theory, the authors stress the fact that a monolamellate system is involved.

In contrast to these morphological properties of the P wall, as defined by Bailey, the S wall is ultrastructurally lamellated and, as a rule, microscopically layered (S_1, S_2, S_3). Further, the amount of anisotropic fibrillar material (cellulose and/or other microfibrils) prevails over the highly hydrated isotropic plastic matrix substances (hemicelluloses, pectins) in such a way that only a *parallel texture* of the fibrils is possible (Frey-Wyssling, 1976: 15). The parallel texture of the S walls is made possible by the tendency of the cellulosic chain lattice to incur lateral fasciations (Frey-Wyssling, 1951; 1969: 15), which fact is named 'mesomorphic assemblage' by Danièle Reis (1978).

2) The physiological concept considers the cell wall as primary as long as it grows in area by elongation or general extension. According to this definition the deposition of multilamellate systems of considerable thickness must be called 'primary' as long as the cell is expanding, whereas such lamellated layers in conifer tracheids are termed 'secondary'.

Examples of extending multilamellate systems are: the angular reinforcements of collenchyma cell walls (Beer & Setterfield, 1958), the sclerenchyma cells of the so-called 'pericycle' in elongating shoots of *Asparagus* (Sterling & Spit, 1957), and even the classical layered wall of *Valonia*. In all these cases a crossed lay-out of parallel textured lamellae allows an areal expansion without the forming of splits in the wall, although splitting of the fasciated fibrillar sheets is observed in the individual lamellae (Steward & Mühlethaler, 1953).

It is evident that according to the physiological definition (2), the walls of the three objects mentioned were primary throughout, and no S wall would be deposited since extension growth and thickening of the wall are simultaneous processes.

At the Cell Wall Meeting 25/26 May 1978 in the Botany Department of the University Nijmegen Holland (Sassen & Wardrop, 1978), this terminological problem was discussed by H. Meier (Fribourg), J.C. Roland (Paris), M.M.A. Sassen (Nijmegen), A.B. Wardrop (Melbourne), and the author (Zürich). During this debate I advocated the following concepts.

The term *Primary Wall* should be reserved for the first lamella of the cell wall. In this way priority is accorded to Bailey's definition which dates back to 1934. All following lamellae and/or layers form the *Secondary Wall*.

Cell walls which expand should be named *Growing Walls*. Not only primary but also secondare walls may extend by growth. As a matter of fact extension and apposition growth are so intimately linked that they cannot be regarded separately, even if it were known whether the matrix substances act as an interfibrillar or as an interlamellar lubricant.

According to these definitions, the primary wall is monolamellate. It is rich in matrix substances and poor in cellulose. Therefore, a dispersed texture of the first fortifying fibrils is possible. Parallel textures in P walls, as observed in the edges of coleoptile parenchyma cells (Wardrop & Cronshaw, 1958) are an exception.

The multi-net theory of Roelofsen deals with the primary wall. It presumes that the fibrils float freely in the matrix. Although this prerequisite is true, no considerable change of the fibrillar direction is possible without a corresponding change in the diameter of the cell. The cellulose microfibrils are extremely long, so that their raising from a more horizontal to a more vertical position involves a diminution of the circumference of the wall.

In the secondary wall with less matrix and much more fibrillar material and, as a rule, parallel textures, the fibrils tend to fasciate with their neighbours. This 'mesomorphic assemblage', known for liquid crystals (Reis, 1978), goes on without any energy controlled morphogenesis; therefore, it cannot explain how the complicated textures of pit membranes, of stomata, and of other highly specialized textures are generated.

There are three stages of 'assemblage' in the organization of the fibrillar wall material: The first is the simultaneous polymerization and crystallization of the chain molecules into fibrils. In the P wall with its dispersed texture no further assemblage occurs. The second stage is a fibrillar assemblage by lateral fasciation (parallel texture) producing lamellar sheets in the S wall. Finally, the morphogenetic arrangement of aggregated fibrillar bundles around pores, into rims etc. is the third stage of these assemblages.

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WOOD ANATOMY NEWS

Note on the anatomy of Eucalypt woods and on the CSIRO wood collection

Dr. H.E. Dadswell of Australia was one of the foundation members of the Association and served as an Office holder for a number of years. His speciality in the field of anatomy was eucalypt woods and it was his intention to prepare an authoritative and comprehensive treatise on them. He collected much data to this end. His intentions were affected first by taking on administrative studies as Chief of the Division of Forest Products, CSIRO in 1960 and then by his sudden death in December 1964.

Dr. W.E. Hillis, who subsequently became leader of Dadswell's section, began the task of salvaging the mass of data. It was found that data for 108 species was completed, and that for 37 species was finished in varying degrees during Dadswell's search for taxonomic relationships. It was decided to use the limited facilities available to prepare the completed data of the 108 species for publication and to preserve the meticulous attention to accuracy for which Dadswell was renowned. The task was a long and laborious one and it involved the assistance of several people and in particular Mary Parsons, Dr. Dadswell's former assistant, Ken Bamber and Joyce Lanyon. Eventually the CSIRO Technological Paper 'The Anatomy of the Eucalypts' by (the late) H.E. Dadswell was published in 1972.

During this period, the Division of Forest Products was broken up and other organizational changes were made. As a result the existence of the Technological Paper is not as widely known among anatomists as it could be. A limited number of copies are still available for distribution. It consists of 28 pages of text, 6 plates and the data is summarized in a Table of 6 large fold-in pages.

