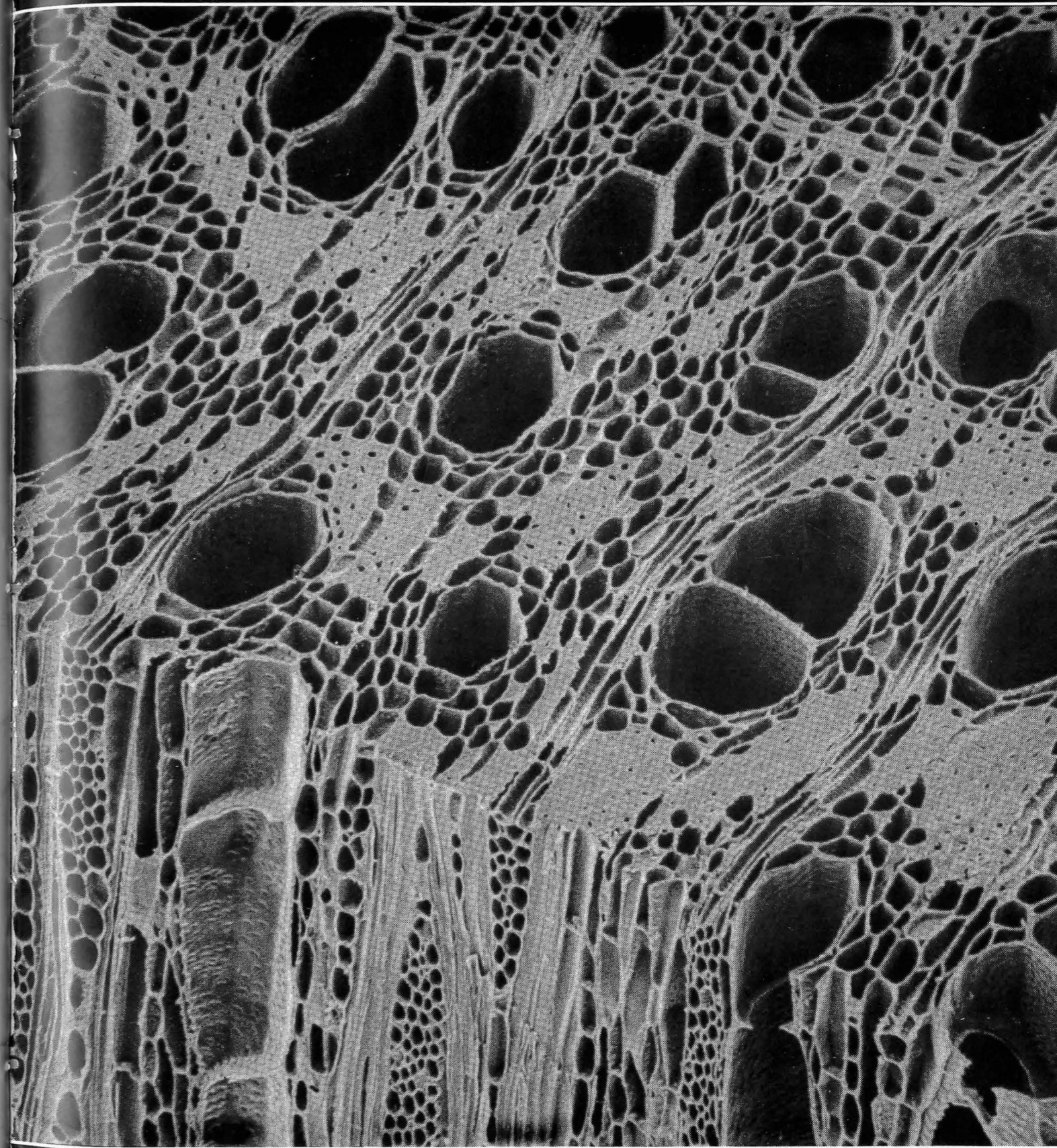


IAWA BULLETIN

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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. Meyland and B.G. Butterfield, Lower Hutt and Christchurch.

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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.

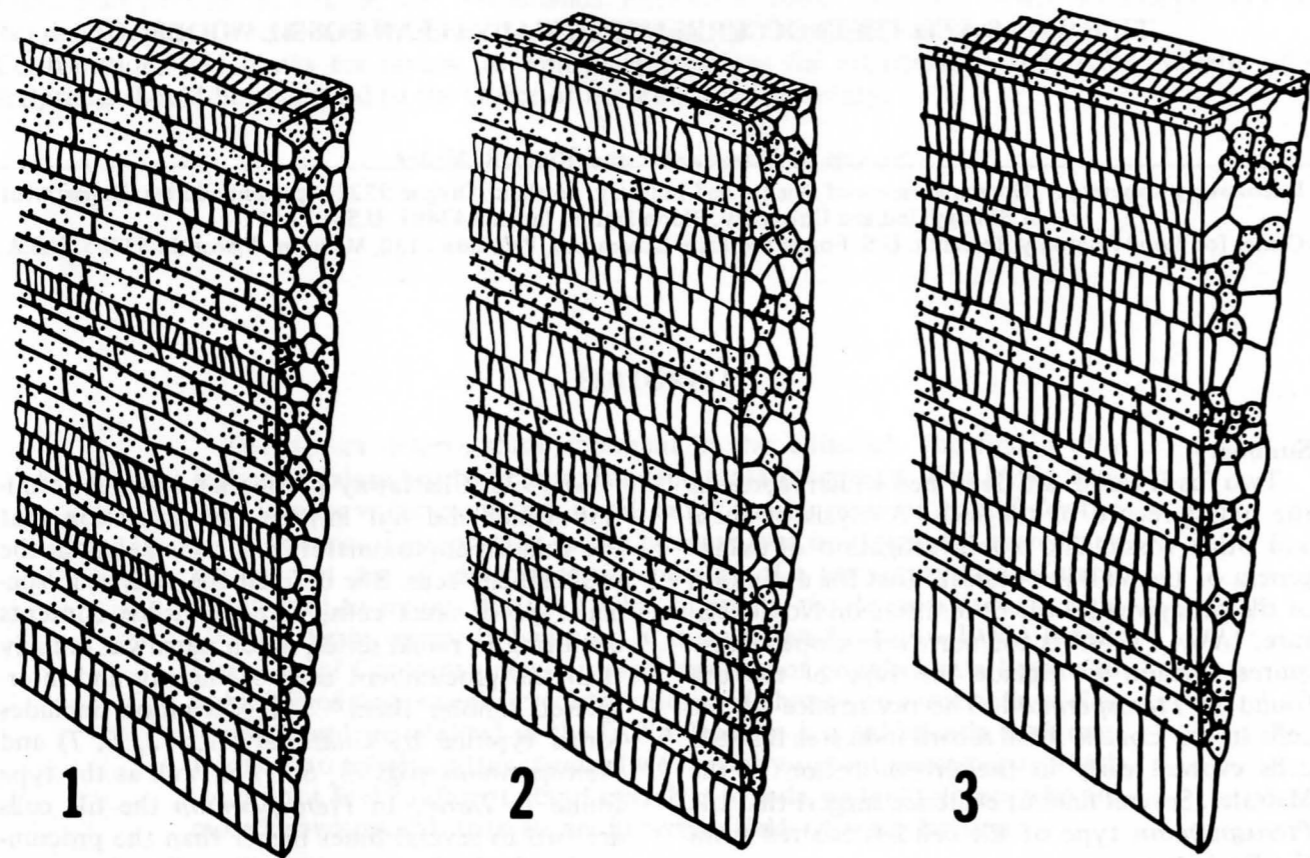
In 1933, Chattaway proposed a broader definition which did not impose the restriction that tile cells be approximately the same height as the procumbent cells. She defined tile cells as a 'special type of erect cells, without visible contents occurring in radial series, much narrower radially than the 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



