



**IAWA
BULLETIN**

1972/4

OUR COVER

The cover of the IAWA Bulletin for 1972 consists of photomicrographs (cross- and tangential sections) of *Apeiba membranacea* Spruce ex Benth., Family Tiliaceae. Broad bands of radially aligned parenchyma cells are prominent features in this species.

The material was collected on 5 August 1933 by Boris A. Krukoff (No. 5304) in the Territory of Acre, on the Rio Purus, Brazilian Amazonia. The slide was prepared by Mr. A. C. Day from specimen BWC_w No. S12437 which was borrowed from the Harry Philip Brown Memorial Wood Collection at State University of New York College of Environmental Science and Forestry. Photomicrographs were prepared with the assistance of Mr. J. J. McKeon. Magnification: 70X

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The International Association of Wood Anatomists was organized in 1931 to advance the knowledge of wood anatomy in all its aspects. It does this in part by attempting to promote and facilitate cooperation among the relatively small number of specialists in wood anatomy.

Prospective members are invited to write to the Office of the Executive Secretary for a copy of the Constitution, an application form, and information about IAWA. Membership dues, which includes a subscription to the IAWA Bulletin, are currently \$3.50 (U. S.) per year.

EDITORIAL

Comments in our last editorial regarding a shortage of technical papers appear to be out of order at the present time. There are actually more papers on hand for this issue than we could handle without a major enlargement. We have had to publish those received first. Please keep them coming. It would even be pleasant for us to be forced into a decision to enlarge the Bulletin.

The appeal for program themes for the IAWA meeting at the XII International Botanical Congress at Leningrad in 1975 has failed to elicit any response from the membership. We wish to remind you that if you have ideas which you want to be considered, they should be submitted soon.

A comment has been received recently on the indexing number system used for the IAWA Bulletin. For some years the issues have been identified by year and a number indicating the quarter of publication. The more usual system is to assign a volume number. Should we change our system to conform to the more usual library notation?

W. A. Côté

C. H. de Zeeuw

Intervessel Pit Membranes in *Knightia excelsa* R.Br.

By

B. G. Butterfield¹ and B. A. Meylan²

The intervessel pit membrane in hardwoods is generally described as a simple structure without visible openings, built up of the two primary walls of the adjacent cells and the intervening middle lamella (Schmid, 1965). Such pit membranes do not have a centrally thickened torus like many conifer pits but are commonly overarched by borders of secondary wall material. Schmid and Machado (1968) have published evidence that intervessel pit membranes may consist of a number of alternating fibrillar and granular layers, the more internal fibrillar layers tending to have a parallel microfibril arrangement continuous with the primary wall of the vessel while the more external ones have a loose crossed texture.

Changes in the nature of pit membranes during differentiation of the vessel member have been discussed by Schmid and Machado (1968) and Yata, Itoh and Kishima (1970). The latter authors suggest that during the later stages of protoplast breakdown, some components of the unlignified vessel member primary walls are degenerated by the action of enzymes.

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This action affects the perforation plate partitions (end walls) and the intervessel pit membranes.

The stages in perforation plate breakdown in *Knightia excelsa* R.Br. (New Zealand honeysuckle or rewarewa) have been illustrated recently by the present authors (Meylan and Butterfield, 1972). During this study a number of scanning electron micrographs of intervessel pit membranes were obtained.

Wood samples from mature trees of *Knightia* were dried by a solvent exchange process similar to that outlined by Collett (1970) and fractured so as to expose different layers of the cell wall. The specimens were then coated with 20 nm of carbon and a similar amount of gold-palladium and examined in the vacuum dry state in the column of a Cambridge Series IIA scanning electron microscope.

The vessel to vessel pit membranes are illustrated in figures 1 to 3. Intervessel pits in *Knightia* are arranged in an alternate pattern on the vessel member walls, the pit apertures being at a slight angle to the horizontal. The secondary walls of the adjoining vessel members overarch the pit chambers, which are separated by almost circular pit membranes. These intervessel pit membranes clearly show a microfibrillar texture under the scanning electron microscope, with a random arrangement of the microfibrils on the surface. None of the membranes exposed by fracture showed any tendency to separate into layers so it was not possible to observe the orientation of the microfibrils at levels inside the pit membrane.

The loose microfibrillar texture of the mature intervessel pit membrane is not a feature of either the mature secondary wall or the immature primary wall as observed in differentiating perforation plates (Meylan and Butterfield, 1972). Our observations with the scanning electron microscope, therefore, would tend to confirm the suggestion that some of the components of intervessel pit membranes, presumably the non-cellulosic components, are removed during vessel member differentiation. There is no evidence, however, to indicate that the pit membranes are subjected to the severe enzymatic action that removes almost all of the components of the perforation partitions.

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FIGURES

Figure 1. A fracture exposing a number of wall layers between two vessel members in *Knightsia*. The inside wall of the near cell can be seen at the top of the photograph pierced by numerous pit apertures. Below this the S3 layer has been removed exposing the horizontal orientated microfibrils of the S2 wall. Where this too has been removed to the lower left of the photograph, the pit membranes have been exposed overlaid by varying amounts of S1 secondary wall. Parts of the secondary wall of the adjacent vessel member are seen to the lower right (2,900X).

Figure 2. Two almost intact intervascular pit membranes exposed by the removal of the secondary wall of the near cell. Note the slit shaped apertures and overarching borders of secondary wall in the adjacent group of pits (15,500X).

