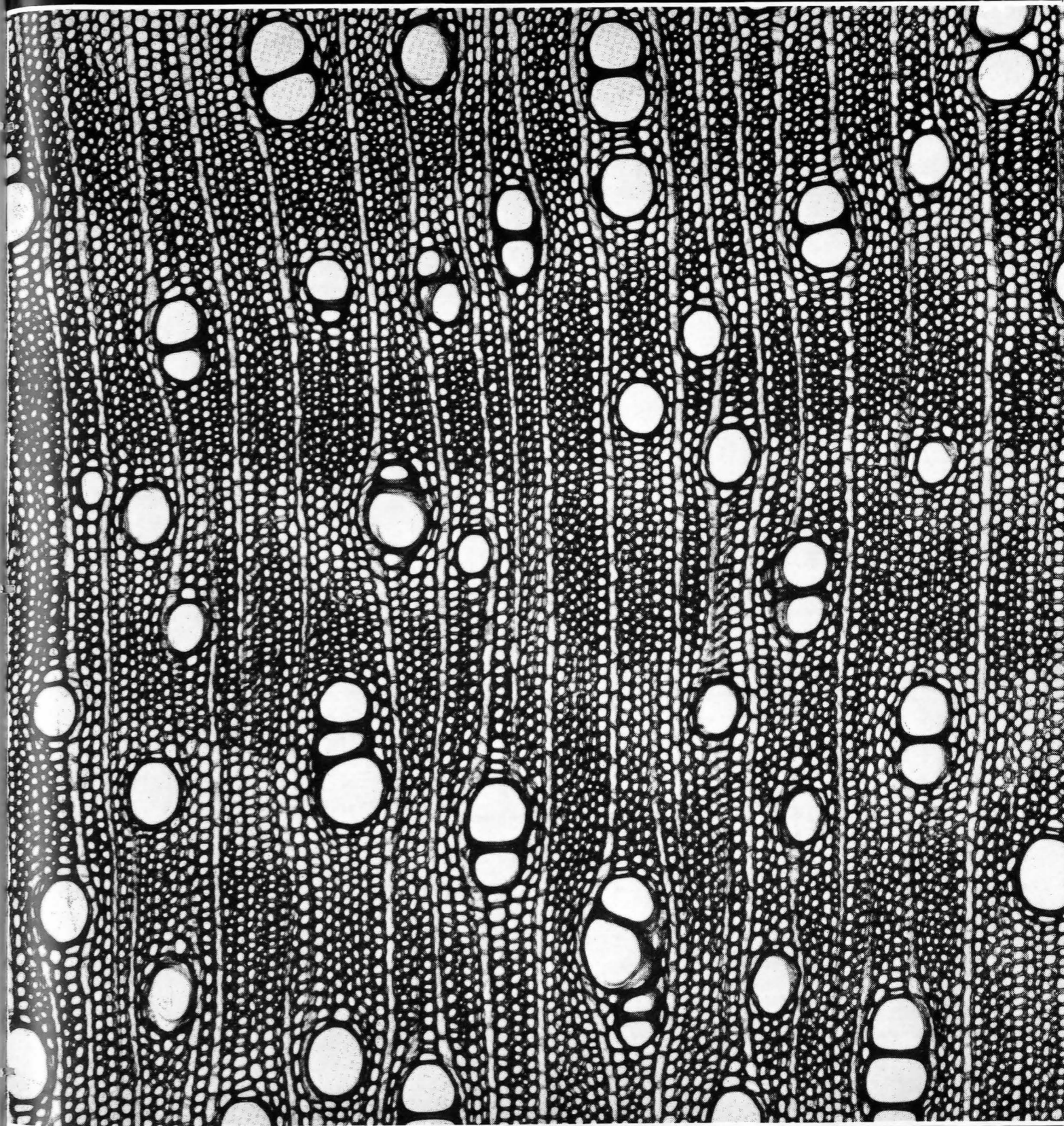


IAWA BULLETIN

Contents

	page
Association affairs	58
L. GOOSEN-DE ROO and P.C. VAN SPRONSEN	
Electron microscopy of the active cambial zone of <i>Fraxinus excelsior</i> L.	59
R.A. GREGORY	
Living elements of the conducting secondary xylem of sugar maple (<i>Acer saccharum</i> Marsh.)	65
Book review	70
KUNG-CHI YANG	
The fine structure of pits in yellow birch (<i>Betula alleghaniensis</i> Britton)	71
A. FREY-WYSSLING	
The concept of the primary cell wall	78
Wood Anatomy news	79
L.J. KUČERA	
Vascular nodules in the pith of yew (<i>Taxus baccata</i> L.)	81
Association affairs (continued)	86
Wood Anatomy news (continued)	87



Front cover: Scanning electron micrograph of the wood of *Eugenia mairi* 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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WOOD ANATOMY NEWS

Late registration for Amsterdam Congress

IAWA Members and others interested who wish to attend the Wood Anatomy Congress in Amsterdam from August 26 through August 30 are urged to register at their earliest convenience. The program may allow for some extra contributed papers submitted after the 15 February deadline. Please contact the office of the Executive Secretary for further details.

Meeting on Xylem Differentiation

Following the success of the 1978 conference on 'Aspects of Xylem Differentiation' in Reading, Dr. J.R. Barnett is organizing jointly with the Royal Microscopical Society a new meeting on the same subject on April 24, 1979 at the University of Reading. The chairman will be Professor R.D. Preston, FRS, and speakers include Dr. J. Dodds, Mr. R. Savidge, Dr. D.S. Skene, Professor P.B. Gahan, Dr. B.G. Butterfield and Dr. J.R. Barnett. Members interested to attend should contact Dr. J.R. Barnett, Department of Botany, Plant Science Laboratories, University of Reading, Whiteknights, Reading RG6 2AS, U.K., for further information.

ASSOCIATION AFFAIRS

New Membership Directory

Dr. R.K. Bamber, from the Forestry Commission of New South Wales, is undertaking the onerous task again to compile an updated, annotated Membership Directory of the IAWA. Membership directories containing information on fields of research of the individual members, are a most important means to stimulate scientific contact and collaboration, and help avoid duplication. May we therefore ask for your active help in compiling the new Directory by completing the questionnaire enclosed in this issue and by sending it to Dr. Bamber at your earliest convenience?

(continued on page 23)

WOOD ANATOMY AND THE USE OF CARBONISED WOOD AS A MATRIX FOR BONE REGENERATION IN ANIMALS

by

James Colville¹, Pieter Baas², Veijo Hoikka³ and Kauko Vainio⁴

Abstract

Wood anatomy appears to be an important factor in successfully using carbonised wood as a matrix for bone regeneration in mice and rabbits. The presence of wide vessels in high frequencies such as in the temperate climber *Clematis vitalba* enables significant bone in-growth.

Introduction

In a recent study (Colville & Hoikka, 1978) it was shown that biocompatibility exists in mice and rabbits to carbonised wood of *Juniperus communis* L. Pieces of carbonised wood of juniper were implanted in the paraspinal soft tissues of mice and in bone defects in rabbits. Results showed not only compatibility but tissue in-growth into the lumina of the tracheids after 25 days. In addition, in rabbits, after 45 days implantation in bone fine trabeculae of cancellous bone could be detected invading the carbon at the margins.

These results, indicating the possible use of carbonised wood as a matrix for regenerating tissues, prompted further experiments with carbonised woods derived from species with a more suitable anatomy than juniper, with its composition of narrow tracheids and ray cells only.

At this stage of the research project, contacts were established between the present authors, and this paper reports on the application of wood anatomy to the field of biomedical research.

Earlier work using wood as a matrix for bone in-growth by Kristen *et al.* (1977) was different in scope, in that these authors selected woods on mechanical criteria and implanted uncarbonised wood fragments. Although they reported considerable success with bone in-growth into wide vessels of birch and ash, biocompatibility of alcohol-extracted and sterilised wood cylinders appeared to be sub-optimal.

Wood anatomical considerations

For the successful application of carbonised wood as a matrix for regenerating bone, the following criteria must be considered.

1. The wood structure should be sufficiently homogeneous to guarantee reproducible results.
2. The wood should retain its porous structure after carbonisation.
3. The carbonised wood should contain pores (vessels) of suitable size to allow the free invasion of bone tissue. Hulbert (1969) has shown that bone in-growth will not occur unless the pore diameter is at least 100 μm and a maximum upper limit of 500 μm has also been reported (Predecki & Mooney, 1971).
4. The percentage porosity is obviously related to fragility of the material (during the carbonisation process) and this factor negates the use of highly porous woods composed of very thin-walled elements.
5. The pores should be devoid of tyloses or other contents, sapwood therefore being more suitable than heartwood.

For the first experiments, wood, chosen more or less at random (Colville & Hoikka, 1978) of *Juniperus communis* satisfies some of the above anatomical considerations in that it has a uniform structure (Fig. 1) but in other respects it was unsuitable having a tracheid lumen diameter of 10–20 μm only. Continuity for invading animal tissue could be expected to be very small in view of the non-perforated nature of the tracheids and the fact that contacts via bordered pits are insufficient because of their limited size and the likelihood that the pit membranes remain intact after carbonisation (cf. Fahn, 1975).

Other woods were thus considered to be more suitable, in particular the vessel containing hardwoods, especially those from tropical rain forests and of woody climbers. Temperate hardwoods are considered unsuitable because if ring-porous they do not provide the necessary homogeneity across the growth ring, or if diffuse-porous the vessels are of a restricted diameter (30–60 μm). Diffuse-porous tropical rain forest specimens often show very wide vessels (200–300 μm) which would seem suitable for the in-growth of bone. However, the wide vessels in these tropical hardwoods are