The wood collection of 34,000 specimens of 237 families, 2225 genera and 9234 species collected by Dr. Dadswell and others is now carefully housed and in frequent use in the Division of Building Research, together with the associated slide collection and other details. The collections contain the partly described mature eucalypt woods, obtained from slow grown trees and consequently different in some aspects from those obtained today from fast-grown eucalypts.

In view of present day needs for rapid quantification of anatomical data and its storage, attention has been given over the past few years to the development of the necessary equipment. A simple device for fibre length measurement and a low-cost electronic image analyser have been developed so far for these purposes. The analyser is presently being used to relate anatomical data with wood properties and details will shortly become available.

Further information regarding the Technological Paper 'The Anatomy of Eucalypt Woods' and other aspects can be obtained from Dr. W.E. Hillis, Division of Building Research, CSIRO, P.O. Box 56, Highett, Victoria 3190, Australia.

Proposals on wood terminology

Thanks to the Multilingual Glossary of Terms Used in Wood Anatomy composed by the Committee on Nomenclature of the International Association of Wood Anatomists in 1964, terminological confusion is limited to a minimum in our disciplin. However, all those who use the glossary regularly will also realize that some of the definitions are open to debate and that more terms could have been included and defined. While discussing the possibilities of revising the Glossary (a very time-consuming enterprise!) at the IAWA Business Meeting in Blacksburg this year, Dr. Keating suggested that for the time being it might suffice to start a column of proposals on new or amended definitions for wood anatomical terms in the IAWA Bulletin, following the example of nomenclatural proposals in the journal Taxon. This suggestion was welcomed by all attendants of the meeting, and is wholeheartedly adopted by the editors of the IAWA Bulletin. All IAWA members are invited to submit seriously considered terminological proposals for this new column in the future. All proposals should be carefully considered by the IAWA membership, and if one finds the proposal unacceptable this should be written to the author and the editors of the Bulletin. Objections will also be published, and only those proposals which do not meet with any opposition for a period of one year can be considered to be generally accepted. In recent IAWA Bulletin papers some formal proposals have been made on the definitions of some terms in the Glossary. The amended or new definitions are repeated here as the first official proposals for this new column, which is hoped to become a useful means for maintaining an up-to-date, uniform terminology in wood anatomy.

Ray initial – The complex of cambial initials giving rise to an entire ray

Ray cell initial – A cambial initial giving rise to a ray cell; usually one of a group and often more or less isodiametric as seen in tangential section
Proposed by Rudolf Schmid, IAWA Bulletin 1976/4: 56.

Protoxylem – First-formed primary xylem (usually with tracheary elements characterized by annular or spiral thickenings)

Metaxylem – Later-formed primary xylem (with scalariform, scalariform-reticulate, or pitted wall thickenings)
Proposed by Rudolf Schmid, IAWA Bulletin 1977/1: 9.

Tile cells – Special type of erect cells, without visible contents occurring in radial series, much narrower radially than the procumbent cells of the ray and interspersed between them
Proposed by S.R. Manchester & R.B. Miller (following Chattaway, 1933), IAWA Bulletin 1978/2&3: 23–28.

Requests for wood samples for sectioning

I. Mrs. T. Baretta-Kuipers, Institute of Systematic Botany, Transitorium 2, De Uithof, Utrecht, The Netherlands, requests sectioning blocks of well-documented and herbarium-backed wood samples for her studies of the systematic wood anatomy of the *Pithecellobium* complex (Leguminosae): *Abarema, Archidendron, Arthrosamania, Cathormion, Cylindrokelupha, Macrosamania, Pithecellobium, Samania* and *Zygia*. Species from SE. Asia, Malesia and Australia are especially wanted.

II. Mr. M. Molenaar, Leiden, has recently embarked on a postgraduate project on the systematic and ecological wood anatomy of Casuarinaceae. Off-cuts for sectioning and scanning electron microscopy of the following species of *Casuarina* (in some institutes possibly partly named *Gymnostoma*) are requested together with detailed collecting data and reference to a herbarium voucher: *Casuarina acuaria, australianum, brachystachys, campestris, chamaecyparis, decussata, diminuta, drummondiana, fibrosa, glaucescens, gracilis, grevilleoides, gymnanthera, helmsii, huegeliana, humilis, intermedium, leucodon, mesostrobilum, microstachya, monifera, nana, nobile, nodiflorum, obesa, orophila, palawense, paludosa, pinaster, pusilla, ramosissima, rigida, riparia, sclerocladа, spicigerum, striata, teres, terminale, trichodon, vitiense.* Sapwood is preferred to heartwood in view of sectioning difficulties. Please send off-cuts to P. Baas, Rijksherbarium, Schelpenkade 6, Leiden, The Netherlands.

