Resin Canals in the Wood of *Larix leptolepis* GORD. (III)
Morphology of Vertical Resin Canals in Compression Wood*

By

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カラマツ材 (*Larix leptolepis*) の樹脂道 (第3報)
あて材に存在する垂直樹脂道の形態*

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Contents

Introduction

The anatomical feature of compression wood in coniferous woods has been investigated by a large number of research workers for many years.[3,10] Their attention is mainly directed to axial tracheids which constitute over 90 percent of the volume of coniferous woods and which also exhibit a noticeable reaction to an angular displacement of tree trunks. The other elements (e.g., epithelial cells, ray parenchyma cells and ray tracheids, etc.) have attracted little attention,[10] hence few data concerning the occurrence and morphology of these elements in compression wood have been published till now.[2,7,9,10,11,14]

TIMELL reports that normal vertical resin canals appear to be somewhat less frequent in compression wood than in normal wood.[10] The frequency of horizontal resin canals is described as the same in normal and compression woods.[7] VERRALL

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reports that epithelial cells have thicker walls in compression wood than in normal wood.[11] YUMOTO et al. also observed expanded thick-walled cells in the epithelium of horizontal canals, in compression wood.[14] On the other hand, TIMELL describes epithelial cells in the epithelium of horizontal canals as similar in normal and compression woods of several species.[9]

The authors of the present paper have already observed the morphology of vertical resin canals in normal wood of Japanese larch (*Larix leptolepis* GORD.).[8] A vertical resin canal complex in Japanese larch is roughly divided into two layers of axial cells, namely, an inner layer and an outer layer. The former (i. e., the epithelium) consists of both thin- (ca. 0.5 microns) and thick-walled (ca. 5 microns) axial epithelial cells. The latter consists of two types of axial parenchymatous cell (i. e., Parenchymatous cell I and II) and strand tracheids. Thin-walled axial epithelial cells are much fewer than thick-walled axial ones. Irregular-shaped epithelial cells are found in the region where uniseriate rays pass through the middle of vertical canals and in the connecting parts between vertical and horizontal canals. Cylindrical epithelial cells are scarcely observed in the epithelium of vertical resin canals.

The aim of the present study is to investigate, using scanning electron microscopy, the morphology of a vertical resin canal complex which consists of epithelial cells, axial parenchymatous cells and strand tracheids in typical compression wood. In the present paper the results obtained from compression wood are compared with those from normal wood stated just above.

Materials and Methods

Materials for the present study were obtained from a larch tree which leaned over on a sloping ground. The tree (*Larix leptolepis* GORD.) was forty-seven years old, about 19 meters in height and 29 centimeters in breast height diameter, grown in a plantation in Tomakomai Experiment Forest, Hokkaido University. A cross-sectional view of the tree trunk exhibited an extreme eccentricity, and augmented growth increments (i. e., compression wood) were found on a lower side of the tree. A disc was cut from the tree at breast height. Compression wood was formed for twenty-five years or so, till the tree was felled down.

A large number of small specimens (R: 1 mm, T: 1 mm, L: 3 mm), which contained one or more vertical canals, were obtained from the outer part of each growth ring in sapwood of the disc. The specimens were dehydrated in a graded series of ethyl alcohol, after aspirated to avoid air bulbs for one or more days, subsequently embedded in methacrylate resin (n-butyl methacrylate : methyl methacrylate=6 : 4). After transverse surfaces of an embedded specimen were planed, a tangential or a radial surface of it was planed to the surface where the vertical canal was apparently observed, with glass knives on LKB Ultrotome 8800. The specimens finished were immersed in acetone or xylene alternatively for one or more weeks to remove the methacrylate resin, and dried in room conditions or by the crytical point drying method, subsequently coated with gold. Principally observations were made with a JSM-2 microscope at 15 kV.

Results and Discussion

Normal vertical resin canals were less frequent in compression wood than in normal wood. Most of them found in compression wood were present in the outer part of growth rings. That is, in compression wood as well as in normal wood normal vertical canals were formed late in the growth period. Normal vertical canals with small inside diameter were more frequently found in compression wood than in normal wood. Generally the small canals found in compression wood were present in the terminal zone of growth rings where depressed latewood tracheids were formed. In the present study traumatic vertical canals were not found in compression wood. All types of axial cell which constituted a vertical resin canal complex in normal wood were also observed in compression wood (Photos 1, 2 and 3).

