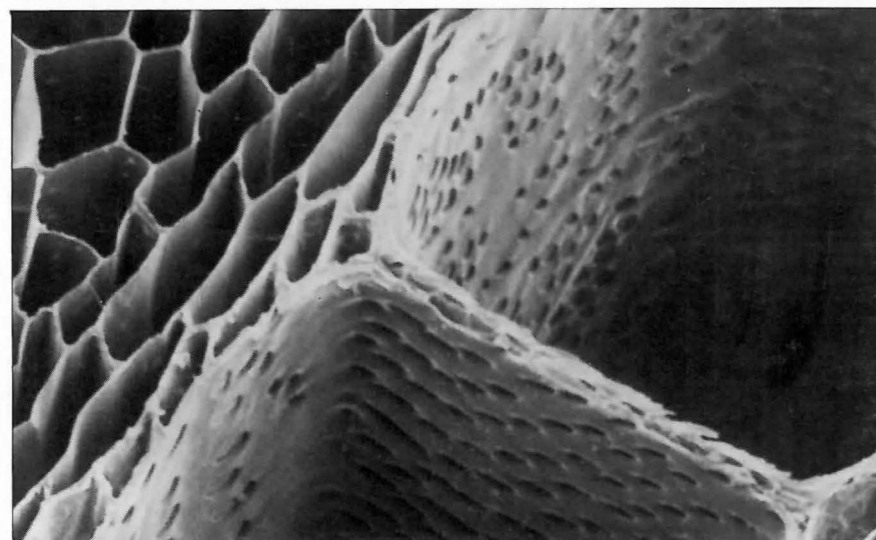


The background of the cover is a composite of two black and white micrographs. The left half shows a cross-section of plant tissue with a central vascular cylinder, characterized by a ring of large, thick-walled cells and a central pith. The right half shows a longitudinal section of plant tissue, displaying a series of parallel, wavy layers of cells, likely representing a secondary growth region or a specific vascular tissue arrangement.

**I A W A  
B U L L E T I N**

1976/4



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INTERNATIONAL ASSOCIATION OF WOOD ANATOMISTS

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## EDITORIAL

Wood Anatomy throughout the years has had its ups and downs as well as changes in fashion. At the present time some of us may feel concerned about the fate of wood anatomical research in certain centres which had a great tradition in classical wood anatomy, and are now faced with staff reductions and directives to pursue research projects of a technological rather than an anatomical nature. However sad and undesirable these developments may appear, it should be stressed that there is also a very positive awareness of the contributions wood anatomy can make to aspects of pure and applied science. We can, therefore, contrast the reduced wood anatomical activity in some institutions by the significant increase in contributions from other quarters. Wood technologists, pulp and paper specialists, plant taxonomists, as well as archeologists and palaeobotanists, may thus be seen to turn into part-time wood anatomists. Similarly, plant morphogenesisists, tree physiologists and geneticists, have come to realize the importance of thorough anatomical knowledge for their work, and sometimes actively contribute to wood anatomy.

It is anticipated that, in the future, students from these diverse disciplines will form an increasing complement to the small core of full-time wood anatomists. Our International Association of Wood Anatomists clearly has to fulfill an important role in providing contacts between these various disciplines. Modesty should not prevent us from saying that our membership has much to offer in the way of broad, as well as detailed, knowledge of wood structure to the less initiated scientists from other allied disciplines. By uniting all scientists interested in wood structure in the IAWA, this knowledge and experience could be shared. We need your help in identifying and contacting those individuals who have not yet joined our Association. We will all benefit from a further expansion of the IAWA. With your effort, this could soon become reality.

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## CHARACTERIZATION OF COMPRESSION WOOD SEVERITY IN *PINUS ECHINATA* MILL.

by

Robert A. Harris<sup>1</sup>

### Introduction

Shortleaf pine (*Pinus echinata* Mill.) is generally characterized by an abrupt transition from earlywood to latewood. In compression wood, however, this abrupt transition is not so apparent. This has been attributed to the thicker-walled earlywood cells found in the reaction wood (1). Microscopic examination indicates that there is a progressive change from abrupt to gradual transition as the compression wood severity increases.

### Procedure

Samples were collected from the compression wood zones of three shortleaf pine trees which were leaning at angles of 10°, 30° and 45° from the vertical. The samples were studied with a scanning electron microscope (SEM). The SEM samples were prepared by a technique described by Exley *et al.* (2), using razor blades to prepare the final surfaces for viewing. The samples were coated with approximately 100-150 Å of gold palladium and examined on an AMR-900 Scanning Electron Microscope.

### Results

Examination of cross-sections from the three compression wood samples indicates that the transition from earlywood to latewood progresses from abrupt to gradual as the compression wood severity increases. The mild compression wood sample has a definite abrupt transition characteristic

of normal wood; however, the latewood tracheids have the pronounced rounded appearance characteristic of compression wood (Fig. 1). The intermediate compression wood sample exhibits a somewhat semi-abrupt transition (Fig. 2), with the line delineating the earlywood and latewood less definite, and the percentage of earlywood less than that found in the mild compression wood. The latewood tracheids exhibit the rounded cross-sectional shape and helical cell wall check characteristic of compression wood. The severe compression wood sample has a definite gradual transition (Fig. 3).

A closer examination of the latewood tracheids of the severe compression wood sample reveals the characteristic rounded cells, intercellular spaces and helical checks in the secondary wall of compression wood (Fig. 4). The earlywood tracheids maintain a four-sided rather than a rounded cross-sectional shape, and some checks were noted in the secondary walls (Fig. 5). The cell wall checks in the earlywood tracheids are sparse and not as pronounced as those found in the latewood tracheids. Figures 6 and 7 illustrate the difference in cell wall checking between

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Table 1. Classification of Compression Wood Severity Based on Selected Anatomical Features

| WOOD TYPE    | TRANSITION  | ROUNDED TRACHEIDS |     | INTERCELLULAR SPACES |          | CELL WALL CHECKS |          |
|--------------|-------------|-------------------|-----|----------------------|----------|------------------|----------|
|              |             | EW                | LW  | EW                   | LW       | EW               | LW       |
| Normal       | Abrupt      | No                | No  | Absent               | Absent   | Absent           | Absent   |
| Mild         | Abrupt      | No                | Yes | Absent               | Sparse   | Absent           | Present  |
| Intermediate | Semi-abrupt | No                | Yes | Absent               | Present  | Absent           | Abundant |
| Severe       | Gradual     | Sometimes         | Yes | Sparse               | Abundant | Sparse           | Abundant |

earlywood and latewood. An examination of the mild and intermediate compression wood samples also indicates that the modification of the tracheids is notably more pronounced in the latewood than in the earlywood.