Figure 3. A surface view of intervascular pit membranes in *Knightsia* showing the dispersed texture of the microfibrils. The small pieces of debris on the membranes were probably deposited during specimen preparation (15,500X).

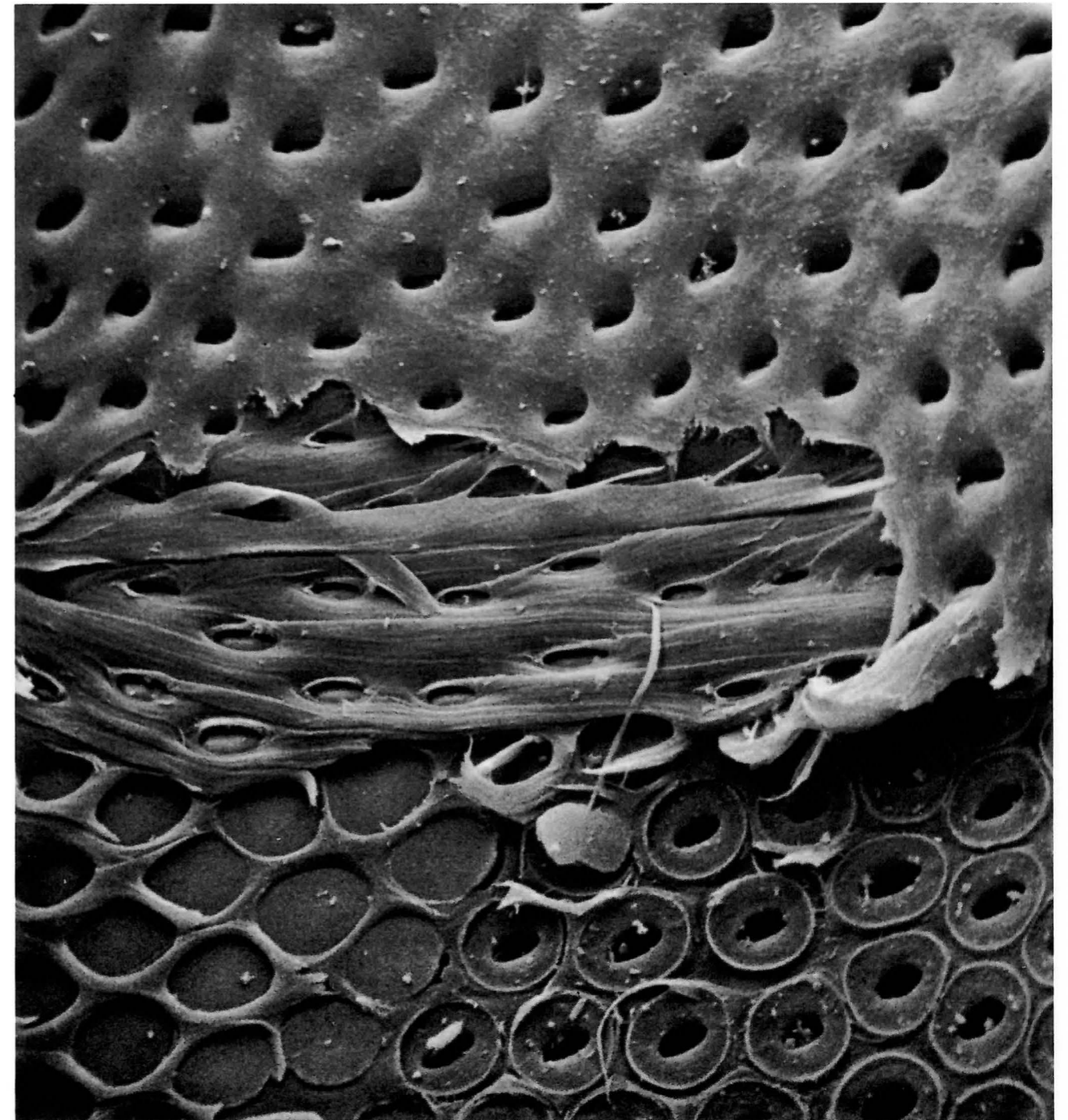


Fig. 1

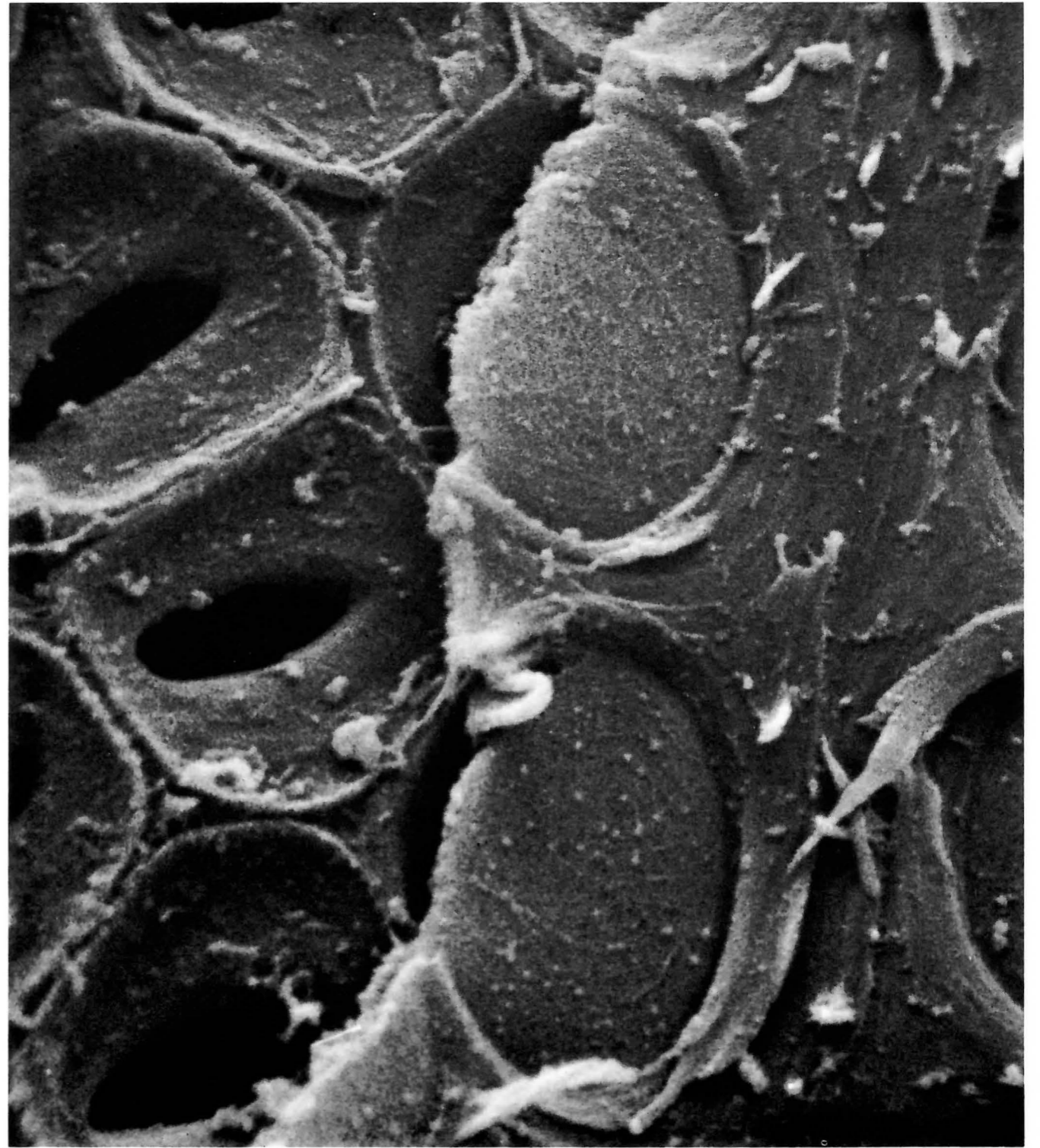


Fig. 2

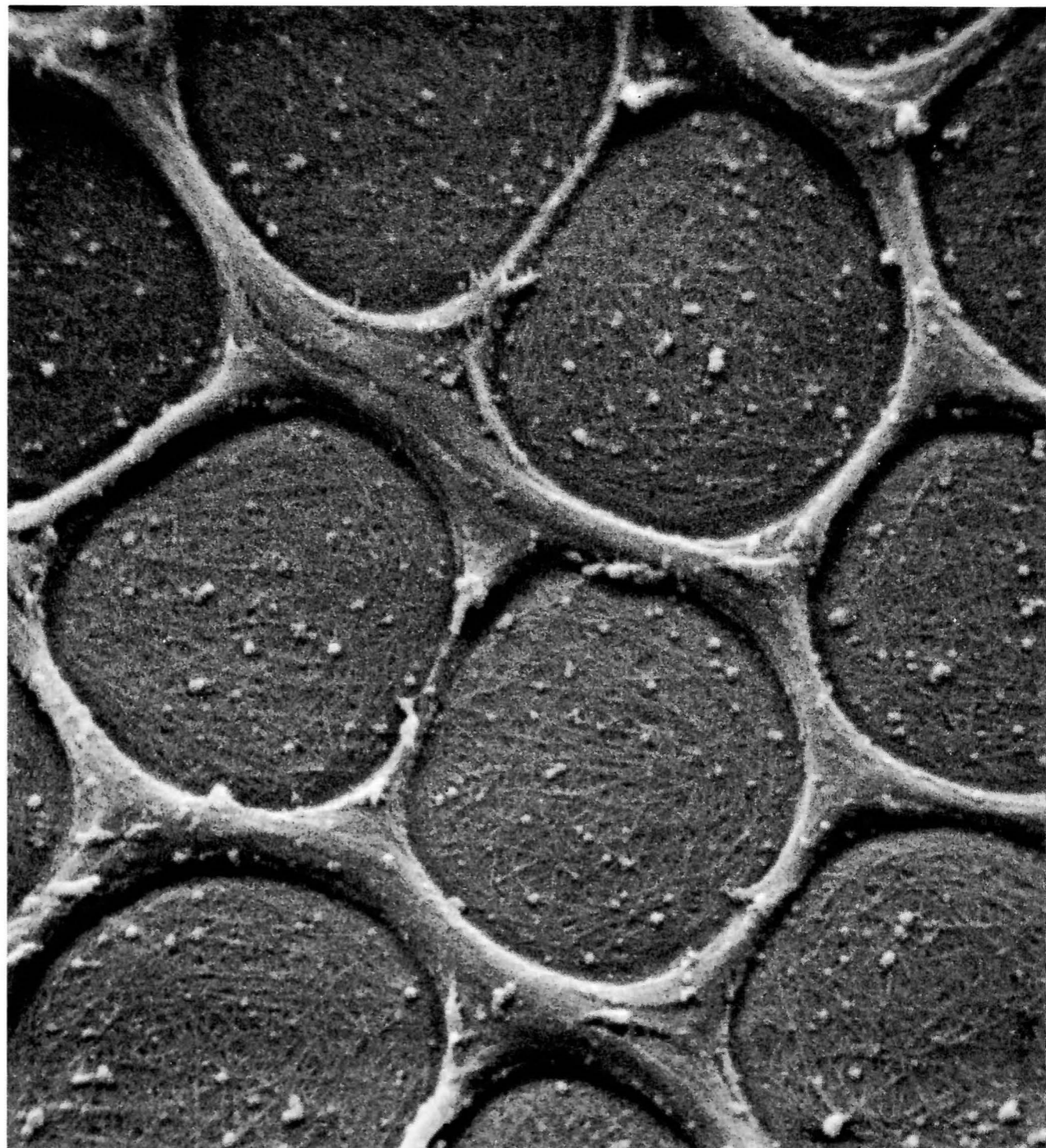


Fig. 3

Nature of the Last-Formed Tracheids in Compression Wood

By

T. E. Timell¹INTRODUCTION

In fully developed compression wood, the terms earlywood and latewood have little meaning, since the major portion of the growth ring consists of the typical compression wood tracheids with their intercellular spaces, rounded outline, and thick cell wall. The first, few rows of tracheids, formed at the beginning of the growing season, are usually different, as they tend to lack intercellular spaces and have an angular outline. In many species, the helical cavities in the inner part of S_2 are also missing. In other ultrastructural characteristics, as well as in their chemical composition and distribution of lignin, these first-formed tracheids are similar to those produced at a later stage (Côté, Day, Kutscha, and Timell 1967).

In both normal and compression woods of conifers the tracheids deposited at the end of the season are flattened in the radial direction, assuming an oblong shape in the latter tissue. Sanio (1873-1874) noted that in one growth ring of *Picea abies* (L.) Karst. the last-formed tracheids lacked spiral striations, but Sonntag (1904) observed that the pits had a slit-like opening in the same wood. According to Krieg (1907),