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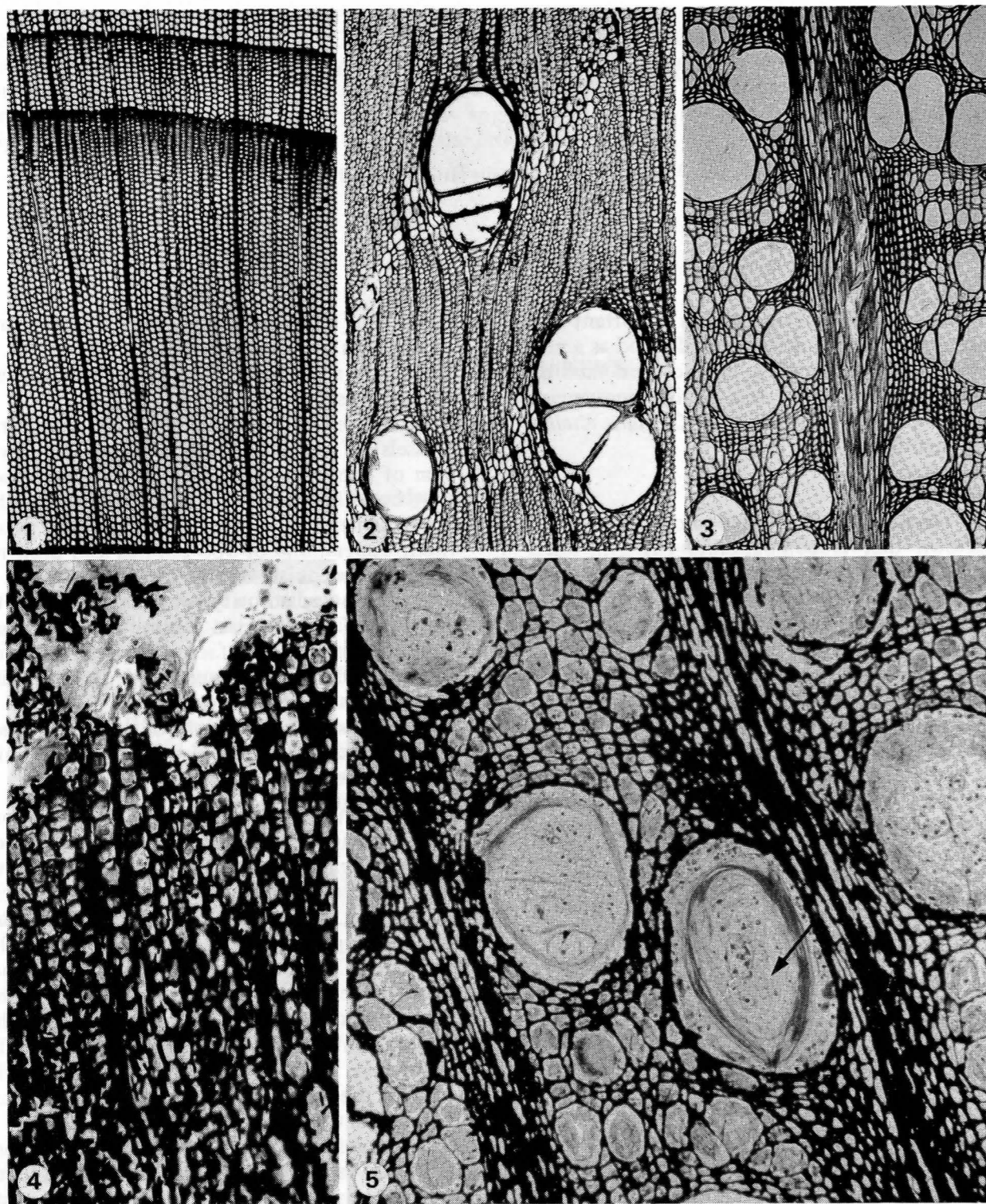


Fig. 1-3. Transverse sections of uncarbonised woods to show different porosities, x 50. — 1. *Juniperus communis*. — 2. *Terminalia superba*. — 3. *Clematis vitalba*. — Fig. 4. Implant of carbonised *Juniperus communis* wood showing in-growth of connective tissue. — Fig. 5. Implant of carbonised wood of *Clematis vitalba*, showing bone in-growth in large vessels in centre of implant after 56 days, and excellent preservation of the microstructure of the wood.

invariably present in comparatively low frequencies and the vessels generally do not occupy more than 10-20% of the total volume. The wood of most climbers is also known for its wide vessels. They are, moreover, usually present in very high frequencies resulting in much higher percentage volumes. In view of the above, the following species were selected for further tests.

1. *Terminalia superba* Engler & Diel (Fig. 2); the well known commercial timber (Limba) and tropical hardwood. In this species the vessels average about 300 μm in diameter, and occupy about 10% of the total volume.
2. *Clematis vitalba* L. (Fig. 3) and *Parthenocissus tricuspidata* (Sieb. & Zucc.) Planch.; temperate climbers which have their entire growth rings almost filled with 'early wood' vessels (150-400 μm diameter), constituting from 50-70% of the total volume. In addition, narrow vessels occur intermingled between the wide vessels in those woods.

Carbonisation of wood

Cellulose is capable of undergoing thermal decomposition without the presence of a melting stage, forming a carbonaceous residue. The actual chemical changes taking place during the process can be conveniently divided into four stages (Gill, 1972). According to Tang & Bacon (1964) the carbon chains are formed along the paths of the original cellulose chains, thus preserving a replica of the original fibre structure.

In this project the wood was cut into small pieces approximately 3 mm² and placed in a vertical furnace. Nitrogen gas at five litres per minute, calculated to normal pressure, was passed over the wood for one hour before heating began. The temperature was then raised to 850° C and kept constant for five hours. When cool, the samples were removed and autoclaved prior to implantation.

Surgical techniques

Biocompatibility tests were first carried out using carbonised *Juniperus communis*, placed in the soft tissues of mice and left *in situ* for variable times (Colville & Hoikka, 1978).

Fifteen New Zealand white adult rabbits were anaesthetised using intramuscular fentanyl citrate 0.3 mgs per kg body weight (Hypnorm Janssen Pharmaceutica).

A 3 mm² defect was created in both iliac crests and filled with a similar sized piece of carbonised wood of *Juniperus communis*. The rabbits were sacrificed at various intervals, see Table 1, and histological preparations made for staining with haematoxylin and eosin.

A further ten New Zealand white immature

rabbits were used and operated on, as above, to assess the relative amount of bone in-growth in the three wood species — *Clematis vitalba*, *Terminalia superba* and *Parthenocissus tricuspidata*.

Results

Excellent biocompatibility was demonstrated using carbonised *Juniperus communis* in the soft tissues of mice (Colville & Hoikka, 1978). Likewise *Juniperus communis* implanted in the iliac bones of rabbits for variable periods of time showed no evidence of foreign body reaction. At 25 days, however, connective tissue could be seen in the tracheids of the *Juniperus communis* and from 50 days onwards fine bone trabeculae could be seen to be growing in at the margins of the implant (Fig. 4).

In the remaining ten immature rabbits, one died on the tenth post operative day (autopsy revealed bilateral pneumonitis). Thus nine rabbits each with three implants were available for examination. There were no technical failures. Macroscopically, the carbon implant was difficult to see because of bone overgrowth in all specimens. However, microscopically bone in-growth occurred only at the margins of *Terminalia superba* and *Parthenocissus tricuspidata*, whereas in *Clematis vitalba* implants, bone could be seen growing throughout the implant (Fig. 5). A summary of the times of implantation and the amount of bone in-growth is shown in Table 1.

Discussion

No substance implanted in living tissue, can ever be said to be completely compatible, this property being reserved for substances manufactured by the body itself i.e. autogenous. Nevertheless, biocompatibility of carbon in many forms has already been reported (Kenner, 1975; Musikant, 1971; Bechtol *et al.*, 1959; and Colville & Hoikka, 1978).

Rabbit Implantation No.	time days	Bone in-growth		
		<i>Parthenocissus tricuspidata</i>	<i>Terminalia superba</i>	<i>Clematis vitalba</i>
R 16*	—	—	—	—
17	47	—	—	—
18	55	—	+	++
19	55	+	+	++
20	65	—	—	++
21	56	+	+	++
22	56	—	+	++
23	56	+	—	++
24	56	+	+	++
25	56	+	+	++

* Died 10th post operative day.

+ : present; ++ : significant; — : absent or limited marginal in-growth only.

Table 1.

One aspect of the compatibility of this form of carbon still requires further investigation, namely an analysis of the concentration of heavy metal ions, known carcinogens.

Bone in-growth is dependent upon many factors — compatibility, pore size, shape and frequency (porosity), site of the implant, technique of implantation, nature of the implant, age and general health of the animal.

Some of the factors in each group of animals — i.e. site of implant, age and general health of the animals, were constant and need not be considered further. The technical procedure was as far as possible standard, the defect being filled on each occasion with an implant of the same size. However, if even a small degree of movement repeatedly occurred between the implant and the tissue interface, the delicate immature tissue could be damaged. This factor may have some bearing on the differing results using the same type of wood.

Preparation (carbonisation) was as far as possible standardised. However, the amount of shrinkage of fibres and hence the shape and size of the pores is known to be dependent upon the rate of heating, furnace atmosphere and humidity. In these respects, it is possible that different woods react in different ways even under standard conditions.

Incompatibility can hinder in-growth, but in all specimens no foreign body reaction could be detected.

Thus regarding bone in-growth pore size and porosity must be considered vitally important.

Juniperus communis, even with a porosity of 90 % could not be expected to allow any in-growth of bone — at least 100 µm pore diameter being necessary for the in-growth of bone (Hulbert, 1969).

Terminalia superba, diffuse-porous and with large pore diameter (200–300 µm) allowed some in-growth at the margins as expected, but the low percentage porosity (10 %) could not be expected to result in significant bone in-growth.

Clematis vitalba and *Parthenocissus tricuspidata*, both temperate climbers and with similar pore diameters and percentage porosity should each have allowed similar i.e. significant bone in-growth. This significant amount of bone in-growth however only occurred in the case of *Clematis vitalba* and somewhat less in-growth in the case of *Parthenocissus tricuspidata*. These different results for two temperate climbers with a rather similar wood structure remain unexplained.

Conclusions

Carbonised woods of *Juniperus communis*, *Terminalia superba*, *Parthenocissus tricuspidata* and *Clematis vitalba* have been shown to be compatible with soft tissues in mice and bone in rabbits.

Connective tissue in-growth will occur in the tracheid lumina of *Juniperus communis*. Bone in-growth in the pores of *Terminalia superba* and *Parthenocissus tricuspidata* was clearly shown in rabbits. A significant amount of bone in-growth was demonstrated in the pores of *Clematis vitalba* throughout the implant.

Hence, the use of carbonised wood of suitable anatomy as a matrix for regenerating new bone is a possibility. Further research is needed and is in progress.

Acknowledgements

The above work was funded in part by a grant from the Medical Research Council of Ireland.

We wish to thank Mr. B.J.H. ter Welle (Utrecht) for providing wood samples suitable for carbonisation.

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THE PICEA–LARIX PROBLEM

by

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Abstract

The woods of *Larix* and *Picea*, hitherto thought to be indistinguishable, can be separated on the structure of the bordered pits in their ray tracheids. *Larix* mostly has relatively large bordered pits with a big aperture, and the margin of the border to the pit aperture is rounded or slightly pointed. The border is often thin. In *Picea* on the other hand the ray tracheid bordered pits are relatively small and have a narrow aperture. The margin of the border to the pit aperture is often edged with 1 or 2 angles and the apertures are channel-like. The border is often thick and can be dentate.

In 1901 the Danish wood anatomist and botanist O.G. Petersen made the following conclusion about this classical problem in the diagnostic wood anatomy:

'I believe I dare say that, in spite of all work done, a good diagnostic histologic character for distinguishing the wood of Larch and Spruce is still to be regarded as a *pium desideratum*'. And I add that, whereas in many other cases I consider it hopeless, in this case I believe one may well expect to find a distinguishing mark in the course of continued investigations or by a coincidence, as the 2 plants in question are morphologically very different.' (Petersen, 1901).

