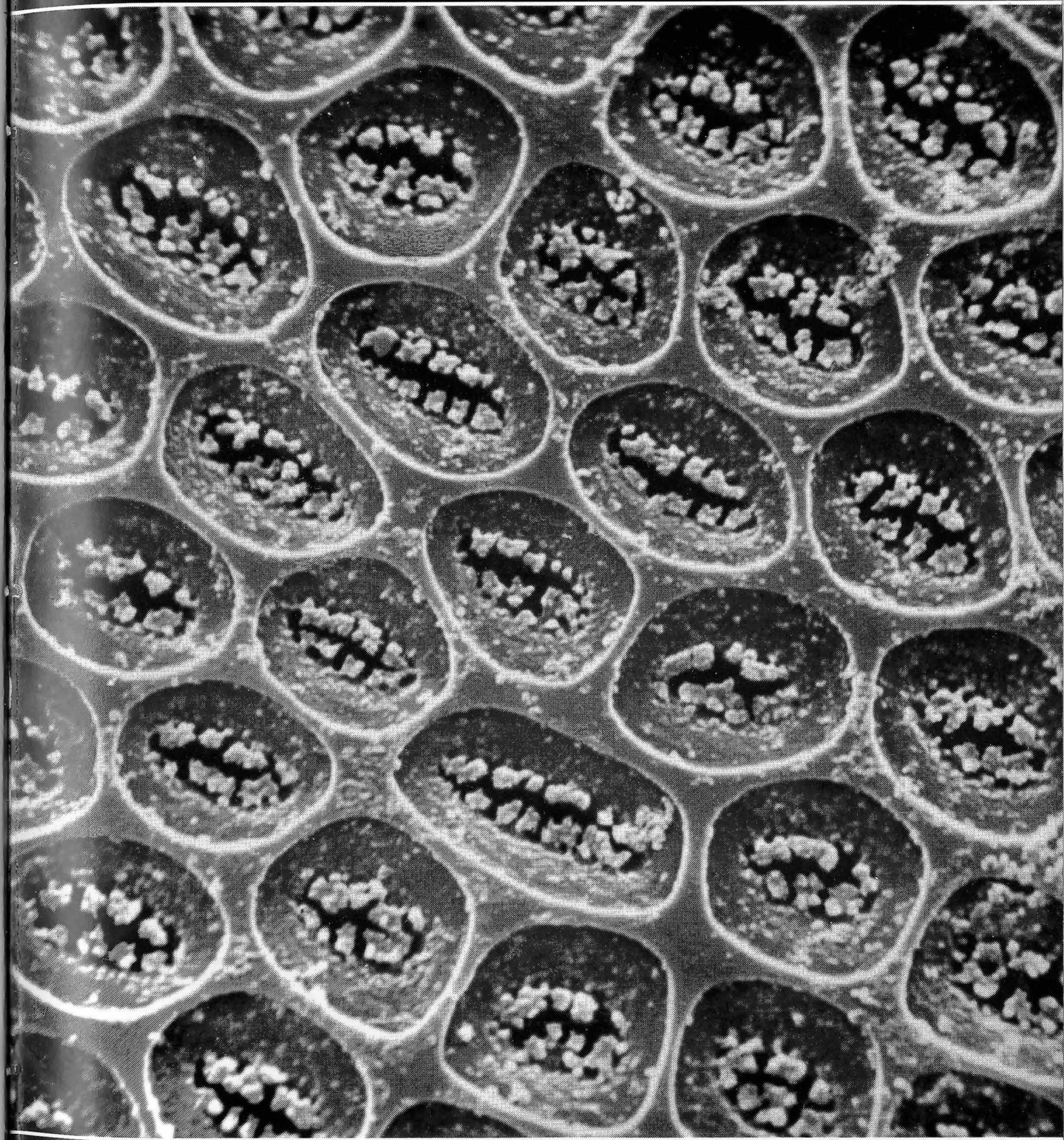


## IAWA BULLETIN

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



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*continued on page 63*

## VESTURED PITS IN BORAGINACEAE

by

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### Summary

Vestured pits were observed with the SEM in *Echium*, *Rochefortia*, and *Pteleocarpa*. Genera without vestured pits include *Auxemma*, *Cordia*, *Ehretia*, *Heliotropium*, *Patagonula*, *Saccellium*, and *Tournefortia*. *Bourreria* and a specimen of *Heliotropium calcicola* have what appear to be rudimentary or partially developed vestures. The presence of vestured pits in Boraginaceae does not follow any taxonomic system. *Echium* is in one subfamily, whereas *Rochefortia* and *Pteleocarpa* are in the other subfamily.

### Introduction

Since the late 1800's, vestured pits have been known to occur in such families as Leguminosae and Myrtaceae. In 1925, Record reviewed the literature and found that members of 20 families had vestured (cribriform) pits. To ascertain the diagnostic and phylogenetic value of vestured pits, Bailey (1933) examined 2,660 species, 979 genera, 152 families, and 33 orders. In that classical paper, he determined that vestures were minute outgrowths of the pit area and not perforations of the pit membrane, and thus he proposed that these structures be called vestured pits and not cribriform pits. In his observations, Bailey found that only 24 families have vestured pits, and refuted the occurrence of vestures in 13 families previously reported to have them. Of the families with vestures, only four did not have vestures throughout every genus, and in only Oleaceae did the occurrence of vestured pits not follow any taxonomic subdivision. Record (1936) and Metcalfe and Chalk (1950) reproduced Bailey's original work but no new research was undertaken until the advent of the electron microscope. Côté and Day (1962), Wardrop *et al.* (1963), and others examined vestured pits with the transmission electron microscope and more recently Scurfield, Silva, and Ingle (1970), Scurfield and Silva (1970), Ishida and Ohtani (1970), and Cassens (1973), observed vestured pits with the scanning electron microscope. For the most part, the investigations of these scientists were

confined to the fine structure of hardwood pits, the cell wall sculpturing, and the basic morphology of vestures. However, for the first time since Bailey's classical paper, Scurfield, Silva, and Ingle (1970) reported the presence of vestured pits in a species (*Gnetum gnemon*) not listed by Bailey. Since then, Butterfield and Meylan (1974) have found vestures in *Persoonia toru* (Proteaceae) and Parameswaran and Liese (1974) made further observations on *Gnetum*. Van Vliet (1975) described and illustrated the different types of vestured pits in Crypteroniaceae *s.l.* Carlquist (1970) alluded to the presence of vestured pits in Boraginaceae (*Echium*), but his suspicions were not confirmed until the present study.

The presence of vestured pits in Boraginaceae was discovered through the routine identification of a wood sample supposedly from the Florida Keys. Initially *Eugenia* (Myrtaceae) was proposed as a possible identification because the unknown seemed to have vestured pits and other characteristics of Myrtaceae, but conclusive evidence was lacking. Dr. B. F. Kukachka of the Forest Products Laboratory examined the sample and suggested *Rochefortia* (Boraginaceae). Comparing the unknown with samples of *Rochefortia* in our collection confirmed Kukachka's suspicion, but the question of the vestured pits remained. Because the intervacular pits were minute (2-4  $\mu$ m), the supposed vestures could not be seen clearly with the light microscope even with an oil immersion objective. To clarify the problem, the scanning electron microscope (SEM) was used. Both *Rochefortia* and the unknown were examined and both were found to have vestured pits, thus confirming the identification and at the same time establishing the question of vestured pits in Boraginaceae.

### Methods and Materials

Samples of Boraginaceae for examination were taken from specimens in the Madison (MADw), Samuel J. Record (SJRw), and Smithsonian (USw) wood collections. Table 1 lists the specimens examined with the SEM. Because no vestured pits

<sup>1</sup>Maintained at Madison, Wis., in cooperation with the University of Wisconsin, U.S.A.



were initially found in some genera, only a few specimens of these genera were examined with the SEM. However, observations were made on additional specimens with the light microscope and in no case were vestures found. A radial and/or tangential surface about 5 by 10 millimeters was split from air-dry wood blocks. The samples were mounted and coated with gold for examination with the SEM.

### Results and Discussion

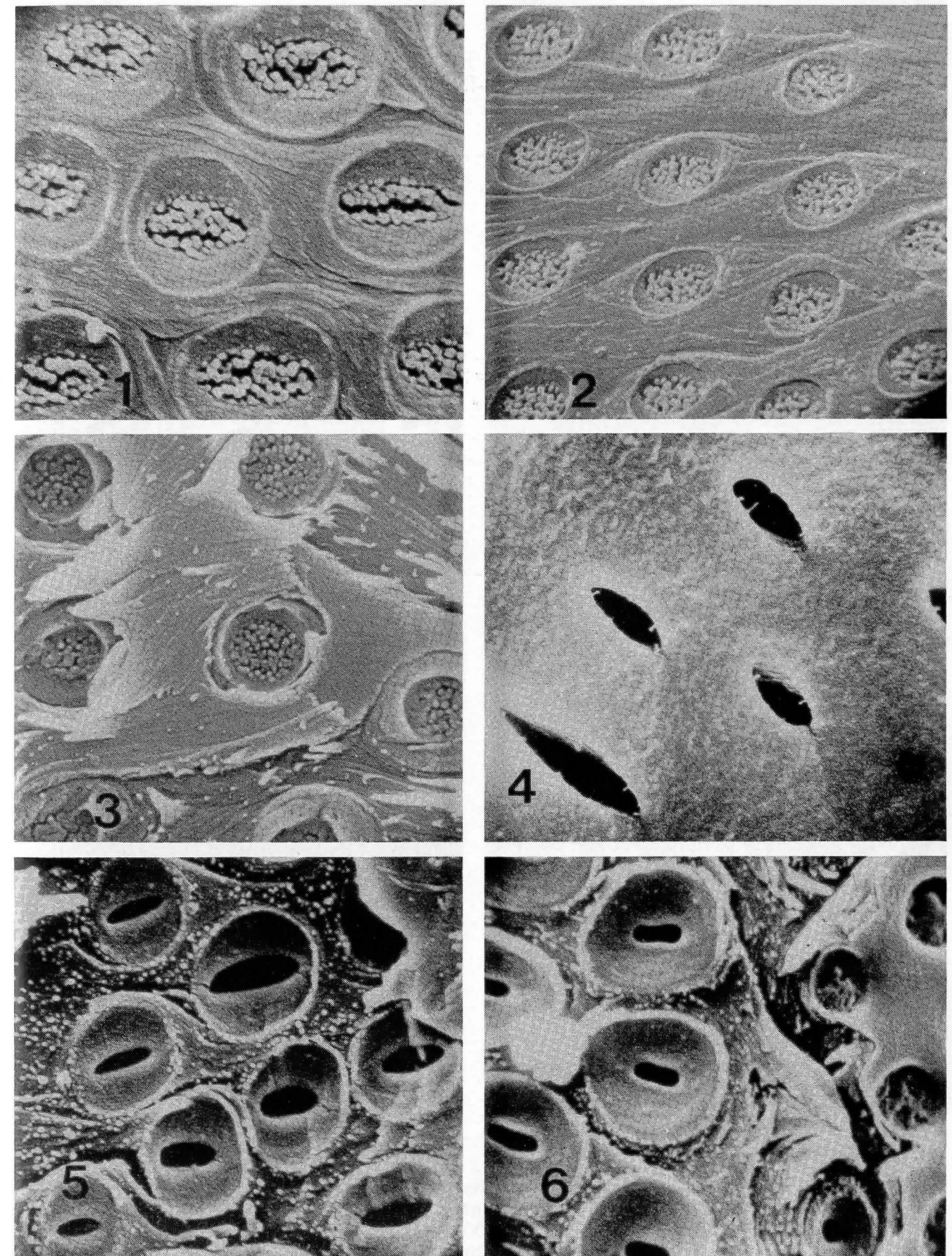
Vestured pits were observed with the SEM in *Echium* (Fig. 1), *Pteleocarpa* (Fig. 2), and *Rochefortia* (Fig. 3) of the Boraginaceae (Table 1). For the most part the vessel-ray, intervacular, and imperforate tracheary element pits were vestured in the three genera. However, in *Rochefortia* few intervacular pits are available for examination as the pores are mostly solitary.