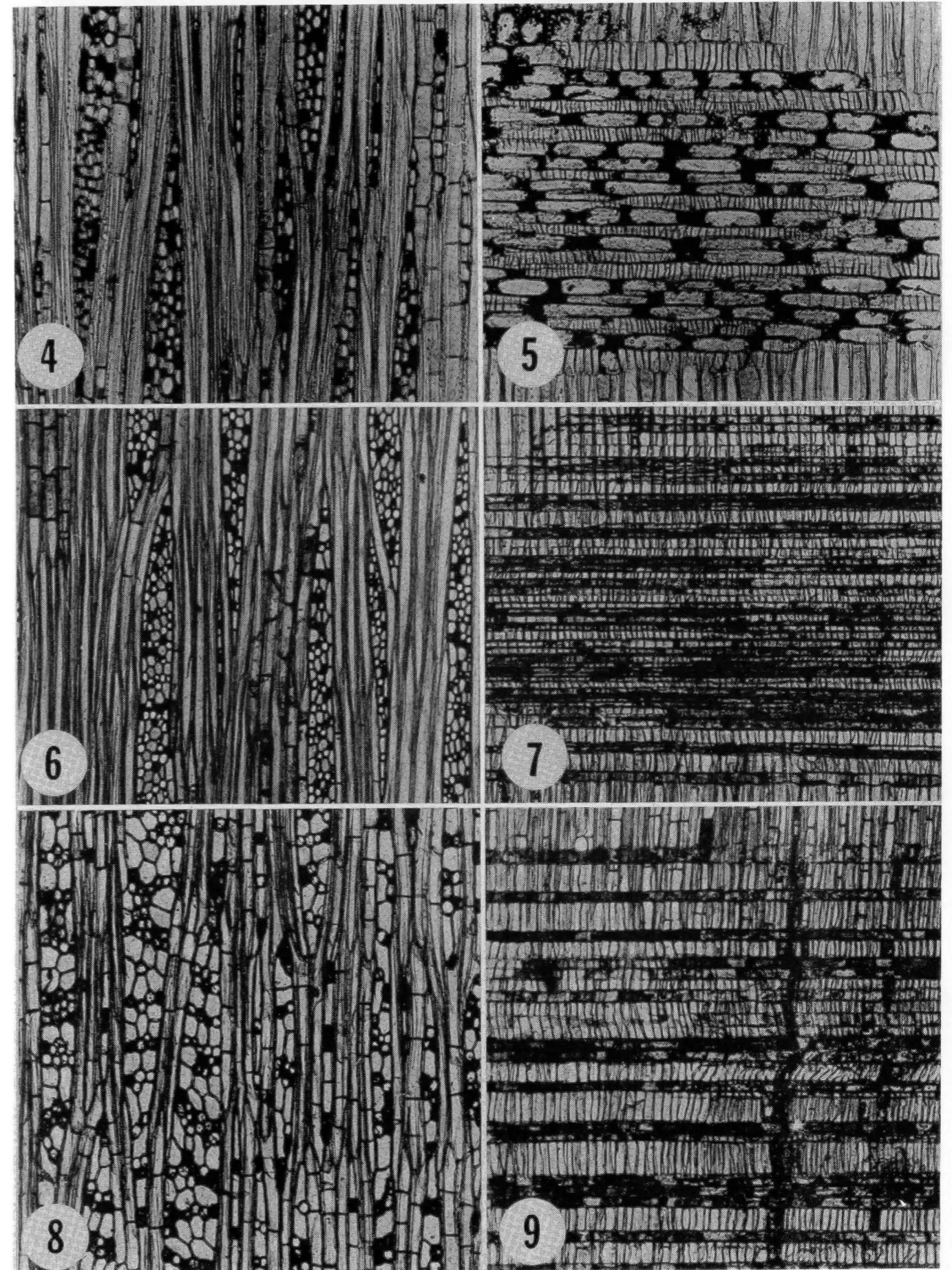
Figures 1–3: Cutaway diagrams of multiseriate rays showing different types of tile cells. Procumbent cells stipled, tile cells not stipled. About x 200. — 1. *Durio zibethinus* Murr. Tile cells of the *Durio* type, approximately the same height as the procumbent cells; not easily recognized in tangential 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.

