Resin Canals in the Wood of *Larix leptolepis* GORD. (V) Formation of Vertical Resin Canals.*

By

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カラマツ材 (*Larix leptolepis*) の樹脂道 (第5報) 垂直樹脂道の形成*

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Introduction

In *Larix*, *Picea*, *Pseudotsuga* and *Pinus* the occurrence of resin canals is regarded as a normal feature, while in such genera as *Abies*, *Tsuga* and *Cedrus* resin canals are considered to arise as a result of injury. The former group of genera also has traumatic resin canals, i. e., canals arising as a result of injury. Normal canals occur in both vertical and horizontal directions in wood, whereas the direction of traumatic canals is usually either vertical or horizontal in the same sample.[7] Axial and ray (i. e., radially oriented) epithelial cells are traceable to daughter cells arising from fusiform initials in the cambium and cambial ray cell initials, respectively.[7]

In the secondary xylem the formation of normal vertical canals already occurs in xylem mother cells. The first change of these mother cells into axial epithelial cells is a transverse division, i. e., a segmentation.[1,6,7,8,12,13] The mother cells, which

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are destined to differentiate into axial epithelial cells, are generally four in number at first, and these four cells are present in two radial files, two ones each.[8,13] Before the separation of the mother cells, true middle lamellae between them are thought to be dissolved by lytic enzymes which are carried by Golgi vesicles in themselves.[2] The separation which produces an intercellular space, in the first place, arises schizogenously near the centre of a cluster of the mother cells, i. e., at corners between these cells in cross sections.[2,8,13] Subsequently the schizogenous separation arises between tangential or radial walls of the mother cells, and thus an intercellular space which is called a resin canal is formed in wood.[2,6,8,13] During the separation, cell compartments derived from the mother cells divide periclinally or anticlinally into a number of smaller cells.[8,13] In addition, several cambial parenchyma cells around the mother cells also divide transversely or sometimes longitudinally into small cells.[8,12] Eventually vertical resin canals are enclosed with axial epithelial cells which are surrounded with axial parenchymatous cells and strand tracheids.[5,6,7,8,9,12,13]

Traumatic resin canals are described as arising from the separation of epithelial cells in a manner entirely comparable to that occurring in the formation of normal canals.[7]

The studies on the formation of normal resin canals have been made in detail in *Pinus*.[2,5,8,13] However in *Larix, Picea* and *Pseudotsuga* the studies on it were not yet investigated sufficiently. Therefore the authors have made a research on the formation of normal vertical canals in *Larix leptolepis*.*1 Furthermore we have studied the formation of traumatic vertical canals and have compared the development of these with that of normal vertical canals.

Materials and Methods

Twelve larch trees (*Larix leptolepis* GORD.), grown in a plantation in Tomakomai Experiment Forest of Hokkaido University, were used for the present study. On the basis of a diameter at breast height and of widths of annual rings for the last ten years, the trees were divided into two groups. The first group consisted of four trees which were, on an average, 13.6 cm in a breast-height diameter and 2.9 mm in the width of annual ring. The second group consisted of eight trees which were, on an average, 14.2 cm in the diameter and 2.7 mm in the width. Materials for the study of the formation of normal canals were taken separately from the first group fourth times, at regular intervals from July 21 to August 28 in 1980. All trees of the second group were wounded on June 19, 1980. To be precise small blocks including the cambium (L: 2 mm, T: 5 mm, R: a few mm) were removed from the trees by razor blades. Soon thereafter, the wounded area was covered with vaseline. Materials for the study of traumatic canals were taken separately from the second group eighth times, at regular intervals from June 26 to August 14 in 1980.

*1 *Larix kaempferi* (LAMB.) CARR. is used instead of *L. leptolepis* GORD., in the new edition of "Flora of Japan (in Japanese)" by J. OHWI (1982, p. 60).

The materials obtained from both groups were fixed either in Zirkle's reduced chromium solution[15] or in 3 percent glutaraldehyde solution (buffered with sodium cacodylate). Some of the materials fixed in the latter were post-fixed in osmium tetroxide (buffered with sodium cacodylate). After the fixation, small specimens (T : 2–3 mm, R : 4–5 mm, L : 4–5 mm) were dehydrated in a graded series of acetone and were embedded in Epon 812 or Spurr's resin.[11] From the embedded specimens, mainly cross or sometimes radial sections in 5 or 10 microns thickness were cut with a steel knife on a sliding microtome. In addition, 2 microns thick cross or radial sections were also cut with glass knives on LKB Ultrotome 8800. All sections were stained with basic fuchsin and were observed under an optical microscope.

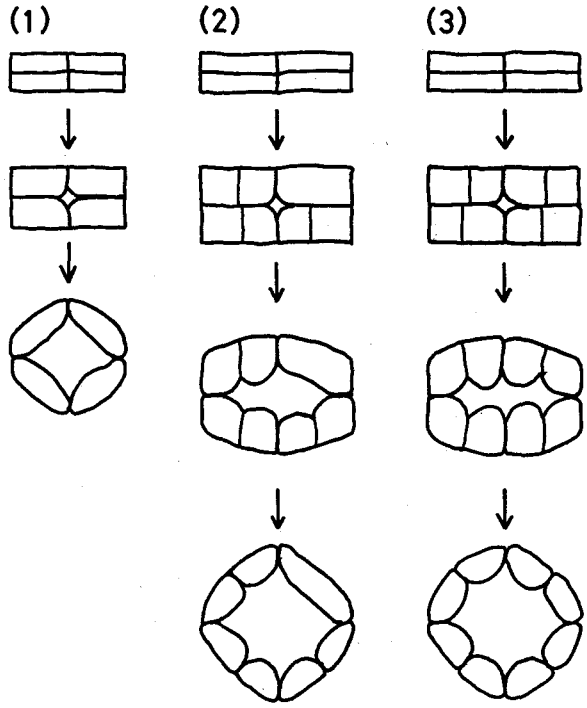
Results and Discussion

1. Normal vertical resin canals

Fusiform parenchyma cells, which were destined to differentiate into axial epithelial cells, already enlarged radially when other parenchyma cells in the cambial zone were still flattened tangentially (Photo 1), as seen in *Pinus halepensis*.[13] In *Pinus silvestris*, initials of axial epithelial cells were rarely two and frequently three or four in number at first, and these initials belonged to two radial files.[8] In the present study, four epithelial initials (i. e., ones which denote initials of epithelial cells in this paper) occurring in two radial files, two ones each, were also seen frequently, but two or three initials present in two files were not found. However five or six epithelial initials in two files were often observed, and in addition, six to eight initials in three files were found at times. Occasionally four epithelial initials in a file and eight ones in four files also occurred. As mentioned above, in *Larix leptolepis* the number of epithelial initials was various to start with, though four ones in two files appeared to occur most frequently.

When epithelial initials were formed only in a radial file, though such a case was scarcely found, they were invariably four in number (Photo 2). Epithelial initials formed in two radial files varied in number from four to six. Four initials occurred in the two files, two ones each (Photo 3). Three of five initials were in a file and the other two were in the other file (Photo 4). Six initials belonged to the two files, three ones each (Photo 5). In the case of five or six initials in the two files, the initials in a file nearly always alternated with the ones in the other file, in other words, corners between the initials in a file were adjacent to radial walls of the ones in the other file. Epithelial initials formed in three radial files varied in number from six to eight. Six initials occurred in the three files, two ones each (Photo 6). Four of seven initials were in two neighboring files, two ones each, and the other three were in another file (Photo 7). Six of eight initials belonged to two neighboring files, three ones each, and the other two belonged to another file (Photo 8). Eight epithelial initials which were present in four files, two ones each, were rarely found in the present study (Photo 9). When initials occurred in four files, commonly one or more files of the four were much narrower in width than the others.

As a rule, each of epithelial initials, in the first place, divided anticlinally into two smaller cells in cross sections (Photos 3 and 6). Sometimes initials with large trangential diameter twice divided anticlinally into three cells (Photos 9 and 17), while initials with small tangential diameter occasionally divided periclinally into two cells (Photo 9). However initials which did not divide mitotically were also seen several times in the present study, for example, two of five initials in two files (Photo 1), a middle initial of the three in either of two files where five initials occurred (Photo 4), two middle initials in each of two files in which six initials were present (Photo 5). On rare occasions, only one of six initials in three files divided anticlinally (Photo 10). Generally small initials in a narrow file did not divide both anticlinally and periclinally. Since cambial fusiform initials were small in diameter in juvenile wood, undivided epithelial initials were supposed to be frequently observed in it. Epithelial initials which divided more than twice were seen only sometimes in the formation of normal canals.



Figs. 1-7. Schematic drawings of the development of six types of mass of epithelial initials.