(continued on page 87)

VASCULAR NODULES IN THE PITH OF YEW (TAXUS BACCATA L.)

by

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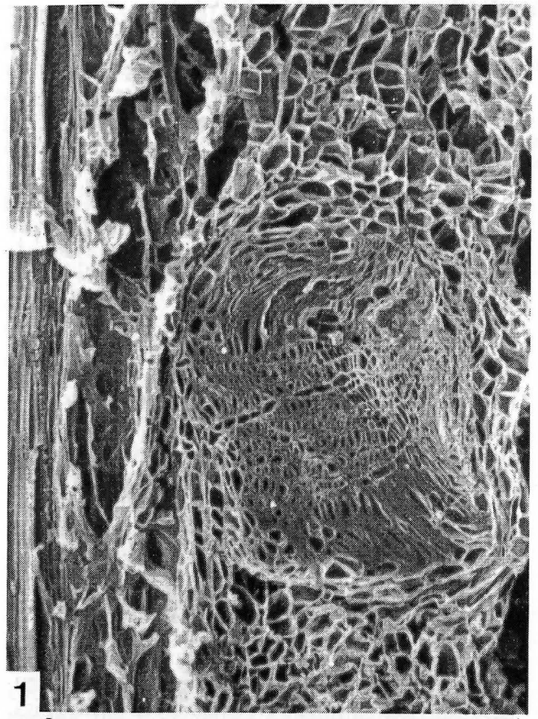
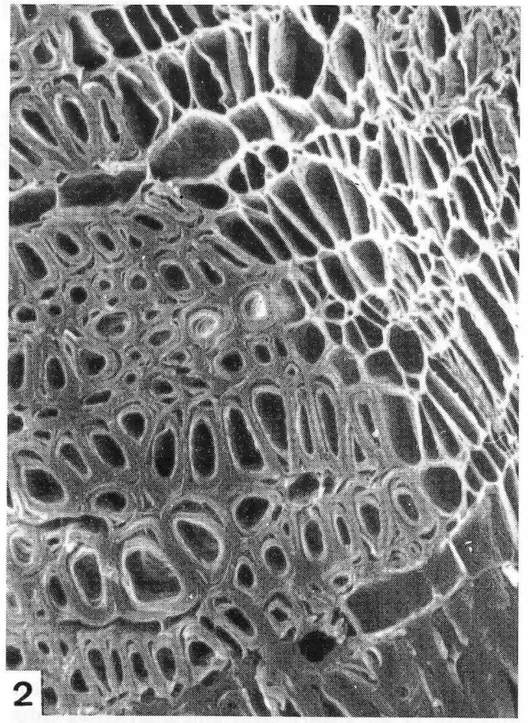
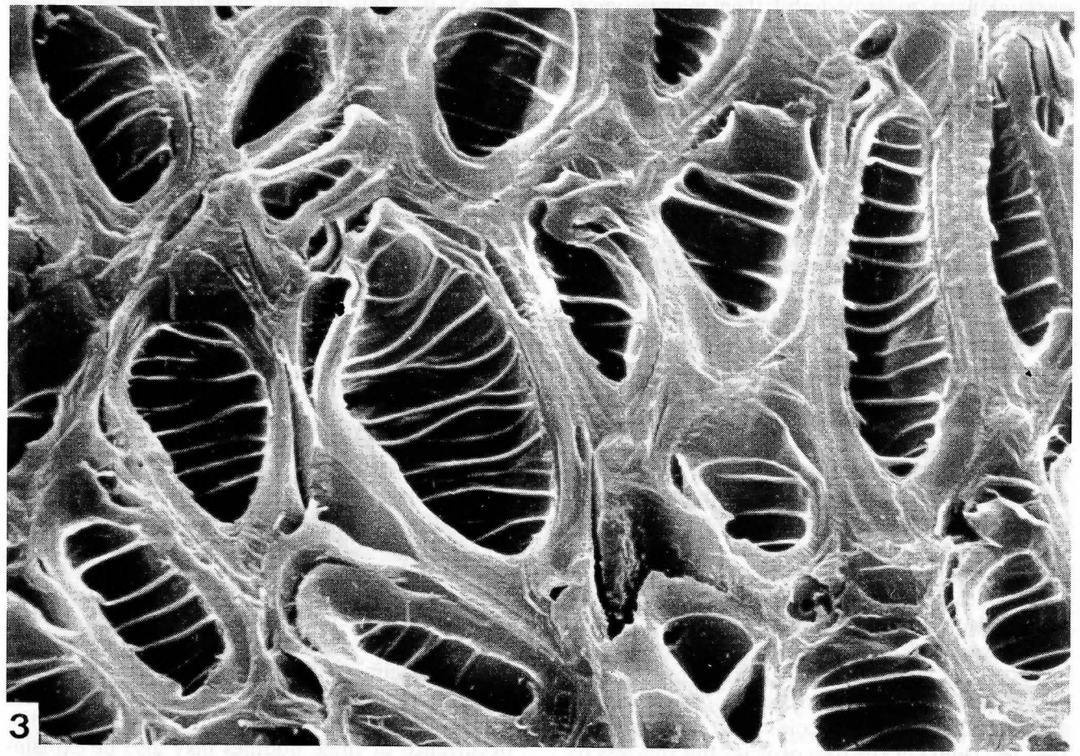
Our knowledge of the anatomy and physiology of the pith in woody plants is scattered in a large number of publications. There are few papers mainly or fully devoted to this subject, and yet the pith structure may often be helpful in diagnosis, render valuable information for systematic considerations and interesting clues from the cell physiological point of view. Perhaps the most comprehensive and extended survey in this field is the earliest one, made by Gris (1872) who studied the anatomy and physiology of the pith in 200 woody angiosperms belonging to 130 genera and 40 families. Gris elaborated a classification of pith types and established the longevity of the pith cells in several species. Kassner (1884) dealt with the pith of 28 woody angiosperms, partly re-examining Gris' results. Kobler's (1908) work on the pith in 23 angiosperms and 5 gymnosperms contains more macroscopical than microscopical data. Tassi (1906) described the pith structure in members of 28 gymnospermous genera. His results were re-examined and completed by Steinböck (1926) in 66 recent and fossil gymnosperms. A detailed study on the pith anatomy in the Taxodiaceae containing data on 13 species belonging to 8 genera and an identification table was published by Doyle and Doyle (1948). The pith structure of 3 *Larix* species investigated by Micek (1958) does not enable a specific identification. Kubart (1924) was probably the first to recognize the diagnostic importance of the pith, particularly in the identification of fossil gymnosperms. For instance, the pith structure allows a clear distinction between *Larix* and *Picea* not rendered by wood anatomy, and the same applies for some genera of the Podocarpaceae (Steinböck, 1926; Kostyniuk, 1949). A comparative study of the pith anatomy, carried out by modern methods, could probably offer some clues for the newly discussed broad taxonomic considerations of the gymnosperms (Keng, 1963, 1975).