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the last tracheids in the growth rings of *Pseudotsuga menziesii* (Mirb.) Franco compression wood lack spiral striations and instead possess helical thickenings. Boutelje (1966) noted that the tracheids on the lower side of knots in *Picea abies* (L.) Karst. and *Pinus sylvestris* L. were angular in outline and that helical thickenings were present in the former species. For these reasons he considered them to be normal tracheids. Hartler (1968) states that the last-formed tracheids in compression wood are normal latewood cells and that they are transparent when viewed in transmitted light. Schultze-Dewitz, Götze, Günther, and Luthardt (1971) observed that in branch compression wood of *Pinus sylvestris* L. the last-formed tracheids were of the normal type.

Judging from these results, the impression could easily be gained that the last tracheids in a growth ring of compression wood generally are of the normal type. However, it is not clear why the gravitational stimulus, usually responsible for the formation of this wood, should cease to act for a short time at the end of each growing season. It is also well known that in compression wood of the mild or moderate, rather than severe, types, the earlywood consists of normal and the latewood of compression wood tracheids. It is the objective of this note to draw attention to the fact that the last-formed cells in all conifer compression woods as a rule are typical compression wood tracheids, that statements to the effect that they should be normal have little foundation, and that the observations to the contrary in the literature constitute rare exceptions.

RESULTS AND DISCUSSION

When thin cross sections of conifer stems or branches are viewed in transmitted light, narrow bright bands are frequently observed in the otherwise dark regions of compression wood. These bands are usually caused by the first-formed tracheids, whereas the last cells are opaque.