Fig. 1. **Type A-1**: four epithelial initials present in two radial files, two ones each. (1) Occasionally none of the four initials divide mitotically; (2) On rare occasions, one or more initials of the four do not divide anticlinally; (3) In general, each of the four initials divides anticlinally into two cells. The schizogenous separation arises, in the first place, at the spot where a corner between initials in a file is adjacent to a corner between initials in the other file.

In the present study, masses of epithelial initials were classified into six types (Figs. 1-7), on the basis of the number of initials in the mass and of the number of radial files in which the initials were present. Type A-1 : four epithelial initials present in two radial files, two ones each (Fig. 1). Type A-2 : six initials present in three files, two ones each (Fig. 2). Type A-3 : eight initials present in four files, two ones each (Fig. 3). Type B : four epithelial initials present in a radial file (Fig. 4). Type C-1 : five or six initials present in two radial files (Figs. 5 and 6). Type C-2 : seven or eight initials present in three files (Fig. 7).

Each of four epithelial initials in tw files (Type A-1) commonly divided anticlinally into two smaller cells (Photo 2). Sometimes one or more initials of the four were thought not to divide anticlinally (cf. Photo 10). However the four initials might occasionally become four epithelial cells without cell divisions, for the minimal number of epithelial cells in the epithelium of vertical canals was described as four

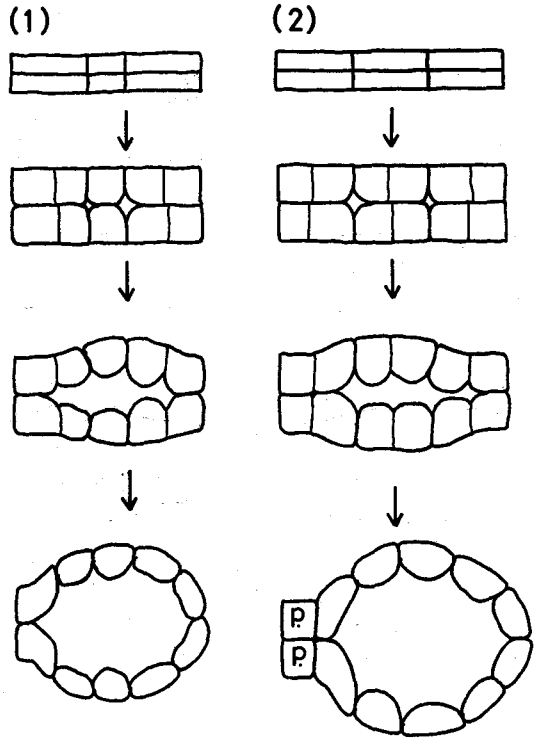


Fig. 2. **Type A-2** : six epithelial initials present in three radial files, two ones each. (1) Sometimes small initials in one or more narrow files constitute the six initials, and such initials rarely divide mitotically; (2) Generally each of the six initials divides anticlinally into two smaller cells, and subsequently, two (p) of the four smaller cells in either of two files except a middle one, which do not face a canal, probably become axial parenchymatous cells (**Type A-2′**). The schizogenous separation, at first, arises possibly at the centre of four initials in two neighboring files of the three as in the case of **Type A-1** and subsequently arises between tangential walls of the smaller cells.

in *Larix Kaempferi*.[8] In general, the four epithelial initials in Type A-1 would differentiate into four to eight axial epithelial cells in the future (Fig. 1).

Each of six epithelial initials in three files (Type A-2) commonly divided anticlinally into two smaller cells, so that initials summed to twelve in number (Photo 6). After the anticlinal division, four smaller cells in either of two radial files except a middle one of the three were thought to differentiate into two types of cell (Photo 11). That is, two of the four smaller cells, which faced a developing canal, became axial epithelial cells, and the other two were thought to differentiate into slender parenchymatous cells which were called Parenchymatous cell I by SATO and ISHIDA.[9] Eight remaining smaller cells in two neighboring files became epithelial cells. Such differentiations of epithelial initials frequently arised after the anticlinal division. However none of the six initials in Type A-2 might divide occasionally (cf. Photo 10). When epithelial initials in three files were six in number at first, a tangentially elliptical vertical canal which is enclosed probably with six

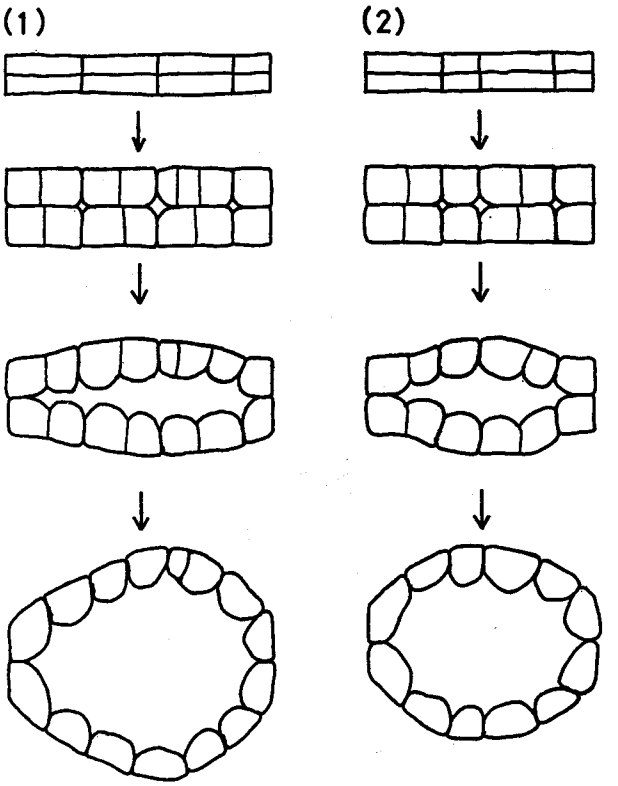


Fig. 3. **Type A-3**: eight epithelial initials present in four radial files, two ones each. Commonly one or more files of the four are much narrower in width than the others. (1) Sometimes an initial with large tangential diameter twice divides anticlinally into three cells. The schizogenous separation might first arise at the centre of four initials in middle two files of the four and secondly arises between tangential walls of the smaller cells as in **Type A-2.**

to ten epithelial cells in cross sections would finally be formed in the three files (Fig. 2). Especially in mature wood, a vertical canal enclosed with ten epithelial cells (Photo 11) appeared to occur most frequently (Type A-2′ in Fig. 2 (2)).

When eight epithelial initials occurred in four radial files, two ones each (Type A-3), one or more files of the four were commonly narrower than the others (Photo 9). Epithelial initials in wide files divided anticlinally into two or sometimes three cells, whereas ones in narrow files scarcely divided mitotically. The four files might not consist of only wide files, nor only narrow files might constitute them. Eight epithelial initials present in four files would differentiate probably into twelve or more epithelial cells in course of time (Fig. 3).

Four epithelial initials in a file (Type B) individually divided anticlinally into eight smaller cells (Photo 2). Since the eight cells were very small in diameter, they would not divide again. In the future, a small vertical canal which is enclosed with six or eight small epithelial cells in cross sections may be formed in the file (Fig. 4).

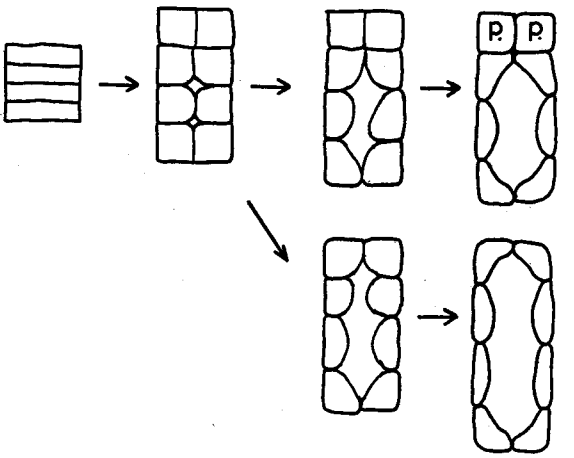


Fig. 4. **Type B**: four epithelial initials present only in a radial file. At all times, the four initials individually divide anticlinally into eight smaller cells and might finally become six or eight epithelial cells (p: axial parenchymatous cells). The schizogenous separation might first arise at the centre of the middle four smaller cells and secondly arises between radial walls of the smaller cells.