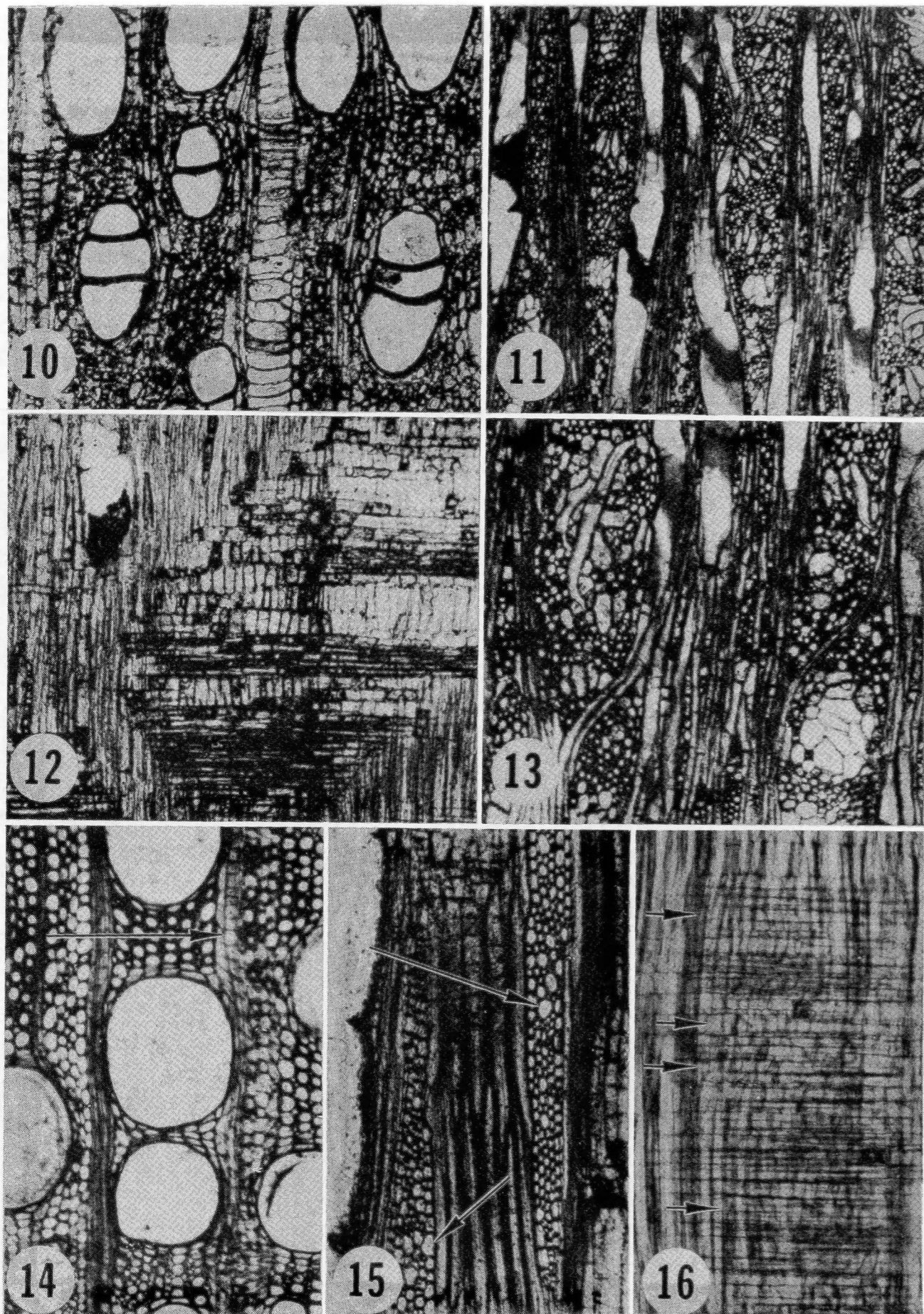
Two fossil wood samples were examined by transmitted light microscopy. Thin sections were prepared by the conventional grinding technique and by the acetate peel method. Type specimens of the fossils are housed in the Natural Sciences Collection of the Oregon Museum of Science and Industry.

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; intervacular pits alternate, 4-6 μm . Fibres non-septate, not storied. Axial parenchyma reticul te, 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; intervacular 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 Ja-

pan 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 interme-

diolate 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.

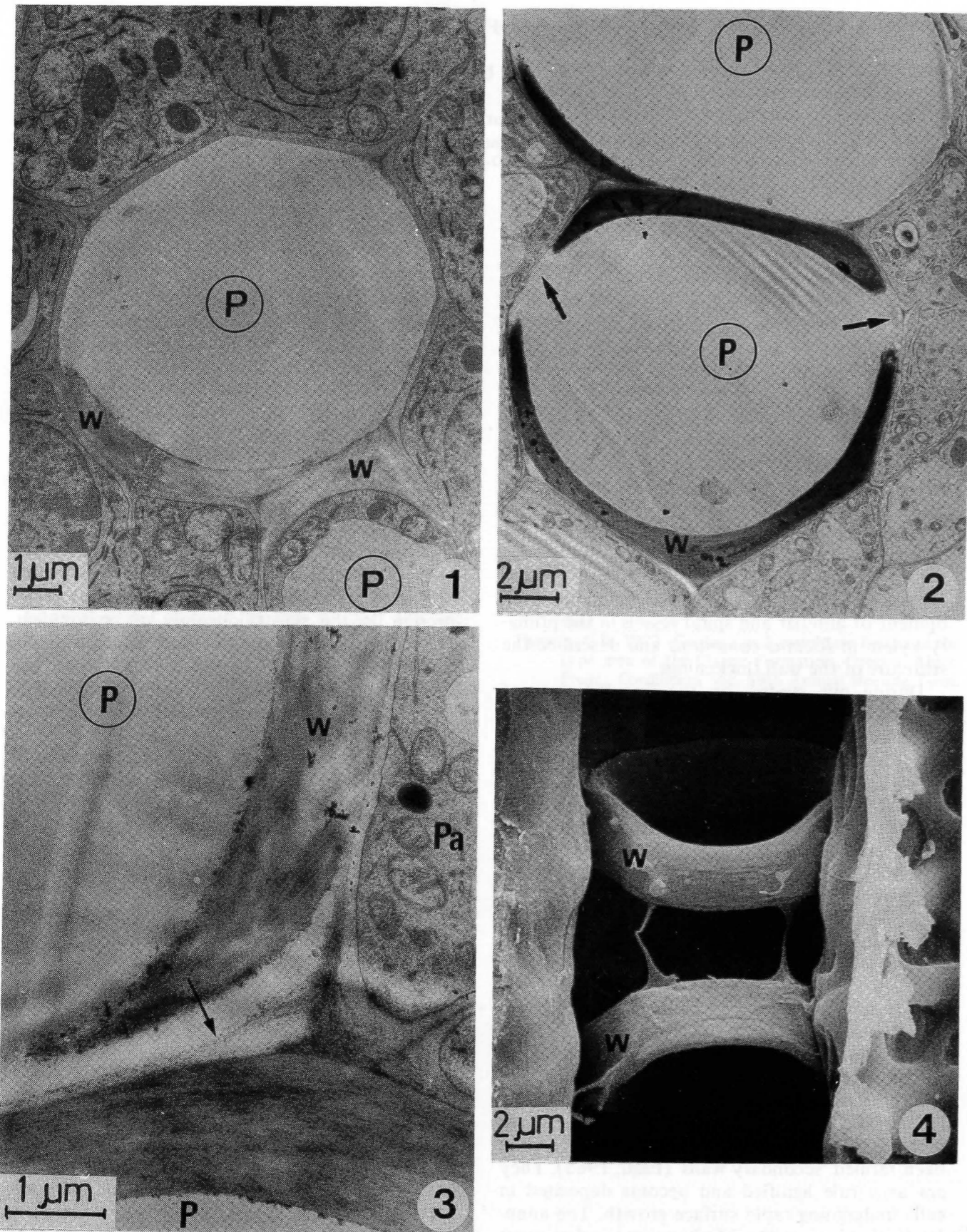
During our studies on the fine structure of bamboo (Parameswaran & Liese, 1976, 1977a, b) some observations were also made on the ultrastructure of protoxylem elements, especially in *Bambusa vulgaris* Schrad. ex Wendl. In most of the bamboo species the protoxylem consists of one or two tracheary elements 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 orig-

inal 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.