To my knowledge the problem was last touched upon by B. Huber in 1970 when he concluded: 'Trotzdem ist seit bald hundert Jahren den wiederholten Bemühungen vieler Holzanatomen vorläufig noch immer versagt geblieben, ein für alle Einzelfälle zutreffendes Unterscheidungsmerkmal für die beiden Gattungen zu finden.' (Huber, 1970).

I am now venturing to return to this problem for the reason that I believe to have found, 'by a coincidence', as O.G. Petersen puts it, a character that makes it possible to distinguish between the two genera *Picea* and *Larix*.

The incentive to a more thorough investigation of the problem is given by the frequent finds of pieces of '*Picea-Larix*' wood in the cultural layers of the Middle Ages in SW Scandinavia (Denmark, SW Sweden, and SW Norway). Wood which must always have been imported, for which reason it is of cultural historical importance to know whether it is *Picea* wood or *Larix* wood. Small stave cups are particularly frequent in these cultural layers (Fig. 1). One reckons that these cups may be drinking cups or that they have somehow been

subjected to a varying degree of moisture. The remainder of a sealing compound is often found along the bottom edge. The quality of the *Larix* wood makes this species preferable for cups of this kind. The oldest stave cups found in Bergen, Norway (Bartholin & Solberg, unpubl.) were often made of *Abies spec.*, which proves importation from Central Europe. *Larix* must therefore not be ruled out beforehand. On the other hand the finds of stave cups are so frequent that it is difficult to relate them to the relatively small natural distribution of *Larix decidua* Mill. The *Picea-Larix* problem in South Scandinavia also crops up in connection with finds in interglacial deposits, where it is of great vegetation-historical importance to know whether finds should be referred to one genus or the other, a problem which cannot be solved with certainty by means of pollen analysis either.

In subfossil wood the wood-anatomical characters can be best seen, as a rule, on radial longitudinal surfaces, as the transverse surface and the tangential longitudinal surface are often deformed because of the pressure in the strata.

In *Picea* (and *Larix*?) the rays seem very resistant to decay, which meant that the investigations were concentrated on the ray cells seen on the radial section.

It turned out that the bordered pits in the ray tracheids showed great variation in size and appearance. A large part of the pits could not be described in an unequivocal way, but 3 types seemed to be of a recognizable and characteristic appearance.

1. The *Larix* type (Fig. 2): The bordered pit is relatively large with a big aperture, the margin of the border to the aperture is rounded or slightly pointed. The border is often thin.
2. The *Picea* type 1 (Fig. 3): The bordered pit is relatively small with a small aperture. The margin of the border to the aperture is often edged with 1 or 2 angles and the aperture looks like a little channel. The border is often thick.
3. The *Picea* type 2 (Fig. 4): Has the same appearance as *Picea* type 1, but the border is dentate.

The distribution of the different types of bordered pits including atypical types of different species is given in Table 1. The distribution is based on measurements of 100 pits each time. (For the

Table 1. Distribution of types of bordered pits in ray tracheids per 100

Sample no.	Tree species	Atypical	Larix type	Picea type 1	Picea type 2
Picea (mean)		31.4	1.9	59.8	7.0
C 3	<i>P. abies</i> (L.) Karst.	39	6	26	29
L 577	ibid. (root)	38	1	53	8
L 578	ibid. (root)	31	2	64	3
C 316	<i>P. engelmannii</i> (Parry) Engelm.	36	2	50	12
L 466	ibid.	29	0	67	4
C 317	<i>P. glauca</i> (Moench) Voss	33	5	45	17
L 460	ibid.	32	0	54	14
L 551	ibid.	31	2	64	3
L 586	ibid.	29	1	67	3
L 552	<i>P. glauca</i> var. <i>albertiana</i> (S. Brown) Sarg.	22	0	78	0
L 561	<i>P. hurstii</i>	28	5	61	6
L 581	<i>P. jezoensis</i> (Sieb. & Zucc.) Carr.	24	1	67	8
L 568	<i>P. mariana</i> (Mill.) Britten, Sterns & Poggenberg	26	2	67	5
L 585	ibid.	26	0	72	2
L 563	<i>P. mariana</i> var. <i>doumetii</i> (Carr.) Schneid.	22	0	73	5
C 315	<i>P. omorika</i> (Pančić) Purkyně	58	6	34	2
L 587	ibid.	27	2	70	1
L 588	ibid.	30	1	64	5
L 461	<i>P. pungens</i> Engelm.	21	1	69	9
L 579	ibid.	21	1	60	18
L 50	<i>P. sitchensis</i> (Bong.) Carr.	69	2	28	1
C 307	ibid.	40	2	56	2
L 457	ibid.	26	0	64	10
L 553	ibid.	15	4	81	0
Larix (mean)		30.5	66.3	3.3	0
C 32	<i>L. decidua</i> Mill.	26	69	5	0
L 73	ibid.	38	58	4	0
C 358	ibid.	42	53	5	0
L 474	ibid.	28	68	4	0
L 576	ibid.	34	63	3	0
L 534	<i>L. x eurolepis</i> Henry	47	46	7	0
C 639	<i>L. gmelinii</i> (Rupr.) Kuzeneva	19	79	2	0
L 83	<i>L. laricina</i> (Du Roi) K. Koch	34	59	7	0
L 464	<i>L. leptolepis</i> (Sieb. & Zucc.) Endl.	29	66	5	0
C 631	ibid.	27	72	1	0
L 481	<i>L. leptolepis</i> x <i>gmelinii</i>	26	72	2	0
L 559	<i>L. occidentalis</i> Nutt.	34	61	5	0
C 343	<i>L. sibirica</i> Ledeb.	18	82	0	0
L 487	ibid.	31	69	0	0
L 498	ibid.	22	77	1	0

L : Samples from the Lund wood collection

C : Samples from the wood collection of the Institut of Plant Anatomy and Cytology, Copenhagen

Lund samples the value is the mean for 200 pits). The samples had been coded with the sample number and the names were unknown when making measurements. The values in the table must only be regarded as normative, as they have been determined by one person only and can therefore hardly be considered quite objective.

In the practical diagnostic work it is not necessary to measure. Having learnt carefully how to distinguish the different types, a general view can lead to a quick determination. Using about x 300 magnification is recommended.

By using these characters on about 2000 inter-

glacial and medieval samples from the area mentioned above, only *Picea spec.* was found!

I hope that my colleagues will give the method a try, for example on subfossil samples from Central Europe, as I am of the opinion that it needs checking critically from another quarter. I want to point out, though, that the method is not applicable on charcoal, where the bordered pits have often been burnt away, nor on thin roots, where ray tracheids are seldom well-developed.

The characters seem so obviously recognizable that I have felt very doubtful about publishing these results, particularly bearing in mind the

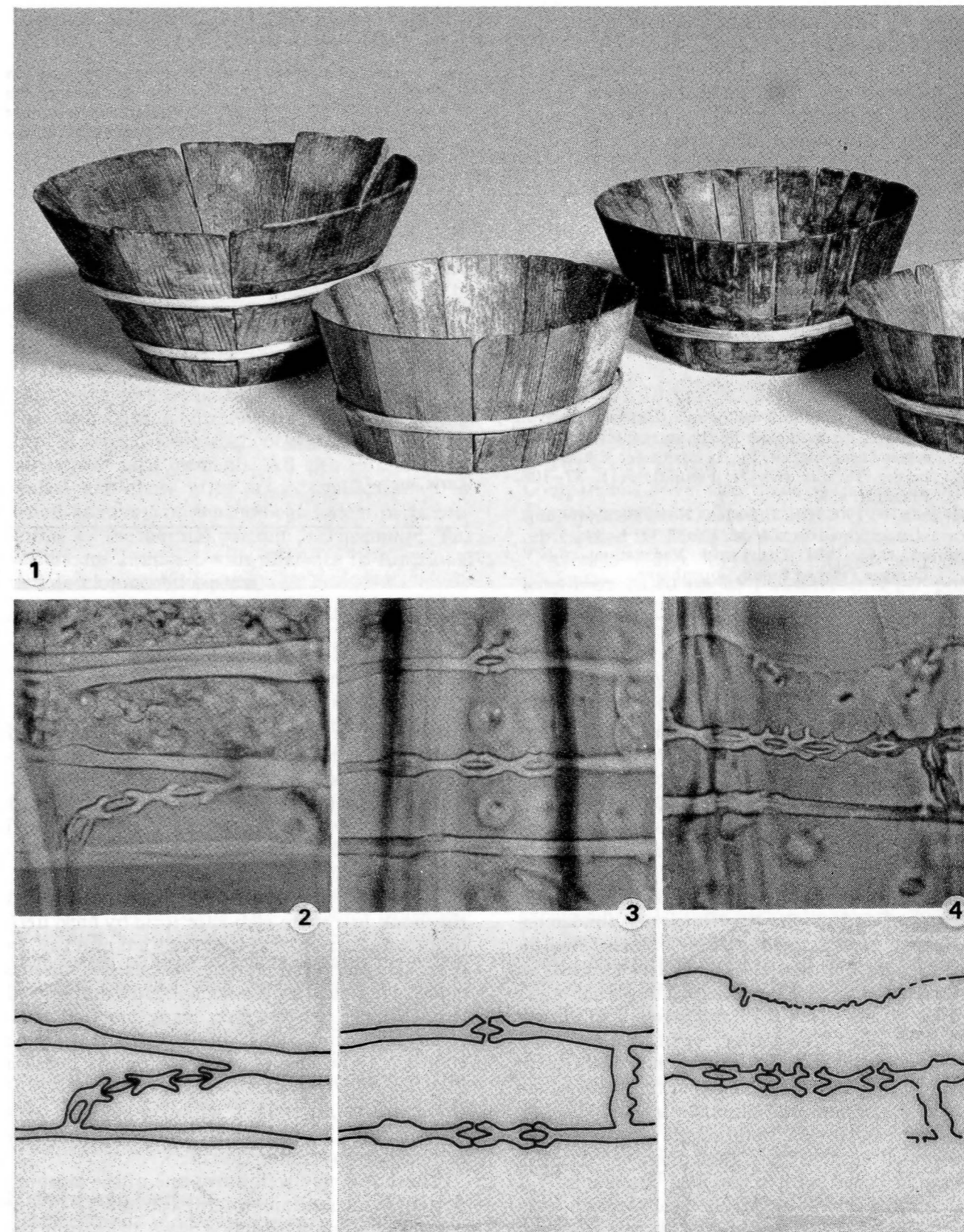


Fig. 1. Stave cups of *Picea spec.* (Photograph: Kulturen, Lund). — Fig. 2. Bordered pits. *Larix* type. — Fig. 3. Bordered pits. *Picea* type 1. — Fig. 4. Bordered pits. *Picea* type 2. (Photographs figures 2–4: Odense University).

words by Huber quoted above. But 'by another coincidence' I found that the same observations were made already in 1903 (Ingvarson, 1903). F. Ingvarson gives the same description of the character of the bordered pits in the ray tracheids with the exception of *Picea* type 2. He also gives measurements of the proportions of the bordered pits, see Table 2, which to a large extent support my observations.