Commonly each of five epithelial initials in two radial files (Type C-1) might divide anticlinally into two smaller cells. However a middle initial of the three in either of the two files often did not divide (Photo 4). Since a vertical canal enclosed with five epithelial cells was found in *Larix Kaempferi*,[3] none of the five initials might not divide occasionally. In the present study, the occurrence of masses of five initials was not sufficient to observe the division of each of them. In the case of six initials in two files, three ones each (Type C-1), commonly either or both of two middle initials in the two files might not divide anticlinally (cf. Photo 5). However both of the middle initials sometimes divided anticlinally into four smaller

cells. After such a division happened, two of the four smaller cells, which faced a developing canal, might have invariably divided again periclinally (cf. Photo 18). The other two cells which did not divide periclinally were thought to differentiate into slender parenchynatous cells (i. e., ones called Parenchymatous cell I[9]). In the

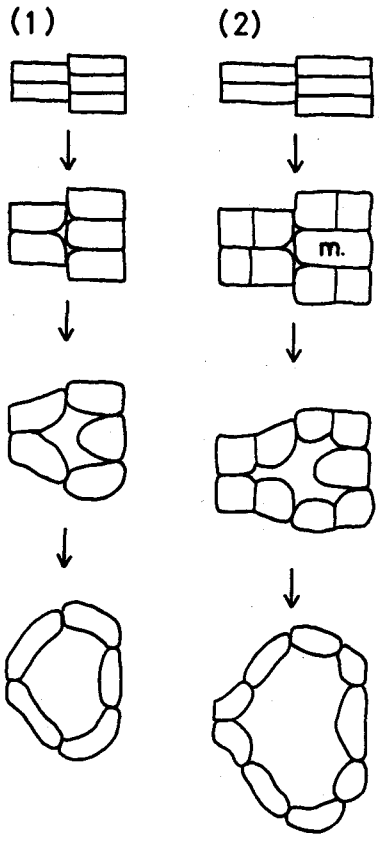


Fig. 5. **Type C-1**: five epithelial initials present in two radial files. (1) Occasionally none of the five initials divide mitotically. (2) Commonly a middle initial (m) in either of the two files does not divide anticlinally. The schizogenous separation first arises probably at the spot where a corner between two initials in a file is adjacent to a radial wall of a middle initial in the other file and secondly arises between radial walls of the initials.

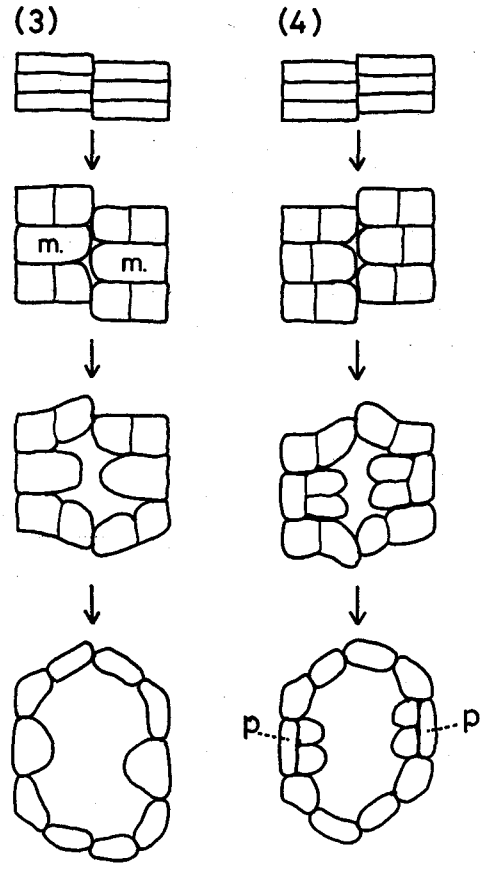


Fig. 6. **Type C-1**: six epithelial initials present in two radial files, three ones each. (1) In general, either or both of middle initials (m) in the two files do not divide anticlinally. (2) After both of the middle initials individually divide anticlinally into four smaller cells, two of these four smaller cells, which face a canal, divide again periclinally (p: axial parenchymatous cells). The shizogenous separation might first arise near the centre of the six initials, i. e., at the places where a corner between initials in a file is adjacent to a radial wall of a middle initial in the other file. Secondly the separation arises between radial walls of the six initials.

case where epithelial initials in two files were five or six in number to start with, a radially elliptical vertical canal which is enclosed probably with five or six to ten or twelve epithelial cells in cross sections would finally be formed in the two files (Figs. 5 and 6).

Seven epithelial initials in three radial files (Type C-2) were composed of four initials in two neighboring files and of the other three in another file (Photo 7). Although a middle initial of the three in another file sometimes did not divide, commonly each of the seven initials divided anticlinally into two cells. Eight initials

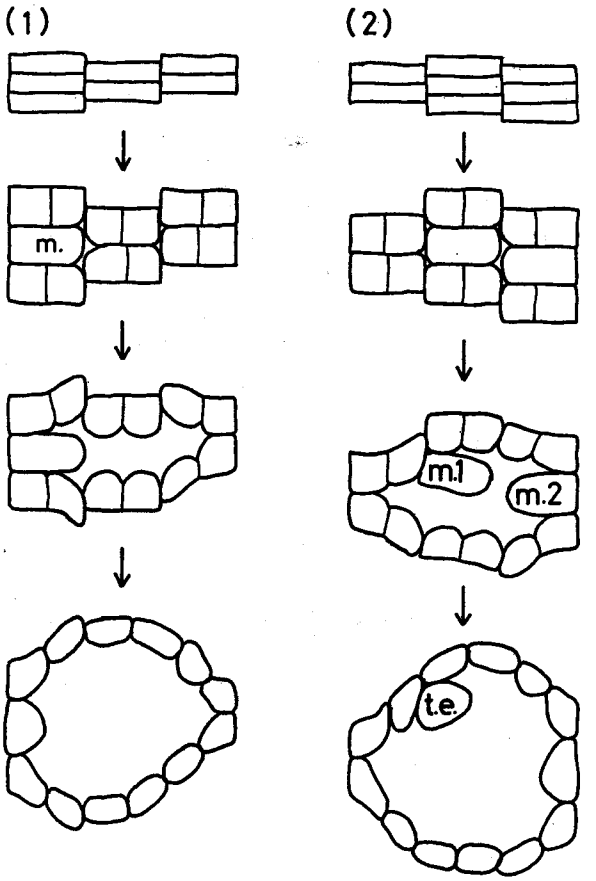


Fig. 7. **Type C-2**: seven or eight epithelial initials present in three radial files. (1) Commonly a middle initial (m) of the three in a file does not divide anticlinally. (2) Both of middle initials (m. 1 and m. 2) in two neighboring files might not sometimes divide anticlinally, and in particular, the middle initial (m. 1) adjacent to a pair of initials in another file might never divide mitotically. The middle initial m. 1 might become a thin-walled epithelial cell (t. e.) in the future. The schizogenous separation first arises probably near the centre of a mass of five or six initials in two neighboring files as in **Type C-1** and secondly arises between radial walls of the five or six initials. Subsequently, the separation arises between tangential walls of the pair in another file.

in three files (Type C-2) were composed of six initials in two neighboring files, three ones each, and of a pair of initials in another file (Photo 8). Both of two middle initials in the two neighboring files might seldom divide mitotically. In particular, a middle initial adjacent to one of the pair in another file might never divide mitotically (cf. Photo 8). Such a middle initial was assumed to become a thin-walled epithelial cell without the thickening and lignification (Fig. 7). Each of six initials except the two middle ones generally divided anticlinally into two cells. When epithelial initials in three files were seven or eight in number at first, a large circular canal would, in course of time, be formed in the three files (Fig. 7). Such a canal would be enclosed probably with seven to fourteen epithelial cells.

A schizogenous separation, as reported by several researchers,[1,2,6,7,8,13] in the first place, arised near the centre of a mass of epithelial initials. The separation appeared to arise as soon as each of the initials divided anticlinally (cf. Photo 1).

In the case of Type A-1, the separation arised, at first, at the centre of four epithelial initials in cross sections, i. e., at the spot where a corner between the two initials in a file was adjacent to a corner between the two in the other file. Subsequently, the separation arised between tangential walls of the four initials (Fig. 1). With regard to Type A-2, the separation appeared to first arise at the centre of four initials in two neighboring files of the three, and secondly arised between tangential walls of the initials (Fig. 2). As regards Type A-3, the first separation appeared to arise at the centre of four initials in middle two files of the four. The second separation arised between tangential walls of the initials, as well as in the case of Types A-1 and A-2 (Fig. 3).

After four epithelial initials in a radial file (Type B) individually divided anticlinally into eight smaller cells, the separation appeared to first arise at the centre of middle four smaller cells in cross sections (Fig. 4). The separation secondly arised between radial walls of the smaller cells (cf. Photo 2).

In the case of Type C-1, the separation first arised, in cross sections, at the places where corners between the initials in a file were adjacent to radial walls of the initials in the other file (Fig. 5 and Photo 5). The separation secondly arised between radial walls of the initials, as dipicted in Fig. 20 by MAYR.[6] With regard to Type C-2, the first separation arised near the centre of five or six initials in two neighboring files of the three and the second separation arised between radial walls of these initials as seen in Type C-1. Subsequently, the separation arised between tangential walls of a pair of initials in another file. Thus in the case of Type C-2, a developing canal had a L-shape transiently (Photo 8).