The transition from normal wood to severe compression wood is summarized in Table 1, which can be used to classify a particular specimen of compression wood according to its severity. Percentage of earlywood, though an indication of compression wood severity, was not included in the table due to its variability in normal wood. A very small percentage of earlywood does, however, indicate severe compression wood.

An interesting effect is produced when a tracheid of compression wood is viewed in three dimensions (Fig. 8). This is done by taking a SEM micrograph, tilting the specimen 7° or 8°, and photographing the tracheid again at the same magnification. When viewed with the aid of a stereoscope, the helical checks appear analogous to a winding staircase viewed from above.

Another feature seen only when viewing in three dimensions is that S<sub>2</sub> layers of the secondary walls are projected above the compound middle lamellae, and S<sub>1</sub> layers, as if pulled out during specimen preparation. This is probably a result of the S<sub>2</sub> wall

layers being compressed during cutting and springing back after the blade passes. It indicates that the framework of the compound middle lamellae and S<sub>1</sub> layers is stiffer than that of the S<sub>2</sub> layers.

#### Summary

The study indicates that as compression wood severity in shortleaf pine increases, the transition from earlywood to latewood changes from abrupt to gradual. The earlywood is less affected by compression wood formation than the latewood, particularly in mild compression wood.

#### References

1. Côté, W.A. Jr. and A.C. Day. Anatomy and Ultrastructure of reaction wood. In: W.A. Côté, Jr., Ed: Cellular Ultrastructure of Woody Plants, Syracuse University Press, Syracuse, N.Y. 603 pp., 1964.
2. Exley, R.R., B.G. Butterfield and B.A. Meylan. Preparation of wood specimens for the scanning electron microscope. *Journal of Microscopy* 101: 21-30, 1974.

Figure 1. Cross-section of mild compression wood. Note the abrupt transition and rounded latewood tracheids (arrow). × 92

Figure 2. Cross-section of intermediate compression wood. Note the semi-abrupt transition. × 45

Figure 3. Cross-section of severe compression wood. Note the definite gradual transition. × 45

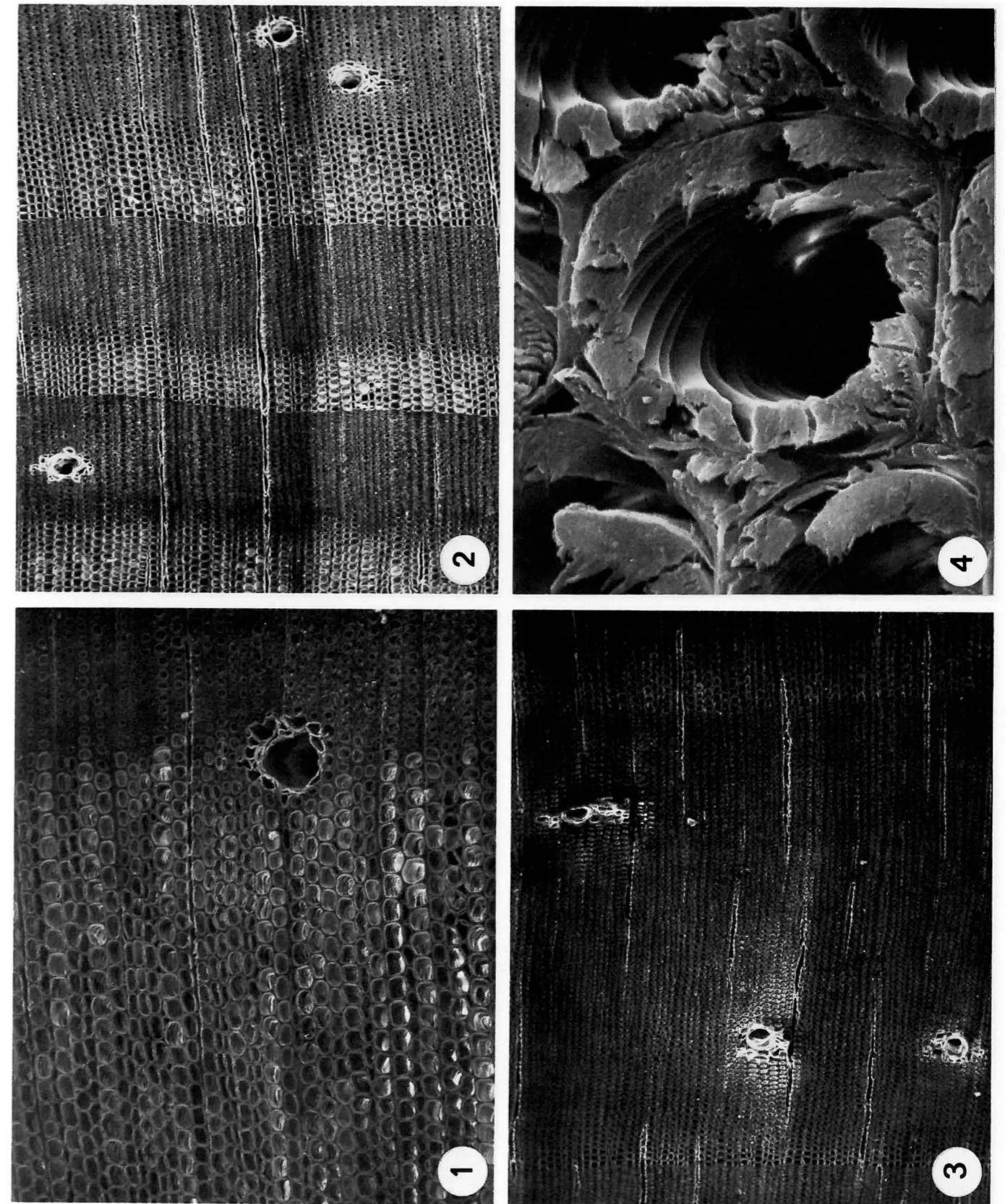
Figure 4. Latewood tracheid of severe compression wood. Note the rounded shape, intercellular spaces and helical checks in the secondary wall. × 2110