Table 1. List of Boraginaceae specimens examined with SEM and occurrence of vestured pits

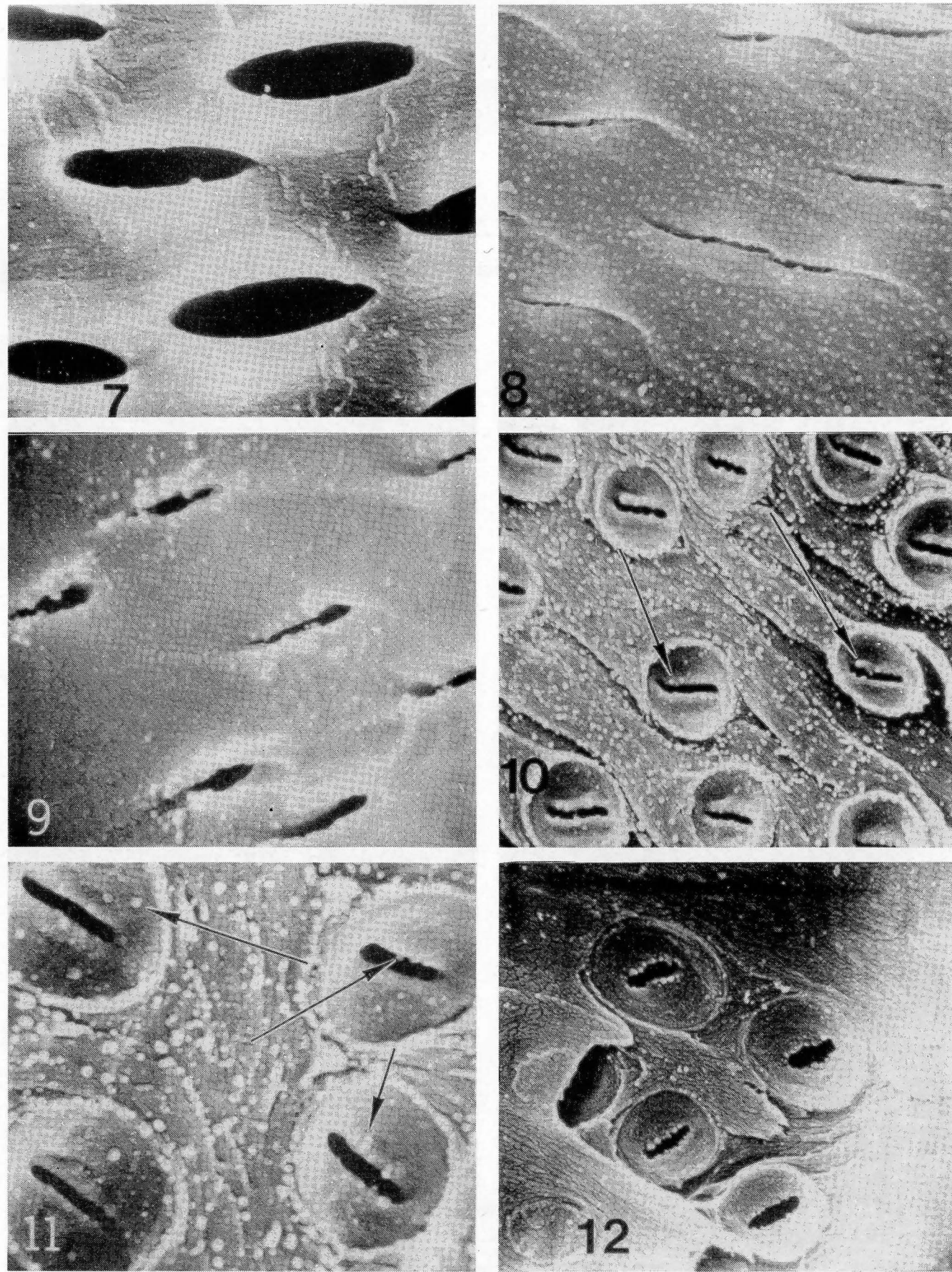
Species	Vestured <sup>1</sup>	Collector	Xylarium
<i>Auxemma oncocalyx</i>	-	Dahlgren	MADw 27846
<i>Bourreria cumanensis</i>	+?	L. Williams 12258	MADw 27843
<i>Bourreria cumanensis</i>	+?	L. Williams 12803	MADw 27844
<i>Bourreria cumanensis</i>	+?	Curran & Haman 589	MADw 27845
<i>Bourreria succulenta</i>	+?	Abbott 2909	MADw 19904
<i>Bourreria succulenta</i>	+?	Stern & Wasshausen 2420	MADw 24135
<i>Bourreria succulenta</i>	+?	Stern & Wasshausen 2455	MADw 24160
<i>Cordia alliodora</i>	-	L. Williams 4306	MADw 6572
<i>Cordia alliodora</i>	-	L. Williams 8292	MADw 8434
<i>Cordia alliodora</i>	-	Capucho 406	MADw 27635
<i>Cordia gerascanthus</i>	-	Record & Kuylen 115	MADw 27659
<i>Cordia glabra</i>	-	L. Williams 8699	MADw 27662
<i>Echium fastuosum</i>	+	E. W. Carl	MADw 27839
<i>Echium fastuosum</i>	+	I. Webber (cult.)	SJRw 23780
<i>Echium fastuosum</i>	+	FHOW 11762	SJRw 33905
<i>Ehretia acuminata</i>	-	Forest Botanist 2848	MADw 27841
<i>Ehretia anacua</i>	-	H. Nogle 279	MADw 13223
<i>Heliotropium angiospermum</i>	-	Stern & Brizicky 168	SJRw 51024
<i>Heliotropium angiospermum</i>	-	Stern & Chambers 314	SJRw 51503
<i>Heliotropium angiospermum</i>	-	R. M. King 4339	USw 27333
<i>Heliotropium calcicola</i>	+?	Hansen & Nee 1793	MADw 36662
<i>Heliotropium ternatum</i>	-	K. L. Chambers 2789	USw 33870
<i>Heliotropium ternatum</i>	-	Stern & Wasshausen 2538	USw 35565
<i>Heliotropium spec.</i>	-	I. Webber (cult.)	SJRw 23214
<i>Patagonula americana</i>	-	Jardim Botanico	MADw 27850
<i>Patagonula americana</i>	-	H. M. Curran 658	SJRw 1688
<i>Patagonula americana</i>	-	H. M. Curran 697	SJRw 1706
<i>Pteleocarpa lamponga</i>	+	For. Dept. Java 3800	SJRw 15470
<i>Rochefortia grandifolia</i>	+	A. Fors 9	SJRw 13358
<i>Rochefortia stellata</i>	+	W. R. Barbour 24	MADw 11052
<i>Rochefortia stellata</i>	+	G. C. Bucher	SJRw 15884
<i>Rochefortia spec.</i>	+	T. Hofmann-Olsen Lum. Co.	MADw 16684
<i>Rochefortia spec.</i>	+	?	MADw 3894
<i>Saccellium lanceolatum</i>	-	Ad. Nac. Bosques	MADw 27858
<i>Saccellium lanceolatum</i>	-	FHOW 9629	SJRw 32601
<i>Tournefortia argentea</i>	-	?	MADw 15717
<i>Tournefortia bicolor</i>	-	Krukoff 8459	MADw 27853
<i>Tournefortia caribaea</i>	-	Stern & Wasshausen 2537	MADw 24222
<i>Tournefortia glabra</i>	-	G. S. Miller 1305	MADw 20739
<i>Tournefortia gnaphalodes</i>	-	Stern & Brizicky 229	MADw 18235
<i>Tournefortia hirsutissima</i>	-	G. S. Miller 1228	MADw 20589
<i>Tournefortia rugosa</i>	-	M. Acosta-Solis 5855	MADw 16621

<sup>1</sup> + = vestured pits present; - = vestured pits absent; +? = vestured pits questionable.

Fig. 1. *Echium fastuosum* (SJRw 23780). Vestured intervacular pits. x 6000. — Fig. 2. *Pteleocarpa lamponga* (SJRw 15470). Vestured intervacular pits. x 5400. — Fig. 3. *Rochefortia spec.* (MADw 16684). Vestured vessel-ray pits. x 5500. — Fig. 4. *Cordia gerascanthus* (MADw 27659). Nonvestured vessel-ray pits. x 5500. — Fig. 5. *Heliotropium angiospermum* (SJRw 51503). Nonvestured intervacular pits. x 6500. — Fig. 6. *Patagonula americana* (SJRw 1688). Nonvestured vessel-ray pits. x 6000.







The vestures are variable in shape, size, and abundance. They seem to be branched, unbranched, or bead-like in different pits of the same sample, sometimes within the same pit. The pit cavity has vestures, but the pit canal and aperture may or may not contain vestures. In some pits, vestures appear to be absent, but in other pits of the same sample vestures are abundant. The classification of vestures proposed by Bailey (1933), Côté and Day (1962), Schmid (1965), and Scurfield, Silva, and Ingle (1970) was inadequate and no new type could be discerned. Cassens (1973), Ishida and Ohtani (1970), and Butterfield and Meylan (1974) also note that too much variability exists for proper classification.

Vestured pits were not observed in *Auxemma*, *Cordia* (Fig. 4), *Ehretia*, *Heliotropium* (Fig. 5), *Patagonula* (Fig. 6), *Saccellium*, and *Tournefortia* (Fig. 7) (Table 1). *Bourreria* and a specimen of *Heliotropium calcicola* are listed as '+?' because typical vestured pits were not seen. In Figure 8, the inside vessel wall of *Bourreria* is dotted with wart-like projections, but vestures are difficult to discern due to the slit-like pit aperture. In Figure 9, however, the wart-like projections occur more often around the pit aperture. Careful examination of the pits suggests that these warts or vestures do not occur within the pit cavity. In Figures 10 and 11 the pit cavities are exposed. The vessel wall between pits appears to have warts. These structures have been seen in other species (Figs. 5 and 6) and are probably artifacts due to the fracturing of the vessel wall. Within the pit cavities, typical vestures are absent, but arrows indicate the presence of small lumps or artifacts in the cavity. These small lumps do not appear to be vestures in either a rudimentary or early developmental stage. The presence of a pronounced warty layer, especially near the pits in *Bourreria* (Figs. 8 and 9), suggests that the lumps within the pit cavity are probably more closely related to warts than to vestures.

In a specimen of *Heliotropium calcicola*, structures similar to those in *Bourreria* were observed (Figs. 12 and 13). The structures in *H. calcicola* are confined to the pit cavity especially near the rim of the pit aperture and protrude slightly into the pit aperture. These structures were scarcely evident in other pits of the same specimen (Fig. 14) and absent in pits of other species of *Helio-*

*tropium* (Fig. 5). The pit in Figure 13 looks like a vestured pit in some stage of development, but inconsistent occurrence of such pits in the same specimen and the absence of such pits in other *Heliotropium* suggest that the structures are artifacts or some extraneous deposits. The possibility of warts seems remote, as no warty layer was observed as in *Bourreria*.