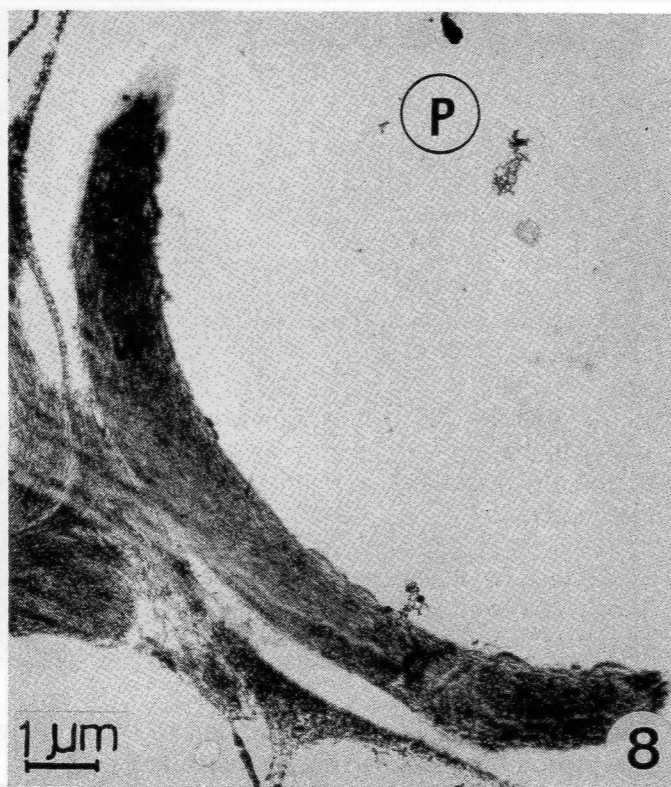
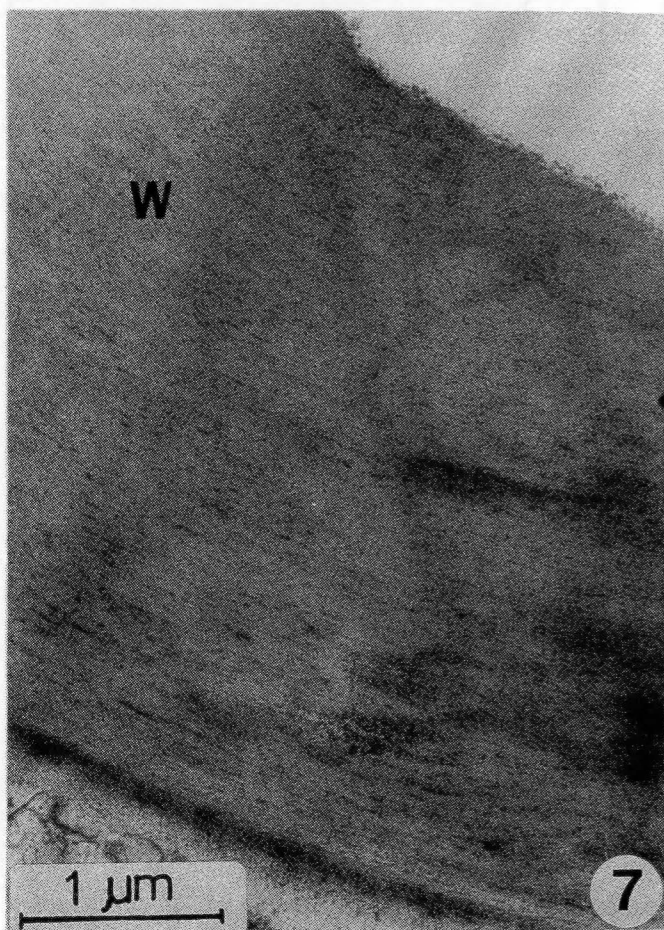
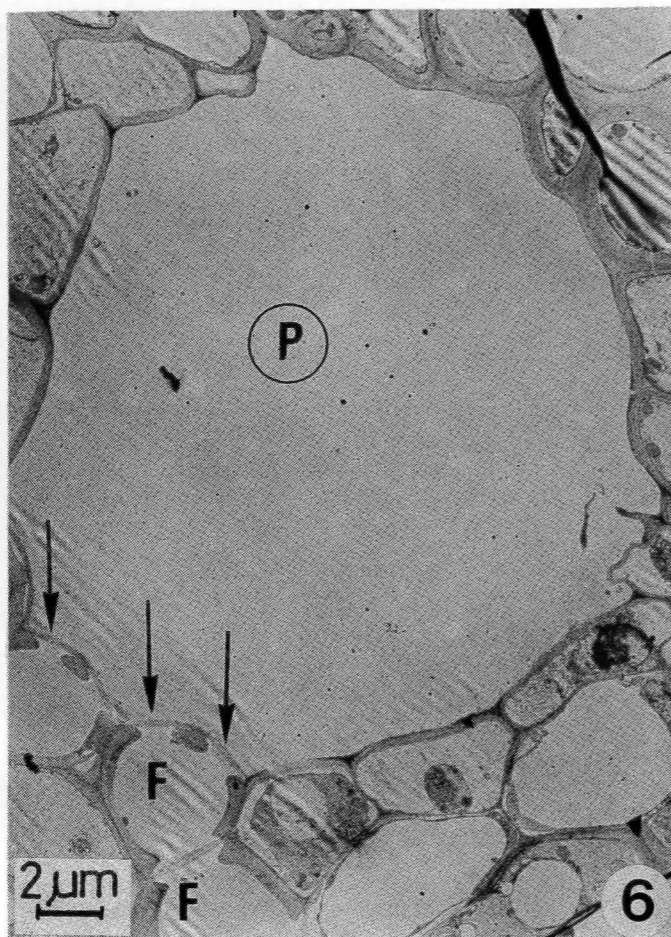
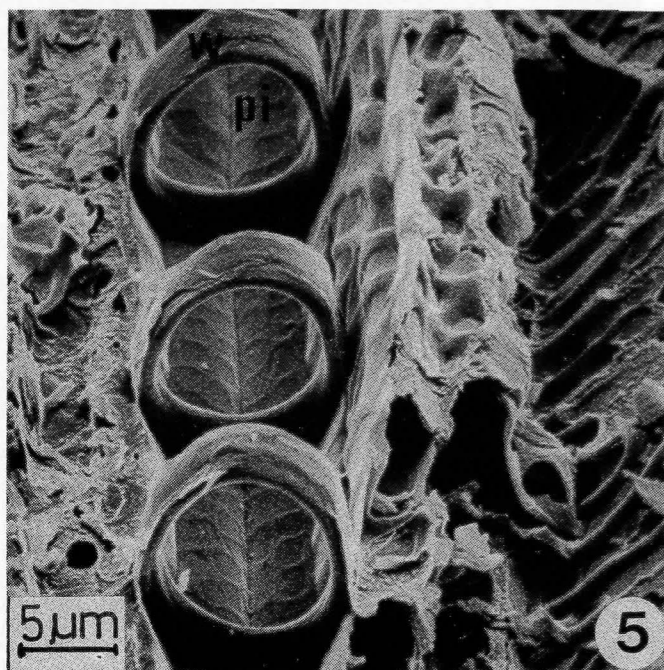
Fig. 5. Highly tilted protoxylem cell to show the arrangement of individual isolated ring thickenings in the protoxylem lacuna together with the pit fields (pi) to adjacent cells in the background. *Melocanna bambusoides*. SEM. — Fig. 6. Protoxylem lacuna (P) at a late stage of development with partly 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 TAXONOMY¹

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

¹ Scientific Article No. A2401, Contribution No. 5420 of the Maryland Agricultural Experiment Station.