Examination of compression wood from some 25 conifer species in this laboratory over the last 10 years has so far failed to reveal a single case where the last portion of a growth ring consisted of normal wood. Radial sections, when examined under the light microscope, contain spiral striations until the very end of the ring (Côté, Day, Kutscha, and Timell 1967). When transverse and longitudinal sections were studied in the electron microscope, the last-formed tracheids were found to be of the same type as those laid down earlier (Schreuder, Côté, and Timell 1966, Côté, Day, Kutscha, and Timell 1967, Côté, Day, and Timell 1968).

In a recent study, tissue consisting of phloem, cambium, and compression wood of *Picea abies* (L.) Karst was fixed with glutaraldehyde-osmium tetroxide, embedded in Epon-Araldite, sectioned, stained with lead citrate and uranyl acetate, and examined in the electron microscope. All tracheids located next to the cambial zone were of the compression wood type, as can be clearly seen from Figs. 1, 2, and 3. These cells, albeit sometimes flattened (Fig. 3), had a cell wall consisting of a thick S_1 layer and an S_2 layer whose inner part was fissured by numerous and well developed cavities. It should be noted that the embedding medium used precludes the possibility that the cavities could be preparation artifacts.

Transverse sections that had been embedded in methacrylate and subsequently stained with germanium are shown in the next four figures. In *Pinus resinosa* Ait. (Fig. 4) both first-formed and last-formed tracheids contained pronounced helical cavities, but in *P. sylvestris* L. (Fig. 5) and in *Tsuga canadensis* (L.) Carr (Fig. 6) the cavities were less well developed, and they were absent in *Sequoia sempervirens* (D. Don) Endl. (Fig. 7).