It is rare that vestured pits occur in only some species of a family. Of the 26 families known to have vestured pits, only 5 families did not have vestured pits throughout every genus, and in only Oleaceae and Proteaceae did the occurrence of vestured pits not follow any taxonomic subdivision. Whether Boraginaceae is considered one large family with both woody and herbaceous taxa or a smaller family with mostly herbaceous taxa, the genera with vestured pits are not all in the same higher taxonomic category. *Echium* is in the subfamily Boraginoideae, tribe Echieae, and *Rochefortia* and *Pteleocarpa* are in either Boraginaceae subfamily Ehretioideae or, according to some authors, Ehretiaceae. The nonvestured genera *Ehretia*, *Saccellium*, *Bourreria*, *Cordia*, *Patagonula*, and *Auxemma* are in the Ehretioideae and *Heliotropium* and *Tournefortia* are in the Boraginaceae. Thus in the Boraginaceae the occurrence of vestured pits does not follow any taxonomic subdivision.

Other wood anatomical features examined suggest heterogeneity. The pore arrangement is either ring, semiring, or diffuse porous. In addition the pores may be in wavy bands, somewhat dendritic, or solitary. The pore size is generally small, but also medium to large. The axial parenchyma may be sparse, reticulate, apotracheal banded, or paratracheal. Variability also is present in the ray width and height, in the type and location of cellular inclusions, and in some features of the gross morphology. The intervascular pit size varies from 2 to 10  $\mu\text{m}$ , but the vessel-ray pits are always similar to the intervascular pits. Other similarities include nonseptate fiber-tracheids, heterocellular rays, and simple perforation plates.

#### Acknowledgements

The author is grateful for the assistance of Dr. I. B. Sachs and Mr. R. E. Kinney of the Electron Microscope Laboratory, Forest Products Laboratory.

Fig. 7. *Tournefortia glabra* (MADw 20739). Nonvestured intervascular pits. x 6000. — Fig. 8. *Bourreria succulenta* (MADw 19904). Wart-like projection on the inside of a vessel wall. Slit-like pit apertures obscure pit cavity and the presence of vestures. x 6000. — Fig. 9. *Bourreria cumanensis* (MADw 27844). Wart-like projections around pit aperture. x 11000. — Fig. 10 and 11. *Bourreria succulenta* (MADw 24135): Fig. 10: Pit cavity exposed. No typical vestures present. Arrows point to small lumps or artifacts. x 6500; Fig. 11: x 13000. — Fig. 12. *Heliotropium calcicola* (MADw 36662). Pits with pit cavity exposed. Note structures which may be vestures in some stage of development or artifacts. x 6500.



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## SOME EFFECTS OF WOUNDING ON TRACHEID DIFFERENTIATION IN *PICEA SITCHENSIS*

by

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### Summary

After wounding the cambium of *Picea sitchensis* with a needle, tracheids which were in the wall-thickening stage of differentiation, and were close to the injury, retained their cytoplasmic contents. Since these cells retained their stage of differentiation at the time of injury, this may provide a method for determining seasonal changes in the duration of the wall-thickening stage of tracheid differentiation. Cells in the wall-thickening stage that were further from the injury produced thicker walls than normal; presumably they were stimulated by growth promoters released by the injury.

### Observations

During an investigation into the distribution of cambial activity within trees of *Picea sitchensis* (Bong) Carr., we used a modification of Wolter's technique (Wolter, 1968) to establish the seasonal course of wood production. The cambial zone was stabbed through the bark at two-week intervals, each time of wounding being colour coded with oil paint. Sections were cut through each mark at the end of the growing season. At the injured point, cells that were in the expanding or wall-thickening stage of xylem differentiation were usually crushed by the needle (Fig. 1, 2). But on each side of the crushed region, it was usually possible to distinguish several layers of cells that had retained their cytoplasmic contents (Fig. 1, 2). These cells appeared to have been 'fossilized' at their stage of development at the time of injury, those nearest to the cambium having the thinnest walls, the walls increasing in thickness in successive tracheids away from the cambium (Fig. 2, 3). Comparison with increment cores taken at the time of wounding showed that the cells with cytoplasmic contents corresponded with those in the wall-thickening stage at that time. Hence, using a time sequence of wounding, it should be possible to follow seasonal changes in the duration of tracheid wall thickening, without destructive sampling until the end of the season.

Conversely, tracheids further from the point of injury, in a comparable part of the growth ring, had thicker walls than had the surrounding tracheids (Fig. 1, 2). Comparison with increment cores suggests that these thicker walled tracheids also corresponded with those in the wall-thickening stage of differentiation at the time of injury. Previous work by Kučera (1971, 1977) has shown similar thick-walled tracheids adjacent to wound tissue in *Taxus baccata* and *Pseudowintera colorata*. Kučera (1977) suggested that the thicker walls might result from an increase in indoleacetic acid associated with the injury.

In stems wounded at the beginning of cambial dormancy, the injury stimulated a short burst of renewed cambial activity (Fig. 4); the presence of bordered pits on tangential tracheid walls was taken to indicate the approach of normal dormancy (Denne and Ledsham, 1976). Since previous work showed that the cambium was not reactivated by application of either indoleacetic acid or gibberellic acid after the beginning of dormancy (Denne and Wilson, 1977), it seems likely that this stimulatory effect of wounding may be associated with the release of other growth promoters.

### Acknowledgement

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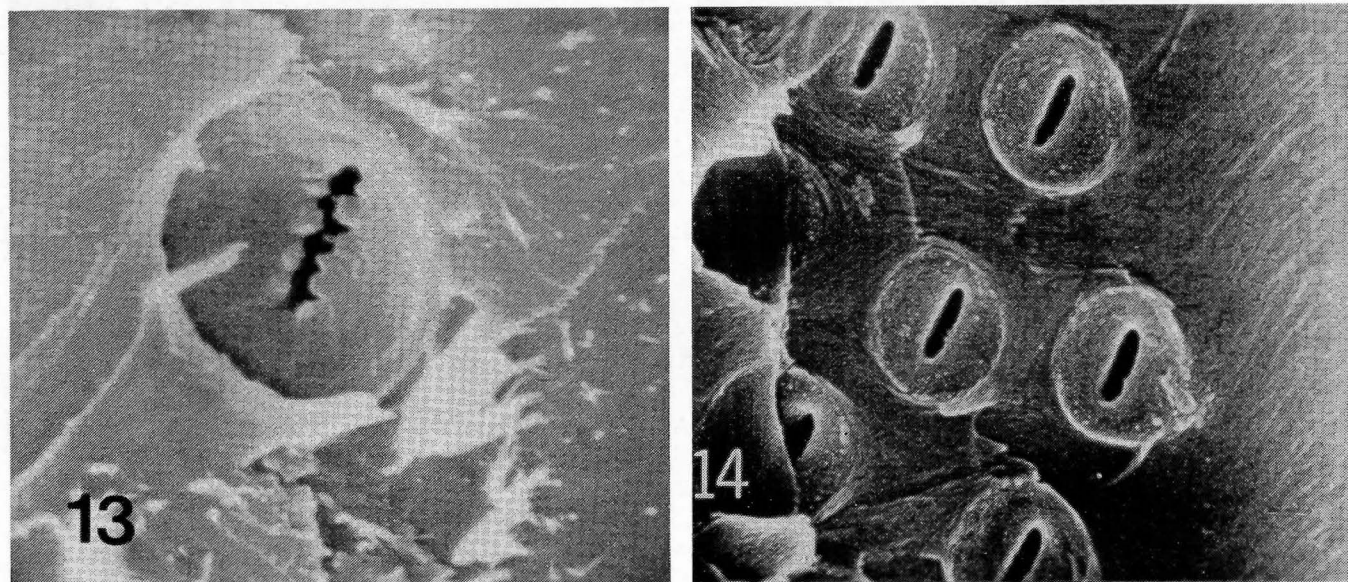


Fig. 13 and 14. *Heliotropium calcicola* (MADw 36662): Fig. 13: x 11000; Fig. 14: Structures seen in Figures 12 and 13 are not present. x 6000.



by

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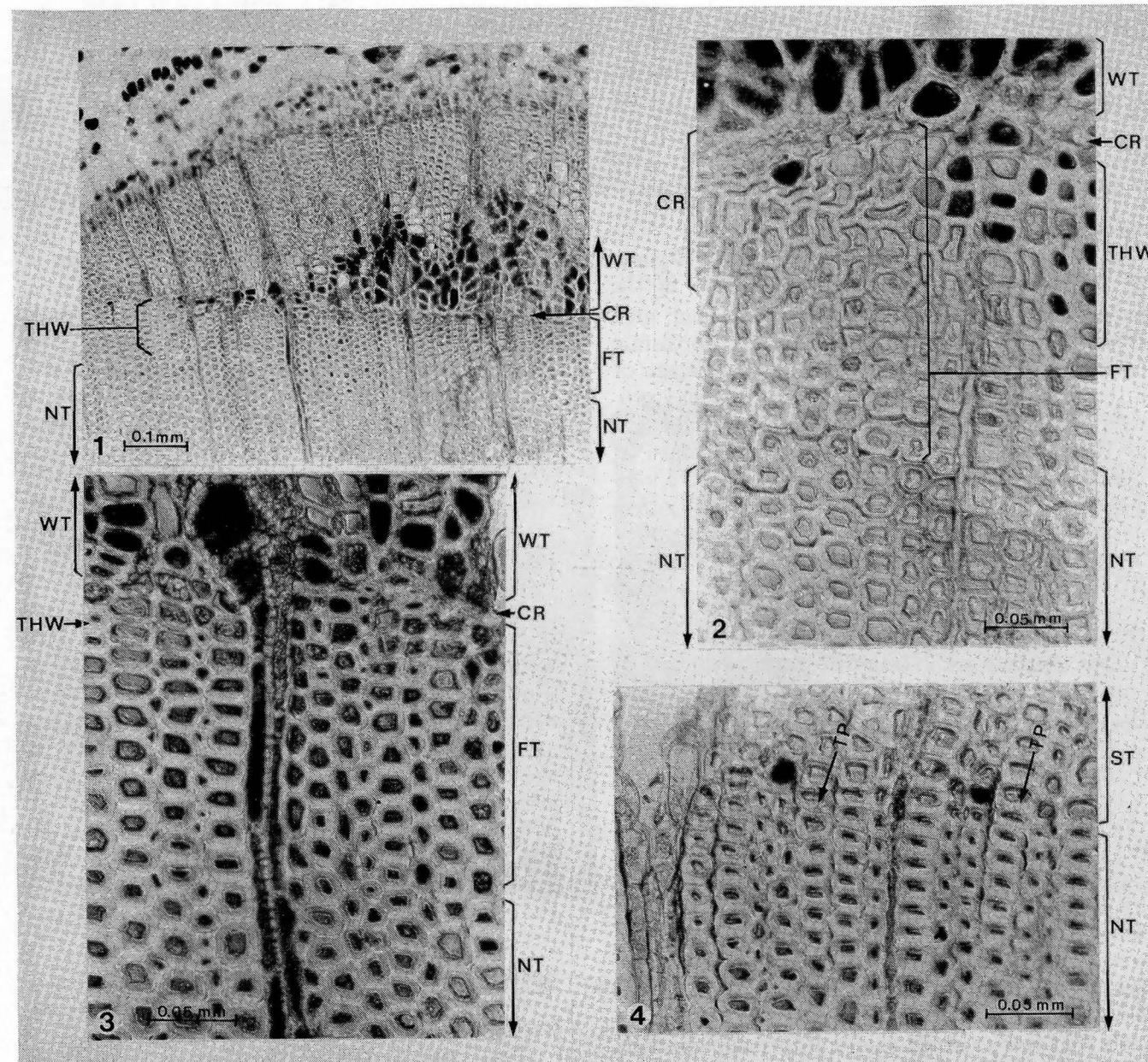


Figure 1. Transverse section of *Picea sitchensis* stem wounded during latewood production. FT = 'fossilized' tracheids (i.e. thinner walled tracheids retaining cytoplasm), below wound tissue; THW = thicker walled tracheids, lateral to wounded area; NT = 'normal' tissue (i.e. tracheids fully differentiated before wounding); CR = crushed cells; WT = wound tissue. ——— Figure 2 and 3. Transverse sections of *Picea sitchensis* stem wounded during latewood production. Symbols as in figure 1. ——— Figure 4. Transverse section of *Picea sitchensis* stem wounded at the beginning of cambial dormancy. ST = tracheids produced after wounding; NT = tracheids produced before wounding; TP = bordered pit in tangential tracheid wall, indicating the end of the normal growth ring.