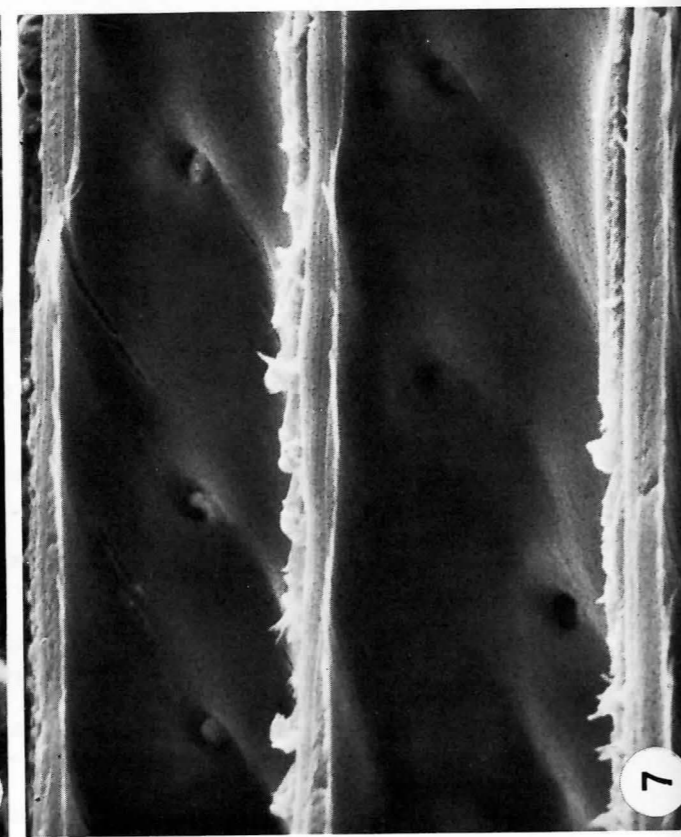
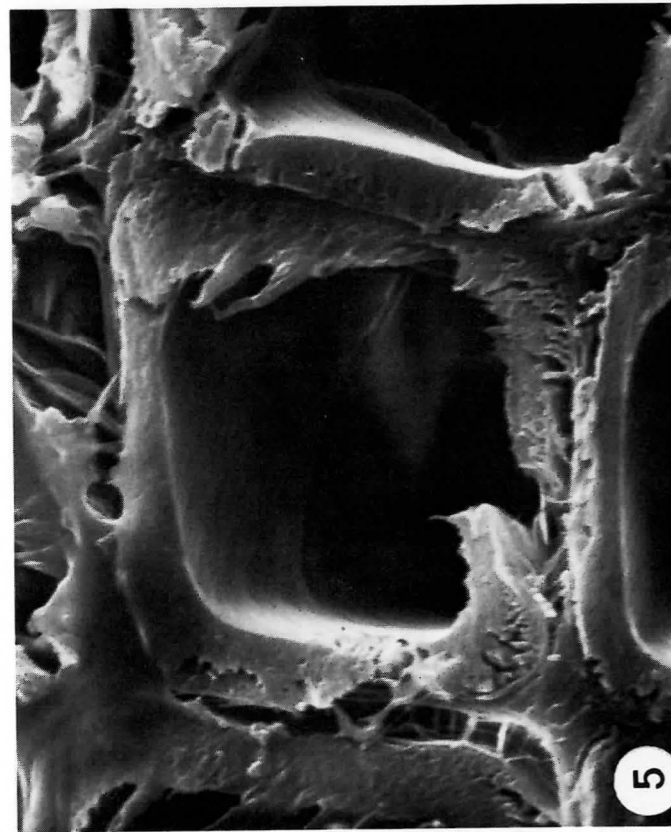
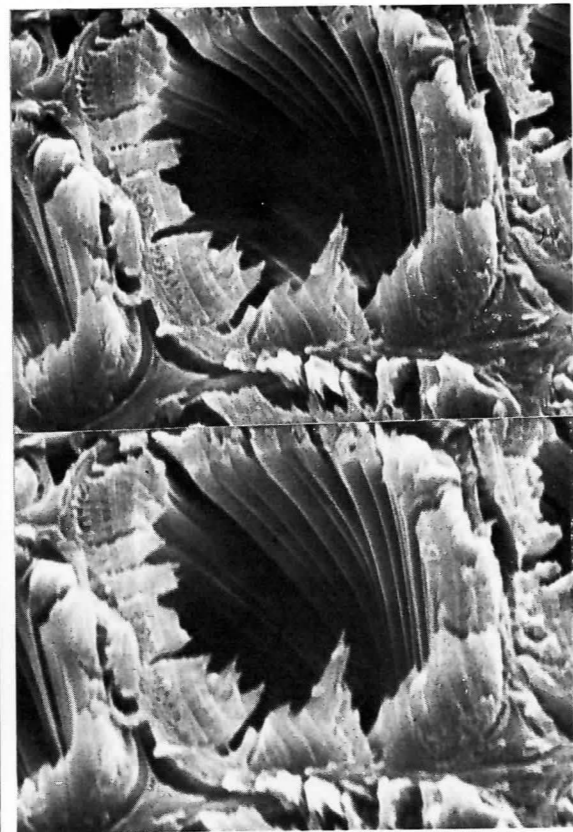
Figure 5. Earlywood tracheid in severe compression wood. Note fewer checks and less rounded shape compared to the tracheids in Figure 4. × 2110

Figure 6. Radial view of severe compression wood latewood tracheid, showing prolific checking in the secondary wall. × 2100

Figure 7. Radial view of severe compression wood earlywood tracheids, with few checks in the secondary walls. × 1068