When examined under polarized light (Côté, Day, Kutscha, and Timell 1967), the last-formed tracheids are found to have an orientation of the microfibrils in both the S_1 and the S_2 layers which is similar to that of the earlier cells and to lack an S_3 layer. Examination of the lignin skeletons remaining after removal of the polysaccharides, as shown for *Larix laricina* (Du Roi) K. Koch in Fig. 8, reveals that the distribution of lignin in these cells is that of compression wood tracheids in general (Côté, Day, and Timell 1968).

The electron micrographs shown are typical of all those examined. The last-formed compression wood lacks the intercellular spaces otherwise characteristic of compression wood, and the tracheids are generally oblong in cross section. The S_1 layer is especially thick at the cell corners, so that the outline of the entire cell often is rectangular, while those of the S_2 layer and the lumen are oval (Figs. 4, 6, and 8). The S_1 contains transversely oriented microfibrils and appears to be somewhat less lignified than the inner portion of S_2 . The $S_2(L)$ layer has a high concentration of lignin and is not fissured. The remaining, inner part of S_2 is not as highly lignified as S_1 . In some cases the helical cavities in this layer

are fully developed, whereas in other instances they are less conspicuous or altogether missing. Since the cavities are of schizogenous origin and appear rather late in the differentiation of the cell (Wardrop and Davies 1964, Côté, Kutscha, and Timell 1968), this variation is not surprising. No S_3 layer is present.

The tracheids formed in compression wood at the termination of the growing season are accordingly in most respects similar to those laid down earlier. The only differences are the oblong or oval rather than spherical cross section of the cells, the occasional poor development or absence of helical cavities, and the lack of intercellular spaces. The lower rate of growth prevailing at the end of the season and the more abundant supply of photosynthate available at this time are probably responsible for the complete lignification of the middle lamella.

ACKNOWLEDGEMENTS

Figs. 4, 5, 6 and 8 were made available through the courtesy of Mr. Arnold C. Day. Figs. 1, 2, and 3 were obtained at the Laboratorium für Elektronenmikroskopie, Institut für Allgemeine Botanik, ETH, Zürich, Switzerland.

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KEY TO LABELING

CC	Cambial cell	M	Middle lamella
EW	Earlywood	P	Primary wall
LW	Latewood	S	Secondary wall

All marks represent 1 μ m

CAPTIONS TO FIGURES

- Figure 1. Transverse section of compression wood and cambial zone of *Picea abies* (L.) Karst. showing last-formed xylem and dormant cambial cells. Note the presence of residual cytoplasm in the lumen of the tracheids.
- Figure 2. Radial longitudinal section of last-formed tracheids in compression wood of *Picea abies* (L.) Karst., showing well developed cavities in the inner part of the layer S₂.
- Figure 3. Transverse section of last-formed tracheids and a few cambial cells in *Picea abies* (L.) Karst. The flattened xylem cells are in all other respects typical compression wood tracheids.

Figure 4. Transverse section of compression wood in *Pinus resinosa*

Ait. at the latewood-earlywood boundary, showing the presence of helical cavities in both types of tracheids.

The S_1 layer is thickened at the cell corners (arrows).

Figure 5. Transverse section of compression wood in *Pinus sylvestris*

L. at the latewood-earlywood boundary. The flat latewood tracheids contain only a few helical cavities.

Figure 6. Transverse section of compression wood in *Tsuga canadensis*

(L.) Carr. at the latewood-earlywood boundary. Only traces of cavities can be seen in the last-formed tracheids.

The S_1 layer is thickened at the cell corners (arrows).