Xylem parenchyma comprises two quite distinct categories of cells:

1. the cells of the storage parenchyma, which belong to the vertical or the horizontal system; besides storage substances, these cells can also contain tannins or crystals of calcium oxalate (cf. Czaninski, 1968 a and b).

2. specialized cells, always contiguous with a vessel; these include transfer cells (cf. Gunning *et al.*, 1968, 1974) characterized by their wall outgrowths, contact cells (Braun, 1970; Sauter, 1972) and vessel-associated cells or v.a.c. (Czaninski, 1964, 1968).

This last cell type possesses some quite characteristic cytological and cytochemical properties. In a fully differentiated v.a.c. of sycamore (Fig. 1), the cytoplasm is dense and rich in ribosomes; it contains short and numerous mitochondria, and very few, poorly differentiated plastids which only rarely contain starch, even during the winter. The endoplasmic reticulum is well developed, with regular profiles; the numerous vacuoles are spherical and small; in every season a peroxidase activity can be demonstrated at the level of the tonoplast or of the intravacuolar precipitates (Fig. 2) (cf. Czaninski and Catesson, 1969). This cytological aspect remains essentially unchanged throughout the year: the v.a.c.'s, in contrast to the cells of the storage parenchyma, do not undergo seasonal modifications. In the pit fields, their primary cell wall remains pecto-cellulosic when it separates a v.a.c. from a vessel; in contrast, it can be lignified when it is situated between two storage parenchyma cells, but in this case, it possesses plasmodesmata (Fig. 3, arrows). It should be pointed out that we have never observed plasmodesmata in the primary wall of a pit common to a living cell and a vessel, even a differentiating vessel; nevertheless, the primary wall of a v.a.c. coupled at the level of a pit to the wall of a tylosis can possess plasmodesmata (perhaps newly-formed) (Czaninski, 1974). After their differentiation, and when the vessel to which they are adjacent is adult, the v.a.c. produce a new pecto-cellulosic layer along the wall common to the vessel (Fig. 4) (O'Brien, 1970; Czaninski, 1973), at least when the v.a.c. possess secondary lignified thickenings. In the primary xylem, the walls of the v.a.c. generally remain cellulosic.

These characteristics are essentially constant, whether the v.a.c. belong to the vertical or the horizontal parenchyma, and to whatever systematic group the xylem studied belonged. We have found them in the v.a.c. of *Robinia pseudoacacia* (1966, 1968a), *Acer pseudoplatanus* (1972), *Ulmus spec.* (1975), *Populus italica*, *Dianthus caryophyllus* (1971), *Daucus carota* (1974) and *Triticum aestivum*. The presence of these specialized cells seems, therefore, to be a general occurrence among the Angiosperms; however, only a portion of the cells contiguous with the vessels may present the characteristic appearance of the v.a.c., the other portion being composed of classical parenchyma cells. In other respects, the specialization of the v.a.c. seems to be more important in the secondary xylem than in the protoxylem or the metaxylem. Outside the Angiosperms, in the vascular plants which possess imperforate tracheary elements instead of vessels, v.a.c. have not yet been described: in the Gymnosperms, if they exist, they are probably infrequent and largely restricted to the horizontal parenchyma; as regards the Pteridophytes, they very rarely have parenchyma cells in the metaxylem and consequently the regular presence of v.a.c. there is unlikely.

Some recent observations allow us to specify the possible roles of the v.a.c. One of these is to react to any perturbation, whether this is in response to a stress or when a vessel ceases to be functional.

First and foremost, they are involved in the formation of tyloses (Fig. 5) which seal the vessels, either naturally in the course of the ageing of the plant, or after wounding or a parasitic attack.

In other respects, when plants sustain an attack by a vascular parasite, whether or not pathogenic, we have observed that the v.a.c. are the first cells to react by the acquisition of a secretory activity characterized by an increase in the number of mitochondria and dictyosomes, and important modifications of the endoplasmic reticulum and vacuoles. This activity leads to the accumulation of the products of secretion (polysaccharides and osmiophilic, probably phenolic, substances) in the extra-cellular compartment, followed by their emptying into the vessels (Fig. 6). The transfer of these products of secretion into the vascular space



implies a considerable permeability of the walls to large molecules. We have described these phenomena in the carnation infected by *Phialophora cinerescens* (Czaninski *et al.*, 1973; Moreau *et al.*, 1973) or by *Verticillium dahliae* (Catesson *et al.*, 1977; Moreau *et al.*, 1977) and in elm attacked by *Ceratocystis ulmi* (Czaninski *et al.*, 1975). These observations ally the v.a.c. with transfer cells which can play an important role in the case of extra-cellular secretions (Gunning and Pate, 1974).

The v.a.c. could also have a role in the conduction of sap for example by acting as a by-pass for blocked vessels (Dimond, 1967). This hypothesis is supported by the cytological appearance of the v.a.c.: they bear a marked resemblance to the companion cells of sieve tubes, even though they do not have the same origin; and they also recall the transfer cells which play a certain role in lateral transport (these could merely be a type of v.a.c. restricted to the primary xylem). Moreover, the pecto-cellulosic layer situated against the wall common to the vessel could be homologous to the wall outgrowths of transfer cells (Yeung and Peterson, 1975; Czaninski, 1977), however, in the v.a.c., it does not increase the surface of the plasmalemma.

Finally, according to the hypothesis of Plumb and Bridgman (1972), long chains of polysaccharides could play a role in the rising of the sap. These chains, if they exist, would be secreted by the v.a.c. and emptied into the vessels. In any case, the v.a.c. seem to be implicated in the general metabolism of polysaccharides and appear altogether analogous to the contact cells described by Sauter (1972) and Sauter *et al.* (1973) and which 'are considered to be the specific sites of a metabolically controlled sucrose release'. Considering their possible roles, the specialized cells of the parenchyma contiguous with the vessels cannot be defined as simple contact cells: they represent a specific cellular category which one may consider analogous with the specialized cells

of the phloem. In fact, following a recent analysis of the analogies between companion cells, albuminous cells, and contact cells (in the haustorium of parasites, Dorr and Kollmann, 1975), Srivastava (1970) proposed calling all these cell types by the general term 'companion cells'; Behnke (1975) prefers to call them 'associate cells'. We propose, in order to harmonise the nomenclature, that the specialized cells of the xylem be likewise defined as associate cells, and, more precisely 'vessel-associated cells' since they are physiologically connected to the vessels.

#### Acknowledgement

I am grateful to Dr. F.A. Williamson for translating the manuscript.