Figure 8. Stereo pair of a latewood tracheid of severe compression wood. × 1338





## THE ELUSIVE CAMBIUM—ANOTHER TERMINOLOGICAL CONTRIBUTION

by

Rudolf Schmid<sup>1</sup>

The vascular cambium is commonly defined as the lateral meristem<sup>2</sup> adding to the girth of an axis (or appendage) by the production of secondary xylem and secondary phloem. This broad definition conceals the fact that there exists some gentle controversy over the nature of this lateral meristem, that is, whether it consists of a single layer of initiating cells versus more than one layer of initiating cells (see Table 1). Proponents of a uniseriate concept of the vascular cambium, which is historically the older view (Mischke, 1890; Sanio, 1873; Schoute, 1902—see Bannan, 1955, Newman, 1956, and Philipson, *et al.*, 1971), have been increasingly countered by proponents of a multiseriate (= pluriseriate) concept of the cambium, which was initially suggested by Raatz (1892); more recent protagonists of various concepts of the cambium will be discussed below. On the other hand, Paliwal and Sajwan (1975: 107) and Srivastava (1973: 51) imply that the controversy is of "little practical significance." Interestingly, a similar debate over a uniseriate versus multiseriate initiating layer does not seem to exist concerning that other famous lateral meristem, the phellogen or cork cambium (note the lack of such discussion in Brown, 1971, Eames and MacDaniels, 1947, Esau, 1953, 1960, 1965, Fahn, 1974, Foster, 1949, Harlow, 1970, Kausmann, 1963, Kozłowski, 1971, McLean and Ivimey-Cook, 1951, Morey, 1973, Panshin and de Zeeuw, 1970, Schoute, 1902, Srivastava, 1963, 1964, and Wetmore and Steeves, 1971). It might also be noted that Hartig's (1853) biseriata concept of the vascular cambium (the outer layer producing phloem, the inner xylem) has long been universally rejected (see Bannan, 1955, Philipson and Ward, 1965, Philipson *et al.*, 1971, and Sanio, 1873).

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<sup>2</sup>As discussed below, "cambium" and "lateral meristem" are not equivalent terms.

<sup>3</sup>By this concept, due to various factors the single layer of initials need not be perfectly aligned tangentially to form a symmetrically cylindrical sheath surrounding the xylem (Brown, 1971; Butterfield, 1975; Murmanis, 1970; Newman, 1956; Philipson and Ward, 1965; Philipson *et al.*, 1971; Steeves and Sussex, 1972; Wodzicki and Brown, 1973). Continuity of the cambial sheath may be interrupted by well-differentiated resin canals (Wodzicki and Brown, 1973) and, additionally, it may be discontinuous in certain types of atypical (= "anomalous") secondary growth (Philipson and Ward, 1965; Philipson *et al.*, 1971) as well as in some roots (Kozłowski, 1971; Philipson *et al.*, 1971—see also Brown, 1971). The cambium, of course, is routinely disrupted by interfascicular regions related to the departure of traces to branches and leaves in young axes.

By the uniseriate concept of the cambium, the "vascular cambium *sensu stricto*" consists of a single layer of initial cells<sup>3</sup>, whereas the "cambial zone" (= "cambial region") consists of the cambial initials plus their immediate derivatives, the phloem mother cells and the xylem mother cells (for alternate terminology of mother cells see note "e" in Table 1). Many modern workers have accepted such a concept of the cambium, to wit: Brown (1971), Cheadle and Esau (1958), Committee on Nomenclature (1964), Eames and MacDaniels (1947), Esau (1953, 1965, and as discussant in Wilson, 1964), Esau and Cheadle (1955), Fahn (1974), Foster (1949), Gregory (1971), Harlow (1970), Kausmann (1963), McLean and Ivimey-Cook (1951), Mahmood (1968), Morey (1973), Murmanis (1970, 1971), Newman (1956), Panshin and de Zeeuw (1970), Philipson and Ward (1965), Philipson *et al.* (1971), Romberger (1963), Tomlinson and Zimmermann (1969), Wardrop (discussant in Wilson, 1964), Wetmore and Steeves (1971), Wilson and Howard (1968), Wilson, Wodzicki, and Zahner (1966), and Wodzicki and Brown (1973).

Also belonging to this school are those workers accepting a single initiating layer of cells, (usually called "cambial initials"), but preferring to call the "cambial zone" (often not mentioned as such) simply, and broadly, "cambium" (see elaboration below): Bailey (1923, and as discussant in Wilson, 1964), Bannan (1955, 1957, 1962, 1966, 1967, 1968), Butterfield (1975), Esau (1948, 1960), Evert (1963), Evert and Deshpande (1970), Kozłowski (1971), Srivastava (1963, 1964), and Steeves and Sussex (1972). On the other hand, some researchers apparently accept the uniseriate concept but are rather noncommittal with regard to designating the meristem as "cambial zone" or "cambium" (Barghoorn, 1964, and as discussant in Wilson, 1964; Cumbie, 1963, 1967a, b; Evert, 1961; Jane, 1970; Lorch, 1967; Paliwal and Sajwan, 1975; Srivastava, 1973; Srivastava and O'Brien, 1966; Zee, 1968).

As numerous workers have pointed out, the crux of the difficulty with such a uniseriate concept of the cambium is that it is often impossible to distinguish in a radial file of cells (so-called tier—a term of Cheadle and Esau, 1958, and Esau and Cheadle, 1955) a cambial initial from other meristematic or meristematic-like cells, a fact that beginning students in plant anatomy quickly become aware of. Furthermore, when it is possible to distinguish a single

initial in a file of cells, this often involves working with gymnosperms or with dormant cambia in this group and in angiosperms.

In contrast, active cambia of dicotyledons generally have, as amply demonstrated by many anatomists (especially the proponents of the multiseriate view of the cambium), a radial file of very similar, actively dividing cells. Such is the basis for the multiseriate concept of the cambium, but the partial (see below) crux of the problem with this concept is whether this zone of dividing cells should be called "cambium" or "cambial zone" (see also Bannan, 1955). The terminology in boldface in Table 1 focuses on these differences.

The preceding discussion has implied that the controversy is between a uniseriate versus a multiseriate concept, but the situation is a bit more complicated than this. In my view there are really three concepts on the nature of the cambium: (1) a uniseriate concept as defined above (references in second paragraph), (2) a multiseriate concept invoking similarity and equivalence among cambial cells, that is, all could be regarded as initials with equivalent powers of multiplication (Catesson, 1964, 1974; Kleinmann, 1923; Priestley, 1930; Raatz, 1892)<sup>4</sup> and (3) a supposed multiseriate concept<sup>5</sup> which in actuality is really a terminological modification of the uniseriate concept (some of the workers cited at the beginning of the third paragraph above). [The already referred to biseriate concept of Hartig (1853) represents a fourth, but absurd alternative.]