Acknowledgements

I want to thank the Institute of Plant Anatomy and Cytology, University of Copenhagen, for lending me coded slides and The Arboretum at Horsholm, Denmark, for most of the samples of the Lund collection.

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BOOK REVIEW

Tropical trees and forests. An architectural analysis. F. Hallé, R. A. A. Oldeman & P. B. Tomlinson, 441 pp., many illustrations. Springer Verlag, Berlin-Heidelberg-New York. Price (Cloth): DM 125 or US\$ 62.50.

This handsome book surveys the complex problems of tree development leading to specific tree architecture, and also has a section on the architecture of forests. Starting from such fundamental phenomena as seedling development, bud diversity, radial growth etc., the authors present an integrated picture of *how* tropical trees and forests are built, and often they also attempt to answer the questions of *why* they are built as they are. The present reviewer is certainly not qualified to evaluate critically the contents of this book which covers much new and hitherto neglected ground. It is not easy for the traditionally narrow-minded wood anatomist to grasp the complex descriptive accounts, laced with theoretical comments. Yet the authors should be commended for their lucid treatment of intricately connected processes and structures. For the IAWA Bulletin it is perhaps most appropriate to dwell on the significance of this book for wood anatomy. Using small sectioning blocks one easily ignores the fact that one is studying a once living part of an ecosystem carrying out vital functions for its maintenance. Although aware of much structural variation within a tree, wood anatomists so far have hardly con-

Table 2 (from Ingvarson, 1903)

Tree species and places of collection	Proportion between the diameter of the outer and the inner pit aperture in ray tracheids
<i>Picea excelsa</i> , Lappland, Sweden	7.8 : 1
ibid., Värmland, Sweden	5.7 : 1
ibid., Jämtland, Sweden	8.3 : 1
ibid., Skåne, Sweden	7.4 : 1
ibid., Jylland, Denmark	13.9 : 1
<i>Picea excelsa</i>, mean	8.62 : 1
<i>Larix europaea</i> , Skåne, Sweden	3.1 : 1
<i>L. americana</i> , Vermont, Canada	2.3 : 1
ibid., Canada	2.2 : 1
ibid., driftwood	1.7 : 1
<i>L. sibirica</i> , Siberia	3.7 : 1
ibid., Siberia	2.9 : 1
<i>Larix</i>, mean	2.65 : 1

cerned themselves with possible correlations of anatomical structure with the diverse developmental modes, finally responsible for the existence of different architectural models and their deviating derivatives in nature. These architectural models were classified in a comprehensive system for the first time by Hallé and Oldeman in 1970. This has stood the test of time and is presented in this book in a more elaborate form by lucid definitions and examples as well as by a useful key. In some chapters the authors themselves discuss wood anatomical aspects such as growth rings and vessel characters. However, many more observations and conclusions offered should become common knowledge to wood anatomists, because they may well have a bearing on some causes of wood structural variation within or amongst trees or species (e.g. syllepsis and prolepsis; orthotropy and plagiotropy; reiteration etc.).

This book may well prove one of the most important contributions to tropical botany of our decade, and since 'Botany needs help from the Tropics; its big plants will engender big thinking' (Corner, cited in this book) it will be of crucial importance for botany as a whole. Especially students of temperate trees, basing their generalizations on observations on these odd, exceptional creatures, should consult this book in order to become a twelfth hour convert before being lost for ever.

Pieter Baas

THE PECULIAR WOOD STRUCTURE OF *VACCINIUM LUCIDUM* (BL.) MIQ. (ERICACEAE)

by

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Abstract

The wood and bark anatomy of *Vaccinium lucidum*, an epiphytic shrub from the wet, montane forests of Malesia, with a distinctly swollen stem basis, is described and discussed. The xylem of the stem basis is characterized by large dilating rays separated from each other by narrow strips of narrow axial elements. All elements are thin-walled and show little or no lignification. The wood anatomy of the non-basal stem parts conforms to the normal pattern of *Vaccinium*. The results are discussed with reference to functional and developmental aspects.

Introduction

Vaccinium lucidum (Bl.) Miq. is an epiphytic (rarely also terrestrial) shrub from the montane, wet forests of Malesia. The plants are characterized by a distinctly swollen stem basis said to be hypocotylar (Sleumer, 1976) or rhizomatous (Von Faber, 1927). Prof. Dr. C.G.G.J. van Steenis drew my attention to this species while I was studying the xylem anatomy of another taxon with swollen stem bases: *Leptospermum crassipes* Lehm. (Baas, 1977). Material of *Vaccinium lucidum* from the Cibodas forest reserve in Java was especially collected by Dr. Soejadmi Dransfield née Soenarko; it included a rather soft swollen stem basis, straight stems of various diameters, and hard, swollen stem portions associated with branching.

The study of this material was considered relevant, because it allows an assessment of the potentialities of a single genome to modify its complex secondary xylem anatomy in different plant parts, and because it may throw light on functional aspects of wood anatomy.

Materials and Methods

Macerations and transverse, tangential and radial sections were prepared according to standard techniques. Sections were stained with safranin and astrablue according to a modified method by Maáčz & Vágás (1961). The following samples were studied:

- A. A thin, straight branch, 8 mm in diameter with a pith of 1 mm in diameter.
- B. A straight stem, 15 mm in diameter with a pith of 3 mm in diameter.

C. A hard, swollen stem part associated with branching, 20 mm in diameter, with a pith of 2 mm.

D. Ibid. but 18 mm in diameter and also with a pith of 2 mm.

E. A soft swollen stem base, 25 mm in diameter with a very narrow pith of 0.1 mm.

Comparisons were also made with several other *Vaccinium* species of normal tree or shrub habit, represented in the Rijksherbarium slide collection.

Average values for vessel member and fibre length are based on 25 measurements per point sample.

Results

The anatomy of the swollen stem base of *Vaccinium lucidum* is illustrated in Figures 1–6. The secondary xylem is dominated by broad rays composed of large cells (c. 30–70 μ m high and wide, and 40–90 μ m long in radial direction). The axial xylem system is confined to narrow strips 2–8 cells wide. The fusiform elements comprise vessel members and fibres of almost identical dimensions as seen in transverse section (c. 20 μ m). The vessels are solitary and provided with exclusively scalariform perforations with (3–)8(–18) very closely spaced bars. Where in contact with fibre-tracheids the vessel wall is provided with circular to oval bordered pits (4–5 μ m) in a diffuse arrangement. Vessel-ray pits are more closely spaced and are opposite to alternate (4–7 μ m in radial diameter), occasionally unilaterally compound. Vessel member length ranges throughout the whole stem base from (80–)310–420(–670) μ m and shows a very unorthodox length-on-age relationship (Fig. 12). The fibres are all thin-walled and can be classified as fibre-tracheids (with bordered pits and included apertures; only rarely septate) mixed with a transitional form between libriform fibres and fusiform parenchyma (with minutely bordered to simple pits and often septate). The latter type of fibre is even more thin-walled than the fibre-tracheids. The length-on-age variation in fibre length is given in Fig. 13. The broad rays are composed of weakly erect to weakly procumbent cells as seen in radial section; besides, narrow rays of erect cells only are present in the strips of axial elements. Some of the ray