The pith of yew (*Taxus baccata* L.) has been repeatedly investigated (Rothert, 1899; Tassi, 1906; Steinböck, 1926) and described as composed solely of parenchyma cells. However, in the course of a routine examination Bosshard and Kučera (1972) found tracheoids (non-prosenchymatous tracheids) in the pith of yew, and this was recently confirmed in an SEM study by Kučera (1977; see also Materials and Methods therein). While studying the tracheoids, several nodules in the pith were found (Fig. 1). These medullary nodules proved to be composed of tracheids, sieve cells, and a cambial zone lying in between them (Fig. 2). As they occur in the pith, it appears to be appropriate to term these cells and tissues medullary tracheids, medullary sieve cells, and medullary cambium. Other possible epitheta are 'local', 'special', or 'internal' (cf. Scott and Brebner, 1889). The shape and size of the medullary tracheids is highly irregular (Fig. 3). Their cell walls are very much thicker than those of the surrounding parenchyma cells. The layering of the secondary wall is clearly visible in the SEM. Prominent helical thickenings with irregular course and frequent branching (or fusion) are a constant feature of the tracheids (Figs. 4 & 5). Bordered pits are irregularly distributed in the tracheidal cell walls (Figs. 4 & 5). In regard to the cell wall thickness, helical thickenings, and size and distribution of the bordered pits, there is basic similarity between the medullary tracheids and the tracheoids in the pith of yew. The occurrence of vascular bundles in the pith is wide-spread within the angiosperms. Metcalfe and Chalk (1950) listed 36 dicotyledonous families where medullary bundles are known to occur in some or all of the members. The presently described vascular nodules are, however, discontinuous and infrequent and thus cannot be compared with the medullary bundles of the angiosperms. The only similar observation to the present one was made by Jaccard (1910) in the pith of spruce (*Picea excelsa* Link). Unfortunately his drawings are of a rather poor quality. Because of their similarity to bird's eye structure and wound xylem, Jaccard considered the tracheids in the pith to be wound tissue and suggested as possible cause of their formation pressure, frost, fungal or insect attack. The material employed in the present investigation did not show any sign of external influence, such as wounding, fungal or insect attack on its surface. All the selected shoots were healthy and vigorous. Nevertheless, the possibility of an external agent (e.g. frost, pressure, pollution by chemicals) causing the development of the vascular nodules cannot be completely excluded. On the other hand, the occurrence of these nodules may also be explained by some rare constellation of the developmental conditions of the pith.







The pith parenchyma cells surrounding the vascular nodules occasionally develop certain morphological modifications.

1. The occurrence of trabeculae. – These rod-like extensions of cell wall material traversing the cell lumen are often associated only with the tracheids of the secondary xylem of the gymnosperms, although their occurrence is far more general (Keith, 1971). They have recently been observed in vessel members of *Knightia excelsa* R. Br., a member of the Proteaceae family (Butterfield and Meylan, 1972). Trabeculae occur in some pith parenchyma cells in the neighbourhood of the vascular nodules (Figs. 6 & 7). To our knowledge this is the first report on trabeculae in parenchyma cells. The trabeculae show a typical increase in diameter where they come into contact with the cell walls (Fig. 6), and they may be hollow (Fig. 7). It is noteworthy that the trabeculae often occur together with certain structural abnormalities, such as bird's eye structure, growth-ring depressions, abnormally large horizontal resin ducts, and wound tissue formation (Keith, 1971).

2. Wrinkled (folded) cell wall. – A wrinkled cell wall was observed in a number of pith parenchyma cells surrounding the vascular nodules (Figs. 8 & 9). The development of the folds does not show a gradual pattern. On the contrary, the folds either completely cover the cell walls or they are absent. Parenchyma cells with heavily wrinkled and smooth cell walls occur often next to each other (Fig. 8). Many folds display branching (Fig. 9). The shape and size of the folds as well as their distributional pattern suggest that they are a developmental abnormality, probably caused by high pressure in the pith, connected with the growth of the vascular nodules. The same may apply for the trabeculae.

Acknowledgement

The award of a post-doctoral fellowship by the University of Canterbury, Christchurch, New Zealand, and a grant of the Huber-Kudlich Stiftung, Zürich, Switzerland, are gratefully acknowledged.