Butterfield (1975), for example, offers the last alternative. To quote Butterfield (1975: 14, emphasis mine), who curiously does not cite his own book on the cambium (Philipson *et al.*, 1971): the "cambium should be defined as a 'multiseriate zone of periclinally dividing cells lying between the differentiating secondary xylem and phloem, with a *distinct initial* capable of both periclinal and anticlinal divisions lying *somewhere* within each radial file of cells.'" Butterfield's definition is essentially like that of the uniseriate school, the chief nomenclatural difference being that the former's "cambium" and "distinct initial" are, respectively, the latter's "cambial zone" and "vascular cambium" (single layer of initiating cells). It is significant that Butterfield never

<sup>4</sup>Wilson's (1964) well-known paper is sometimes cited as accepting the "multiseriate concept" (e.g., Mahmood, 1968; Murmanis, 1970). Although Wilson did generate some discussion on this topic (see discussions by Bailey, Wardrop, Barghoorn, and Esau in Wilson, 1964), he clearly indicated (p. 20) that "the possible existence of true cambial initials . . . is of little significance to [his] study" and subsequently, in fact, definitely accepted a uniseriate concept of the cambium (Wilson and Howard, 1968; Wilson *et al.*, 1966).

<sup>5</sup>According to Butterfield (1975: 13, emphasis mine), "the concept of a multiseriate cambium may or may not include reference to a single initial within each radial file of cells."

mentions "cambial zone" or, more importantly, that he does not advocate Catesson's (1964, 1974) concept of the cambium consisting of many, entirely equivalent, initiating cells in a radial file. The same, of course, can be said regarding other workers with views similar to those of Butterfield (references at beginning of third paragraph). The real difference between the uniseriate concept and the so-called multiseriate concept is, therefore, essentially nomenclatural, terminological, or semantic, *not* conceptual. "Cambium" thus is frequently used with reference to the "cambial zone" because it is difficult to distinguish the cambial initials from their recent derivatives; Esau (1953, 1965) in her well-known textbook noted this some time ago.

The word "meristem" comes from the Greek *meristos*, meaning divisible. As Wodzicki and Brown (1973) correctly point out, "cambium" and "lateral meristem" are not equivalent. By the uniseriate concept, the true cambial meristem, therefore, is the "cambial zone", which includes all the dividing cells, that is, the cambial initials and the xylem and phloem mother cells. This usage of lateral meristem, of course, is directly comparable to the one of apical meristem consisting of a region of apical initials subtended by actively dividing cells (see Esau, 1965; Fahn, 1974; Gifford and Corson, 1971; Romberger, 1963; Steeves and Sussex, 1972). The point of this discussion is that *all* concepts of the cambium (#1, #2, #3 above) recognize a multiseriate *meristem* (Table 1). The dual question, however, is not only what this meristem should be called ("cambial zone" or "cambium"—respectively, concepts #1 versus #2 or #3 above), but also how many initiating layers it has (one or several—respectively, concepts #1 and #3 versus #2).

Consequently, one cannot by fiat restrict "cambium" to a uniseriate layer of dividing cells since, historically (see Lorch, 1967), a "cambium" is merely a meristem with products of division arranged orderly in parallel files (Esau, 1960, 1965). Likewise, "cambium" cannot be applied solely to a multiseriate situation.<sup>6</sup> It seems, therefore, that the definition of "cambium" has to be amplified by criteria other than the number of layers of dividing cells. Suitable criteria would appear to be (1) number of layers of *initiating* cells, (2) the permanency of these cells, (3) the centrifugal and/or centripetal direction of their

<sup>6</sup>Interestingly, the multiseriate application has been more common (in print) than the uniseriate one (Bannan, 1955). However, a "uniseriate cambium" has had greater popularity since it has been adopted in most of the anatomy textbooks, especially the ones in English (Eames and MacDaniels, 1947; Esau, 1953, 1960, 1965; Fahn, 1974; Foster, 1949; Panshin and de Zeeuw, 1970, and earlier 1949 and 1964 editions; other texts cited in Bannan, 1955). On the other hand, a multiseriate application has been advocated especially by researchers and Europeans (see Bannan, 1955, and citations at the beginning of third paragraph).

division products, and (4) anticlinal cell division. These amplificatory criteria, of course, are subject to debate depending on which particular concept of the cambium is adopted.

In summary, a concept of the vascular cambium as a uniseriate initiating layer is advocated. Recognizing the difficulty and frequent impossibility of distinguishing a given initial from other meristematic cells in a radial file of cells, *I believe that one can still think of a cambial initial (or cambium) from a theoretical viewpoint to refer only to that single layer of essentially permanent cells (or cambium) which divides anticlinally and which is also positionally capable of producing cells in both a centrifugal and a centripetal direction, all the periclinally dividing cells thus constituting a meristematic zone referred to as the "cambial zone" (= "cambial region")* (Table 1). Other than nomenclature, this definition is identical to the so-called multiseriate one of Butterfield (1975), among others (see beginning of third paragraph), although different from the true multiseriate view of Catesson (1964, 1974).

By the foregoing uniseriate concept, "cambial zone" is applied to the actual meristematic layer and "cambium" is retained for the actual initiating layer (this obviously then consisting of "cambial initials").<sup>7</sup> To apply "cambium" to the entire meristematic layer, as done by proponents of the multiseriate concept (see Table 1), would necessitate by the uniseriate view a new designation for the initiating layer. Although "cambial initials" is, of course, an acceptable designation, I would retain "cambium" as equivalent to "initiating layer" not only because of the wide usage of the latter by proponents of the uniseriate concept, but also because, in agreement with Eames and MacDaniels (1947), "cambium" applied to the entire differentiating region might lead to the conception that the cambium is a multiseriate layer of initials. Furthermore, to equate "cambial zone" and "cambium", or not to mention the former term at all, as done by many workers, seems to offer no greater terminological clarity.

It is recognized, however, that in some cases "initial function" (*sensu* Newman, 1956) may be temporarily lost so that there may be no cells in a file or tier meriting the designation "initial," but only "tissue mother cells" (Bannan, 1968; Evert, 1963). Likewise, it is also recognized, in agreement with Philipson *et al.* (1971), that present knowledge is inadequate to say

<sup>7</sup>There are a number of combinations of terms to refer to, respectively, the uniseriate layer of initials *versus* these initials plus their tissue mother cells: (1) "cambium" *versus* "cambial zone" (this paper, and many advocates—references in second paragraph), (2) "cambial initials" *versus* "cambial zone" (e.g., Newman, 1956), (3) "cambial initials" *versus* "cambium" (many advocates—references at beginning of third paragraph), and (4) "cambial initials" *versus* "cambial zone" or "cambium" (e.g., Kozłowski, 1971; Srivastava, 1963, 1964).

conclusively that a single initiating layer is invariable or even general in dicotyledons.