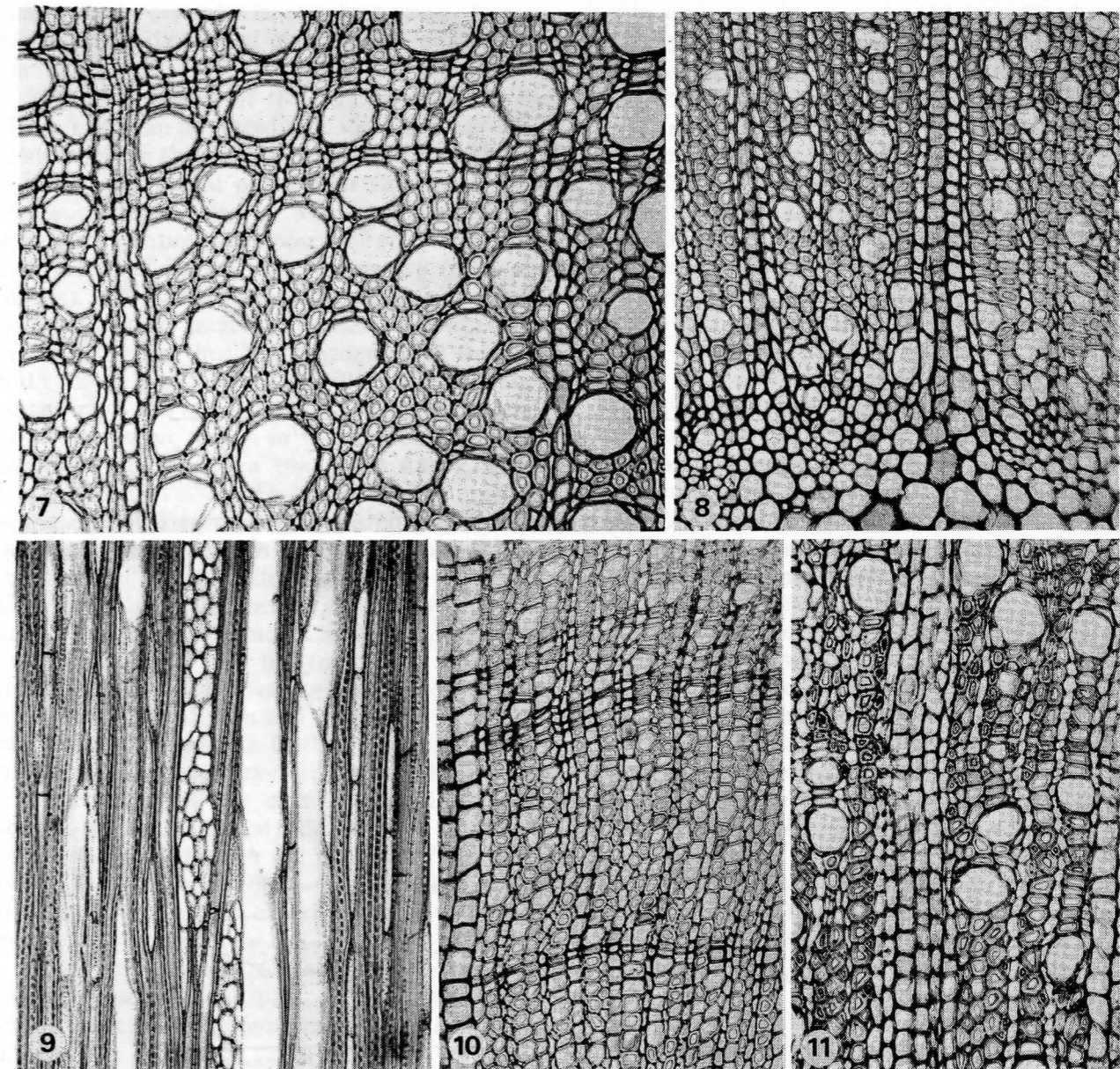
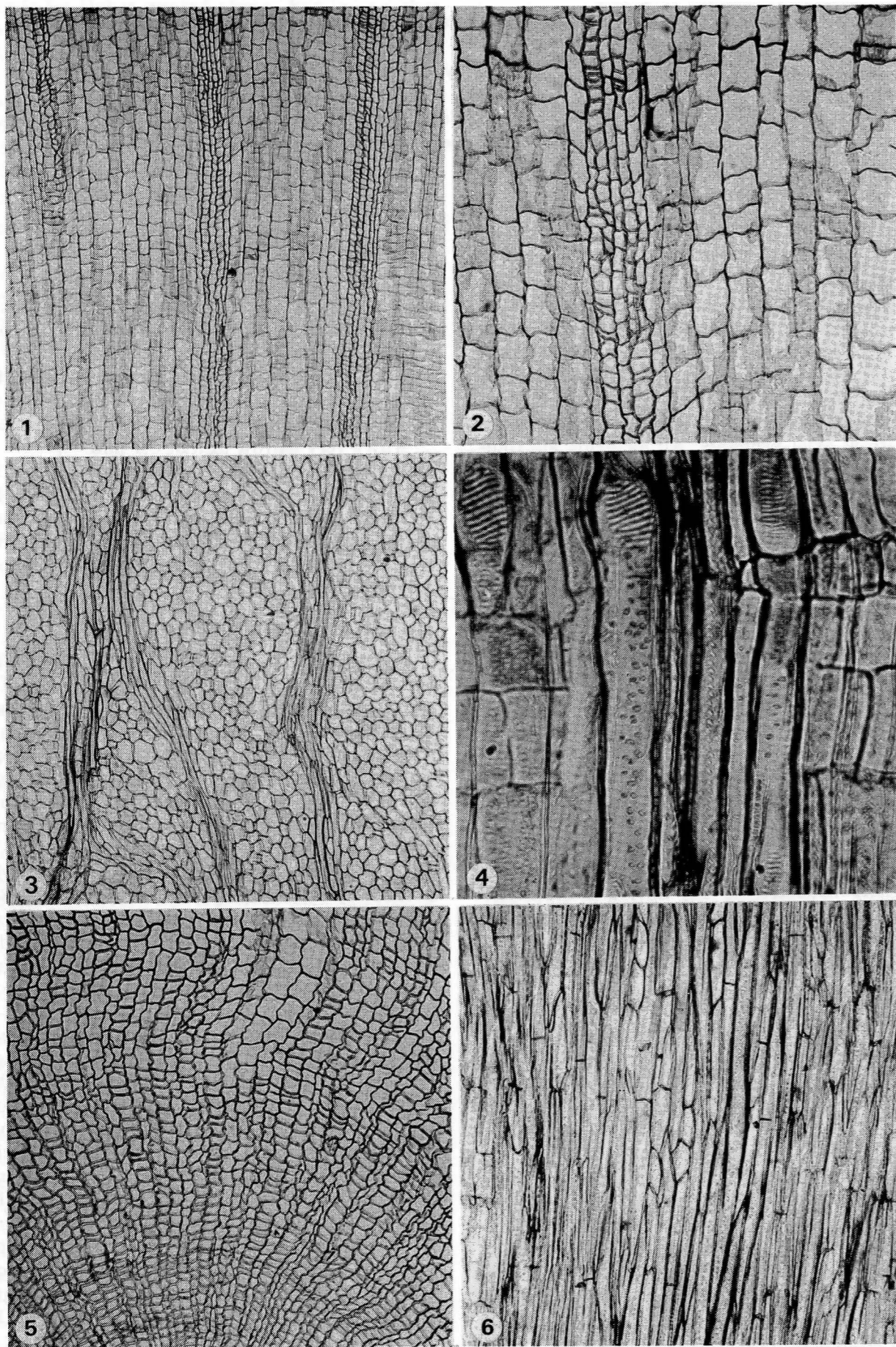


Fig. 7-11. *Vaccinium lucidum* (Bl.) Miq. Secondary xylem of non-basal stem parts, all x 130. — 7-9. Transverse and tangential section of normal stem (sample B), 7 near periphery, 8 near centre of stem; 9 showing 'normal' rays and fibre-tracheids, (septate) libriform fibres and vessel members. — 10. Transverse section of thin twig (sample A). — 11. Transverse section of hard, swollen stem part (sample C).

Fig. 1-6. *Vaccinium lucidum* (Bl.) Miq. Secondary xylem of swollen stem basis. — 1. & 2. Transverse section near periphery, resp. x 50 and x 130. — 3. Tangential section showing abundance of ray tissue, x 50. — 4. Radial section showing ray cells, vessel members, and a fibre-tracheid (arrow) flanked by cells intermediate between libriform fibres and axial parenchyma cells, x 330. — 5. Transverse section near pith, showing onset of dilatation of rays, x 130. — 6. Tangential section near pith, showing narrow rays of upright cells and abundance of axial elements, x 130.

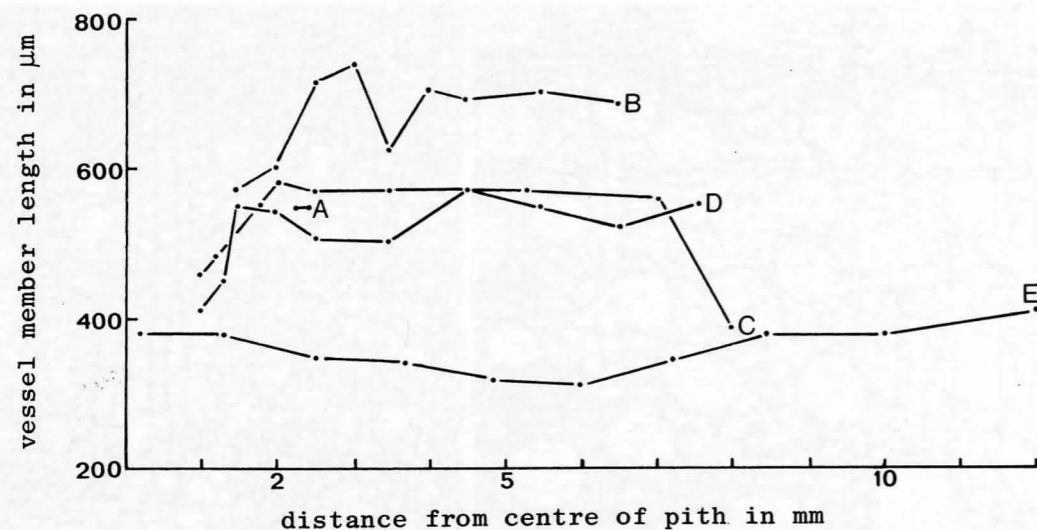


Fig. 12. Length-on-age graphs for vessel member length in different stems and stem parts of *Vaccinium lucidum*. A: thin branch (measured near periphery only); B: normal stem; C & D: hard, swollen stem portions associated with branching; E: swollen stem basis.

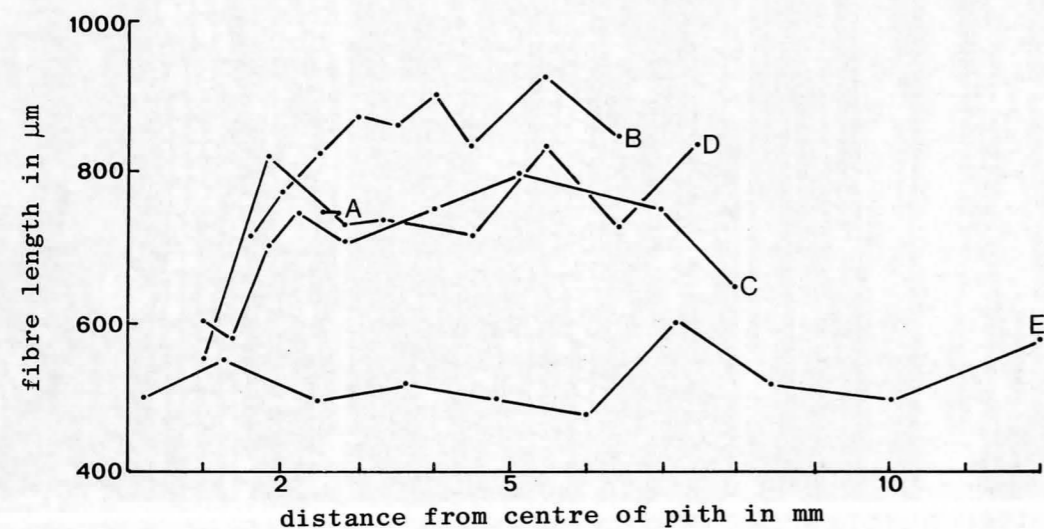


Fig. 13. Length-on-age graphs for fibre length in different stems and stem parts of *Vaccinium lucidum* (see figure 12 for further legends).

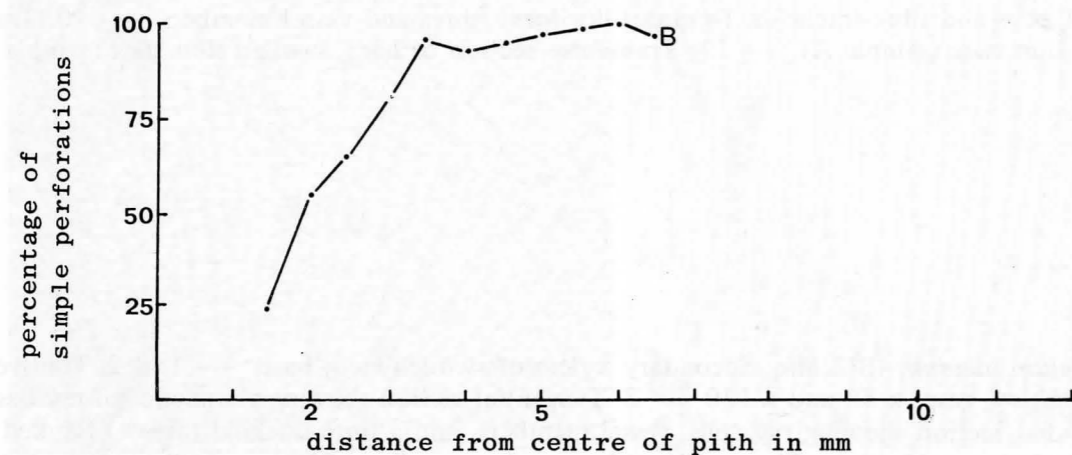


Fig. 14. Percentage of simply perforated vessel member end walls in normal stem (sample B) of *Vaccinium lucidum* as related to distance from the pith.

cells contain crystals: large solitary ones, two or more irregularly shaped ones per cell, or even regular clusters.