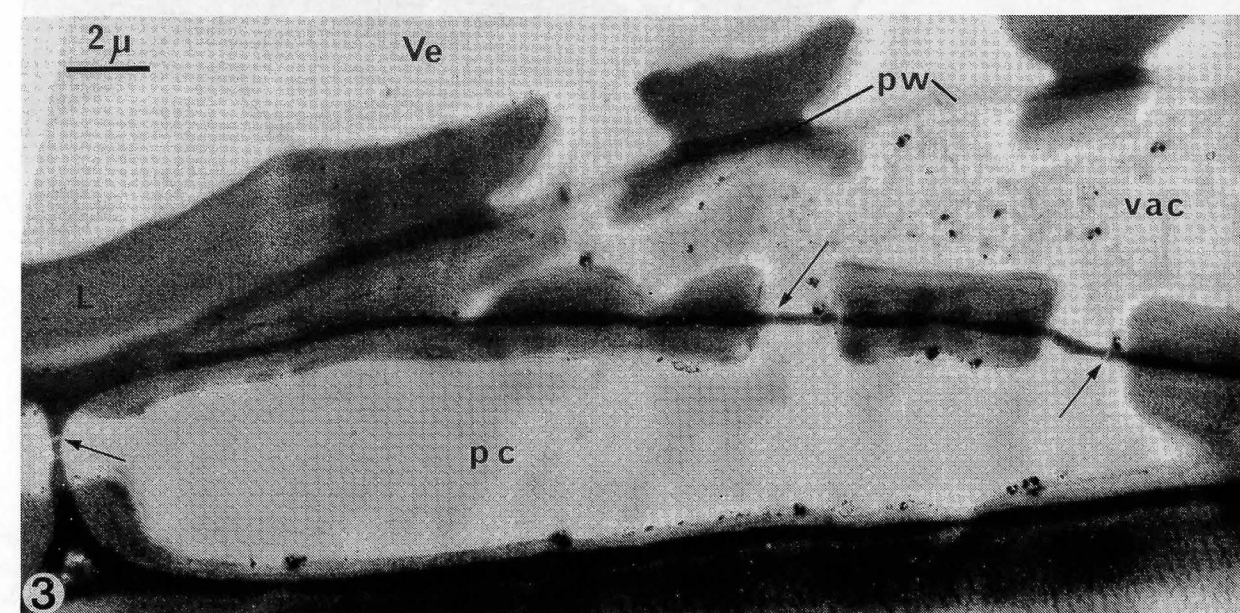
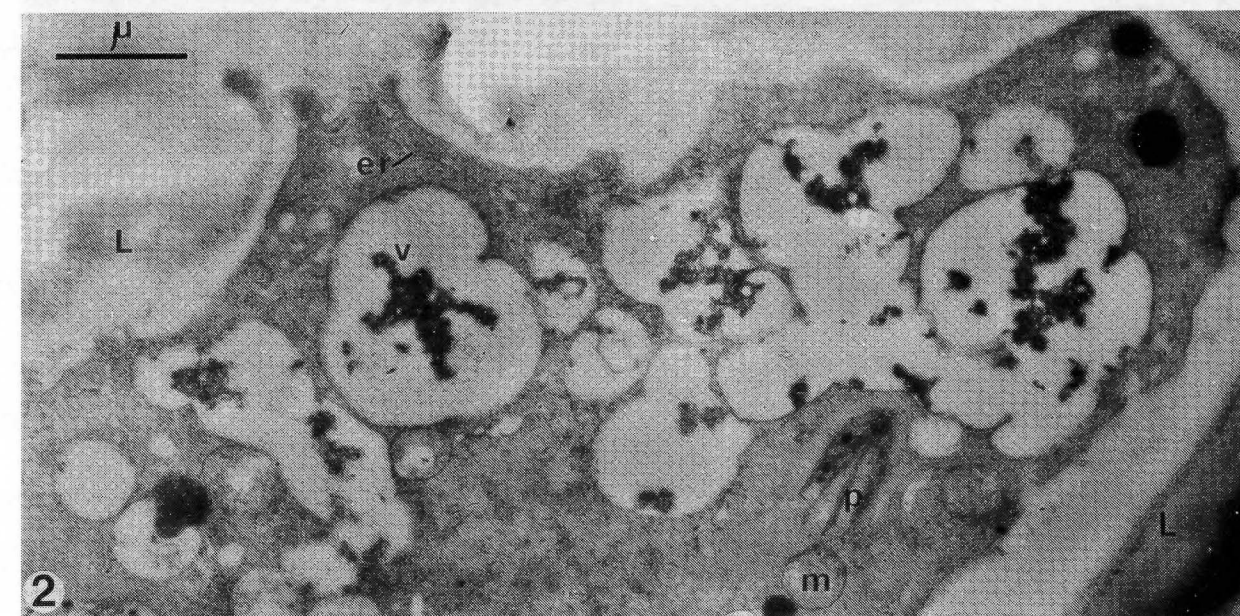
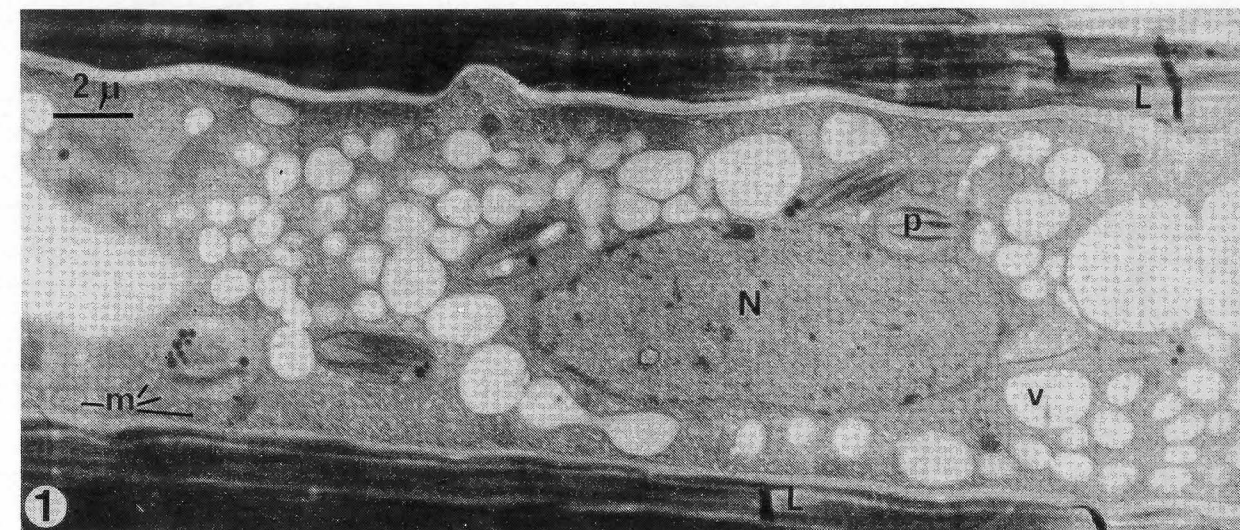
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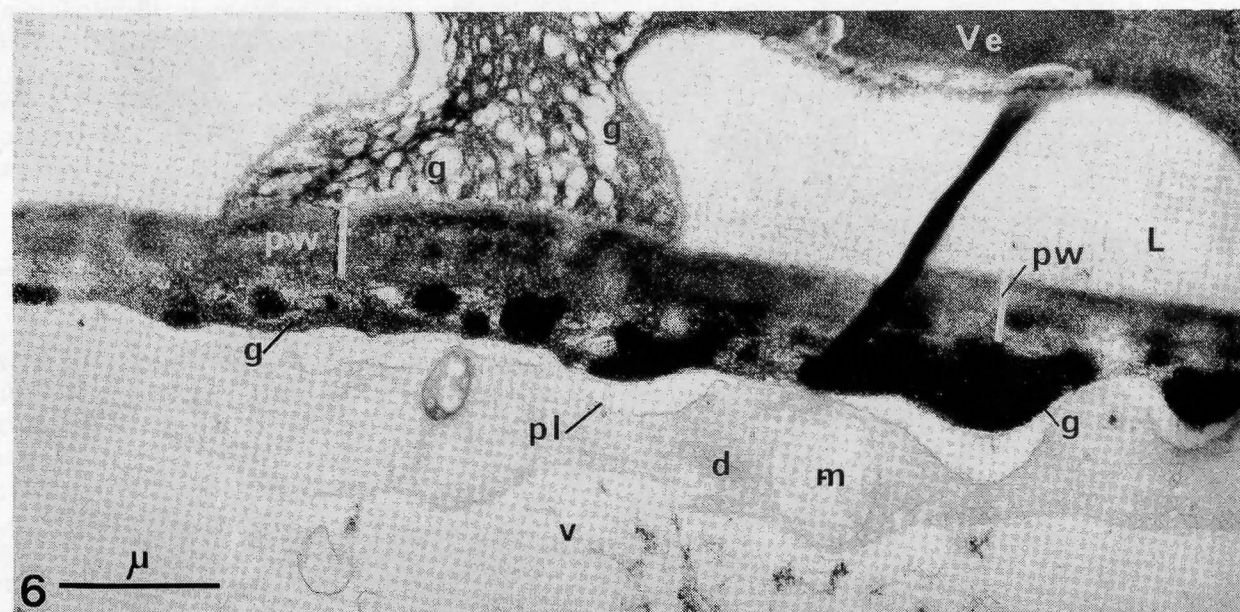
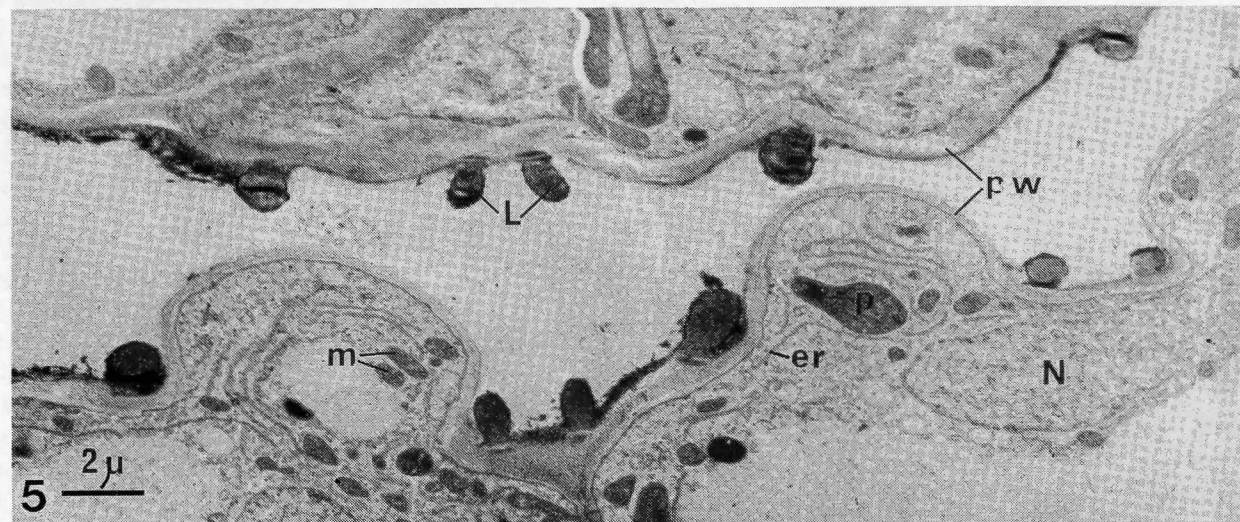
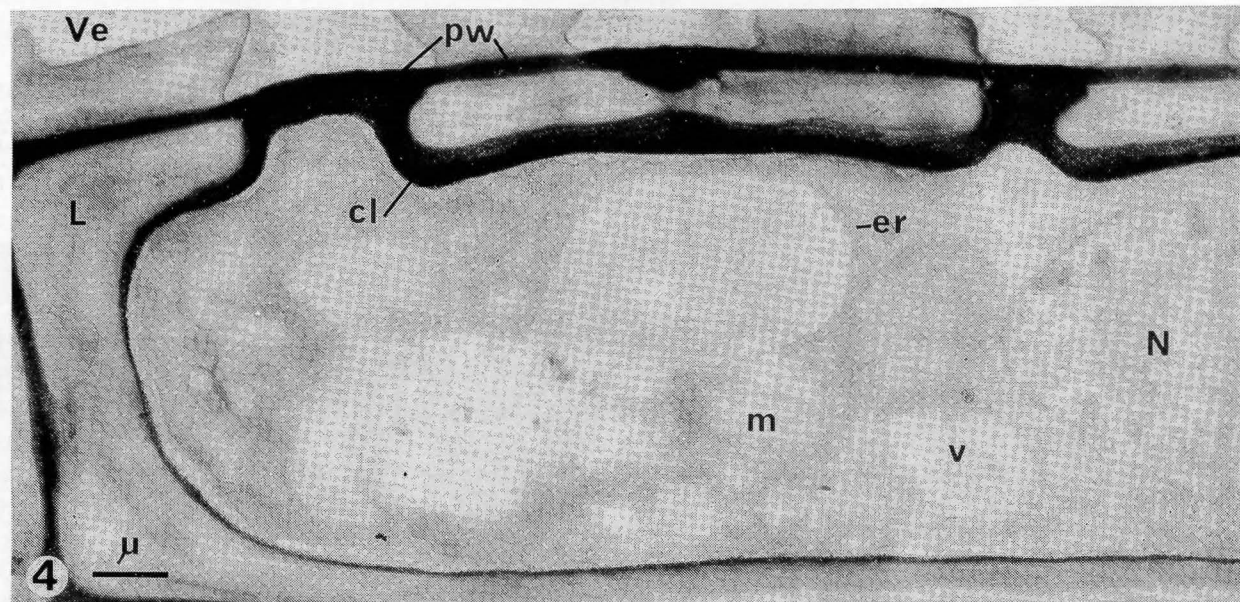
**Explanation of plates:** Fig. 1–6: radial sections of vascular associated cells. All micrographs except figure 3 from samples fixed with glutaraldehyde-osmium tetroxide.

**Key to abbreviations:** d : dictyosome; e r : endoplasmic reticulum; L : lignified secondary wall; m : mitochondria; N : nucleus; p : plastid; p c : parenchyma cell; pl : plasmalemma; p w : primary wall; v : vacuole; v a c : vessel associated cell; Ve : vessel.

Figure 1. *Acer pseudoplatanus*. Section of v.a.c. stained with 1% aqueous  $KMnO_4$ . The cytoplasm is very dense with many small vacuoles. — Figure 2. *Robinia pseudoacacia*. Section incubated in the DAB (diaminobenzidine) reaction mixture : peroxidase activities are localized in vacuoles (tonoplast and precipitates). — Figure 3. *Populus italica*. Sample treated by ethanolamine-silver nitrate (Chafe & Chauret, 1974) for lignin detection. V.a.c.-vessel pit areas showing unligified primary wall. Pit membranes between two living cells are lignified and possess plasmodesmata (arrows).







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Figure 4. *Robinia pseudoacacia*. V.a.c. : sections treated by periodic acid-thiocarbohydrazide-silver proteinate (Thiéry, 1967) and showing cellulosic layer (cl) ('protective layer?') formed along the vessel adjacent wall. — Figure 5. *Daucus carota*. Section showing the commencement of tyloses formation.  $KMnO_4$ . — Figure 6. *Dianthus caryophyllus* infected by *Verticillium dahliae*. Section contrasted by periodic acid-thiocarbohydrazide-silver proteinate and showing secretion products (g) in extra-cellular compartment and in vascular lumen.