The complex in normal wood sometimes lacks the outer layer, that is, the epithelium is sometimes adjacent to axial tracheids in the wood.[8] However the complex without the outer layer was more frequently observed in compression wood than in normal wood. The outer layer observed in compression wood, as well as that in normal wood,[8] was composed of slender axial parenchymatous cells (Parenchymatous cell I, P-1), large axial ones (Parenchymatous cell II, P-2) and strand tracheids (Photos 1 and 2). The two types of axial parenchymatous cell were less frequent in compression wood than in normal wood. In the case of P-1, it was more apparent. Strand tracheids appeared to be more frequent in compression wood than in normal wood. Therefore the proportion of strand tracheids to the axial parenchymatous cells (P-1 and P-2) was higher in compression wood than in normal wood. Strand tracheids next to axial tracheids with well developed spiral grooves were often lacking in spiral grooves (Photos 1 and 9). Sometimes an element of strand tracheids was also lacking in spiral grooves (Photo 9), though the other elements adjoining it had noticeable spiral grooves. In a tangential or a radial view, in compression wood (Photos 1, 2 and 9) as well as in normal wood all the three types of axial cell were rectangular. In a transverse view, in compression wood (Photo 3) as well as in normal wood P-1 was crescent, and both P-2 and strand tracheids were square. Thus the morphology of the three types of axial cell in compression wood was similar to that in normal wood.

The low proportion of the axial parenchymatous cells to strand tracheids was thought to be one of the anatomical characteristics of compression wood. LAMING states that strand tracheids may be regarded as transitional elements between epithelial cells or axial parenchyma cells and axial tracheids.[6] JEFFREY proposed that axial parenchyma elements were derived from modified tracheary cells.[4] We supposed that fusiform cambial cells which had been destined to differentiate into axial parenchymatous cells were modified into strand tracheids. In order to clarify the question mentioned above, it is necessary that the process of the formation of vertical canal complex is investigated. The outline of the three types of axial cell, in a transverse and a longitudinal view, can be also observed at the optical microscopic level. The number of them should be measured under the optical microscope. Therefore we will make the detailed study on the morphology of vertical canals in compression wood using optical microscopy.

In compression wood as well as in normal wood, the inner layer (i. e., the epithelium) was an epithelial cell thick and partly two epithelial cells thick, and was composed of thin- and thick-walled axial epithelial cells. Thin-walled axial epithelial cells (ca. 0.5 microns) in compression wood (Photo 4), as well as those in normal wood,[8] were contiguous to thick-walled axial ones (ca. 5 microns). Bridge-like thin-walled cells in the epithelium of vertical canals (Photo 5) were found beside the penetrating rays (i. e., rays which penetrate the middle of vertical canals and split them into two channels temporarily[8]), and both large axial epithelial cells with thin wall (Photo 6) and cylindrical ray epithelial cells (i. e., ones lining horizontal canals) with thin wall (Photo 7) were found in the connecting parts between vertical and horizontal canals, in compression wood as well as in normal wood.

The proportion of thin-walled axial epithelial cells to the total number of epithelial cells in normal wood is lowest in *Larix* (10 percent or less), in the Pineae that consists of *Larix, Pseudotsuga, Picea* and *Pinus*.[1] In the present study thin-walled axial ones were fewer in number in compression wood than in normal wood ; thin-walled axial ones were scarcely observed in compression wood. Axial epithelial cells with relatively thin wall (ca. 1 micron), which were not found in normal wood, sometimes occurred in compression wood (Photo 8). The structural difference between thin-walled and relatively thin-walled axial epithelial cells is not yet evident. In a transverse view, axial epithelial cells with thick wall were flat or crescent in normal wood,[8] while many of them had an expanded outline in compression wood (cf., Photo 3). In a tangential or a radial plane, most of axial ones with thick wall had a rectangular outline and an even surface in normal wood,[8] whereas many of them did not have a rectangular outline and had an uneven surface in compression wood (Photo 9). A thick-walled axial epithelial cell with a projection, which was not found in normal wood, sometimes occurred in compression wood (Photo 10). The large axial epithelial cells in the connecting part in sapwood of normal wood were thin-walled,[8] whereas many of them in sapwood of compression wood were thick-walled.