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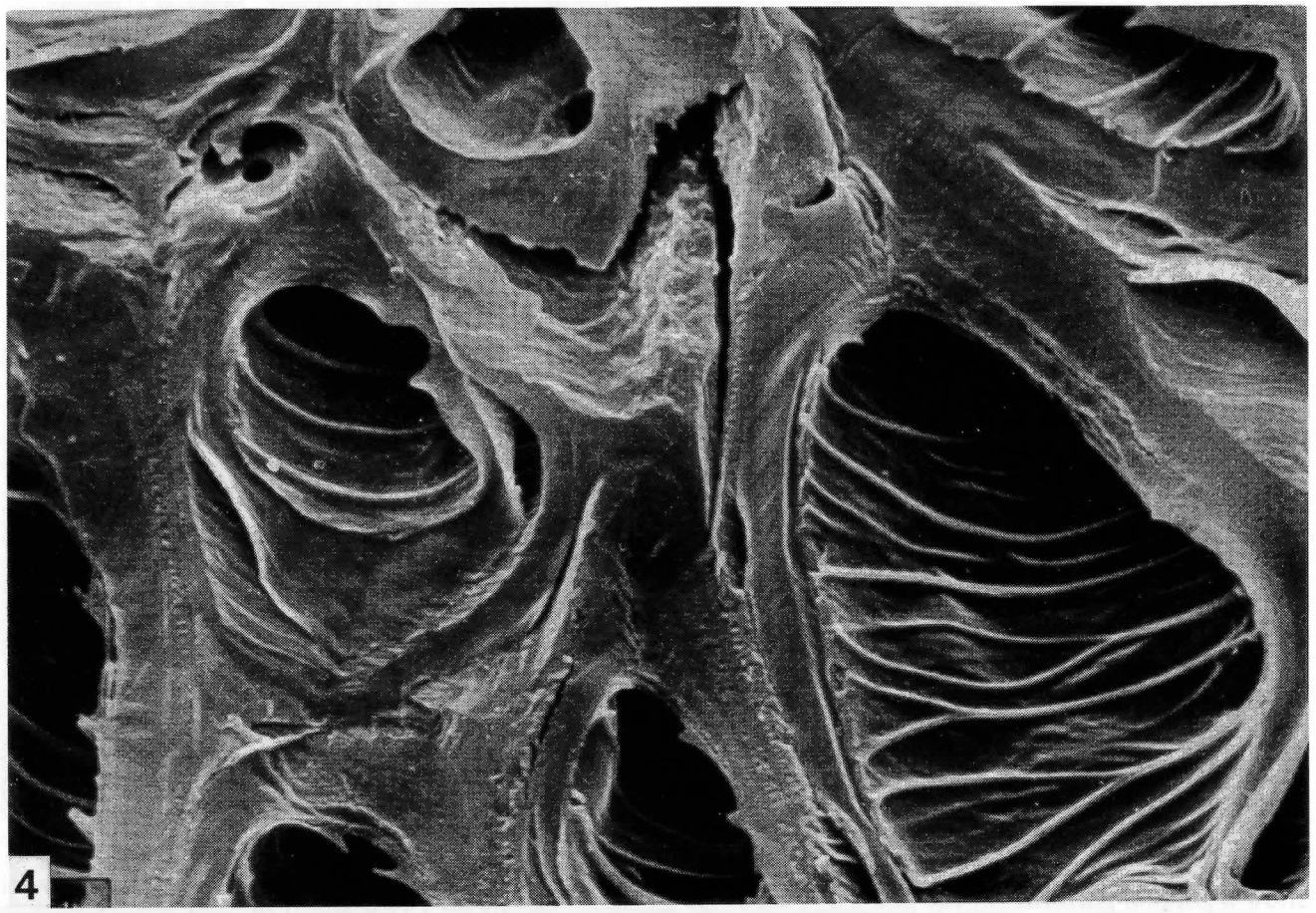
Fig. 1. Vascular nodule in the pith of yew. Below and above pith parenchyma, to the left side xylem tracheids; x 120. — Fig. 2. Central part of a medullary nodule; medullary tracheids to the left, medullary sieve cells to the right, and a medullary cambium in between. Note the obliterated sieve cells in the right upper corner; x 610. — Fig. 3. The xylem-part of a medullary nodule. Note the variability in the shape and size of the tracheids; x 1170.

Fig. 4. Medullary tracheids. Note the cell wall thickness, the course of the spiral thickenings, and a bordered pit in the top left corner; x 2090. — Fig. 5. Medullary tracheids. Note the course of the spiral thickenings and the distribution of the bordered pits; x 2410.