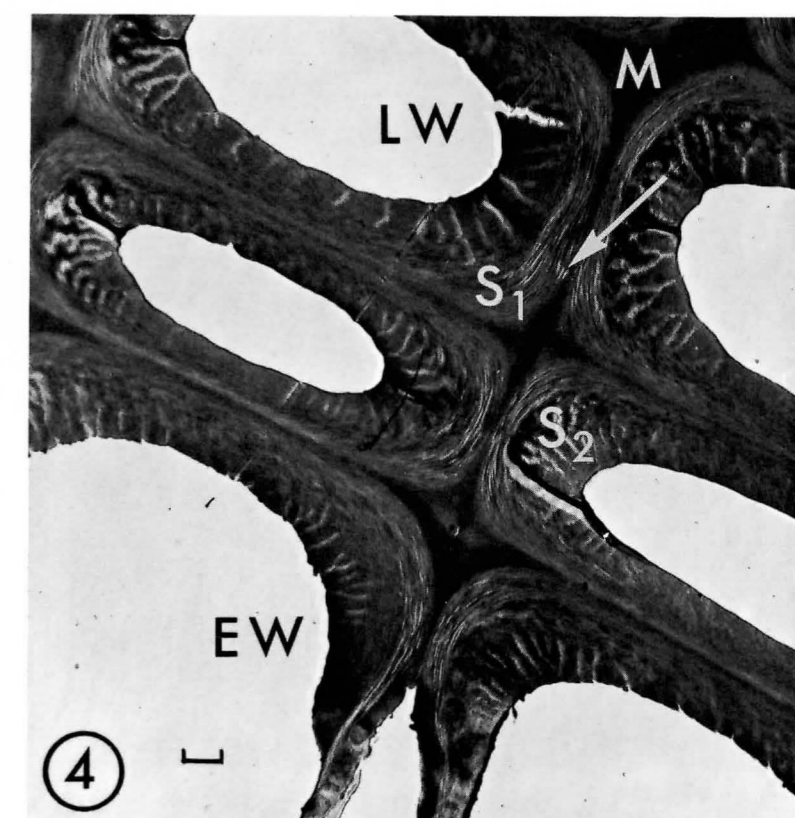
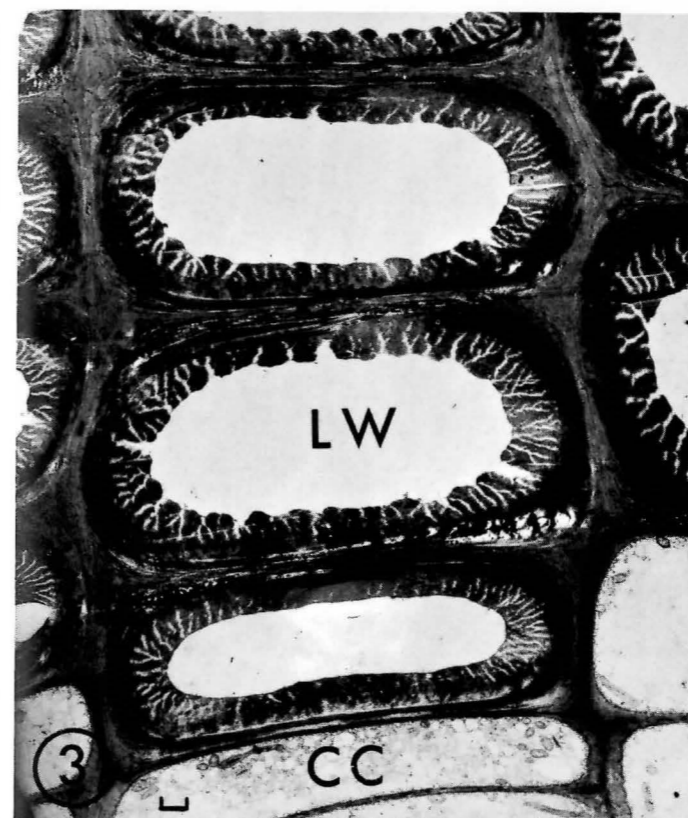
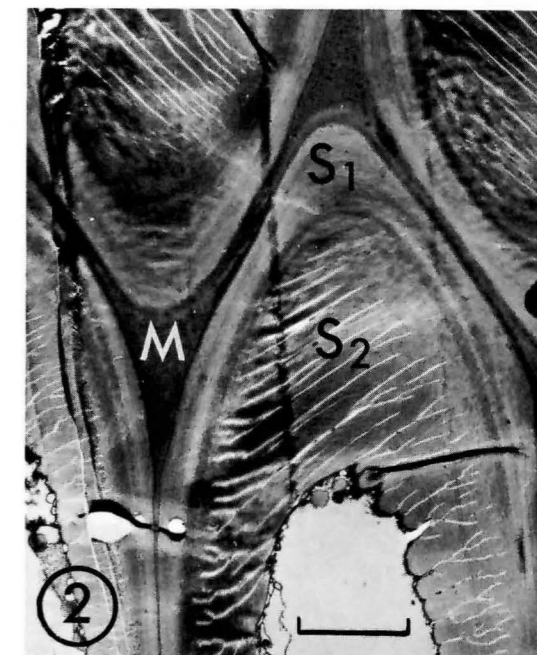
Figure 7. Transverse section of latewood tracheids from compression