The following criteria (from Wilson *et al.*, 1966) can be used to distinguish between the various regions designated in Table 1 (left half). The outer limits of the cambial zone may be determined by observing where most mitoses actually occur, and by the relatively small radial diameter of the cells of the cambial zone as compared to adjacent cells which have started enlarging. As noted above, the cambial initial itself may be almost impossible to identify in a radial file of cells. Some researchers (Bannan, 1955; Mahmood, 1968; Mischke, 1892; Murmanis, 1970, 1971; Newman, 1956; Sanio, 1873—see also Philipson and Ward, 1965, Philipson *et al.*, 1971, and Steeves and Sussex, 1972), however, have established criteria for the recognition of cambial initials based on anticlinal divisions (see point #4 on page 55), cell length, cell diameter, cell shape, cell groupings, and tangential cell wall thickness. The boundary between differentiating cells and maturing cells is marked by the thickening of cell walls, especially in formation of secondary walls, and by the lack of additional radial enlargement of cells. Cytoplasmic breakdown in fusiform xylary elements and disappearance of nuclei in phloic sieve elements prior to assumption of their normal functions of transport of water and solutes then mark the end of maturation.

The distinction between procambium (= provascular tissue) and cambium is another problem, but one beyond the scope of this paper and, at any rate, one not really relevant to studies of wood anatomy. For consideration of this problem, however, see Catesson (1964, 1974), Cumbie (1976b), Esau (1965), Fahn (1974), Fahn, Ben-Sasson, and Sachs (1972), Philipson and Ward (1965), Philipson *et al.* (1971), Priestley (1930), Romberger (1963), and Tomlinson and Zimmermann (1969).

There are several reasons for following the above definition of a cambium consisting of a uniseriate layer of initials:

(1) Recognizing a single layer as the sole initiating layer is consistent with the situation concerning the phellogen or cork cambium (references in introductory paragraph) and also, apparently, with that concerning the cambium of monocotyledons (see Eames and MacDaniels, 1947; Esau, 1965; Fahn, 1974; Foster, 1949; Kausmann, 1963; Philipson and Ward, 1965; Philipson *et al.*, 1971; Schoute, 1902; Tomlinson and Zimmermann, 1969), although data are particularly sparse for the latter. This is a minor point, but any consistency in terminology of meristems is desirable.

(2) In a similar vein, my definition is also comparable to recent representations of zonation and growth in shoot apices (Gifford and Corson, 1971, especially Fig. 11 therein) in which there is recognized

**Table 1. Comparison of Terminology Used to Describe Tissues Associated with the Vascular Cambium<sup>a</sup>**

| TERMINOLOGY OF "UNISERiate CONCEPT"           |                                 | CYTOLOGICAL EVENTS <sup>a</sup>  | TERMINOLOGY OF "MULTISERiate CONCEPT" |
|---|---------------------------------|--|---------------------------------------|
| Secondary phloem                              |                                 | Mature tissue (conductive, supportive, etc.)   | Secondary phloem                      |
| Maturing secondary phloem <sup>b</sup>        |                                 | Nuclear breakdown in sieve elements<br>Secondary cell wall deposition in fibers and sclereids              | Maturing secondary phloem             |
| Differentiating secondary phloem <sup>b</sup> |                                 | Cell enlargement, especially radial<br>Limited cell division (transverse and longitudinal) <sup>c, d</sup> | Differentiating secondary phloem      |
| Vascular cambium                              | Cambial zone (=meristem)        | Phloem mother cells <sup>e</sup>   | Phloem mother cells <sup>e, f</sup>   |
|   |                                 | Cambial initials (ray and fusiform)  | Cambial initials (ray and fusiform)   |
|   | Xylem mother cells <sup>e</sup> | Xylem mother cells <sup>e, f</sup>   |                                       |
| Differentiating secondary xylem <sup>b</sup>  |                                 | Limited cell division (transverse) <sup>d</sup><br>Cell enlargement, especially radial                     | Differentiating secondary xylem       |
| Maturing secondary xylem <sup>b</sup>         |                                 | Secondary cell wall deposition<br>Cytoplasmic breakdown in fusiform elements                               | Maturing secondary xylem              |
| Secondary xylem                               |                                 | Mature tissue (conductive, supportive, etc.)   | Secondary xylem                       |

<sup>a</sup> Modified especially from Butterfield (1975) and Wilson *et al.* (1966). See text for elaboration and for additional criteria characterizing the various regions.

<sup>b</sup> I follow Steeves and Sussex (1972) in defining "development" as representing *all* events contributing to the progressive elaboration of the organism and thus consisting of two major aspects—growth and differentiation. Maturation refers to the last stages of growth and development. This usage differs somewhat from that of Butterfield (1975) and Wilson *et al.* (1966).

<sup>c</sup> Some transverse and longitudinal divisions associated with development of sieve elements and companion cells.

<sup>d</sup> Some transverse divisions associated with development of axial parenchyma strands.

<sup>e</sup> Designated as phloem (= phloic) initials or xylem (= xylary, xylic) initials by some workers. "Mother cells" and "initials" are used either synonymously or with slightly different meaning (for the latter see Cheadle and Esau, 1958, and especially the glossary in Esau, 1960). The "mother cell" terminology is preferred since the "initial" terminology obscures the importance of the true "cambial initials." Zee (1968) recently introduced the term "transitional cell" for "phloem mother cell" (*sensu* Esau, 1960).

<sup>f</sup> Regarded as cambial initials by the true multiseriate concept of the vascular cambium (see text).

a zone of apical initials (admittedly not a uniseriate layer) set off by a subjacent pith-rib meristem and a peripheral zone of actively dividing cells, all of this being subtended by regions of maturation. As noted above, there is no nomenclatural and historical basis either for an inclusive use of "cambium" comparable to the entire "apical meristem" (Bannan, 1955; Steeves and Sussex, 1972) or for a restrictive one of "cambium" comparable to the "apical initials" (Wodzicki and Brown, 1973, and the usage adopted here). On the other hand, such comparisons may well be futile if apical and lateral meristems are so markedly dissimilar that certain workers (Steeves and Sussex, 1972: 241) question the desirability of using a single term, *meristem*, to designate both categories. This appears to be an isolated opinion, however, for many researchers have compared the cambial zone with the apical meristem (Bannan, 1955; Evert, 1963; Newman, 1956; Priestley, 1930; Wodzicki and Brown, 1973; and the present contribution).