Fig. 6. Trabecula in a pith parenchyma cell. Note the increase in diameter at both ends; x 2350. — Fig. 7. Cross-cut hollow trabecula; x 2230. — Fig. 8. Wrinkled (folded) cell wall of a pith parenchyma cell. Note the shape and distribution of folds and their absence in the neighbouring cells; x 2160. — Fig. 9. Detail of folds in a parenchyma cell wall; x 5180.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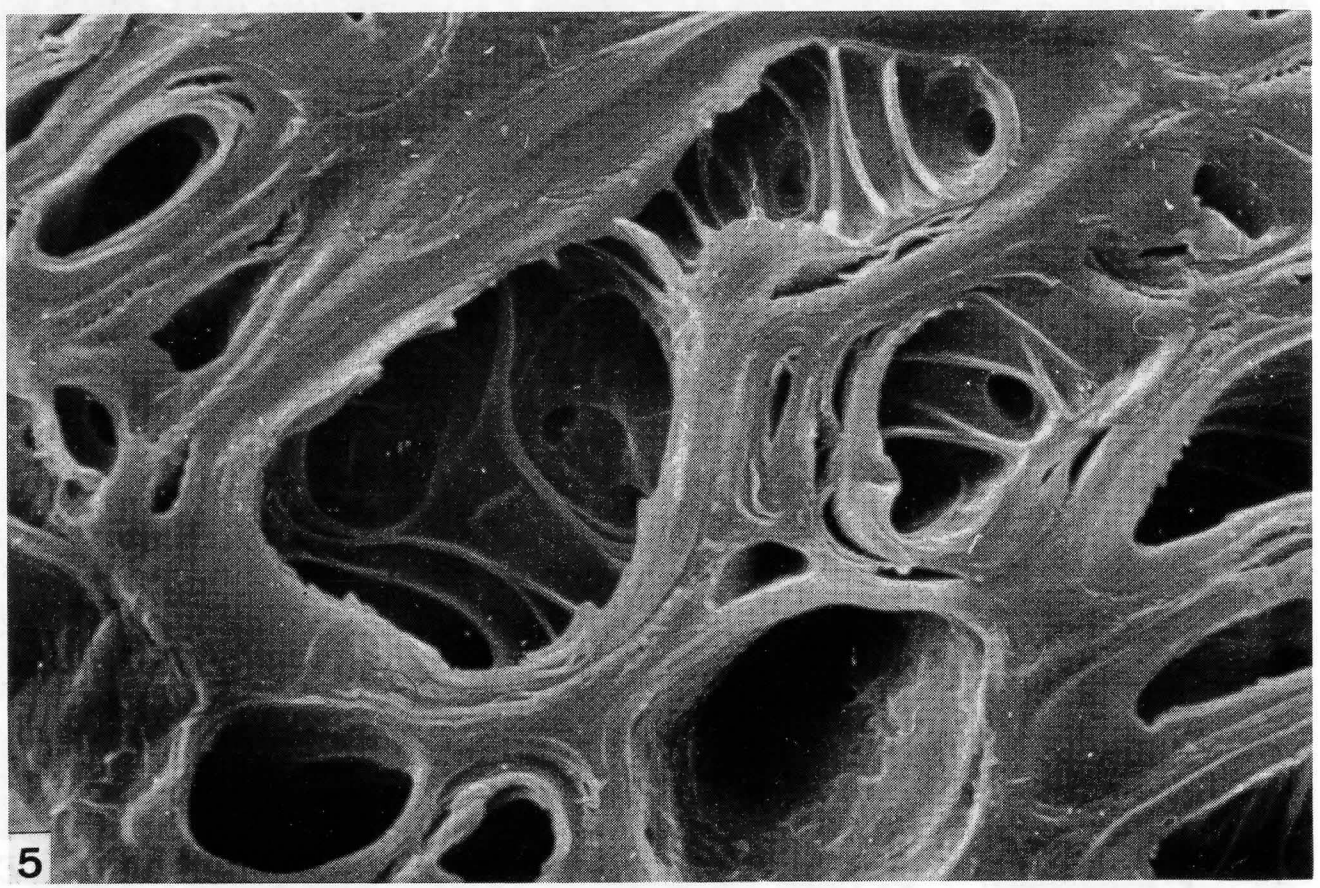