The epithelium in *Larix leptolepis* was surrounded with two types of axial parenchymatous cell (i. e., Parenchymatous cell I and II) and strand tracheids.[9] As mentioned earlier on, the smaller cells derived from epithelial initials might sometimes differentiate into slender parenchymatous cells (i. e., Parenchymatous cell I), that is, both epithelial cells and the slender parenchymatous cells might be present in the same radial file (cf. Photos 11 and 18). Some of fusiform cambial cells which surrounded epithelial initials divided transversely, possibly after these initials had divided in the same direction (Photo 12). The fusiform cambial cells which divided

transversely were thought to differentiate into parenchymatous cells with square or rectangular outline in cross sections (i. e., Parenchymatous cell II) or strand tracheids. Furthermore, cell compartments originated from the cambial cells sometimes divided longitudinally, possibly after the initials had divided in the same direction. Such cells would become small Parenchymatous cells II (Photo 13). If the division of the cambial cells around epithelial initials undoubtedly followed that of the initials, the differentiation and maturation of the cambial cells would also follow that of the initials. YUMOTO et al. report that axial cells around a vertical canal would remain sensitive to the geotropic stimulus for a longer period than usual.[14] Therefore, whether an element of a parenchyma strand differentiated into a parenchymatous cell or a strand tracheid might have not yet been destined when axial tracheids began to thicken and lignify. This might be the reason that parenchyma strands consist in part of strand tracheids in coniferous woods with resin canals.

2. Traumatic vertical resin canals

While initials of axial epithelial cells produced as a result of wounding were not distinguishable in the cambial zone of cross sections, in other words, while these epithelial initials did not yet enlarge radially, they had already divided transversely into small compartments (Photo 14). In the formation of traumatic vertical canals as well as in that of normal canals, longitudinal divisions of initials invariably followed transverse divisions of them.

A large number of masses of epithelial initials, which were lined up tangentially, were produced in two weeks after wounding (Photo 15). Six types of mass of initials occurring in the formation of normal canals were also seen in that of traumatic canals. Type A-2 and Type C-1 more frequently appeared in the formation of traumatic canals than in that of normal canals. In the present study, masses of seven initials in three files (Type C-1) were seldom found. Seven or more initials formed in two files were, at times, found (Photo 16), and in addition, a large mass of initials, which belonged to five or more files (probably up to eight files), was often observed in the development of traumatic canals. Such a large one was thought to be formed by the combination of masses of initials which were seen in the formation of normal canals, for example, the combination of Types A-2 and C-2 (Photo 17). The largest mass was supposed to be formed when A-3 type ones combined each other. Various combinations of masses of initials were observed but a combination of more than three ones appeared not to arise. A combination of two of A-2 type masses may occur most frequently of all kinds of combinations.

Epithelial initials, as a rule, once divided anticlinally into smaller cells in the formative period of traumatic canals, as well as in that of normal canals. However epithelial initials which divided again thereafter, that is, ones which divided more than twice were more frequently observed in the development of traumatic canals than in that of normal canals. Smaller cells derived from the initials divided in various directions, namely, periclinally or anticlinally or obliquely (Photo 18). A

main direction of the division of these cells might be periclinal to a developing canal, as seen in *Pinus halepensis.*[13] The smaller cells and tiny cells originated from these were often deformed. To be exact, the smaller cell sometimes had a semicircular projection facing a developing canal, and most of the tiny cells jutted into a developing canal (Photo 19). In addition to the prominent cells mentioned above, cylindrical cells which radially traversed a developing canal were also found several times (Photo 20). Epithelial initials which were situated on the border between different types of mass or the same-type masses might usually become the cylindrical cells. A large number of irregularly shaped epithelial cells were seen in the epithelium of traumatic canals in *Larix leptolepis.*[9] Numerous small and irregular-shaped epithelial cells would be invariably present in the epithelium of typical traumatic canals.

In the development of normal canals, cambial cells around epithelial initials sometimes divided anticlinally into smaller cells, on the other hand, in that of traumatic canals such cambial cells often divided anticlinally. However the cambial cells which divided more than twice were a few in number in the present study (Photo 19). Smaller cells originated from the cambial cells would become axial parenchymatous cells. Since the cambial cells which differentiate into strand tracheids should not divide anticlinally, strand trancheids might occur less frequently in the formation of traumatic canals than in that of normal canals.

Epithelial initials produced as a result of injury schizogenously separated each other in a manner comparable to that arising in the formation of normal canals. However the schizogenous separation mainly arised between tangential walls of epithelial initials in the formation of traumatic canals, because large masses of the initials present in several files were seen frequently (cf. Photo 17). A cylindrical epithelial cell in the epithelium of traumatic canals traversed a vertical canal only radially in *Larix leptolepis.*[9] Since the direction of the separation was mainly radial, only radially transverse cells would be formed in the epithelium of traumatic canals.

Disorganized materials were, at times, found in developing canals (Photo 21). Since an epithelial initial was sometimes detached from the initials around a developing canal (Photo 22), such an initial was supposed to disintegrate into the materials. One of the three main characteristics of lysigenous cavities was the presence of disorganized cytoplasm in a duct cavity.[4] Typical traumatic canals might be formed schizo-lysigenously in *Larix leptolepis.* Another characteristic of lysigenous cavities was the presence of specific intercellular spaces at the cell corners facing a duct lumen, and such spaces were triangular in cross sections.[4] The triangular intercellular spaces were not found in the present study. Only an epithelial initial detached from the initials around a developing canal would possibly disintegrate into the disorganized materials.

After the formation of traumatic vertical canals produced as a result of injury in the growth period (Photo 23), horizontal resin canals temporarily increased in number per square centimeter, that is, traumatic horizontal canals occurred temporarily. These traumatic canals appeared not to differ anatomically from normal

horizontal canals. On the contrary, after traumatic vertical canals were formed on annual ring boundaries (Photo 24), traumatic horizontal canals did not occur. However fusiform rays which came in contact with the traumatic vertical canals on the ring boundary expanded tangentially (Photo 25), and subsequently, such expanded fusiform rays were transformed gradually into uniseriate rays (Photos 26 and 27). We have already made the report mentioned above.[10] The injury that causes the formation of traumatic vertical canals would also affect cambial ray cell initials. Whether or not traumatic horizontal canals occur in the secondary xylem would depend on the activity of cambial ray cell initials.

Conclusions

Epithelial initials (i. e., initials of epithelial cells) were observed invariably in a mass in the present study. Masses occurring in the formation of normal vertical canals were classified into six types in this paper (Figs. 1–7). The classification was based on the number of initials in the mass and on the number of radial files in which the initials were present. In the formative period of traumatic vertical canals the six types of mass were also observed, and furthermore, a large one of initials, which was thought to be formed by the combination of two or more ones was often found. In any case, in the formation of traumatic vertical canals as well as in that of normal ones, masses of epithelial initials would fundamentally be classified into the six types.

Type A–1 might develop into Types A–2, A–3, C–1 and C–2. In other words, when a pair of epithelial initials in a file occurred tangentially at either side of Type A–1, the Type A–1 was thought to have developed into Type A–2. The pairs which occurred tangentially at both sides of Type A–1 were thought to have transformed the Type A–1 into Type A–3. On the other hand, one or two epithelial initials which arised radially at a side of Type A–1 near the cambium were thought to have modified the Type A–1 into Type C–1. When such one or two initials arised radially at that side of Type A–1 and, in addition, the pair occurred tangentially at either side of it, the Type A–1 was thought to have become Type C–2. If the hypothesis mentioned above was true, only Type A–1 would, at first, exist in the cambial zone. After all, the six types of mass are considered to be made in the course of the formation of both normal and traumatic vertical canals.

In the formation of traumatic vertical canals as well as in that of normal ones, longitudinal divisions of epithelial initials invariably followed transverse divisions of them and also periclinal divisions nearly always followed anticlinal ones, furthermore, each of the initials once divided, as a rule, anticlinally into two smaller cells. Although epithelial initials which divided mitotically more than twice were much more frequently seen in the development of traumatic vertical canals than in that of normal ones, traumatic vertical canals might be ontogenetically similar to normal ones. Because the six types of mass were seen in the formation of both traumatic and normal vertical canals and moreover, the manner of divisions arising in the formation of the former was, early in the formative period, entirely comparable to

that arising in the formation of the latter. Traumatic vertical canals were anatomically different from normal ones in *Larix leptolepis*.[9] However the cause of formation of the former might be similar to that of the latter. The stimuli that caused the formation of normal vertical canals were so intense that traumatic vertical canals might have occurred in wood.