The development of this anomalous histology (Figs. 1-4) can be traced by comparing the wood anatomy near the pith (Figs. 5 & 6) with that of the more peripheral parts. Near the narrow pith the wood is traversed by numerous slender, uniseriate rays entirely composed of erect cells. Ray cells and axial elements are very narrow (c. 10 µm or less). At a short distance from the pith all elements show an increase in their tangential and radial diameters, but the broadening of the rays both through an increase in cell size and number of cell rows per ray is the most striking phenomenon. This soon results in the unusual histology described above. When the rays reach a 'maximum' width of about 16 cell rows they may become dissected through the 'de novo' origin of narrow strips of axial tissue: apparently ray cell initials have been transformed into fusiform initials because at the inception of new strips of axial elements cells identical in cell shape and size to the normal ray cells but tracheal or tracheidal in nature due to cell wall or perforation characters occur in profusion and intergrade with 'normal' fusiform elements further towards the periphery. Dissection of rays also occurs by gradual transformation of ray cells into axial elements starting from the lateral side of rays. Dilatation may also occur through the increase of the number of broad rays by the transformation of a narrow ray within a strip of axial tissue into a broad ray.

All xylem elements of the swollen stem base, except those near the pith, are very thin-walled and are very weakly lignified or not lignified at all.

The anatomy of the non-basal stem parts of *Vaccinium lucidum* is strikingly different and in line with what is known of *Vaccinium* wood anatomy in other species (cf. Metcalfe & Chalk, 1950). An important difference is the greater wall thickness of all elements and much stronger lignification (cf. Figs. 7-11).

Near the pith of branch A the situation is still reminiscent of the secondary xylem in the center of the swollen stem basis: vessel members and fibre-tracheids and libriform fibres have much the same diameter (c. 15 µm) and the rays are almost exclusively uniseriate and composed of erect cells only. Towards the periphery the rays become up to 4-seriate: the uniseriate are here also composed of erect cells only, but the multiseriate rays contain a fair proportion of square to weakly procumbent cells. The vessels are only slightly wider than the fibre-tracheids and libriform fibres (Fig. 10). All vessel perforations in branch A are scalariform.

In stem B, with its wide pith, the first-formed secondary xylem is traversed with uniseriate as well as multiseriate (primary) rays composed exclusively of erect cells. Toward the periphery the rays are like in branch A and can be considered as intermediate between Kribs' heterogeneous types I and II. The vessels are distinctly wider than the fibre-tracheids and libriform fibres from the onset and there are numerous vessel members with simply perforated end walls, especially towards the periphery (see Fig. 14). The bars in scalariform perforations are usually widely spaced and range from (1-)-4-8(-17) in number per perforation plate. The vessel wall pitting is somewhat coarser than in the swollen base and in branch A: vessel-fibre-tracheid pits measure 5-6 µm, and the vessel-ray pits are coarse and simple, measuring 4-14 µm in radial dimension (transitional to scalariform). Vessel member and fibre length curves show a more traditional course: an increase near the pith until a more or less constant level is reached (Figs. 12 & 13).

The wood anatomy of the hard, swollen stem parts associated with branching (samples C and D, cf. Fig. 11) is much similar to that of stem B. Only the rays are significantly wider in these parts, viz. up to 8-seriate. Furthermore both samples have aberrant peripheral zones (traumatic?), characterized by abundant axial parenchyma strands of 2 cells and a steep decline in vessel member and fibre length (see curves for sample C in Figs. 12 & 13 which was taken through such a parenchymatous zone). In the hard swollen stem parts the percentage of simply perforated vessel members is even higher than in stem B.

In samples A-D solitary or irregular crystals have also been observed in some of the ray cells.

The bark anatomy of *Vaccinium lucidum* is in all parts characterized by a superficial cork tissue of numerous cell layers, a number of parenchymatous to sclerenchymatous cortical layers, a perivascular region usually composed of sclerified cells, and a rather homogeneous secondary phloem composed of sieve tubes and parenchymatous cells, and only few phloem fibres (scattered or in short, thin bands). Sclerification is least in the swollen stem basis: here the cortex is wholly parenchymatous and the perivascular sclerenchyma is very poorly or hardly developed. Crystals occur in the phloem and are most abundant in the swollen stem basis. Remarkably enough phloem fibres are most abundant in the (young) twig sample A, and are here present in several, more or less regular, tangential bands. In sample B some of the broader phloem rays are sclerified.

Discussion

Von Faber (1927) suggested that the swollen stem bases of *Vaccinium lucidum* function as wa-

ter storage organs during periods of less abundant water supply. He substantiated this by recording their shrunken appearance during the drier periods. The wood anatomy of the swollen stem of *V. lucidum* would be compatible with such a function. The thin-walled and hardly lignified elements — especially the ray cells — allow for reversible shrinking and swelling and allow for the storage of a considerable volume of water. The limitation of the water conducting cells to a minor portion of the total xylem tissue, together with the fact that all vessel members are very narrow and provided with extremely closely spaced bars in their perforations might provide a guarantee that the water supply from the swollen stem basis to transpiring upper parts would be extremely slow so that it cannot be quickly exhausted. The water conducting capacity of the non-basal stem parts is certainly much greater in view of the higher proportion of vessels, the wider diameter of the latter, and the preponderance of simply perforated vessels in the wider stems and stem parts.

This attractive, functionally adaptive, hypothesis should of course be viewed against the ecological background of *V. lucidum*: although an epiphyte it grows in highly mesic localities and water stress can only by very great exception be severe (Van Steenis, 1972). The functional anatomist would almost like to transplant this species to more xeric environments where it could take more advantage of its specialized xylem structure! It is interesting to compare the swollen stem anatomy of *V. lucidum* with that of *Leptospermum crassipes*. The latter might benefit from a type of wood anatomy facilitating water storage during the hot, dry season in Western Australia. However, the xylem of *L. crassipes* is almost entirely composed of conducting cells (vessel members and tracheids), which — although capable of water storage to some degree — would seem less suitable elements than the ray parenchyma cells of *Vaccinium lucidum*.

Massive parenchyma development has also been recorded for hard, subterranean tubers (lignotubers or 'Xylopodien') in numerous species of the open campos vegetation of Brazil by Dusén and Neger (1921). These authors also hypothesized a water storage function for the parenchyma here, which makes sense when considering the xeric conditions these species are subdued to during the dry season. Here storage of starch was also often found; in the *Vaccinium lucidum* material studied by me no reserve carbohydrate storage was observed at all.

From a developmental wood anatomical point of view the stem base swellings of *V. lucidum* are also interesting. The joint occurrence of a 'juvenilistic' length-on-age graph for vessel members and of a very narrow pith implies another negation of the theories by Philipson & Butterfield (1967)

and Mabberley (1974) for explaining length-on-age graphs for fusiform cambial derivatives (cf. Baas, 1976 & 1977). As in *Leptospermum crassipes*, the 'release-from-mechanical-strength' hypothesis, proposed by Carlquist (1975) would seem a better explanation: Mechanical support of the swollen stem basis in *Vaccinium lucidum* must almost certainly be derived from turgor pressure and hardly or not from its fibres. The presumed conversion of ray initials into fusiform initials resulting in the dissection of broad rays by strips of axial parenchyma is also of interest. The conversion of ray initials into fusiform initials was also reported by e.g. Chattaway (1933) and Braun (1970), but they observed only conversion of marginal ray cells. The latter phenomenon is also common in *V. lucidum*, but here conversion also occurs in the center of the rays, far removed from other fusiform initials.

Acknowledgements

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A NOTE ON THE FINE STRUCTURE OF TRABECULAE IN AGATHIS ALBA

by

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The problem of clarification of the fine structure of trabeculae as they occur in gymnospermous and angiospermous woods has been discussed by Keith (1971) and Ohtani (1977). In a recent communication Keith *et al.* (1978) have described the structure of trabeculae in conifers using various microscopic techniques including transmission electron microscopy. Supplementing these results and encouraged by Dr. Keith it was deemed appropriate to present further details of transmission electron micrography of the trabeculae in the secondary xylem of *Agathis alba*.

The general characteristics of the trabeculae in *Agathis alba* are similar to those already reported. They traverse the lumina of several tracheids in the radial direction, and possess a bar-like structure (Fig. 1). Their average diameter amounts to 4 μ m. At places of contact with the tangential wall, the trabeculae are slightly expanded, thus creating the impression of a dumbbell shape. In the TEM the trabeculae evince their cross-wall-like nature possessing substructural units. The middle lamella of the tracheid wall is apparently continued into the connecting region of the trabecula up to a certain distance. Also the S₂ of the tracheid wall flows into the trabecula as a direct continuation (Fig. 2). Thus the central part of the trabecula comes to possess a highly contrasted

core region of about 1 μ m diameter with a bundle of fibrils oriented parallel to the trabecula (Fig. 3). On both sides of this core the wall layers exhibit a parallel orientation of fibrils; these layers are the direct continuation of the S₂ layer of the tracheid secondary wall. In the polarizing microscope a transection of the trabecula confirms this horizontal orientation of fibrils inasmuch as they show an extinction and the base of the trabecula wall near to the tracheid-wall contact a distinct birefringence. Keith (1978, private communication) expressed the same opinion about the continuity of trabecular structures with the tracheid wall.