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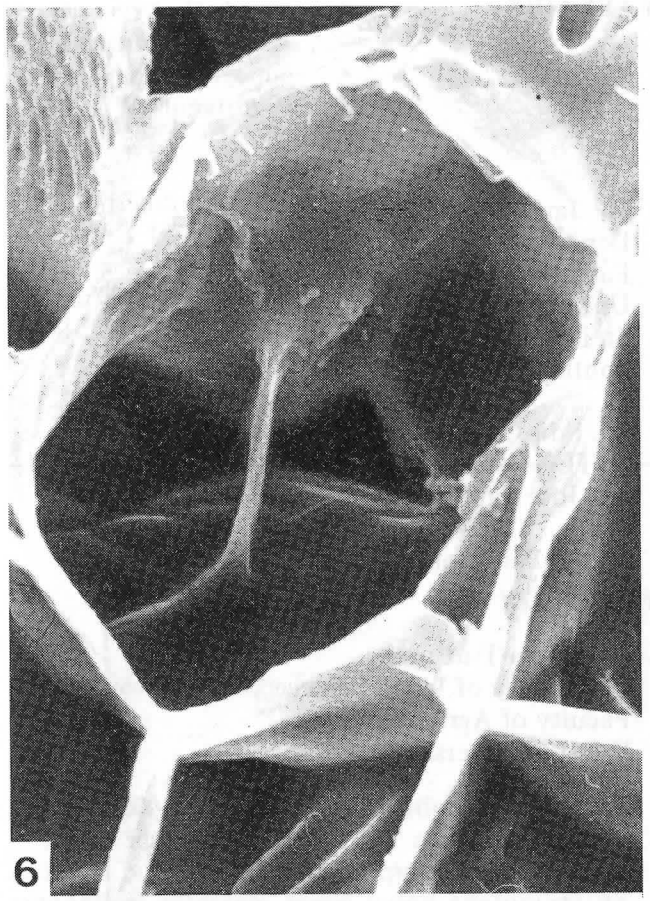
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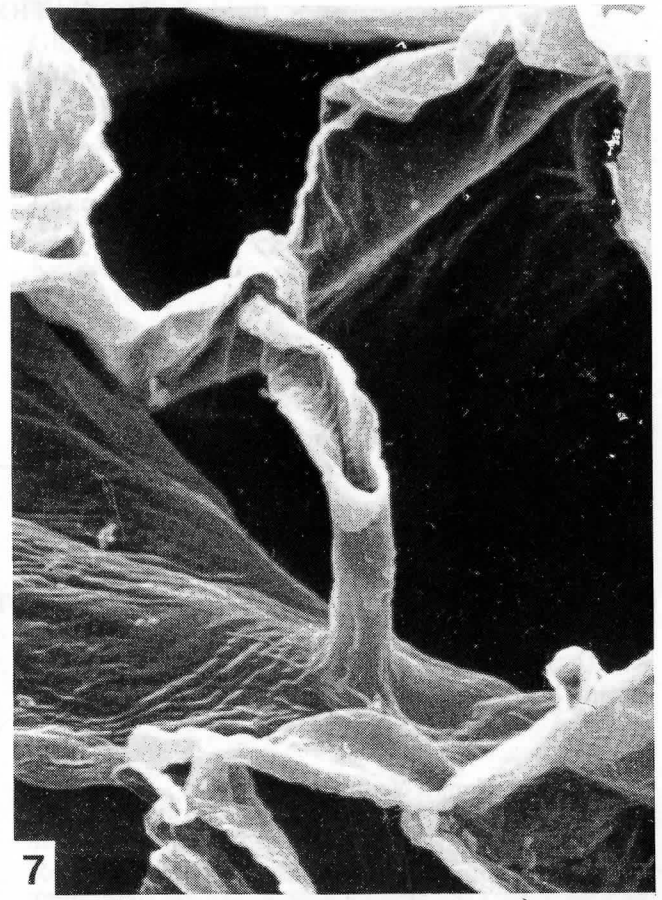
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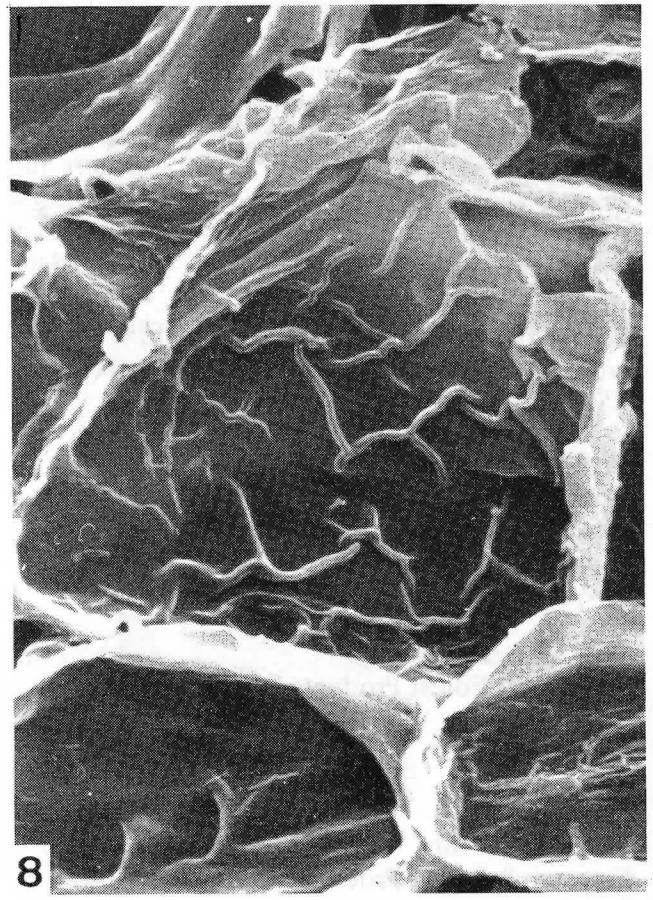
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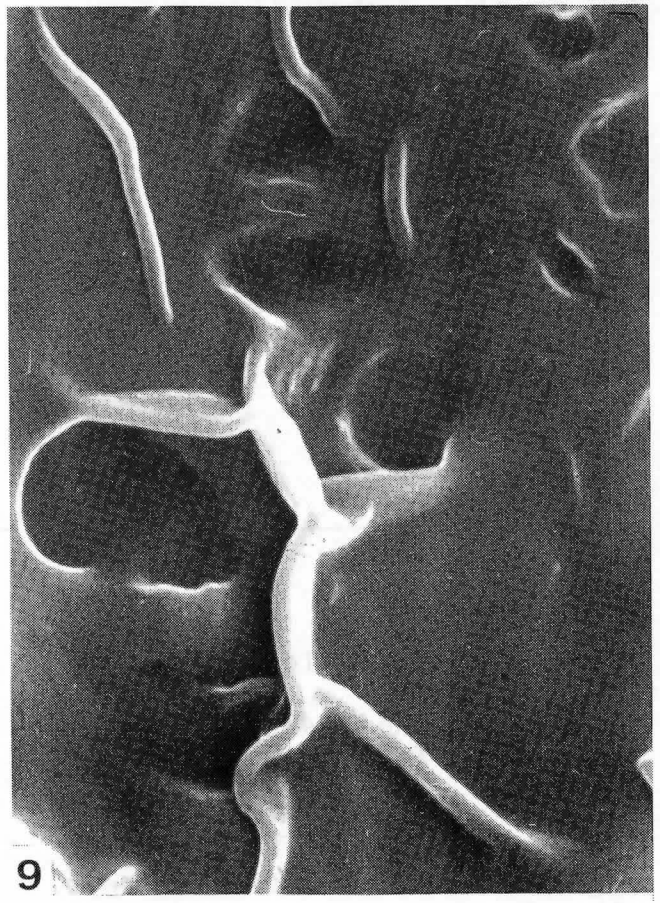
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(continued from page 80)