(3) Recognizing a single layer as the sole initiating layer is consistent with those situations, admittedly almost all in gymnosperms, where such has been conclusively demonstrated (Bannan, 1955, 1968; Mahmood, 1968; Mischke, 1890; Murmanis, 1970, 1971; Newman, 1956; Sanio, 1873; Esau, 1948, contrary to the interpretation by Catesson, 1974; etc.) yet avoids the restrictiveness of Catesson's (1964, 1974) definition of many initiating cells in a radial file. The latter view is apparently supported by the lack of protoplasmic differences between initials and derivatives at the level of resolution of the electron microscope (Catesson, 1974; Evert and Deshpande, 1970; Mahmood, 1968; Murmanis, 1970, 1971; Srivastava and O'Brien, 1966; and references therein—but see Zee, 1968), but a broader definition seems more desirable not only in lieu of much more knowledge from the ultrastructural viewpoint, but also and especially since *cell wall* and *cell size/shape* differences between initials and derivatives are apparent with the electron microscope (Mahmood, 1968; Murmanis, 1970, 1971; Zee, 1968).

(4) The known dynamics of activity of the vascular cambium generally support a concept of a uniseriate initiating layer. As originally noted by Sanio (1873) and subsequently by many other workers (Bannan, 1955, 1962, 1968; Brown, 1971; Butterfield, 1975; Eames and MacDaniels, 1947; Philipson and Ward, 1965; Philipson *et al.*, 1971; Schoute, 1902; Steeves and Sussex, 1972), the simultaneous changes occurring in individual rows on both sides of the cambium (e.g., a doubling or loss of a row on both sides, replacement of such rows by rays, etc.) necessitate changes having occurred in single initial cells that are relatively permanent. In addition, and a fact less often stressed, most multiplicative (= anticlinal, predominantly pseudotransverse) cell divisions are

restricted to initials rather than to mother cells (Bannan, 1955, 1957, 1966, 1967, 1968; Brown, 1971; Butterfield, 1975; Cumbie, 1967a; Evert, 1963; Murmanis, 1970; Newman, 1956; Philipson and Ward, 1965; Philipson *et al.*, 1971; Romberger, 1963). For example, Bannan (1957, 1966, respectively) determined the ratio of pseudotransverse divisions in cambial initials versus those in derived xylem mother cells as about 67:1 in twelve species of conifers and approximately 300:1 in *Sequoia sempervirens*. In a more recent study of an even larger sample (over 43,000 anticlinal divisions observed in the cambial zone of 28 species of conifers) Bannan (1968; see also 1967) found an over-all average of less than 3% pseudotransverse divisions in presumed xylem mother cells. In some cases, however, such anticlinal divisions may be distributed over several layers of cambial cells (Catesson, 1964, 1974; Cumbie, 1963; Murmanis, 1970).

(5) My definition (see also Esau as discussant in Wilson, 1964) stresses the permanency of initials and their capability of anticlinal division and bidirectional periclinal production of derivatives. The latter point does not seem to have been sufficiently emphasized. Bannan (1957), Wilson and Howard (1968), and Philipson *et al.* (1971; also Philipson and Ward, 1965) discuss the controversy concerning the frequency of (periclinal) redivision of the mother cells on either side of the initials. The last noted that one mother cell may produce more than twenty derivatives, but as yet there seem to be little data whether this production is mostly or entirely unidirectional versus frequently bidirectional. The latter situation would, of course, support Catesson's (1964, 1974) multiseriate concept.

(6) "Cambial zone" is an integral part of my concept of the cambium. This expression (or "cambial region") should be readily comprehensible to non-specialists as meaning a meristematic region of cell division. Steeves and Sussex (1972: 258) argue the same for "cambium," but after a century of a well-entrenched uniseriate concept of the cambium it would seem, conversely, that "cambium" to non-specialists would have reference more to a single layer of cells than to the whole lateral meristem (see also footnote 5).

As has been noted by several workers, the uniseriate concept of the vascular cambium is particularly prevalent in American literature. Judging from inadequate and misleading descriptions in elementary botany textbooks, as well as responses to questions I have posed to graduate students on doctoral qualifying examinations, many persons believe or, at least, imply that additive divisions occur only in the cambial initial itself and not also in the mother cells (a falsehood recognized long ago by Mischke, 1890, and Sanio, 1873, Schoute, 1902, among others). In other words, "cambium" is equated with "meristem" (see

above discussion), and a meristematic "cambial zone" is not sufficiently appreciated. This misimpression of a single cell "grinding out" anticlinally and periclinally numerous other cells is perhaps a major defect of the uniseriate concept of the cambium (similar notions about apical meristems died long ago with the denial of the universality of the apical cell concept—see Romberger, 1963), but not of a multiseriate concept. Broader usage of the designation "cambial zone" in a uniseriate concept, however, would eventually seem to remedy this disadvantage.

Use of the expressions "uniseriate" versus "multiseriate," especially in "uniseriate cambium" or "multiseriate cambium,"<sup>8</sup> as done here and by Brown (1971), Butterfield (1975), Philipson *et al.* (1971), Srivastava (1963, 1964), and Wodzicki and Brown (1973), probably only muddles an already complicated terminological situation. As indicated above, every worker recognizes a multilayered or multiseriate zone of dividing cambial cells (=meristem) and thus, by extension, a "multiseriate cambium", but differs with regard to what this zone should be called ("cambial zone" or "cambium"). The correct application of "uniseriate" and "multiseriate", therefore, is really in the expressions "uniseriate initiating layer" or "uniseriate layer of initials" versus "multiseriate initiating layer" or "multiseriate layer of initials," or their equivalents. These concessions to clarity generally have not been adopted by writers, with the notable exception of Bannan (1955, 1957, 1962, 1968), Eames and MacDaniels (1947), and Kozlowski (1971).

The preceding discussion evokes the image of "the elusive cambium." I would thus like to call attention to an interesting historical paper of the same title by Jacob Lorch (1967). This work, which I have never seen cited, focuses on the different sort of cambial elusiveness which existed up to 1840, when Unger (1840) became the first person to stress the cellular, rather than liquid, nature of the vascular cambium (see also Bannan, 1955).