## WHATS GOING ON IN WOOD ANATOMY

by

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I have taken the opportunity presented by the recently compiled Directory of Members of IAWA to examine the current pattern of research in wood anatomy. This pattern is evident from the following table which is based on the information contained in the completed questionnaires. The table shows the number of people working in each of a number of general research areas.

Research area	Number of researchers <sup>1</sup>
Development of normal and reaction wood/wood physiology	64
Relationship of anatomy and gross properties	56
Systematic wood anatomy	52
Structure of cells and cell walls	33
Ultrastructural studies	32
Relationship of growth and wood quality	17
Secondary changes (sapwood-heartwood)	5
Dendrochronology	4
Bark anatomy/taxonomy	4
Anatomy of leaves	2

<sup>1</sup> Many members who completed the questionnaire are engaged in more than one research area.

It appears that most research is being directed at those aspects bearing some relationship to the gross properties of wood, such as, physiology of wood formation, development of reaction wood and the relationship of wood anatomy and properties. Within this general area a wide range of investigations are taking place for example, studies of the effect of day length/night temperature on cell dimensions, determination of the factors controlling differential wood increment in leaning trees, genetical and environmental effects on density and the mechanism of wood failure. This emphasis on the fundamental aspects of gross properties is obviously due in part to the realisation these days by foresters that in successful forestry not only must the growth rate be good but also the wood quality. No doubt there is also a greater appreciation among wood technologists that the gross properties of wood are determined by the properties of the cells and the way in which they are held together.

While it may not be very evident from the wood literature, the questionnaire has revealed that there is a considerable amount of research going on in systematic wood anatomy. The pat-

tern of this research appears to have substantially changed from the 'traditional' studies of basic wood structure and is now directed at specific taxonomic problems where wood characteristics can be an aid to general plant classification. A number of revisions of important taxonomic works such as Metcalfe and Chalk's 'Anatomy of the Dicotyledons' are under way. It is unfortunate that few taxonomic studies of bark anatomy appear to be being made. This is no doubt due to the lack of appreciation of the role that bark anatomy can play in taxonomy. Although bark histology is much more difficult than wood, in my experience the taxonomic significance of the bark anatomy is at least as great as that of wood anatomy.

Another area of considerable interest is the structure of cells and cell walls. While it may have been thought some years ago that all was known here, the development and increased availability of electron microscopes has opened up fresh fields of research. Because of its relevance to the permeability of wood one of the major interests in this work is the structure of pits.

There is comparatively little work being undertaken on secondary changes (heartwood formation). This is surprising as there are few wood phenomena of such practical importance. Likewise few members appear to be interested in dendrochronology despite the significance of such studies in climatology and also in mineral cycling.

In conclusion the questionnaire has shown that wood anatomy research is being directed at the practical problem of understanding the gross properties of wood. It is also clear that the questionnaire does not show the scope of research in certain areas. This is probably due to lack of membership in certain fields, for example dendrochronology, tree physiology, breeding (few of the better known dendrochronologists or tree breeders are members of IAWA). It is also probably due to lack of support of some members who did not return completed questionnaires. It is hoped that when the Directory is revised in 1978 that all members will make the time to complete the questionnaire.

On behalf of the IAWA I wish to thank those members who took the time and trouble to complete and return the questionnaire so promptly.

## THE RELATIONSHIP BETWEEN WOOD RAY SHAPE AND RAY VOLUME PERCENTAGE IN BEECH

by

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### Summary

The volume percentage of wood rays in beech shows a very high negative linear correlation ( $r = -0.81$ ) with ray slenderness. This relationship can be expressed by the following equation:

$$y = 29.228 - 1.034x$$

where  $y$  = slenderness, and  $x$  = volume percentage of the rays.

### Introduction

When we investigated the volume percentages of wood rays in certain commercial hardwoods indigenous to Yugoslavia, a rather high variability was found for beech: *Fagus sylvatica* L. (Petrić & Šćukanec, 1975). Subsequent examination showed that in some trees the multiseriate rays were

high and narrow, while in other trees they were short and wide (Fig. 1 and 2).

Considering the influence of volume percentage and shape of wood rays on the anisotropic transverse shrinkage and swelling of wood according to the ray restraint theory (Skaar, 1972), and considering the influence of rays on radial permeability because they more or less represent the only conducting paths for radial movement of liquids in wood (Siau, 1971), as well as assuming an influence of ray shape on bending and splitting properties of wood, this investigation was undertaken in order to study any possible relationship between the shape of wood rays and their volume percentage in beech.

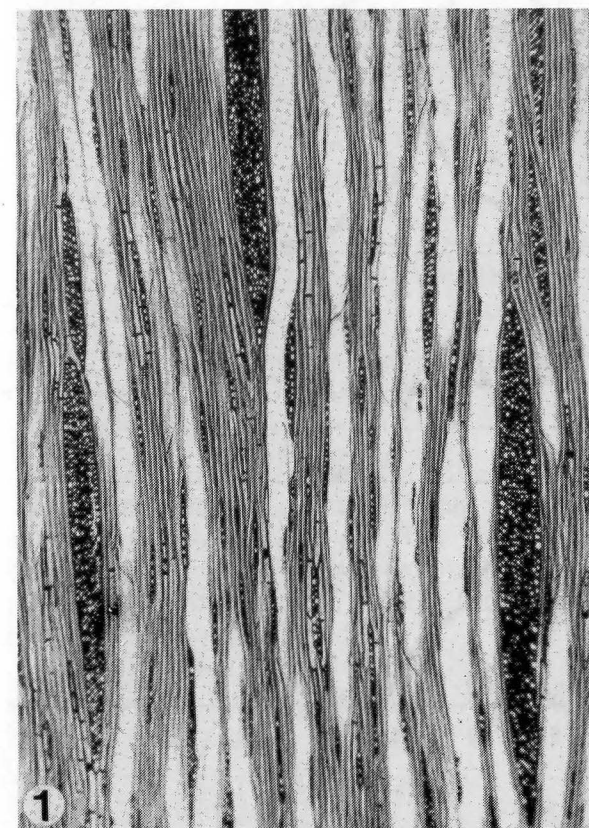


Fig. 1. Tangential section, tree 1, x 40.

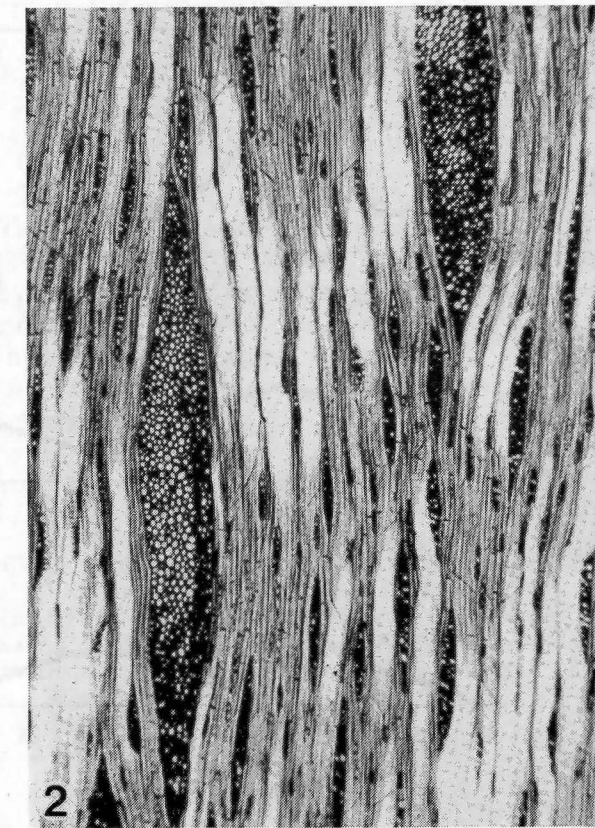


Fig. 2. Tangential section, tree 8, x 40.



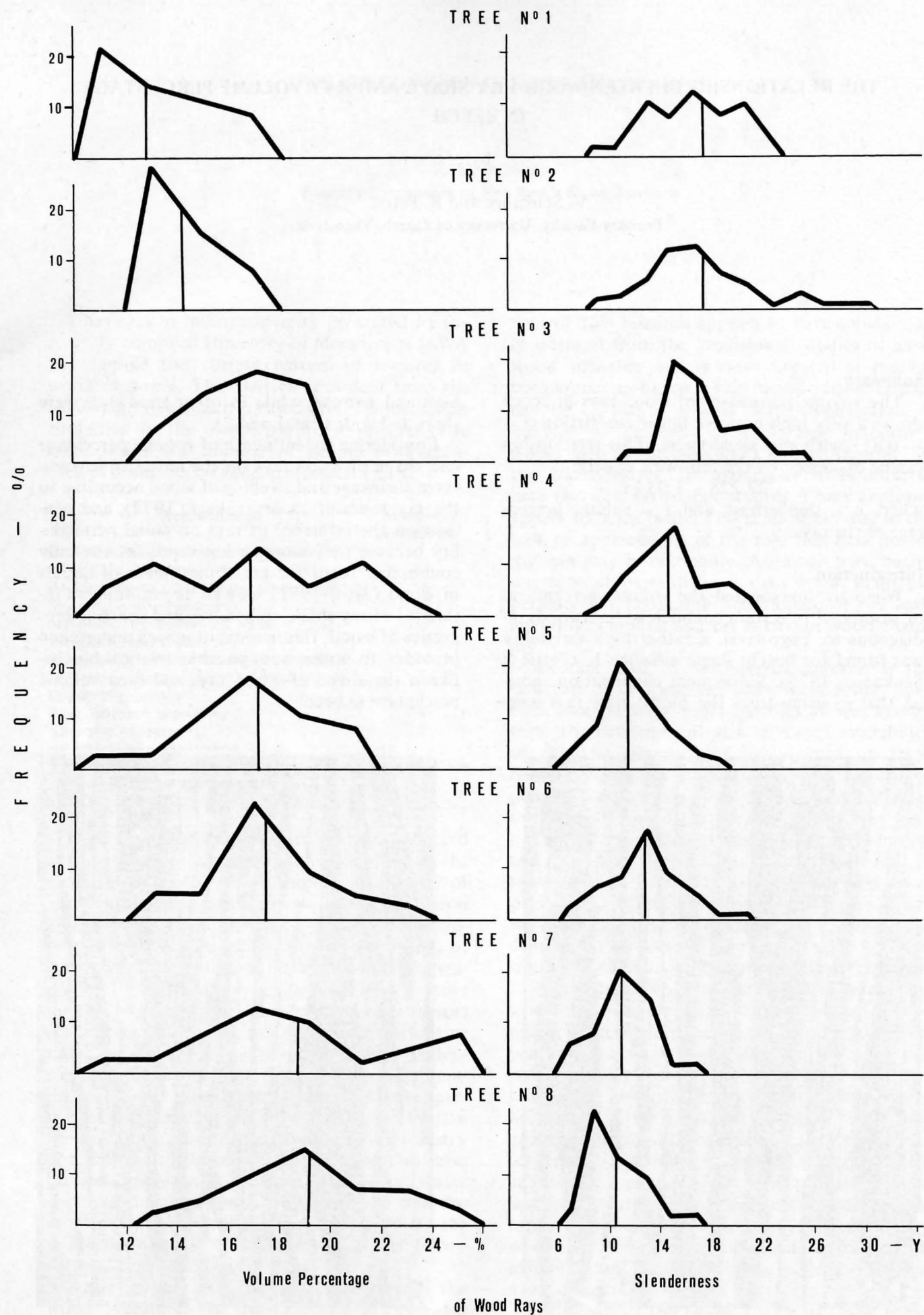


Fig. 3. Frequency polygons of volume percentage and slenderness of rays in 8 beech trees.