A large number of thin-walled ray epithelial cells whose thickness was about 0.5 microns were observed in the epithelium of horizontal canals in normal wood,[8] whereas those observed in compression wood were not numerous (cf., Photo 6).

Cylindrical epithelial cells and stretchings of epithelial cells in the epithelium of vertical canals were scarcely found in normal wood,[8] while they were found frequently in compression wood (Photos 11–16). In the present paper, a cylinder (Photos 11–14) denotes the one that traverses a vertical canal radially and that is composed of one or more axial epithelial cells, while a stretching (Photos 15 and 16) denotes the one that obliquely traverses a vertical canal radially or tangentially and that is formed by the elongation of a part of an axial epithelial cell or rarely by that of an axial one itself. The tangentially transverse cylinders were not found in the present study. Most of the cylinders were found beside the penetrating rays. The thin-walled cylinders were scarcely observed in compression wood (Photo 11). The diameter of the cylinders was various (cf., Photo 11). Sometimes the hollow bridge-like cylinder was found, though might not traverse a vertical canal radially (Photo 12). The cylinder in compression wood was composed not only of an axial epithelial cell (Photo 13) but also of two axial ones (Photo 14). In Photo 14 a transverse wall is shown in the middle of the cylinder (an arrow). It is not evident what percentage of the cylinders is composed of two or more axial epithelial cells. The oblique stretchings, which were thin-walled (Photo 15) or thick-walled (Photo 16), traversed vertical canals radially or tangentially. The thin-walled stretchings appeared to be fewer in number than the thick-walled ones in compression wood.

The low proportion of thin-walled axial epithelial cells to the total number of axial ones was thought to be one of the anatomical characteristics of compression wood. Axial epithelial cells might be thickened and lignified more quickly in compression wood than in normal wood. Most of axial ones in compression wood would be thickened and lignified during the first year. In order to accurately calculate the percentage of thin-walled axial ones, it is necessary that the study with a large amount of material is made at the optical microscopic level. The high proportion of irregular-shaped axial epithelial cells to usual axial ones would also be one of the anatomical characteristics of compression wood. Resin canals arise by a schizogenous separation which occurs in the center of the mass of parenchyma cells (i. e., future epithelial cells).[1,13] The stretching of the epithelial cells across the vertical canal is reported to be formed in *Picea canadensis*[1] and in *Pinus elliottii* ENGELM[5] when they have not entirely separated from each other but have maintained contact at one or more points. While having an uneven surface and having contact at one or more points to each other after the schizogenous separation had begun, many of axial epithelial cells were supposed to be thickened and lignified in compression wood. Therefore irregular-shaped axial epithelial cells were thought to be often formed in compression wood.

Whether the cylinder consists of one or more axial epithelial cells is thought to depend on the sizes of axial ones. Thick-walled axial epithelial cells are approximately uniform in size in normal wood.[8] Since the cylinder was occasionally composed of two axial ones, small axial ones might more frequently occur in compression wood than in normal wood. WARDROP and DADSWELL conclude that short tracheids in compression wood are a consequence of the high rate of anticlinal divisions in the cambial zone of this tissue.[12] Axial parenchyma cells, namely, future axial epithelial cells in compression wood might also have the high rate of cell divisions in the cambial zone.

All the cylinders observed in the present study traversed vertical canals radially. The tangentially transverse cylinders were not found. The presence of the radially transverse cylinders is thought to suggest that axial epithelial cells separate radially from one another. It is probable that the schizogenous separation of axial epithelial cells from one another principally occurs between their tangential walls.

Conclusions

In comparison with the morphology of vertical resin canals in normal wood, those in compression wood have various anatomical characteristics: (1) small number of vertical canals; (2) frequent occurrence of the small vertical canals; (3) frequent absence of the axial parenchymatous cells; (4) low proportion of thin-walled axial epithelial cells; (5) high proportion of the irregular-shaped axial epithelial cells. Considered from the characteristics mentioned above, the morphology of vertical resin canals would be apparently influenced by the stimulus of the inclination of tree trunks.