By whatever concept of the vascular cambium that is adopted, the cambium since Schacht in 1854 (see Lorch, 1967) has been almost universally regarded as consisting of two kinds of initiating cells: *fusiform initials* giving rise to the axial (= vertical) system of the secondary xylem and secondary phloem, and *ray initials*<sup>9</sup> giving rise to the radial (= horizontal) system

<sup>8</sup>"Uniseriate (multiseriate) concept of the cambium," which is used throughout this paper, is semantically different from "concept of a uniseriate (multiseriate) cambium," which is used by Butterfield (1975) and Wodzicki and Brown (1973). The former is preferred not only by analogy with other controversies (it is "the classical concept of the flower," not "the concept of a classical flower"), but also because the differences really involve the concept (uniseriate versus multiseriate) and not the cambium itself, which at any rate is almost always a "multiseriate meristem."

<sup>9</sup>Wodzicki and Brown (1973) note that ray cell initials may be radially elongate and erect as opposed to the common description of "more or less isodiametric."

of the secondary xylem and secondary phloem. No one seems to have pointed out in print, however, the ambiguity of "ray initial." A more precise terminology involving the latter type of initial (Charles B. Beck, pers. comm., 1966) would restrict *ray initial* to the complex of initials of an entire ray and then use *ray cell initial*<sup>9</sup> for the individual initiating cells. In other words, a vascular ray five cells high would be initiated by one ray initial consisting of five ray cell initials. This terminology, however, seems to have been adopted only by Beck and his students (e.g., Schmid). Although such usage of "ray initial" and "ray cell initial" is, of course, contrary to that in the glossary issued by the Committee on Nomenclature, International Association of Wood Anatomists (1964), wood anatomists should seriously consider the merits of the above proposed terminology with a view to introducing it, hopefully, in a future edition of the "glossary."

#### Summary

Arguments are advanced for a uniseriate concept of the vascular cambium, which recognizes a self-perpetuating, single layer of cambial initials ("vascular cambium") within a region of actively dividing xylem and phloic cells ("tissue mother cells" or "initials"). The entire meristematic zone is referred to as a "cambial zone." The actual initials are often difficult or impossible to locate visually in a file of cells, but are positionally capable of producing cells in both a centrifugal and a centripetal direction. Anticlinical cell divisions generally predominate in the cambial initials as opposed to their derivatives. Some so-called multiseriate concepts of the cambium (e.g., Butterfield, 1975, in this Bulletin) are essentially nomenclatural or terminological modifications of such a uniseriate concept of the cambium in that both still accept a single layer of initials. This contrasts with a true multiseriate concept (Catesson, 1964, 1974) advocating several layers of initials. Finally, a more precise usage for "ray initial" would restrict "ray initial" to the complex of initials of an entire ray; the term *ray cell initial* should therefore be used for the individual initiating cells.

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## ASSOCIATION AFFAIRS

### Deputy Executive Secretary

The Council has appointed Mr. P. B. Laming, Forest Products Research Institute TNO, Delft, The Netherlands, a Deputy Executive Secretary. Mr. Laming joined the IAWA in 1967 and has worked in the field of wood identification and structure-property relationships.

### Increase in Annual Dues

By the time this Bulletin has reached you, you will probably have received a dues notice for 1977. In view of the very precarious financial situation of the IAWA, the Council has agreed on a slight increase in annual dues from US\$10.00 to f 30.00 (Dutch guilders = c. \$11.00). If dues are paid by international postal money order, we will be able to avoid considerable banking costs. For those who prefer payment by cheque, it would be appreciated if the equivalent of our banking costs ( f 5.00) could be added on a voluntary basis.

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### Deceased Member

Word has been received from the brother of Ing. Jorge L. Flamand, from ICATEC Consultores, Mexico, that he passed away two years ago. Mr. Flamand joined our association in 1965.

## WOOD ANATOMY ACTIVITIES AROUND THE WORLD

### Exchange of Duplicate Slides

Miss Dorothy Catling from the Metropolitan Police Forensic Science Laboratory, 109 Lambeth Road, London SE1 7 LP, England, informed us that her division has sets of duplicates available of more than one hundred timber slides. She is anxious to exchange these with other institutes.

### A Computer Generated Catalogue on Micro-cards of the Wood Collection at Tervuren

With the aid of the Centre d'Informatique appliquée au Développement et à l'Agriculture tropicale (C.I.D.A.T.) at the Royal Museum for Central Africa in Tervuren, it has been possible to publish an extensive inventory of the wood collection at Tervuren. The collection comprised 5500 species and 30,000 wood samples from all over the world when the inventory was made. The methods employed are described in detail elsewhere (Dechamps, Ergo & de Haes, 1975). It is felt that other curators of wood collections or colleagues using our material for study may find it useful to be informed about the main aspects of the catalogue. Perhaps similar inventories could be carried out in other large wood collections along the same line.

The wood collection at Tervuren has been classified according to botanical affinity as well as according to geographic origin. In the systematic catalogue the families are arranged in alphabetical order. For convenience, the genera and species are also arranged alphabetically within the families. Species of which the wood of at least one sample is backed by a herbarium voucher are marked with an asterisk. Synonyms are given as well as codified information on geographic origin.

Besides this systematic catalogue according to families, there is also an alphabetical catalogue to the genera and species. This is thought to be useful for genera poorly known to the reader.

In the third and final catalogue, lists of wood samples are given for geographical areas (countries, districts and/or provinces). This allows the reader to anticipate which species or genera to expect from a certain area.

We think this type of catalogue is useful for a variety of purposes: it allows a quick judgment on the availability of material for study of selected groups, as well as on the desirability to embark on collecting trips in under-explored areas. Moreover, it contains much nomenclature and taxonomic information—often not easily accessible to the wood anatomist.

The publication of the catalogue in printing would have resulted in a book of 726 pages. Because of the costs involved, and in view of the fact that this catalogue would become out of date after some time due to new acquisitions, it was decided to use the much cheaper means of publication on micro-cards. Four cards of 15 × 9.5 cm to be read with a lector at 42 × magnification thus contain the three catalogues. Additionally, a booklet of 50 pages has been published, giving the table of contents for the micro-cards, the meaning of the geographic codes used, as well as information on methodology of the computer work.

We hope to have provided our colleagues and our institute with a daily working tool in this way, which will save time and perhaps stimulate others to use similar techniques for cataloguing their collections. We will be happy to provide further details to those interested.

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Dechamps, R., A.B. Ergo & W. de Haes. 1975. Inventaire et origine géographique des échantillons de la xylothèque du Musée Royal de l'Afrique Centrale, Tervuren (B). 49 pp., 4 figs., 4 micro-cards. Published by the Musée Royal de l'Afrique Centrale, Tervuren, Belgium. Price 450 FB or US\$12 postage included (if ordered directly from the Museum).

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