It was reported by many researchers that resin canals were formed schizogenously in coniferous woods.[1,2,6,7,8,13] In the present study, normal vertical canals were undoubtedly formed schizogenously, whereas traumatic ones might occur schizo-lysigenously. Epithelial initials which disintegrated into disorganized materials were supposed to be a few in number, but the lysigeny would probably arise in the course of the formation of typical traumatic canals. To explain whether typical traumatic canals are formed only schizogenously or shizo-lysigenously, it is necessary to investigate the development of typical ones using TEM.

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要　　約

樹脂道の存在は，重要な樹種識別拠点のひとつとして古くから注目されており，これらの形態観察は幾人もの研究者によって行なわれている。しかし，樹脂道の形成経過の詳細は *Pinus* で明らかにされているのみであり，正常樹脂道を持つ他の樹種 (*Larix, Picea, Pseudotsuga*) については，ほとんど知られていない。それ故今回は，カラマツ (*Larix leptolepis*) を用いて正常垂直樹脂道の形成経過を調査した。また，傷害垂直樹脂道の形成経過も観察し，正常樹脂道の場合と比較検討した。

1. エピセリウム細胞の始原細胞 (epithelial initials, 以下 E. I. と略記する。) は，形成後直ちに半径方向に拡張する為，木口面切片では，形成層の近辺ですでに他の形成層細胞から識別される。それら E. I. は，常に数個ずつ集まり細胞塊を形成する。本報告では，これら E. I. の集合は 6 種類に分けられた (Figs. 1-7)。Type A-1：2 半径列 (radial file) に 4 個の E. I. (1 列に 2 個ずつ) が存在する。Type A-2：3 半径列に 6 個の E. I. (1 列に 2 個ずつ) が存在する。Type A-3：4 半径列に 8 個の E. I. (1 列に 2 個ずつ) が存在する。Type B：1 半径列に 4 個の E. I. が存在する。Type C-1：2 半径列に 5 個 (1 列に 2 個，他列に 3 個) あるいは 6 個 (1 列に 3 個ずつ) の E. I. が存在する。Type C-2：3 半径列に 7 個 (隣接する 2 列に 2 個ずつ，他の 1 列に 3 個) あるいは 8 個 (隣接する 2 列に 3 個ずつ，他の 1 列に 2 個) の E. I. が存在する 。

2. 個々の E. I. は，木口面切片上では，通常一度垂層分裂を起こし 2 細胞になる。接線方向径の大きい E. I. は，時折り二度垂層分裂を起こし 3 細胞になるが，一方，接線径の小さい E. I. はまれに並層分裂を起こし 2 細胞になる。しかし，接線径の小さい E. I. は，ほとんどの場合分裂しなかった。また，二度以上分裂する E. I. の数は少なかった。

3. 最終的には，Type A-1 からは円形の小型の樹脂道 (Fig. 1) が，Type A-2 と Type A-3 からは接線方向にだ円形の樹脂道 (Figs. 2 と 3) が形成されるであろう。一方，Type B からは半径方向に細長い樹脂道 (Fig. 4) が，Type C-1 からは半径方向にだ円形の樹脂道 (Figs. 5 と 6) ができるであろう。さらに Type C-2 からは，円形の大型の樹脂道 (Fig. 7) が形成されると思われる。

4. 正常樹脂道は，多くの報告に記述されている様に，離生的な細胞分離により形成された。この分離は常に，E. I. の集合の中央部で最初に起こる。その後，Type A-1, Type A-2,

Type A-3 の場合は隣接する E.I. の接線壁間で分離が起こり，Type B, Type C-1, Type C-2 の場合はそれらの半径壁間で起こった。

5. 正常樹脂道形成時に観察された6種類の E.I. の集合が，傷害樹脂道形成時にも見られたが，前者に比べ後者の形成時には，Type A-2 と Type C-1 がより多く出現した。また，2半径列に7個の E.I. が存在する集合も見られ，さらには，5ないし8半径列に渡る大きな集合も多数見られた。これら大きな集合は，正常樹脂道形成時に観察された6種の集合の中の，異なるあるいは同種の2ないし3個の集合が結合して形成されたと考えられる。

6. 個々の E.I. は，正常樹脂道形成時に見られた様に木口面切片上では，通常一度垂層分裂を起こし2細胞になるが，傷害樹脂道形成時にはその後さらに分裂する細胞，すなわち，二回以上分裂する E.I. が頻繁に見られた。また，細胞分裂は様々な方向に起こり，この様にして形成された小型の細胞は，大概その後変形し，異形エピセリウム細胞になった。

7. 傷害樹脂道は，初期には，離生的に形成される。しかし，発達途上の傷害樹脂道中に，しばしば細胞の残骸が見つけられた。樹脂道中に孤立している細胞が，木口面切片で観察されており，これらが破壊すると思われる。*Larix leptolepis* では，傷害樹脂道は離破生的に形成されると考えられる。

Explanation of photographs

Photo 1. Five epithelial initials which increase in radial diameter are present in two neighboring radial files. In the cambial zone the initials are distinguished from other parenchyma cells which are still flattened tangentially. Two of the three initials in the right file (R) do not divide anticlinally.

Photo 2. Four epithelial initials formed only in a radial file (L) and six initials formed in two files (R). Each of the four initials divides anticlinally into two smaller cells.

Photo 3. Four epithelial initials present in two files, two ones each. Each of the initials once divides anticlinally into two smaller cells.

Photo 4. Five initials in two files. Three of the five initials are in the left file (L) and the other two are in the right file (R). A middle initial (m) in the left file does not divide anticlinally.

Photo 5. Six initials occurring in two files, three ones each. A middle initial (m) in the right file (R) does not divide anticlinally.

Photo 6. Six initials occurring in three files, two ones each. Each of the initials divides anticlinally into two cells.

Photo 7. Seven initials in three files. Four initials are in two neighboring files, two ones each, and the other three are in another file. Two initials in the middle narrow file (F) do not divide anticlinally. (p: axial parenchyma cells.)

Photo 8. Eight initials in three files. Six initials are in two neighboring files, three ones each, and the other two are in another file. Two middle initials (a and b) in the two neighboring files do not divide anticlinally. Especially the initial 'a' adjacent to one of a pair of initials in another file might never divide. A developing canal has a L-shape.

Photo 9. Eight initials present in four files (No. 1, 2, 3 and 4), two ones each. A large initial (a) in the wide file (3) twice divides anticlinally into three cells. A small initial (b) in the narrow file (4) divides periclinally into two.

Photo 10. A vertical canal enclosed with seven epithelial cells. Only an epithelial initial (a+b) divides anticlinally.

Photo 11. A vertical canal enclosed with ten epithelial cells which are originated from six initials. Two of the four smaller cells (e) in the file 1 become epithelial cells. The other two cells of the four (p) are thought to become axial parenchymatous cells. A cell (c) in the file 2 might differentiate into an epithelial cell.

Photo 12. A developing vertical canal in a radial section. Contents in epithelial cells are commonly put aside to a developing canal. The distance between transverse walls is various in both epithelial and axial parenchyma strands.

Photo 13. A vertical canal enclosed probably with six epithelial initials in two files (1 and 2). A parenchyma cell in the file 3, which divides anticlinally into two, would become small axial parenchymatous cells.

Photo 14. A transverse wall (t) of a cambial cell shown in a radial section. Transverse divisions were found in specimens which were obtained in a week after wounding.

Photo 15. Numerous epithelial initials produced in two weeks after wounding.

Photo 16. Seven initials in two files formed as a result of wounding. A middle initial (m) in the left file (L) divides obliquely into two cells.

Photo 17. A large mass of initials present in six files (No. 1–6). This mass consists of Type C–2 (files 1–3) and Type A–2 (files 4–6). A large initial in the wide file 5 twice divides anticlinally into three cells.

Photo 18. A vertical canal enclosed with six initials. Two of the three initials except a middle one in the left file (L) twice divide anticlinally into three cells. A smaller cell (a) of the two derived from an upper initial in the right file (R) divides obliquely into two. A lower initial (b) in the right file appears to divide fourth times. Two smaller cells (c and d) of the four derived from two middle initials, which face a vertical canal, divide again periclinally. The other two cells (e and f) would become axial parenchymatous cells (Parenchymatous cell I).

Photo 19. A large vertical canal formed as a result of wounding. Each of epithelial cells (a and b) has a semicircular projection facing a canal and four slender cells (c, d, e and f) jut into the canal. Large parenchyma cells (g, h and i) in the wide file (F) divide more than twice in various directions.

Photo 20. Cylindrical cells (c) situated on the border between Types C-2 (files 1-3) and A-2 (files 4-6). Three cells marked 'e' would become epithelial cells.

Photo 21. A traumatic vertical canal in course of development. Disorganized materials are shown in the canal.