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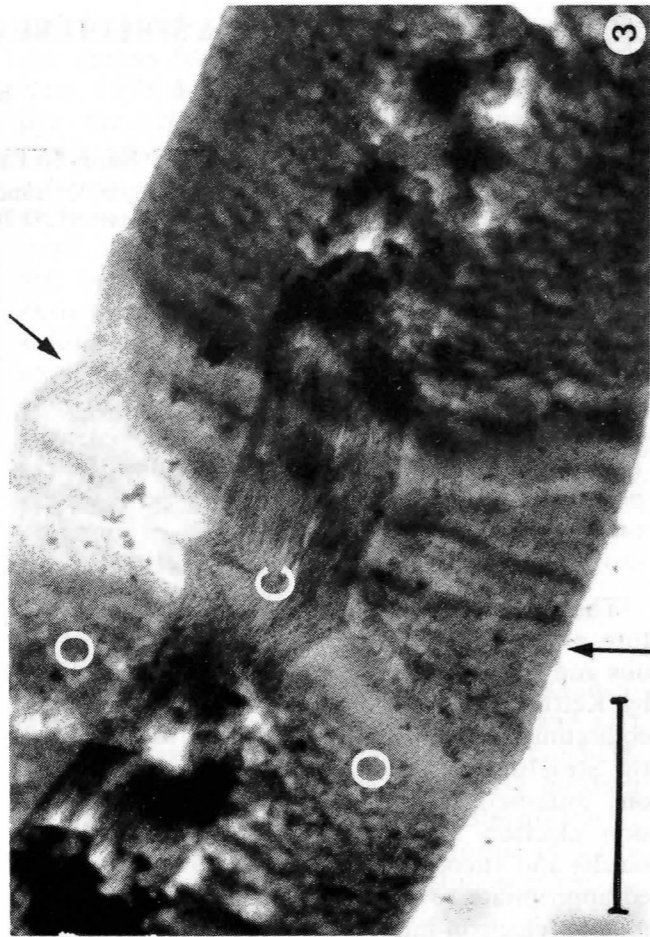
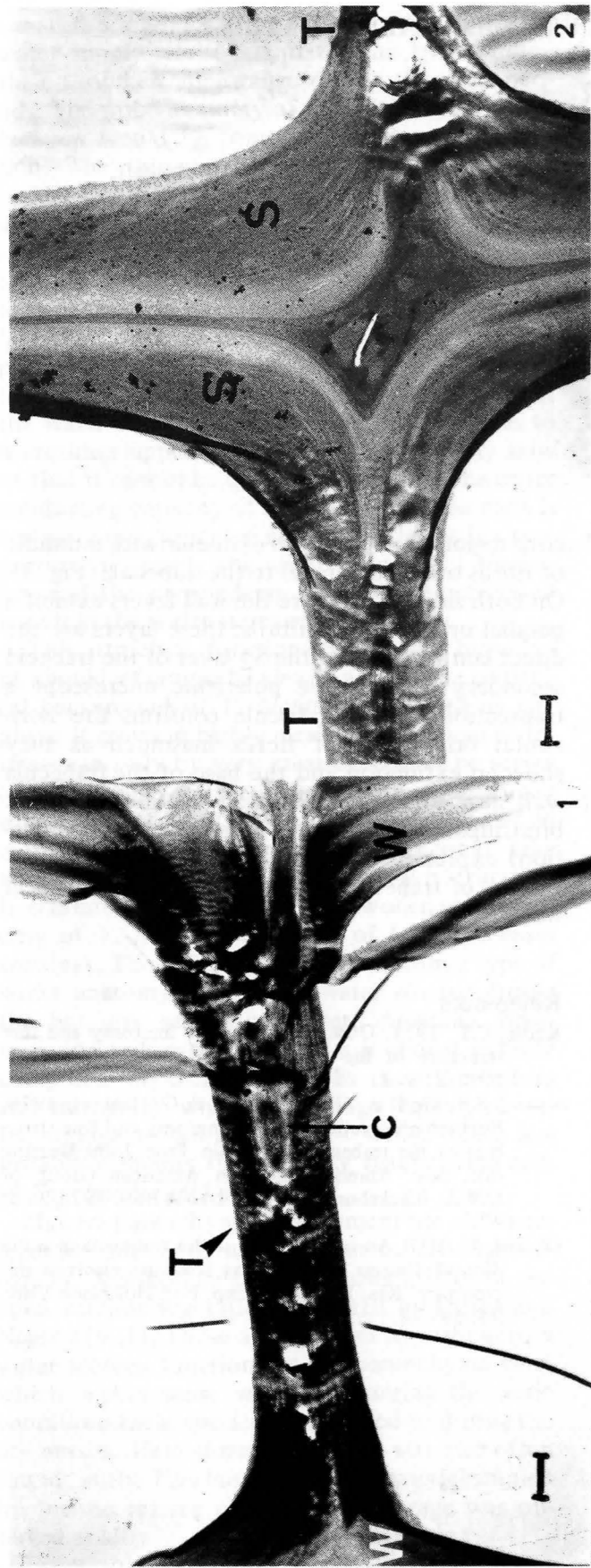


Fig. 1. Cross-wall-like nature of the trabecula stretched between the longitudinal walls of the tracheid (W); core-like region partly visible (C). Bars in all figures: 1 μ m. — Fig. 2. Longitudinal section of a tracheid showing the nature of contact between tracheid wall and trabecula; note the continuity of the secondary wall (S) of the tracheid into the trabecula. — Fig. 3. Enlarged view of the trabecula in longitudinal section with the inner core region (C) and the outer layers (O) with parallel orientation of fibrils; arrows indicate regions of compression resembling slip-planes.

A NOTE ON THE SPATIAL RELATIONSHIP BETWEEN RAYS AND AXIAL RESIN CANALS IN *PICEA ABIES*

by

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Introduction

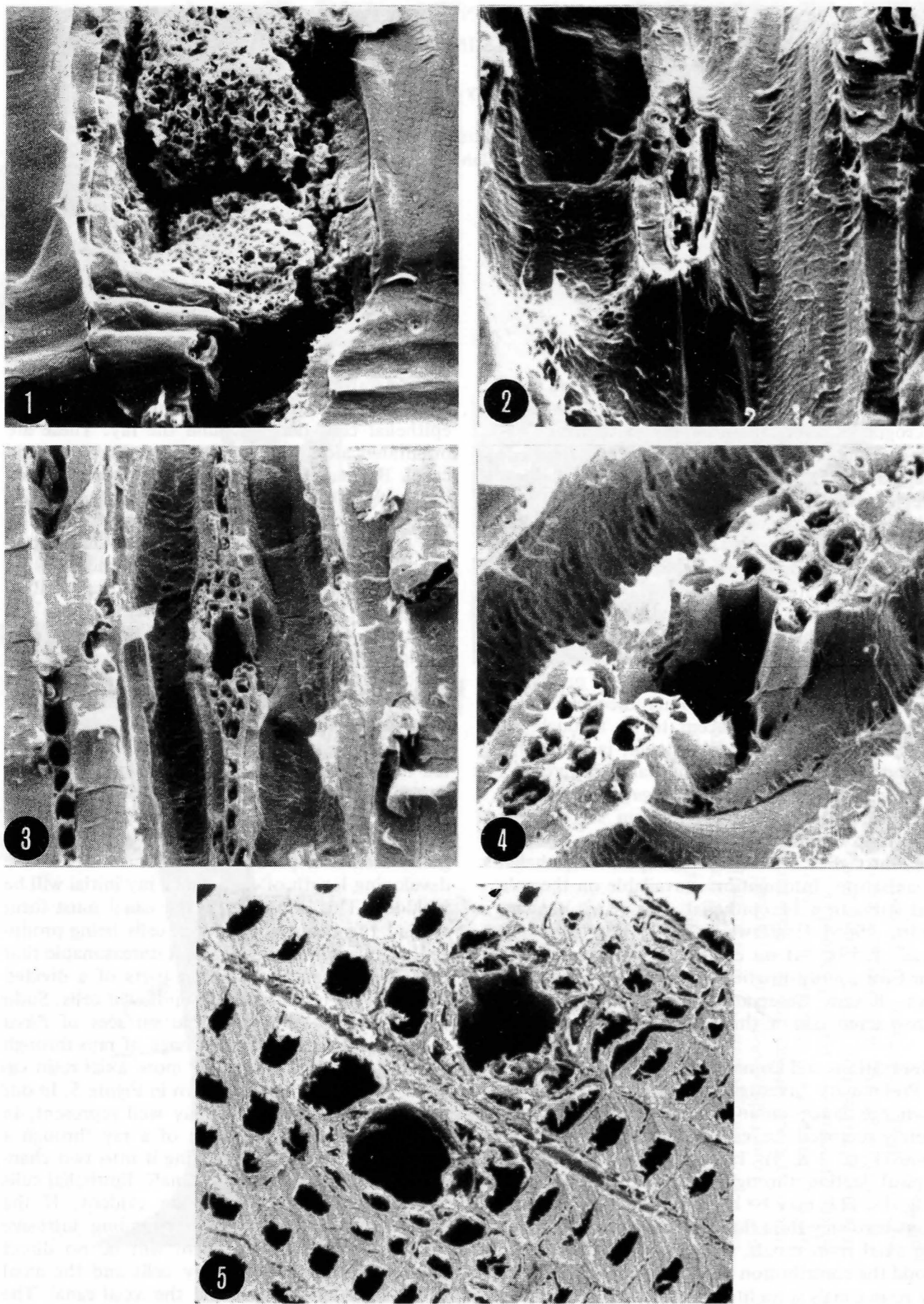
The spatial relationship between rays and axial resin canals has received scant investigation. Few micrographs revealing either the existence or nature of such a relationship have been published. Greguss (1955) states that 'there commonly exists direct communication between longitudinal and radial resin ducts' but provides little direct evidence to substantiate this claim. Chattaway (1951) has suggested a mechanism whereby radial resin canals are initiated in conjunction with axial resin canals in response to a common cambial stimulus. This implies that fusiform rays and axial resin canals should be joined in at least one position. Furthermore, Chattaway (1951) has published evidence that uniseriate rays may become multi-seriate after passing adjacent to, or through, an axial resin canal. Rays are shown, in transverse section, to pass through solitary axial resin canals in *Picea smithiana* and *Pseudotsuga menziesii*.

Consideration of the epithelium surrounding axial resin canals is of interest because a ray passing through a canal must disrupt the epithelial organisation. Information is available on the role and formation of epithelial cells (e.g., Bannan, 1936, 1965; Chattaway, 1951; Engström and Back, 1959), but no evidence has been put forward for a reorganisation of the epithelium around rays. Recent observations in this Department throw some light on this question.

Observations and Comment

Preliminary investigation showed that solvent exchange to acetone and critical point drying completely removed the resin from the canals of *Picea abies* (Figs. 2 & 3). This may be compared to a typical section through an air dried resin canal (Fig. 1). This may be of significance to investigations involving fluid flow through species containing axial resin canals, since even in solvent dried wood the contribution to total conductivity made by resin canals is traditionally ignored. The occurrence of uniseriate rays passing through axial resin canals is fairly common in *Picea abies* (about 2–3 per mm of canal length). Figures 2 and 3 show

the general features associated with intrusive rays in axial resin canals. Of particular note are the epithelial cells that surround the ray. These are orientated along the long axis of the axial resin canal. Bannan (1965) indicates that vertical resin canals are formed in the cambium initially as a bundle of parenchyma cells. These are formed by the segmentation of the fusiform initial. Subsequently, an intercellular canal is formed on the accumulation of resin between developing epithelial cells. Chattaway (1951) points out that the formation of the vertical canals is the result of a change within the daughter cells, and not the cambial initial, since normal vertical elements are formed after the axial resin canal. She also suggests that a radial resin canal is formed when a ray initial occurs in the cambial area that is stimulated to form an axial resin canal. Once this has occurred, the ray initial is permanently altered to produce a continuous radial canal. If an axial resin canal develops in the manner Bannan suggests, then it is probable that somewhere in the developing length of the canal a ray initial will be included. This implies that the canal must form around the continuum of ray cells being produced. If this is the case, it is not unreasonable that the tissue separating the two parts of a divided canal should be sheathed in epithelial cells. Sudo (1968) studied the transverse surfaces of *Picea* species, and reported the passage of rays through tangential groups of two or more axial resin canals. Similar evidence is shown in Figure 5. In our opinion, this observation may well represent, in transverse view, the passage of a ray through a single axial resin canal dividing it into two channels, rather than a pair of canals. Epithelial cells surrounding each channel are evident. If the sheath of epithelial cells surrounding intrusive rays is complete, then there will be no direct communication between ray cells and the axial canal, or a radial canal and the axial canal. The present study has not provided any conclusive evidence of such direct communication: it is extremely difficult to be certain whether the apparent



communication observed in some cases (e.g., Fig. 4) is real or artifactual. Even if the epithelial sheath is complete, indirect communication through the epithelial cells may occur, since Laming (1974) has shown there to be pitting between epithelial cells and ray parenchyma in this species. The question of communication between axial and radial resin canals deserves further study.