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 *Selagi-*

nella, *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 per-

forations 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	%
Prevailing 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 Bailey 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 eco-

logical 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 <i>Hydrangea</i>	Section <i>Cornidia</i>
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 $0.041 \mu\text{m}$ 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.

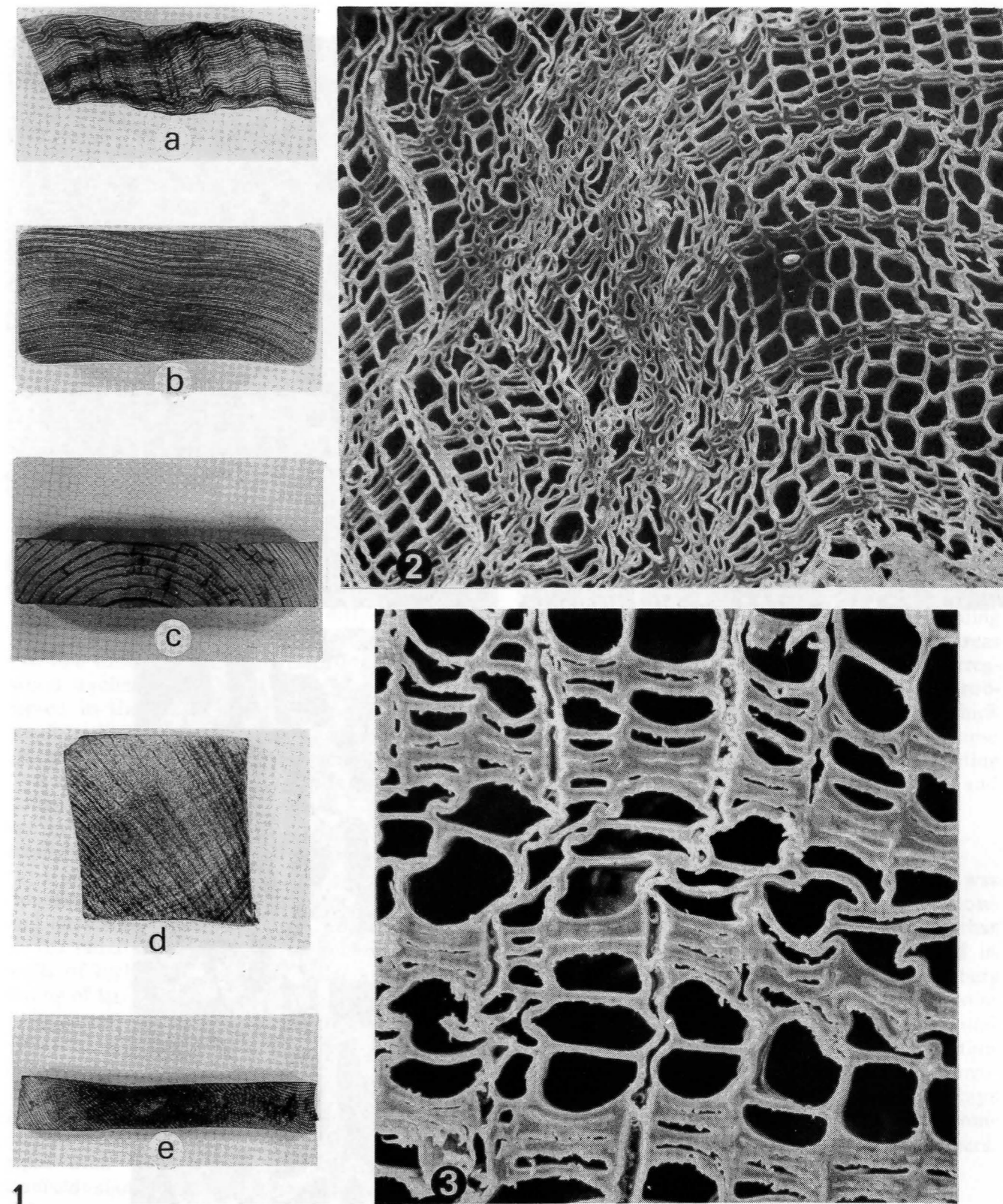


Fig. 1. Cross section views of the wood samples studied: a. Redwood, collapsed heartwood sample. Note the wavy distortion of the piece and wavy pattern of the growth rings. b. Redwood, heartwood sample with a mild collapse condition. Note the abnormal radial shrinkage. c. White fir, showing honeycombs 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.