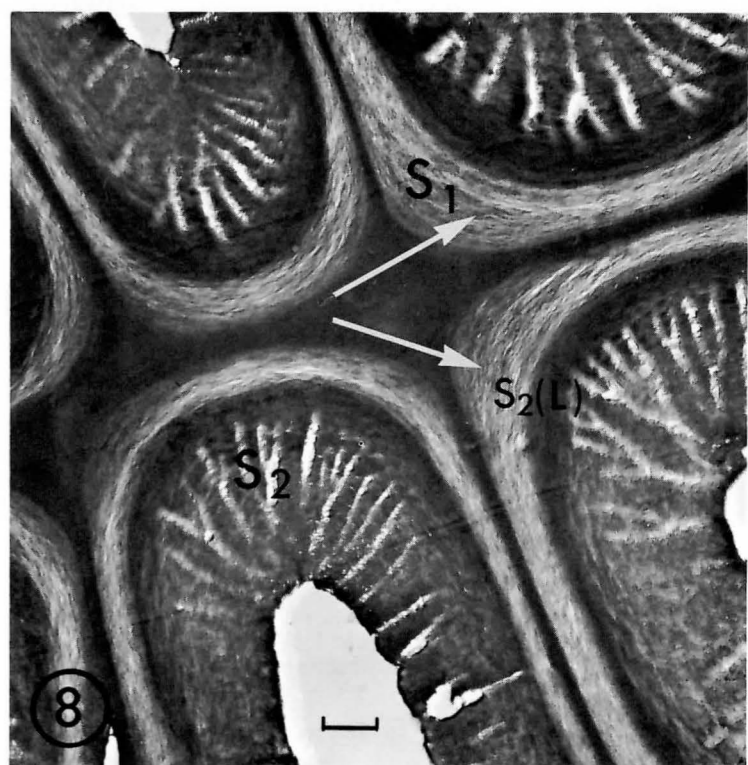
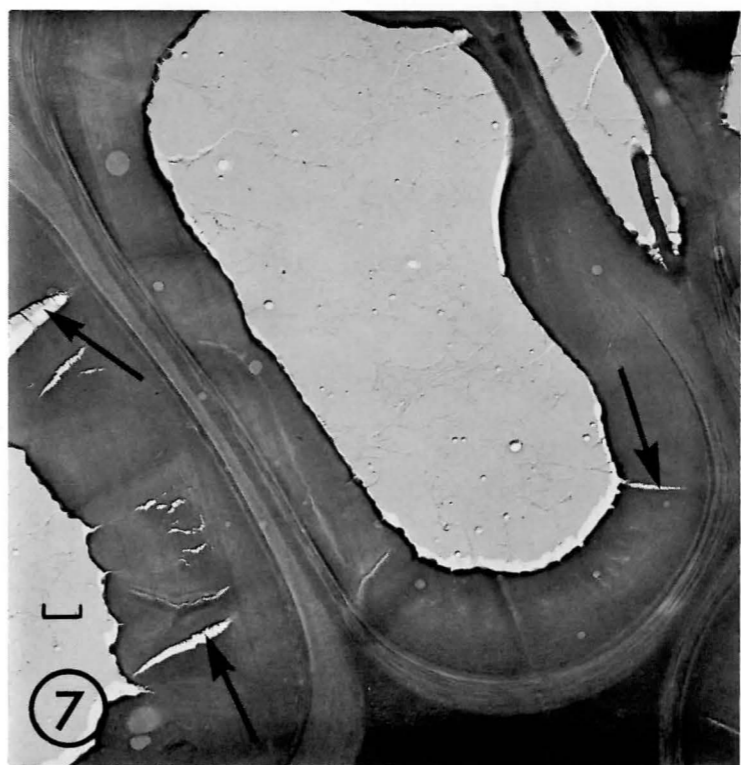
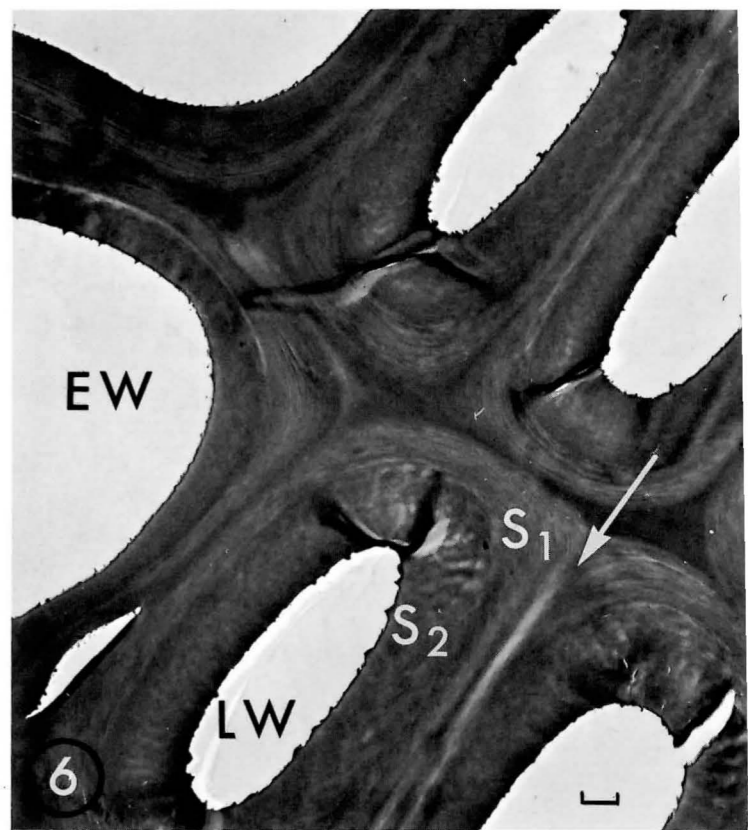
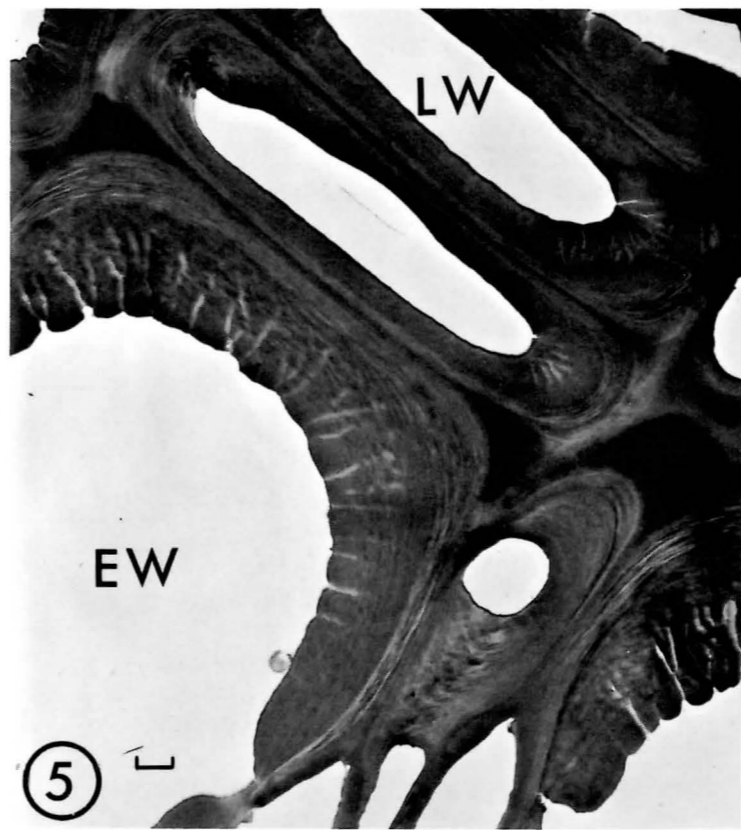
wood of *Sequoia sempervirens* (D. Don) Endl., containing spiral checks (arrows) but no helical cavities.