A feature of axial resin canals in *Picea abies*, particularly adjacent to an intrusive ray, is the fibrillar bridging that occurs between epithelial cells surrounding the canal (Fig. 2). This is reminiscent of the fibrils spanning intercellular spaces reported in a number of conifer species, although in the present case the fibrils seem more robust. Bolton *et al.* (1975) suggest that the fibrils spanning longitudinal intercellular spaces are the remnants of the stretched parental cell wall. It is possible that the fibrillar bridging observed in the present study is similarly vestigial; if not, its function remains to be elucidated.

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Fig. 1. A typical axial resin canal after air drying. A substantial amount of resin remains. Split radial surface, x 1722. — Fig. 2. A uniseriate ray passing through an axial resin canal. Split tangential surface, x 2460. — Fig. 3. A fusiform ray passing through an axial resin canal. Split tangential surface, x 984. — Fig. 4. Detail of Figure 3, x 2460. — Fig. 5. A ray flanked on either side by an axial resin canal (or the two halves of a bifurcated canal). Microtomed transverse surface, x 1722. — Figures 2–5 are of material solvent exchanged to acetone and critical point dried.

The structure of New Zealand woods. B.A. Meyland & B.G. Butterfield, 250 pp., 805 scanning electron micrographs. DSIR Bulletin 222, New Zealand Dept. Sci. & Industr. Res., Wellington, 1978. Price not known.

This book summarizes the results of an extensive survey of the three dimensional structure of 115 New Zealand woods, carried out over the years by Drs. Meylan and Butterfield. Part of their results has been published previously in numerous fine papers which appeared mostly in the New Zealand Journal of Botany and also partly in the IAWA Bulletin. The present book contains much new information and is a landmark in the history of wood anatomy, because it is the first truly detailed survey of the wood anatomy of a temperate flora from the Southern Hemisphere. Twenty softwood species and ninety-five hardwood species are pictured by 7 scanning electron micrographs each, showing most or all salient features for each species. The illustrations are accompanied by data on tree or shrub size, distribution and ecology, and by descriptions of what can be observed using scanning electron microscopy (of course most features described can be observed by light microscopy as well). The micrographs are all of unrivalled quality and the reproduction in print is very good. It is a delight to go through this book and be lost in wonder at the diversity of structural detail in such characters as pitting, wall sculpturing, perforations, intercellular spaces, etc. The overall histology is also well illustrated by low power magnifications of transverse and tangential (sometimes also radial) surfaces.

The texts of both the introductory parts and the descriptions are brief, but adequate in view of the apparently modest aims of the authors. One may wonder why these aims have not been extended in scope. The tremendous wealth of microstructural data presented for the interesting woody flora of New Zealand so obviously invites comment and synthesis on a comparative basis that one does not know whether one should admire or criticize the authors for withstanding this temptation and for limiting themselves to a top quality SEM atlas.

Riding one's own hobby horses, one is struck

by the solid pit membranes in the vesselless hardwood of *Pseudowintera* species, pictured for the first time, and leaving questions to be answered by physiologists who base models of flow in softwood on the porous nature of the membrane margo in tracheid pits. The relatively high incidence of spiral thickenings and scalariform perforations in genera from largely tropical families, not normally showing these features is another interesting result one can deduce from this atlas, but which is left uncommented. Moreover, the data on these carefully selected common tree and shrub species in all their anatomical diversity could easily have resulted in a most useful key to genera or families of New Zealand woods. However, no key is given, not even a tabular summary of the most strikingly varying features in the 95 hardwood species. This would have facilitated access to the overall results of the survey. Perhaps the high standards set by the authors themselves have led them to refrain from elaborate commentary and from the construction of keys, in view of still existing gaps in the knowledge of New Zealand species not included in the book, or in view of the desirability of combining SEM results with detailed light microscopical data. Yet it would seem that at this stage preliminary conclusions and tentative keys could have been brought together in the same book. The present comments are of course only aimed at inspiring the authors to comply with the wish that a companion volume will be produced highlighting the implications for pure and applied anatomy of this survey.

Meanwhile this manual offers a unique data bank, not only for the benefit of those who are interested in New Zealand woods, but for all students of wood anatomy, because it excellently illustrates most or perhaps all structural variations possible in xylem elements. Whatever its price (not known when this review went to the press) this book is a must for reference and teaching libraries and deserves a wide distribution in private libraries as well, where it will stun the layman visitor with the microstructural beauty of wood.

Pieter Baas

(continued from page 2)

New IAWA Council elected

The new IAWA Council for the 1979-1981 term has been elected. For the next three years the following Members will govern our Association in accordance with our Constitution.

Dr. R.K. Bamber (Australia) – Dr. J. Bauch (BRD) – Dr. J. Burley (UK) – Dr. B.G. Butterfield (New Zealand) – Dr. Z. Koran (Canada) – Dr. L.J. Kučera (Switzerland) – Mr. P.B. Laming (The Netherlands) – Dr. E.D. Lobjanidze (USSR) – Mr. C. Manieri (Brazil) – Dr. S. Sudo (Japan) – Dr. A.B. Wardrop (Australia) – Dr. Elisabeth A. Wheeler (USA).

It seems appropriate at this stage to record our appreciation for Members of the previous Council who have served IAWA for two consecutive terms and who were instrumental in the implementation of new policies for our Association over this important period.

New terms of office for Executive Secretary and Deputy

The previous Council has elected Dr. P. Baas for another three year term to serve as Executive Secretary of IAWA. Mr. P.B. Laming has been appointed for a new term as Deputy Executive Secretary.

Deceased Member

We received information that our Member Dr. Jaromir Rak from the Eastern Forest Products Laboratory in Ottawa passed away in April 1978. Dr. Rak had been a Member of IAWA from 1970 onwards.

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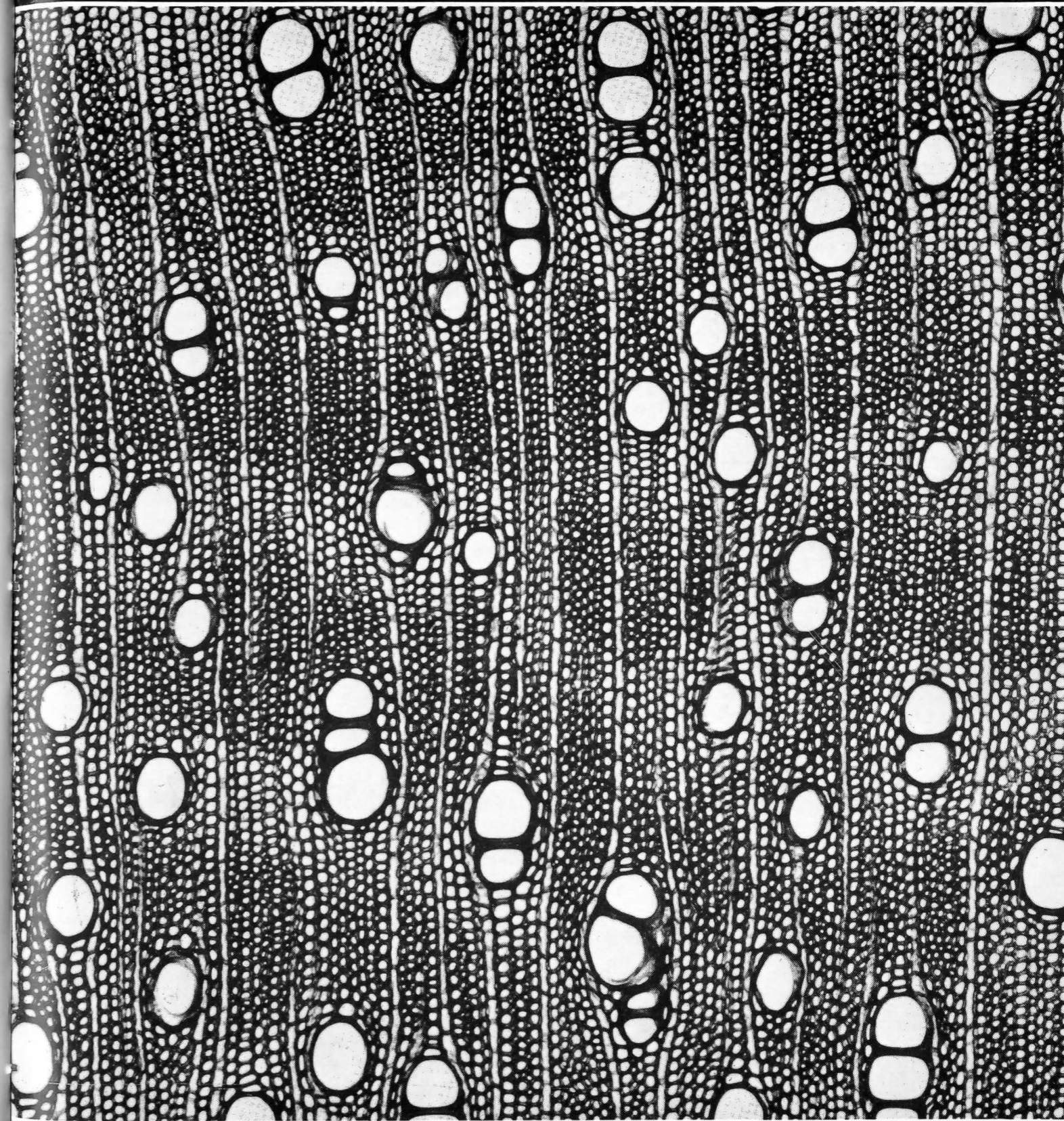
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IAWA BULLETIN

Contents

	page
Wood Anatomy news	2
Association affairs	2
J. COLVILLE, P. BAAS, V. HOIKKA and K. VAINIO	
Wood anatomy and the use of carbonised wood as a matrix for bone regeneration in animals	3
TH. BARTHOLIN	
The <i>Picea-Larix</i> pollen. <i>P. Abies</i>	7
Book review	10
P. BAAS	
The peculiar wood structure of <i>Vaccinium lucidum</i> (Bl.) Miq. (Ericaceae)	11
N. PARAMESWARAN	
A note on the fine structure of trabeculae in <i>Agathis alba</i>	17
S.H. TURNER, A.P. BUSH and A.J. BOLTON	
A note on the spatial relationship between rays and axial resin canals in <i>Picea abies</i> ..	19
Book review	22
Association affairs (continued)	23



Front cover: Transverse section of *Lagerstroemia indica* L. (Lythraceae). The banded pattern in this and some other *Lagerstroemia* species is due to fibre dimorphism and not to parenchyma differentiation (cf. P. Baas & R.C.V.J. Zweyppfenning: Wood anatomy of the Lythraceae. Acta Botanica Neerlandica 28 (2), in the press).

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