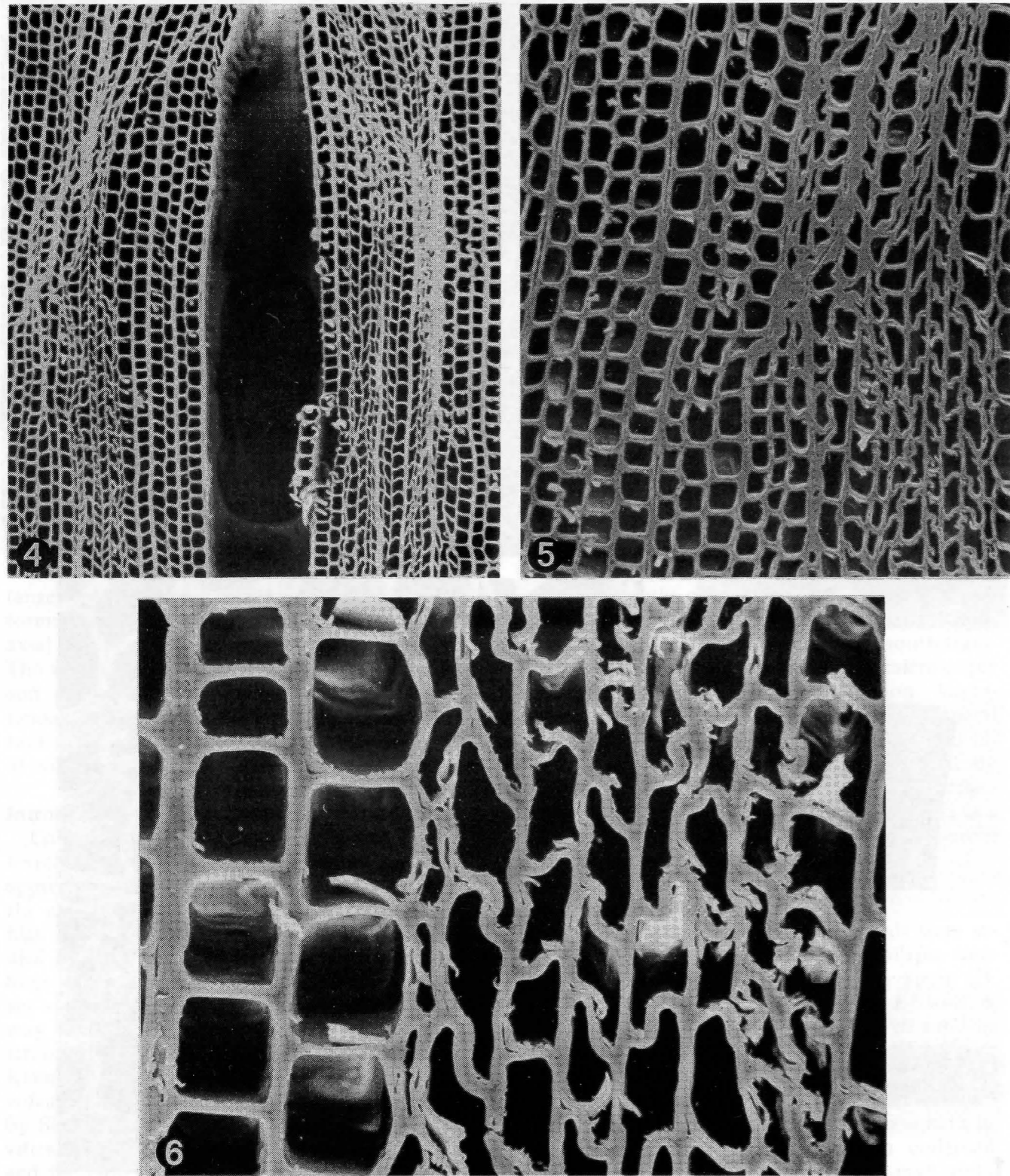


Fig. 4. SEM micrograph of a white fir honeycomb, showing collapse of earlywood tracheids on both sides of the honeycomb fissure. x 33. — Fig. 5. SEM micrograph of collapsed tracheids at the left side of the honeycomb fissure shown in Fig. 4. Earlywood tracheids collapsed tangentially. x 66. — Fig. 6. 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.

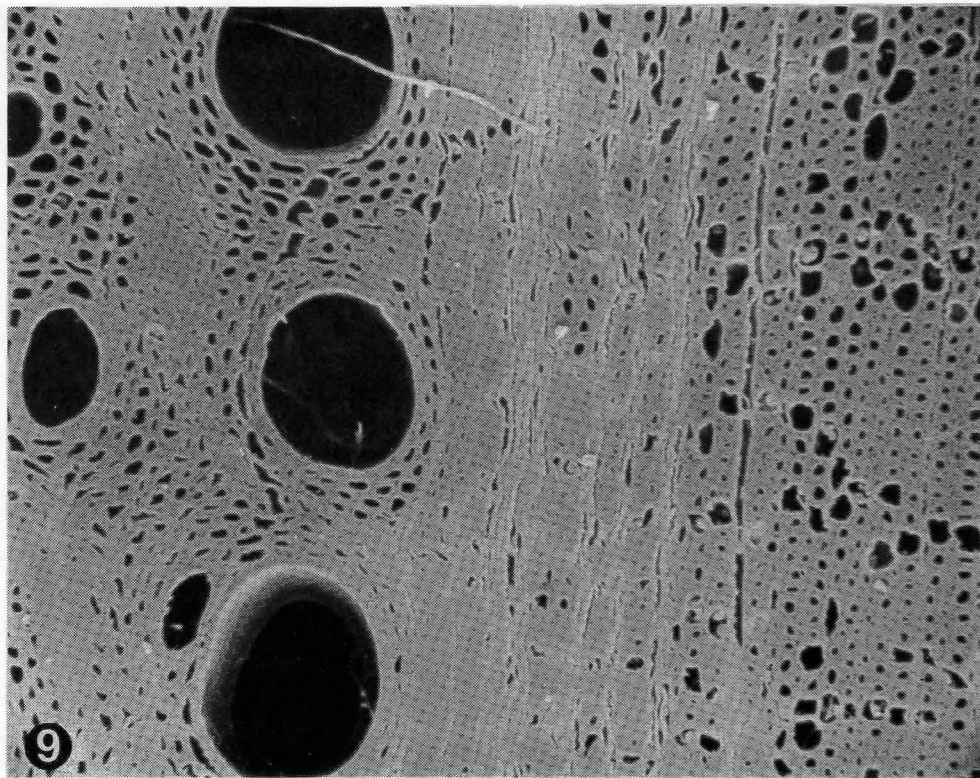
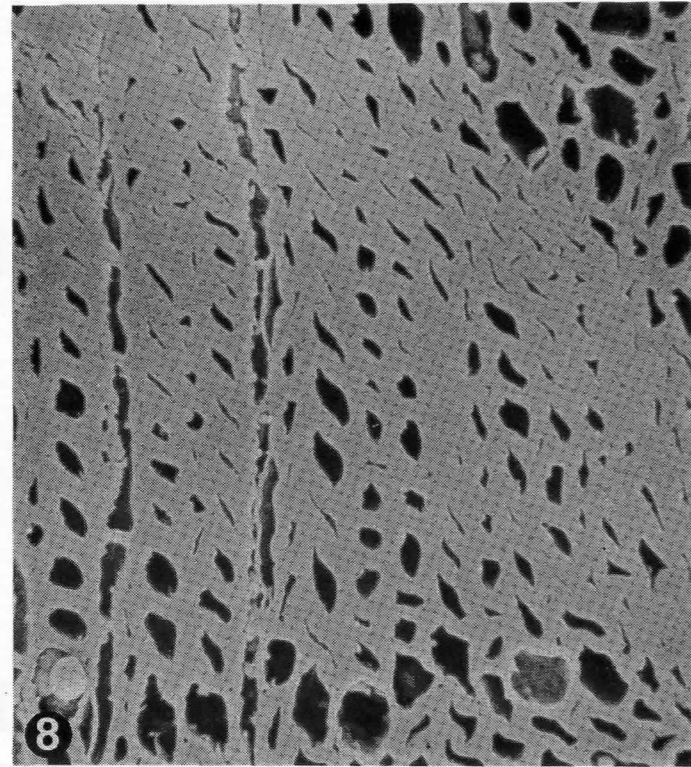
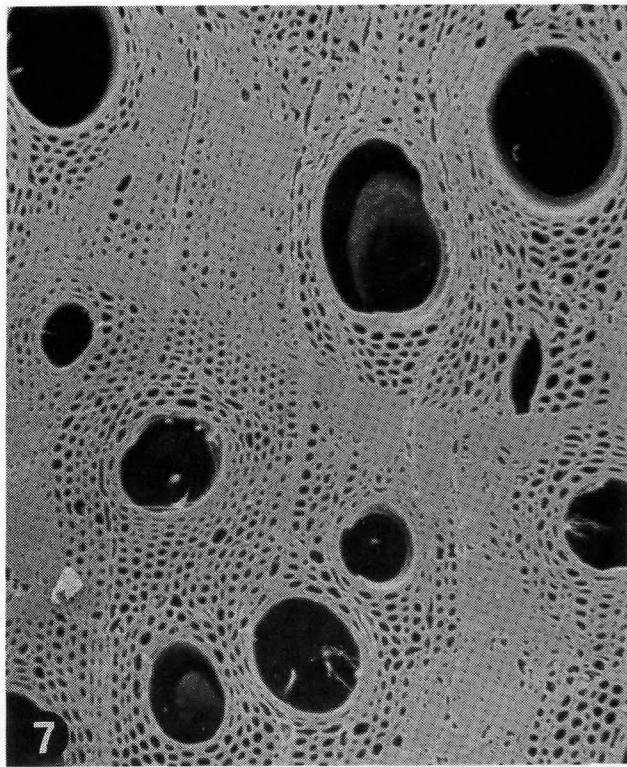