Figure 8. Transverse section of lignin skeleton of last-formed tracheids

in compression wood of *Larix laricina* (Du Roi) K. Koch from which the polysaccharides had been removed with hydrofluoric acid. The S_1 layer is thickened at the cell corners (arrows).

The S_2 (L) layer is highly lignified.





ASSOCIATION AFFAIRSRatification of Constitutional Amendment

Voting on the constitutional amendment specifying a new classification of membership for those who retire from full-time professional employment has been completed. The amendment has been ratified with 59 votes for approval and 2 votes disapproving the action.

Bibliography of Wood Anatomy

Three comments have been received from members on Mr. W. C. Dickison's suggestion in IAWA Bulletin (1972/3) that we publish a yearly Bibliography of Wood Anatomy. B. G. Butterfield comments that "Forestry Abstracts" does cover this area of bibliography quite well and that we would be duplicating their efforts. Dr. Mennega points out that such a system would be particularly useful to the persons and institutions lacking ready access to "Forestry Abstracts".

It would appear that there are several questions which need resolution. Would this be a bibliography of current work by members only? Would the purpose be to supply a handy list to supplement the entries in "Forestry Abstracts"? How much effort and money is the Association prepared to spend on this project? Should the bibliography be expanded into a larger project as for example a general bibliography of literature on wood anatomy?

Appeal for Information

A notification has been received from our bank in August that a check numbered Liv. 020701, from Barclay's Bank Ltd. (Liverpool) through

the New York Foreign Branch, dated 7/3/72 in the amount of \$10.50 (U.S.) has been deposited to the IAWA account. Our difficulty is that there is no name given and no letter received which can be tied to this payment. If this check can be identified by any member, please write to us so that credit can be assigned properly.

Dr. Côté on Leave in Denmark

Dr. Côté is in Copenhagen on a temporary affiliation with the Technical University of Denmark. He can be reached at the address below until approximately December 10.

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Membership Directory Changes

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WOOD ANATOMY ACTIVITIES AROUND THE WORLD

Request for Wood Specimens

The Department of Wood Anatomy of the Institute for Systematic Botany of the State University of Utrecht would much appreciate receiving wood samples for preparing sections of a number of genera not or insufficiently represented in its collection.

Mrs. Jifke Koek-Noorman M.Sc. intends to write a fifth paper on the wood anatomy of the Rubiaceae and urgently needs material or additional material of the following genera: *Bathysa*, *Bikkia*, *Chimarrhis*, *Condaminea*, *Deppea*, *Gleasonia*, *Greenea*, *Isidorea*, *Lindenia*, *Morierina*, *Pallasia*, *Phitopsis*, *Pogonopus*, *Portlandia*, *Rustia*, *Sickingia*, *Simira*, *Tresanthera*, *Ucriana*, *Warszewiczia*, *Wendlandia*.

Mrs. T. Baretta-Kuipers M.Sc. is starting a study of the wood anatomy of *Caraipa* (Guttiferae) in its relation to that of other members of the family and of the Theaceae, i.e., Bonnetioideae. She would appreciate

therefore receiving wood samples of: *Caraipa*, *Kielmeyera*, *Marila*; *Archytaea* (except *A. multiflora*); *Bonnetia*, *Ploiarum*, *Tetramerista*; *Asteropeia*; and *Foetidia*.

For my own work on the wood anatomy of the Celastraceae I should like to receive samples of the genera listed to complete an otherwise fairly representative collection: *Brassiantha*, *Fraunhoferia*, *Glyptopetalum*, *Hartogia*, *Herya*, *Lauridia*, *Maurocena*, *Menepetalum*, *Monimopetalum*, *Moya*, *Otherodendron*, *Peripterygia*, *Polycardia*, *Psammomoya* and *Putterlickia*.

It will be greatly appreciated if the collector's number and the place of deposit of the corresponding herbarium vouchers are indicated on the labels or cards pertaining to the specimens.

Alberta M. W. Mennega

Dutch Version of the Multilingual Glossary of Terms Used in Wood Anatomy

Laming, P. B. and A. M. W. Mennega: Verklarende Woordenlijst van in de Houtanatomie Gebruikte Termen, Houtinstituut TNO, Delft, September 1972, 68 pages. Litho-offset.

This Dutch version of the Glossary of Terms is now available from the Houtinstituut TNO, Schoemakerstraat 97, Postbus 151, Delft, Netherlands, at a cost of \$2.00 (U.S.).

The publication consists of two parts. The first part (52 pages) is an alphabetical listing of Dutch terms, followed by the reference number assigned to the English term in the 1964 Multilingual Glossary, the definition of the term in Dutch, and lastly the English term in parentheses. The second part consists of nine pages of English to Dutch alphabetical listing of terminology.