In the present paper various questions are brought out. Considered from the first, second and third results, in compression wood axial parenchymatous cells are thought to decrease in number. Especially the third one is supposed to indicate the modification of axial parenchyma cells into strand tracheids. Considered from the fourth result, the thickening and lignification of axial epithelial cells might occur more quickly in compression wood than in normal wood. The cause of the fifth result is supposed to be the incomplete separation of axial epithelial cells and the unnatural thickening and lignification of them. Furthermore, the absence of the tangentially transverse cylinders is thought to indicate that the main direction of the schizogenous separation is radial. In order to clarify the questions mentioned above, we will study further the morphology of vertical canals and the process of the formation of them and so on, in compression wood as well as in normal wood.

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要　　約

針葉樹あて材の研究は，材の90％以上を構成し，幹の傾斜に対して顕著な反応を示す仮道管を対象にして古くから行なわれているが，他の材構成要素を対象とした研究は，ほとんどない。本研究の目的は，傾斜したカラマツ (*Larix leptolepis* GROD.) を供試木とし，その典型的なあて材に存在する垂直樹脂道 (Resin Canal Complex) の形態を，SEM を用いて観察することである。得られた結果は以下の通りである。

1. 垂直樹脂道数は，正常材に比べ，あて材ではかなり少ない。

2. あて材では，成長輪の最終部（へん平な晩材仮道管が存在する部分）に，内径の小さい垂直樹脂道が見られた。

3. Complex を構成する軸方向柔細胞は，正常材よりもあて材において少ない。またストランド仮道管はやや多い。

4. 正常材における薄壁の軸方向エピセリウム細胞の出現率は，正常樹脂道を持つ針葉樹の中では *Larix* が一番低いが，あて材においてはさらに低く観察数は極めて少なかった。

5. 正常材ではまれにしか観察されなかった特異な形態をした軸方向エピセリウム細胞（表面に凹凸のあるもの，円筒状のものなど）が，あて材ではひん繁に観察された。また，あて材において最も特徴的な円筒状のエピセリウム細胞は，すべて半径方向に垂直樹脂道を横断していた。

Explanation of photographs

Note: All the photographs were taken from specimens in compression wood. The specimens were obtained from the outer part of growth rings in sapwood. **V**: vertical resin canals. **H**: horizontal resin canals. **R**: rays.

Photo 1. Vertical resin canal complex. The epithelium is an epithelial cell thick and partly two epithelial cells thick. A strand tracheid on the left side of a vertical canal does not have noticeable spiral grooves. 2: Parenchymatous cell II. st: strand tracheids (rectangular outline). Tangential view.

Photo 2. Vertical resin canal complex. The epithelium is an epithelial cell thick on both sides of a vertical canal. 1: Parenchymatous cell I (rectangular outline). 2: Parenchymatous cell II (rectangular outline). Tangential view.

Photo 3. Thick-walled axial epithelial cells with an expanded outline (e) and a thin-walled axial one (t) are shown. 1: Parenchymatous cell I (crescent outline). 2: Parenchymatous cell II (square outline). Transverse view.

Photo 4. A thin-walled axial epithelial cell which is contiguous to a thick-walled axial one. Tangential view.

Photo 5. Bridge-like axial epithelial cells with thin wall (b) and an axial one with expanded thick wall (e) are shown. Tangential view.

Photo 6. Thin-walled ray epithelial cells (r) and a large axial epithelial cell with relatively thin wall (a) are shown. Tangential view.

Photo 7. Cylindrical ray epithelial cells with thin wall (r) are shown. Radial view.

Photo 8. Axial epithelial cells with relatively thin wall (e). Radial view.

Photo 9. Thick-walled axial epithelial cells without a rectangular outline and with an uneven surface (e), and an element of a strand tracheid (st) without noticeable spiral grooves are shown. Tangential view.

Photo 10. Thick-walled axial epithelial cells with a projection. "P" denotes a projection. Radial view.

Photo 11. Cylindrical axial epithelial cells. A slender cylinder with thin wall (c_1) and a big one with thick wall (c_2) are shown. Radial view.