Fig. 7. SEM micrograph of collapsed tanoak wood. Collapse of fibers resulted in distortion of the growth ring and the radial filing of cells. x 33. — Fig. 8. SEM micrograph of collapsed tanoak fibers in the vicinity of vessels. Earlywood fibers collapsed obliquely while the ray and parenchyma cells did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

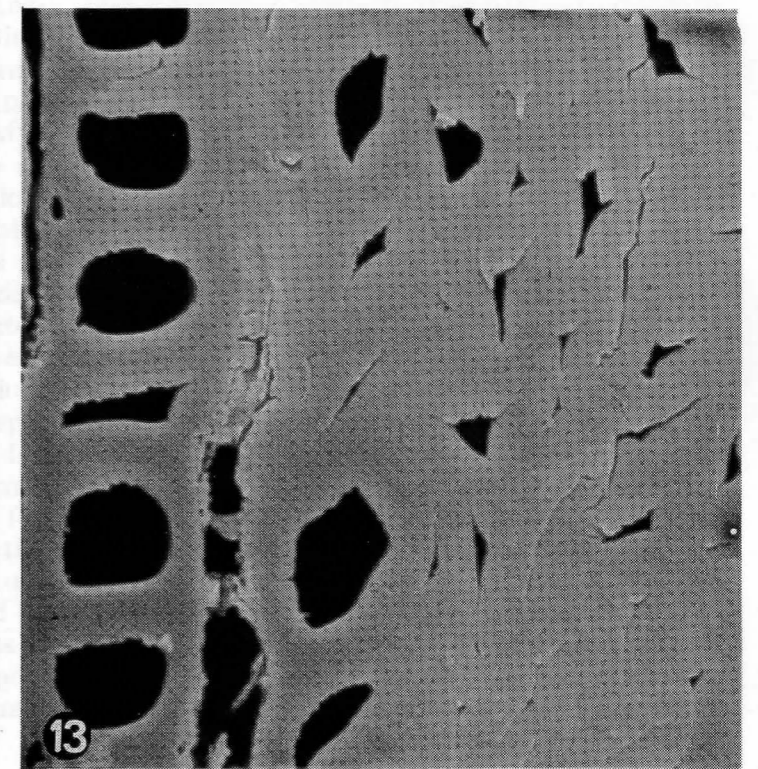
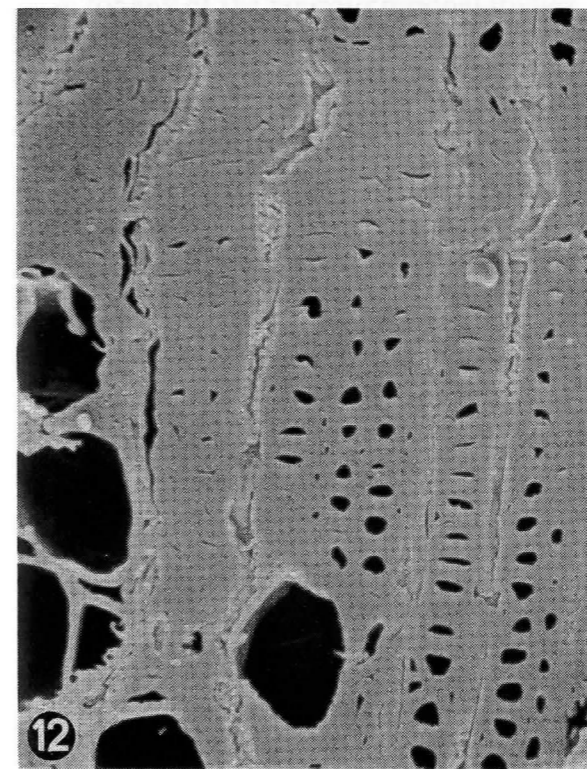
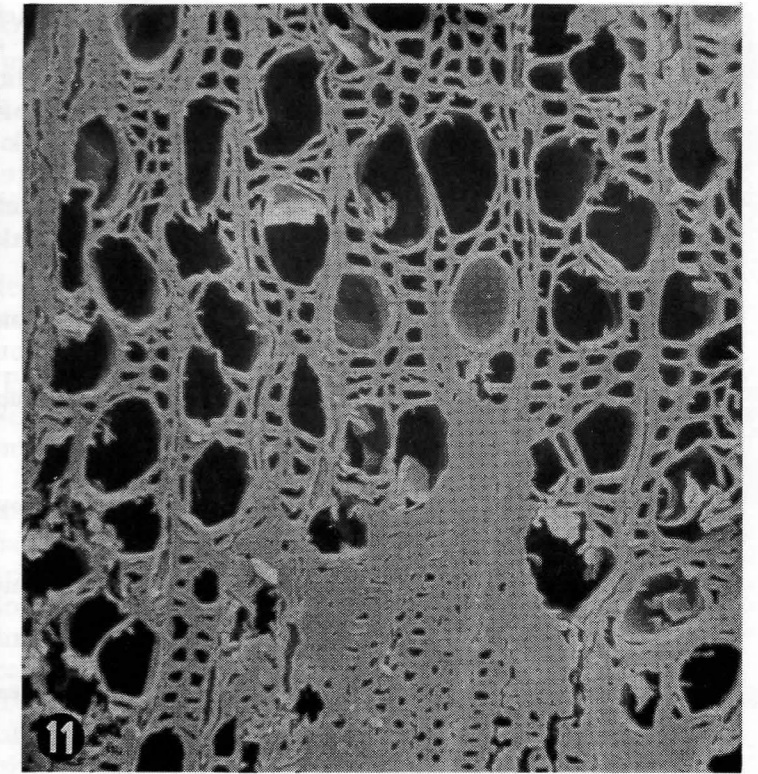
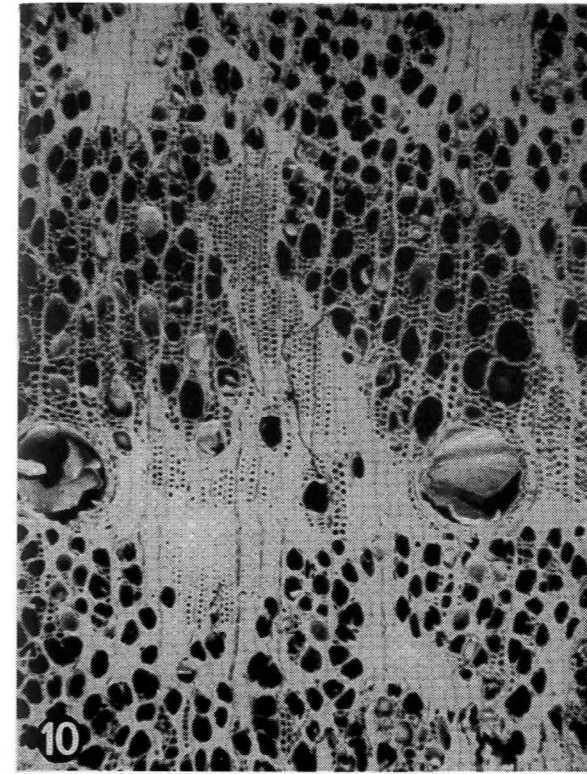