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WOOD ANATOMY NEWS

(continued from page 58)

Bibliography on wood identification

Wood identification has for a long time been and still is one of the major applications of wood anatomical research. Some wood anatomists devote most of their working hours to identification while many of us indulge in the thrill of 'wood detection' only from time to time in order to answer enquiries from an increasingly diverse group of customers. Dr. Martin H. Zimmermann drew our attention to the desirability of an annotated, selected bibliography on wood identification especially for the latter category of wood anatomists. A vast amount of literature exists on the subject but most of it is not easily accessible through sheer lack of a good bibliography. Miss Mary M. Gregory, Systematic Plant Anatomist and Documentalist at the Jodrell Laboratory, Royal Botanic Gardens Kew, Richmond, Surrey, TW9 3DS, England has been found prepared to compose such a bibliography for publication in a future issue of the IAWA Bulletin. This bibliography will have four entries: one by authors, one by geographical region or country, one by taxonomic grouping (for some of the major families only), and one especially for important timbers of commerce.

A number of IAWA members will be consulted for commenting on and adding to a preliminary draft of the bibliography. Meanwhile any suggestions will be welcomed by Miss Gregory.

IAWA BULLETIN

Contents

Front cover: Scanning electron micrograph of the wood of *Eugenia maire* A. Cunn. (Myrtaceae), one of the numerous New Zealand Woods pictured and described by B.A. Meylan and B.G. Butterfield in their 'Structure of New Zealand Wood', N.Z. Government Printer, Wellington, 1978. Courtesy B.A. Meylan and B.G. Butterfield, Lower Hutt and Christchurch.

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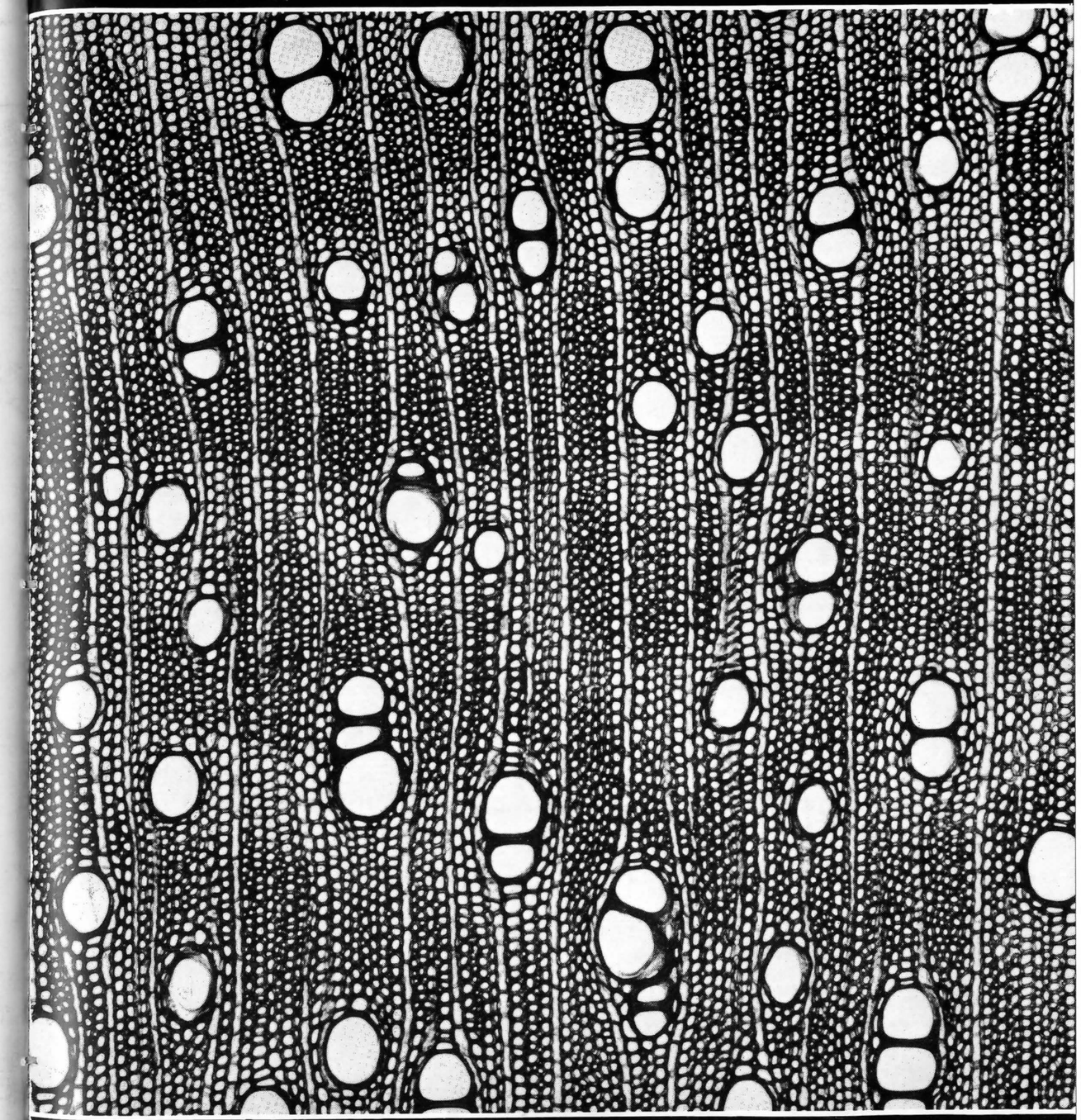

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