#### Materials and methods

The material for this study originated from the area of Zagrebačka Gora, forest district Zagreb. The forest represents a pure beech stand. The green slate parent rock is covered with a brown acid soil, representing site class III for beech. Altitude: 800–850 m, aspect: north, slope: 20–22°. The trees were selected by a random sampling method. This was, however, restricted to sound, straight, upright and dominant or codominant trees. Eight trees, varying in age from 75 to 161 years, were felled for this study.

Disks, 5 cm thick, were cut from each tree at breast height, in order to avoid the influence of within-a-tree variation. Two samples were taken from each disk in the north–south direction. Adult wood in the zone between the 70th and 80th growth ring from the pith was used for study. The growth ring width in the samples varied from 1.40 to 4.49 mm.

each were determined using a Leitz integration eyepiece (Leitz-Integrationsokular). The heights and widths of all three- to multiseriate wood rays were measured in ten fields of view of a Reichert fibroscope (KI D/E).

The height to width ratio of the wood rays was expressed as the slenderness ( $y$ ) of the rays:  $y = h/w$  ( $h$  = height;  $w$  = width). For each section the means of volume percentage and slenderness of wood rays were calculated. These means were used for analysing the correlation between these two characters.

#### Results

The results of the measurements of volume percentage and slenderness of the wood rays in beech, and their deviation from the mean value, as based on 160 measurements and on 8 trees, are depicted in the frequency polygons of Figure 3.

The volume percentages and slenderness values have been classified in classes of 2% and 2 respectively. From Figure 3 it is evident that trees with a high volume percentage of wood rays have a low slenderness value and vice versa.

In order to establish which type of correlation exists between volume percentage and ray slenderness, different possibilities for regression curves were considered. It appeared that a linear equation fits the existing data most satisfactorily. The following equation was obtained after calculating the parameters of equation using the method of the least squares:

$$y = 29.228 - 1.034x$$

( $y$  = slenderness of the rays;  $x$  = volume percentage of the rays). The correlation coefficient ( $r$ ) was calculated on the basis of this equation:  $r = -0.81$ .

In accordance with Reemer-Orphals table (Tavčar, 1946) this correlation coefficient demonstrates that the volume percentage of wood rays in beech shows a very high negative linear correlation with the slenderness of wood rays. This is also demonstrated in Figure 4.

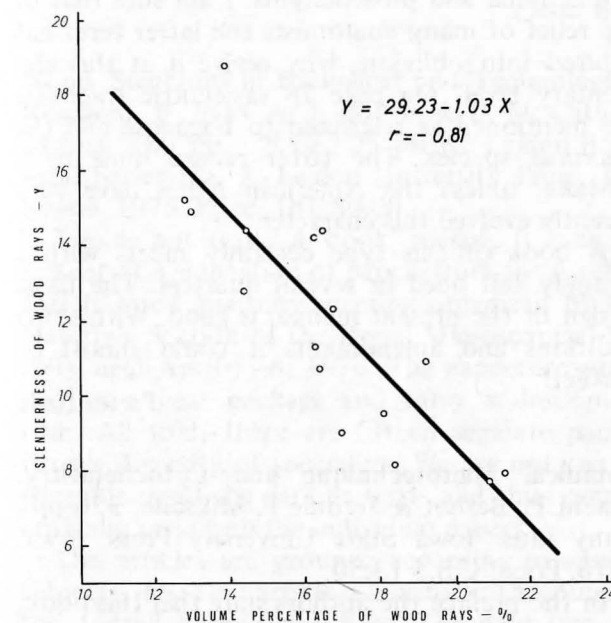


Fig. 4. Correlation between slenderness and volume percentage of wood rays.

After softening the samples in boiling water for 4 hours, tangential sections of 20  $\mu\text{m}$  were cut on a Reichert sledge microtome. The sections were stained in safranin, dehydrated in alcohol and mounted in Canada balsam (FPRL, 1956). A total of 16 sections was prepared.

In each section the volume percentages of all wood rays in ten fields of view of 2.4 square mm

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**Wood Structure and Identification.** H.A. Core, W.A. Côté & A.C. Day, xii + 168 pp., many illus. Syracuse Wood Science Series 6 (ed. W.A. Côté), Syracuse University Press, 1976. Price: U.S.\$ 17.95 (cloth) or \$ 12.95 (spiral bound).

This is a delightful book, introducing the subjects of wood structure and identification. It is not intended as a substitute for textbooks with a wider scope, but aims at serving forestry students, teachers of woodworking or shop in high school or junior college, as well as any persons who are interested in wood structure. The book is restricted to timber species of the United States. There are chapters explaining the basic structure of wood from the submicroscopic up to the macroscopic level, and on microscope and lense characters useful for the identification of North American softwoods and hardwoods, there are also keys to the relevant timber species employing both lense and microscope characters. Finally there are useful appendices on specimen preparation, microscopy, and on the individual species included in the key.

The strength of this book lies in the unrivalled collection of illustrations accompanying the text, which clearly show the features of wood structure of relevance for understanding its three-dimensional architecture and for use in identification. Through its excellent light- and scanning electron micrographs (there are some transmission electron micrographs as well) this manual in a way combines the virtues of Brazier and Franklin's illustrations in their *Identification of Hardwoods - a microscope key* (a publication which has unfortunately been omitted from the bibliography) and Meylan and Butterfield's *Three Dimensional Structure of Wood*. For this reason alone, the book will be highly welcome to student and teacher alike. The text gives a good insight into the various aspects of wood structure and identification. There are, however, some points one might feel unhappy about, particularly in view of the most probable use of the book as a teaching manual. The following points of criticism should be regarded as suggestions for improvements if this publication might live to see a - deserved - second edition.

No attempt has been made in this edition to give clear definitions of the various features illustrated; this is particularly painful for characters like fibre types, vascular and vasicentric tracheids, and types of cross-field pitting. Although it is fully realized that wood elements often do not allow being pigeon-holed into a particular type, I think that some definitions are essential, particularly at this elementary level. Not even the best illustra-

tions can remedy the uncertainty in the mind of the student ensuing from the lack of a delimitation in words of the type of structure pictured. To do justice to the authors, it should, however, be stressed that in the keys 'difficult' characters have been avoided as much as possible. Another weakness of the book is that it rightfully emphasizes the use of lense characters for efficient identifications but, that the features involved are all illustrated by scanning electron- and light micrographs at relatively high magnifications. Why not add a few low magnification incident light photographs, to give the student an idea of what he can expect to see with a hand lense? Two more minor criticisms. In the elementary introduction the wood cell types are classified into two classes: parenchyma and prosenchyma. I am sure that to the relief of many anatomists the latter term has entered into oblivion; why revive it at this elementary level? On page 78 vasicentric tracheids are mentioned as restricted to Fagaceae and the *Fraxinus* species. The latter record must be a mistake, unless the American Ashes have very recently evolved this character.

A book of this type certainly meets with a strongly felt need in several quarters. The basic design of the present manual is good. With some additions and amendments it could almost be perfect!

Pieter Baas

**Botanical Microtechnique and Cytochemistry.** Graem P. Berlyn & Jerome P. Miksche, 326 pp., many illus. Iowa State University Press, Iowa, 1976. Price: U.S.\$ 13.50.

In the preface the authors state that this book, which is a greatly revised and modified version of Sass's well known *Botanical Microtechnique* is to serve as a training manual and *not* as a reference work. Emphasis therefore lies on principles, starting from an elementary level, rather than on giving comprehensive compilations of techniques.

Major parts of the book are devoted to diverse aspects of microscopy (including electron microscopy); the sections on fixation, embedding, microtomy and staining are more restricted in scope. The chapter on cytochemistry lists several methods from this more recent offshoot of botanical microtechnique.

Wood anatomists will look in vain for answers to their microtechnical problems in this book. HF softening is recommended for wood sectioning, thereby ignoring the excellent results generations of skilled technicians have obtained by just boiling their specimens and by making use of well-sharpened knives. This criticism should not

be taken too seriously, however, because the present book obviously aims at introducing a diversity of methods to a wide botanical audience, rather than that it pretends to give answers to specialists' problems.

The book will undoubtedly have its use as an additional source of microtechnical information. However, with the appearance of another general treatise on Botanical Microtechnique one cannot help longing for the day that someone will take up the challenge to provide a really comprehensive reference book on all diverse aspects of microtechnique, starting from the various parts of the plants, and giving directives of how to proceed for demonstrating and analysing the various components of cytoplasm and cell wall. In this respect the almost century-old *Das Botanische Praktikum* by Strassburger and its later revised editions by Koernicke are often more helpful than recent texts on the same subject, including the book reviewed here.

Pieter Baas

**Wood Structure in Biological and Technological Research.** P. Baas, A. J. Bolton & D. M. Catling, editors, 280 pp., 28 fig., 25 plates. Leiden Botanical Series No. 3, Leiden University Press, The Hague, 1976. Price: Dfl. 80.00.

This is not really a 'book' review. It is an assessment of a collection of papers from the Anglo-Dutch wood anatomy meeting organized by the Materials Section of the Royal Microscopical Society held April 5-8, 1976. The papers are wrapped in a neat package and carry a descriptive title. All told, there are fifteen separate papers from a diversity of specialists. We are not knowledgeable in all the various fields and thus cannot critically review all the individual papers.

The articles are grouped according to similar subjects. The first article is a historical account of the Jodrell Laboratory, Kew. The next two papers are traditional studies in systematic wood anatomy. The fourth, fifth, and sixth articles deal with wood identification, silica grains, and root wood anatomy, respectively. The next article is entitled, *Some Functional and Adaptive Aspects of Vessel Member Morphology*. The subjects of the following three papers are variation in wood anatomy of tropical species, branch abscission layers, and wood structure in relation to bud activity. The last five papers include studies in variation in tracheid development, liquid flow through conifer wood, brashness, fracture behavior, and some structural aspects of wood/plastic combinations.

That indefatigable Mr. Plant Anatomy, C. R. Metcalfe, writes about the history of the Jodrell Lab in a delightful manner. Initially one wonders why this article should appear with papers dedicated to wood structure. The editors, P. Baas, A. J.

Bolten, and D. M. Catling, explain in the preface that the Jodrell celebrated its 100th anniversary on May 6, 1976, and 'a biohistorical paper revealing the important events within and around its walls has its rightful place in these proceedings.' A joy to read even though it's not wood structure.

The *Wood Anatomy of the Rhizophoraceae* by Van Vliet and *Comparative Wood Anatomy of Bonnetiaceae, Theaceae, and Guttiferae* by Baretta-Kuipers are two excellent systematic anatomy papers. Both are very comprehensive, but we were a little disappointed in the absence of a key to Bonnetiaceae. We found the use of numbers as column headings in Tables 2-8 in the paper on Rhizophoraceae very inconvenient and less than informative.

John Brazier's paper entitled *Observations of Some Anatomical Features Used in Identification and Taxonomy* is four pages long without illustrations. Although easy to read and interesting, it might have been more comprehensive and less a history of wood identification methods at the Princes Risborough laboratory. Ter Welle's comprehensive listing of species with silica grains will be of great interest to anatomists and wood technologists alike. The presence of silica is a useful character in wood identification, and the wood-using industry needs to be aware of its presence because of the dulling effect this mineral has on woodworking saws and knives. On root anatomy, Cutler demonstrates that some published generalizations on root anatomy need critical review. This much neglected area of research should attract new workers; we know little of root anatomy, particularly of large forest trees.