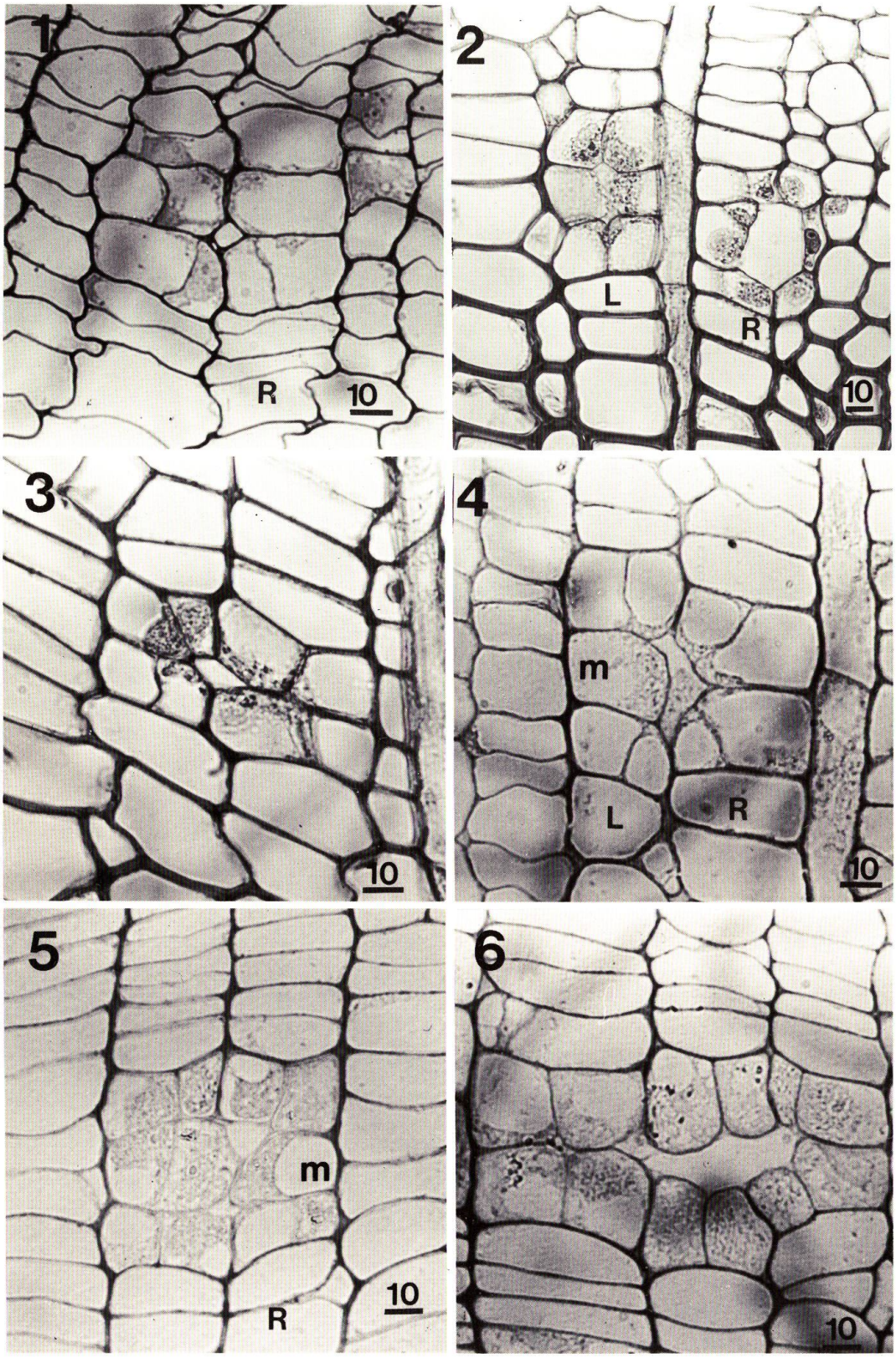
Photo 22. A traumatic vertical canal in course of development. An epithelial initial (e) detached from the initials around this canal is shown in the centre of the canal.

Photo 23. Traumatic vertical canals in early wood.

Photo 24. Traumatic vertical canals on an annual ring boundary.

Photo 25. A fusiform ray with tangentially expanded outline.