Fig. 10. SEM micrograph of collapsed chinkapin heartwood, showing collapse concentrated in the areas composed mainly of fibers. x 33. — Fig. 11. SEM micrograph of collapsed chinkapin with fibers between small vessels relatively free from collapse. x 100. — Fig. 12. SEM micrograph of chinkapin with fibers 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

A NSF grant GB-38359, made to the Electron Microscope Laboratory of the University of California, Berkeley, used to purchase the SEM employed is gratefully acknowledged.

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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 obtain-

ed 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 S₁ and S₂ 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 oven-dry 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 oven-dry 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 re-

leasing compound. Groups of leaves were sprayed to saturation with a 10⁻²M 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 Łódź, 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 Tecnológicas, 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 μ m and fibre length remains fairly constant at about 600 μ m. The vessel elements are specialized with oblique

end walls, simple perforations, and alternate intervascular pitting. Vessels are relatively uniform in diameter (125 μ m) 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 μ m) 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 amorphous 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 BaCl₂ 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 ex-

pected 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 larinan 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 S₂ 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 S₂ 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, Winzerstrasse 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. — *Albizia 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 odoratum Soland. — *Nicotiana glauca* Graham.

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

Paliurus spina-christi Mill. — *Periploca graeca* L. — *Phyladelphus 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 suberrata 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 prop-

erties 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
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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 meet-

ing 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 un-animously accepted. This procedure was much preferred to the alternative of revising the Multi-lingual 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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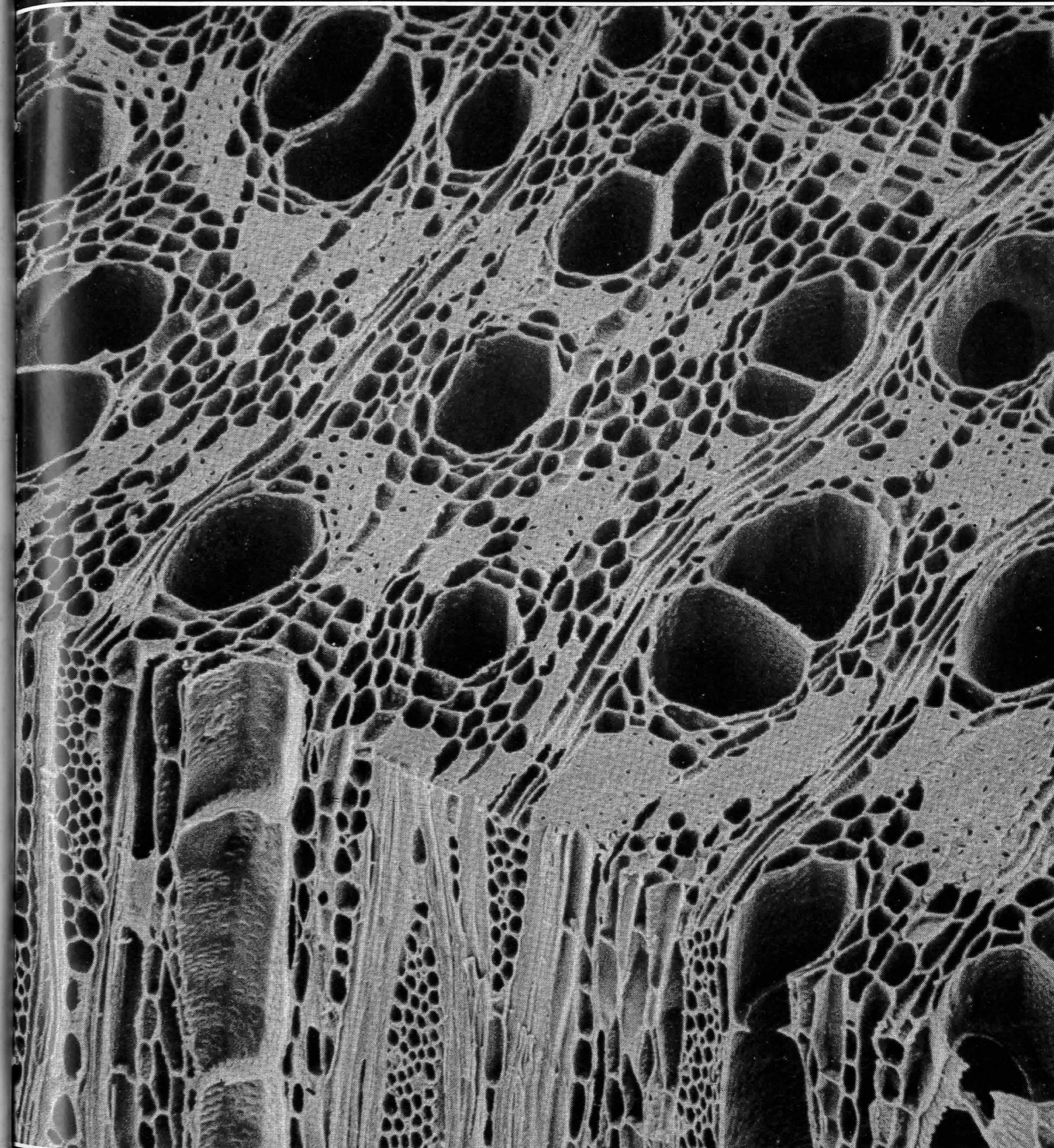
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IAWA BULLETIN

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Front cover: Scanning electron micrograph of the wood of *Eugenia mairé* 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.



International Association of Wood Anatomists

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