Baas has elected to explore the developmental basis of xylem modification through his attempt to demonstrate whether this has happened through selective pressures which impart survival advantages to the plant, or whether it has occurred as a series of haphazard mutations which impart neither selective advantages nor disadvantages to the plant. Baas disputes the views of Sherwin Carlquist who holds that changes in anatomy are perpetuated through advantages conferred by certain functionally adaptive modifications. Baas opts for xylem evolution 'as a random process leading to wood anatomy diversity which is not necessarily advantageous or disadvantageous for efficient water transport or for mechanical requirements.' For readers with a sufficient background in xylem anatomy and variation, in ecology, physiology, and evolution, the ramifications of Baas's analyses and conclusions are sure to be provocative.

Anatomists and wood technologists who have studied the variation in woods of temperate species will want to examine thoroughly the article by Den Outer and Van Veenendaal. These authors studied the wood of 30 tree species each with a distribution in both rain forest and savanna areas



of the Ivory Coast. Variation within characters was tested statistically and shown to be significantly different for a number of features. They conclude that the differences can be attributed largely to the influence of environment, but they hesitate to interpret these differences in a functional or adaptive manner.

The following three articles deviate from wood anatomy in the strict sense, and are more inclined to plant morphology and developmental anatomy with some relations to plant physiology. Koek-Noorman and Ter Welle examine branch abscission in two species of Moraceae. Denne's article discusses the relationship between wood production and bud activity. Next, Ford and Robards study the *Short Term Variation in Tracheid Development in the Early Wood of Picea sitchensis*. This study is similar to Den Outer and Van Veenendaal's work since both relate environmental factors to changes in growth. Ford and Robards examine the delicate changes in radial cell diameter and radial cell wall thickness along a radial file of tracheids.

The four remaining papers are not closely related to the preceding studies but they do bridge the gap between botanical and technological emphases in wood anatomy. *Biological Implications of a Model Describing Liquid Flow Through Conifer Wood*, by Bolton, is a paper for the physiologist and mathematically inclined wood technologist. After constructing the mathematical model, predicted and experimental results are shown to be reasonably similar. However, the predicted differences between early wood and late wood cells are not easily explained. *Causes of Brashness in Timber* is aimed at wood technologists and engineers. Dinwoodie discusses the factors influencing the development of brashness, a review of existing information presented in a very readable manner. Only mathematicians, engineers, and perhaps some wood technologists will completely understand Jeronimidis's article on *The Fracture of Wood in Relation to its Structure*. The derivation of a mathematical model based on various mor-

phological aspects of wood structure and the experimental results of work of fracture of wood is complex, especially for the botanist/anatomist. Only in the discussion is there any discussion of anatomy. In the last article, Laming examines samples of spruce, vacuum-impregnated with methylmethacrylate to determine the position of the polymer in the cells. The lumina of ray and longitudinal tracheids, but rarely the ray parenchyma cells, were filled with polymer. Bordered pit cavities also contained polymer, but there was no evidence to suggest that the cell wall and polymer were attached. Swelling tests conducted on the impregnated wood blocks indicate that the polymer 'does not influence, especially reduce, the hydrophilic nature of the cell wall substantially.'

The editors and publisher are to be commended; the paper quality of this book is excellent, though the photographs are sometimes lacking in contrast and the adhesive strips used to separate adjacent figures are unsightly, but apparently cheaper than engraver's tooling. Drawings, graphs, and tables are professionally executed. There is no index, but since this is a publication of proceedings, this lack is not a serious problem. Extensive detailed bibliographies are generally present at the end of each paper but one can only deplore the editorial style which accounts for abbreviated citations for books where publishers and places of publication have been omitted.

Although these proceedings touch many fields, the entire collection is probably not for everyone's personal bookshelf. A few individual reprints would probably satisfy most workers. The collection does, however, belong in every library that includes publications on botany, forestry, and wood technology. *Wood Structure in Biological and Technological Research* comprises a collection of useful, up-to-date, provocative studies that bridge the gaps among students of wood technology, silviculture, and botany.

Regis B. Miller  
William Louis Stern

#### WOOD ANATOMY ACTIVITIES AROUND THE WORLD

##### IAWA meeting in Amsterdam 1979

The regional group meeting for the European and African members of IAWA has been scheduled for August 29 until September 1, 1979. Conference facilities of the Royal Tropical Institute will be available during these 4 days. It is hoped that many IAWA members will contribute papers on a diversity of wood structural topics. A ques-

tionnaire will be circulated among the African and European members later this year. Members from outside the 'region' will of course also be welcome to attend and deliver a paper. They should write to the Executive Secretary for further details. In view of the economic situation members are advised to start fund raising for travel and accommodation expenses now.

##### Other important meetings

American IAWA members are reminded that the Pan American Regional Group will organize a joint session with the Structural Section of the Botanical Society of America at Virginia Polytechnic Institute and State University, Blacksburg, from August 20-25, 1978 (see IAWA Bulletin 1977/2:37).

From the numerous IUFRO meetings announced in IUFRO News 15/16 from May 1977, the following may be of special interest to the IAWA membership: 'Wood Quality of Tropical Species' to be held in Malaysia in October 1978; 'Protection of Hardwoods and Pulpwood in the Tropics' to be held in Central America, early 1978. The 17th IUFRO World Congress will be in Japan in 1981. In the same year the 13th International Botanical Congress will be held in Sydney, Australia; hopefully with the usual IAWA participation.

##### Wood Anatomy Happenings in Utrecht

On August 26, the section of Plant Morphology and Anatomy of the Royal Dutch Botanical Society held a meeting largely devoted to wood anatomy, to mark the retirement of our member Dr. Alberta M. W. Mennega from the division of

Wood Anatomy of the Institute for Systematic Botany, Utrecht, The Netherlands. Simultaneously the division of wood anatomy in Utrecht had organized an impressive exhibition entitled 'Do you like Wood?' (in Dutch: 'Houdt U van Hout?'), which will also be on view in Amsterdam later this year. Dr. Mennega will remain active in the field of systematic wood anatomy.

##### Request for Wood Samples

Mr. Philip M. Rury, IAWA member at the Botany Department of the University of North Carolina, Chapel Hill, N.C. 27514, U.S.A., is anxious to obtain more wood and bark samples for his anatomical study of the Old & New World Erythroxylaceae (*sensu* Hutchinson - including *Nectaropetalum* and *Pinacopodium*, which are sometimes referred to the Nectaropetalaceae).

##### Personal request from Executive Secretary

Several IAWA members kindly send me reprints of their publications. It would be highly appreciated if all members would adopt this generous habit. This would help in adapting IAWA policies to most recent trends in wood structural research. More substantial publications can of course always be offered for review in the Bulletin.

#### ASSOCIATION AFFAIRS

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##### The IAWA Constitution

The amendments to the IAWA constitution submitted to the membership last year have been approved of by a vast majority of IAWA members so that the amended constitution can be enclosed with this Bulletin.

##### The New Membership Directory

The IAWA owes a great debt of gratitude to Councillor Dr. Ken Bamber and to the Forestry Commission of New South Wales for collecting data for, and collating and typing the New Membership Directory which was enclosed with the previous Bulletin issue. Due to a small deficiency in the long distance communication from the Office of the Executive Secretary, Associate Mem-

bers are still listed as a separate category. This is by now in conflict with the amended Constitution. Moreover, the unofficial category of 'student members' which replaces the associate members is much larger than the list in the directory.

##### Tougher measure against non-paying members

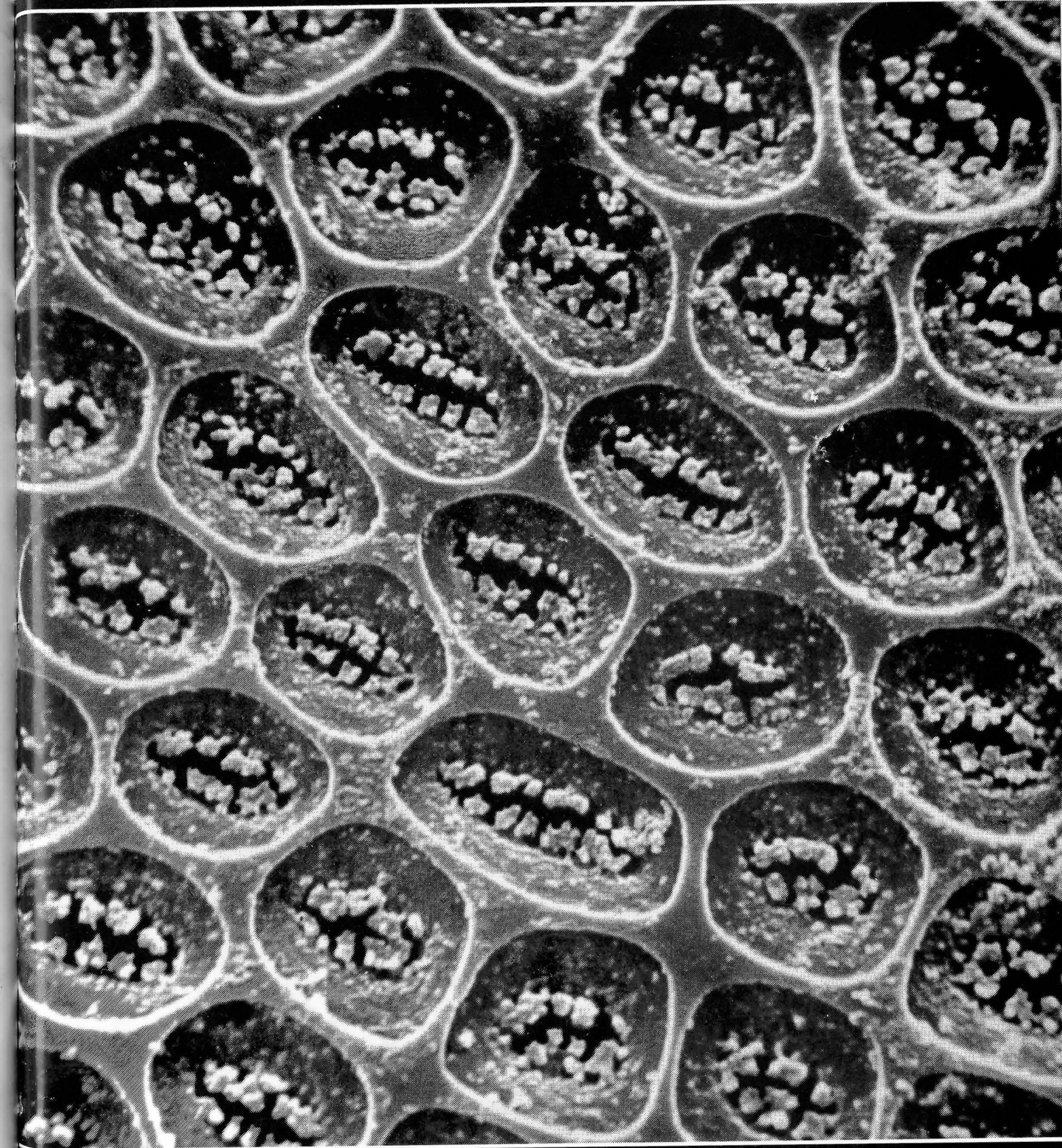
The Council has authorized the Executive Secretary to delete those members from the membership list who have not paid their due for two consecutive years. The names of these members will be listed in the Bulletin. Of course, exceptions will be considered for members in those few countries where currency problems prevent normal payment.



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