Photos 26 and 27. The expanded fusiform ray in **Photo 25** is transformed gradually, as shown in **Photo 26**, into an uniseriate ray shown in **Photo 27**.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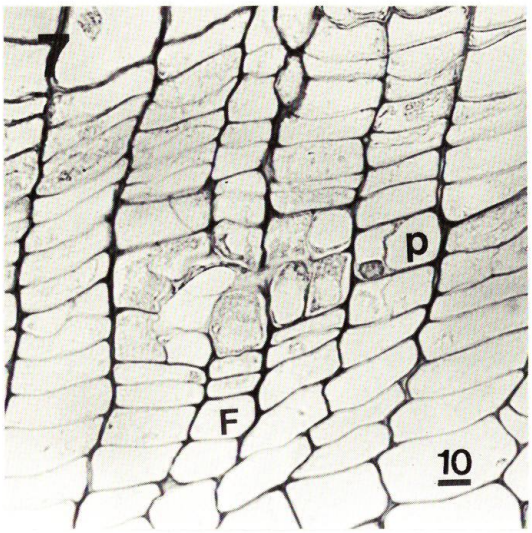
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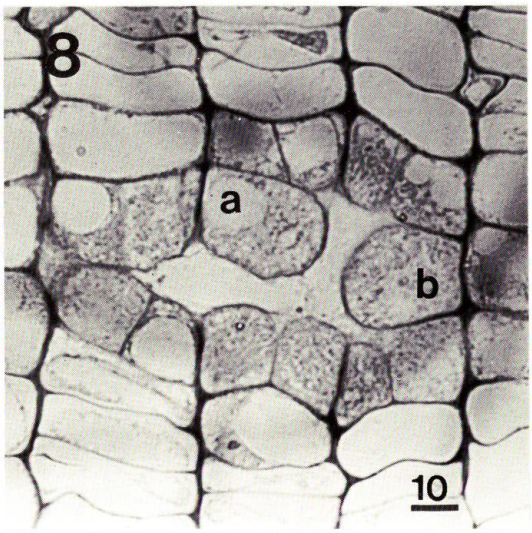
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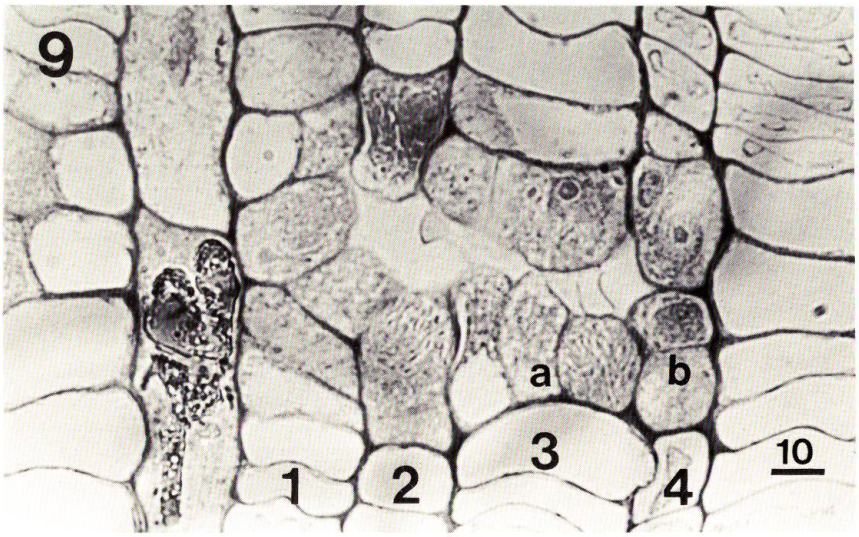
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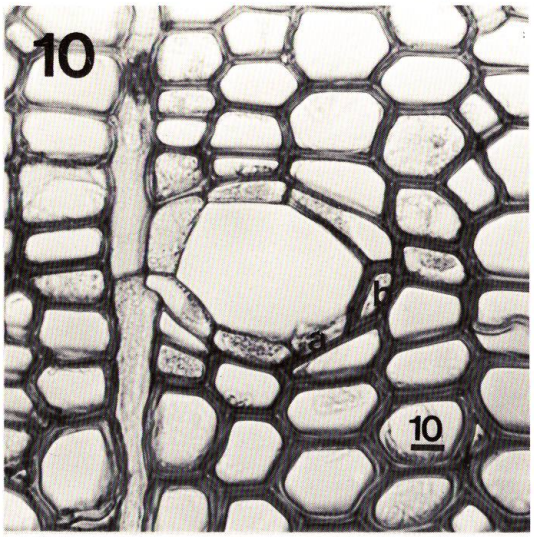
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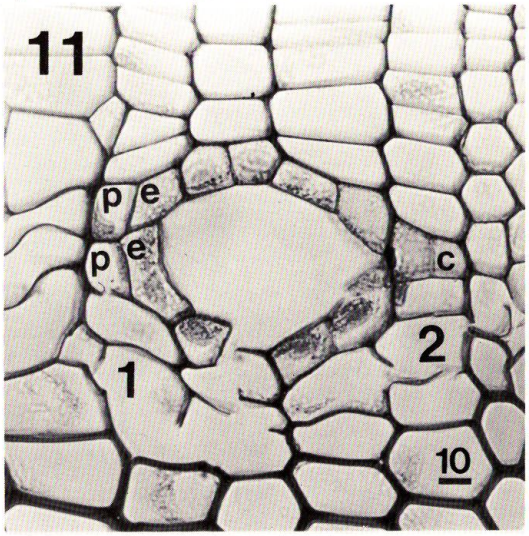
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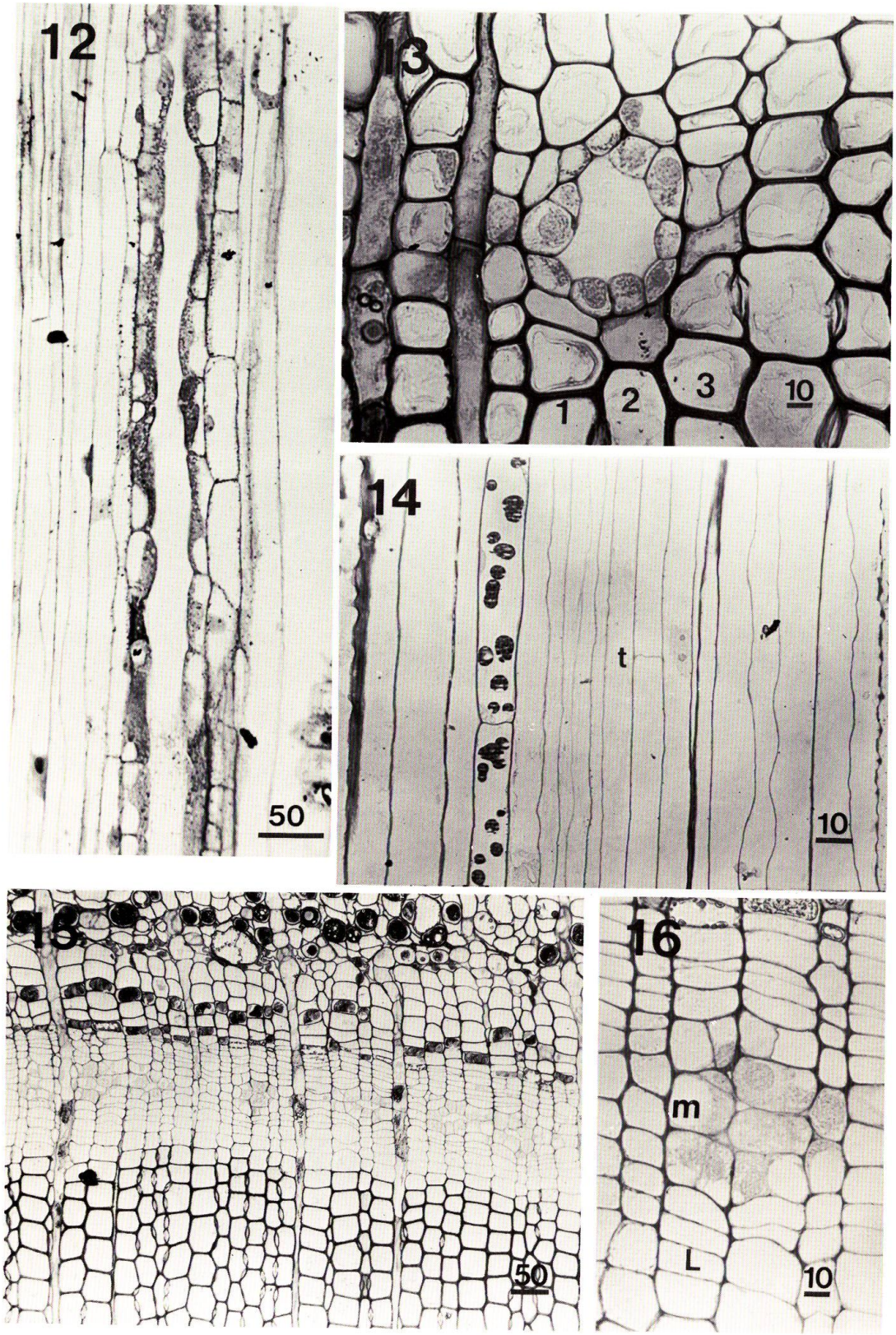
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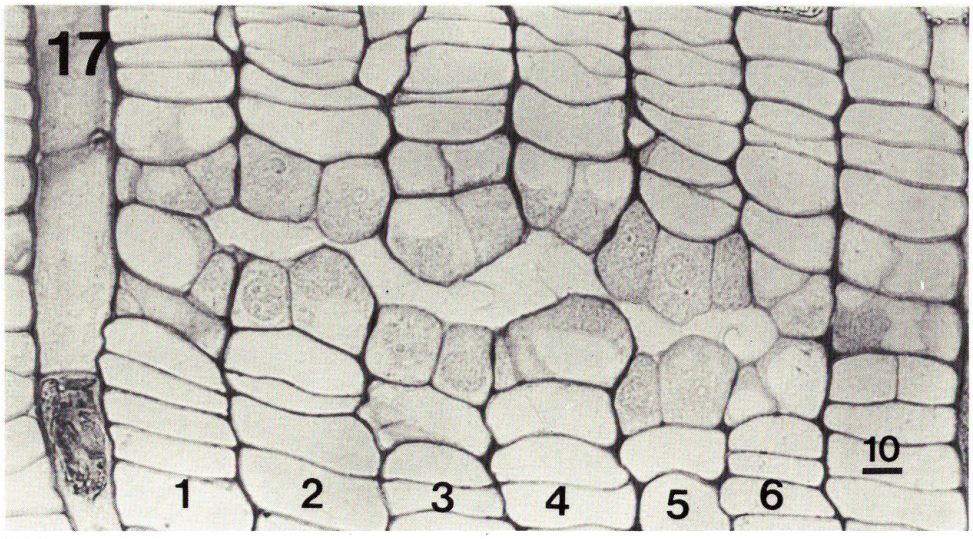
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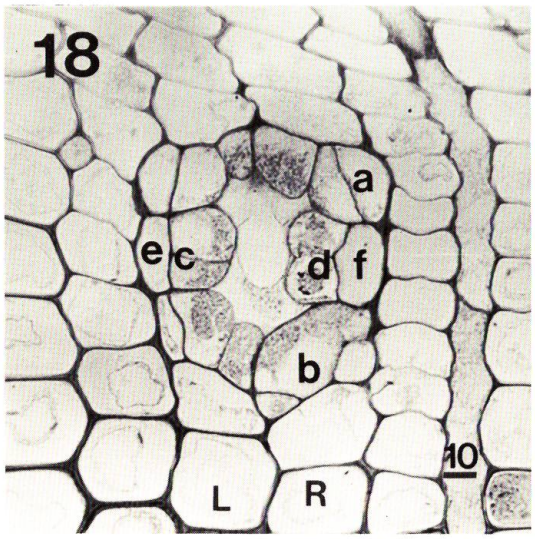
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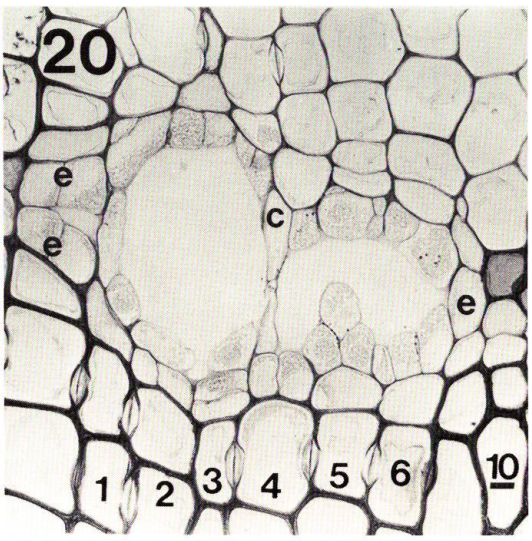
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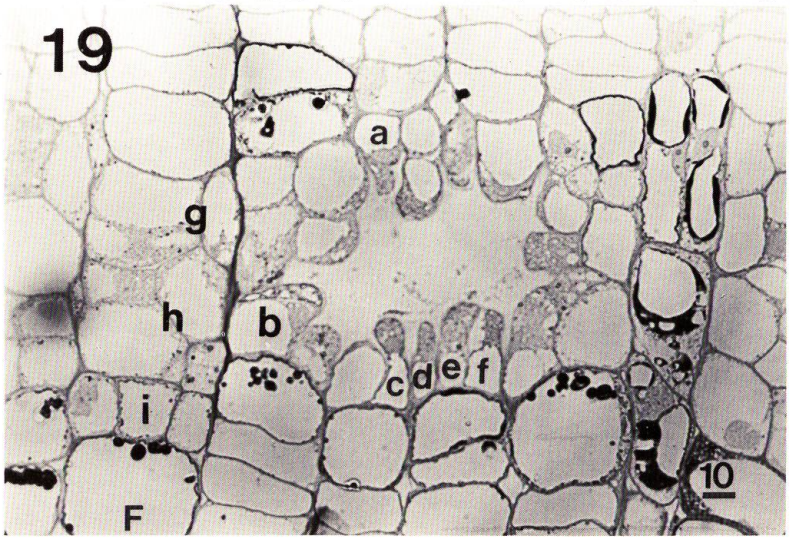
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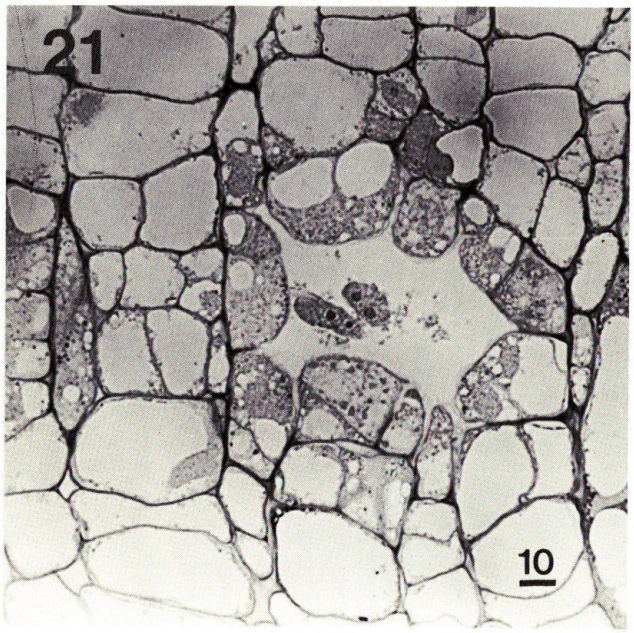
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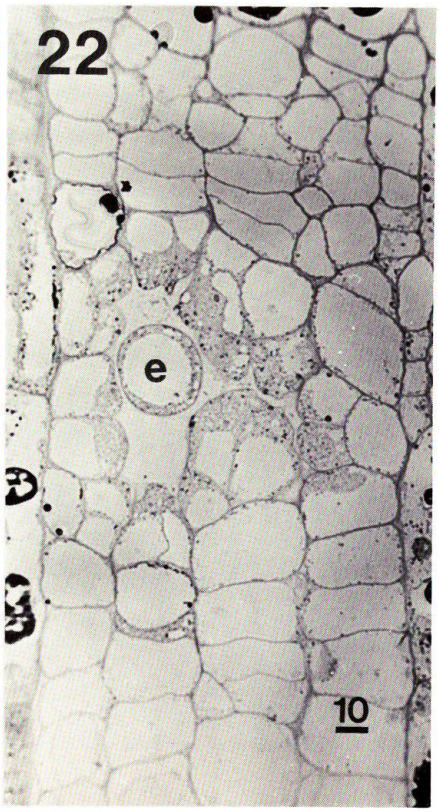
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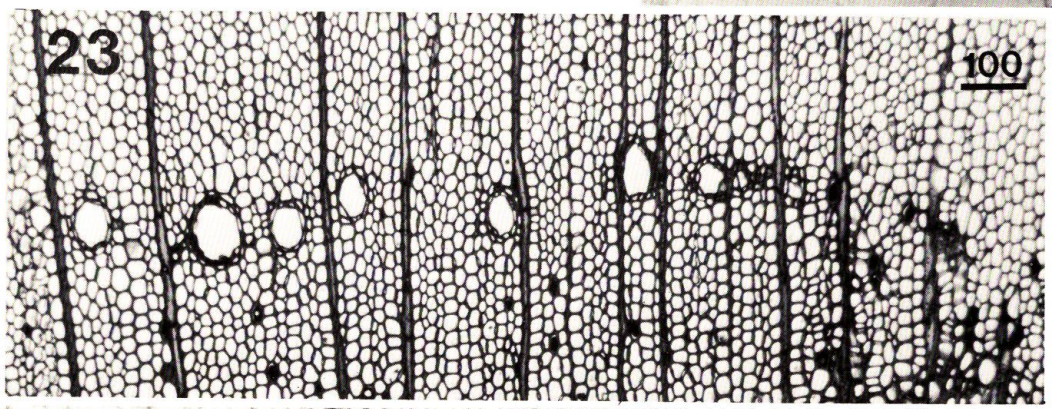
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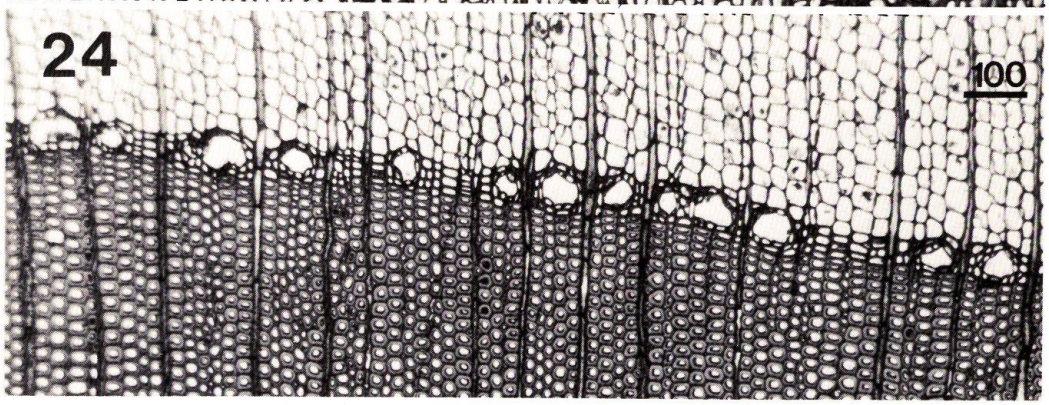
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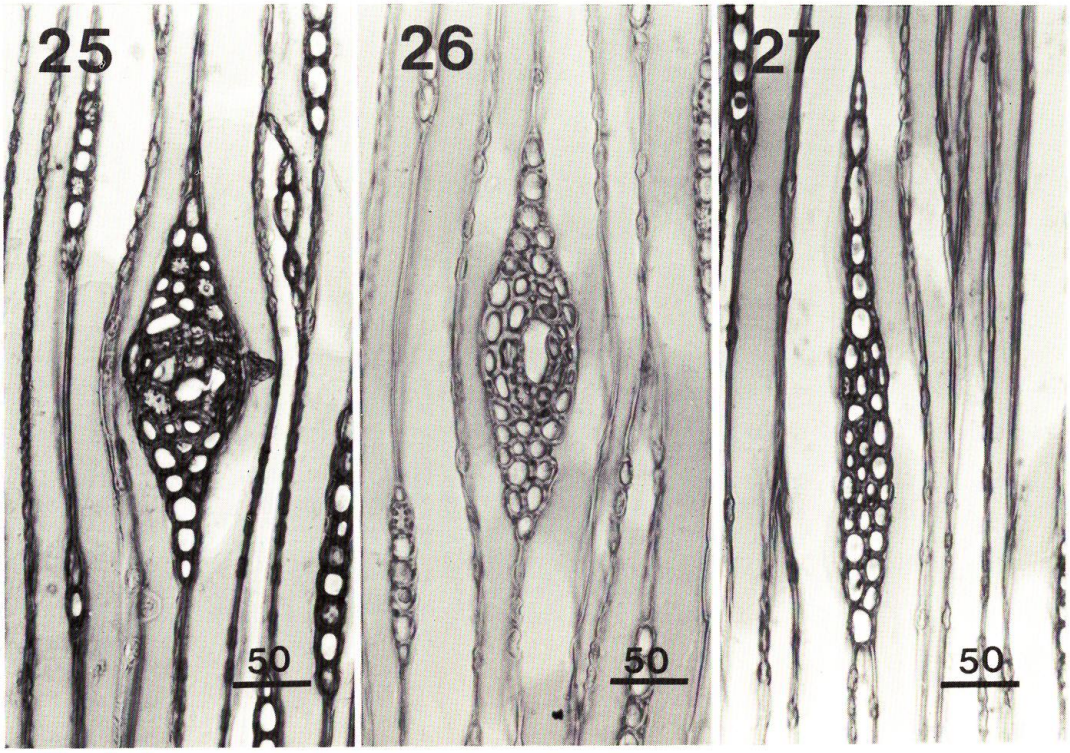
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