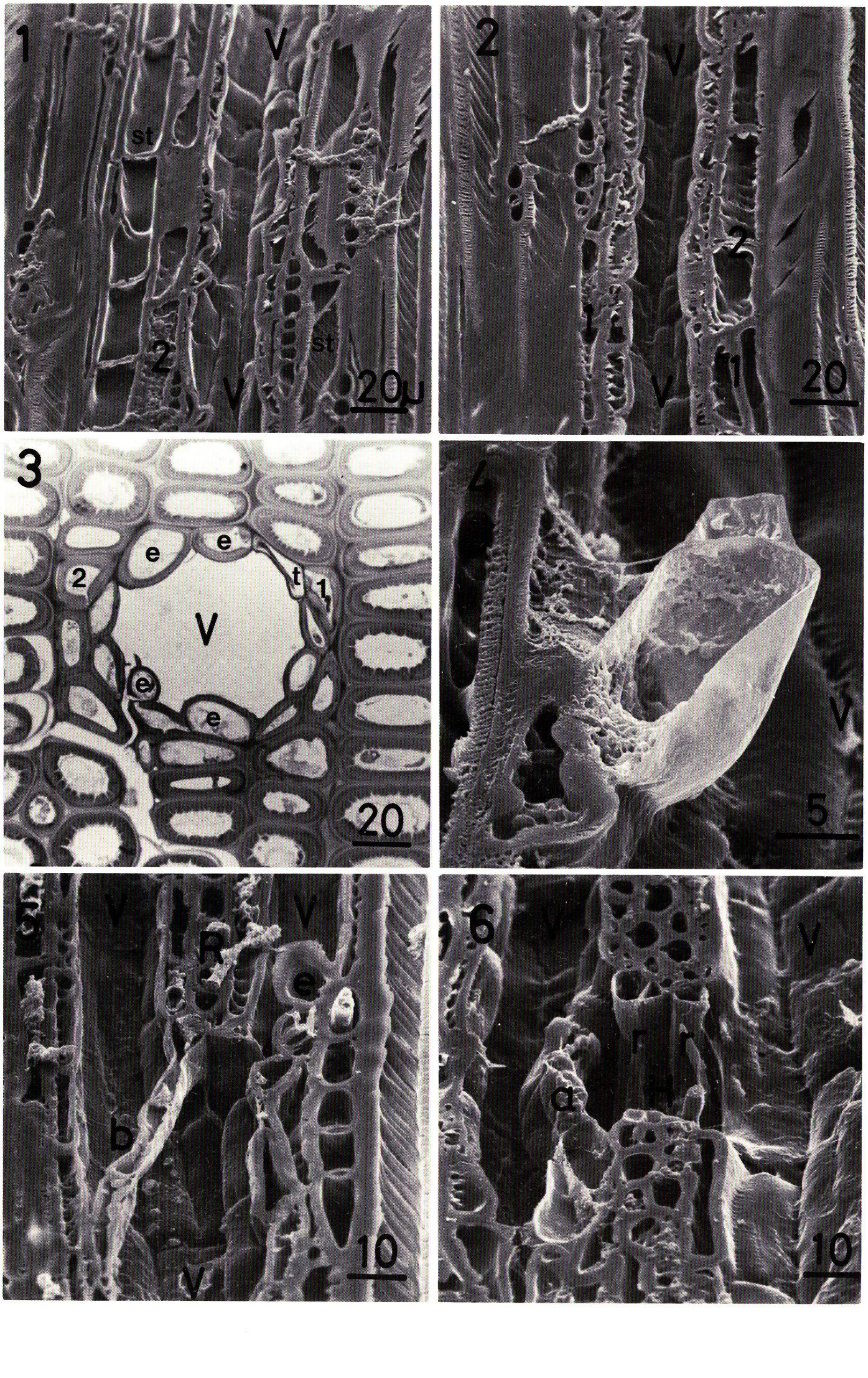
Photo 12. A hollow bridge-like cylinder with thick wall (h) is shown. Tangential view.

Photo 13. A cylinder in the epithelium of a vertical canal (c) is composed of an axial epithelial cell. Radial view.

Photo 14. A cylinder in the epithelium of a vertical canal (c) is composed of two axial epithelial cells. A transverse wall is shown in the middle of the cylinder (an arrow). Radial view.

Photo 15. A tangentially oblique stretching with thin wall (s) is shown. Tangential view.

Photo 16. Tangentially oblique stretchings with thick wall (s) are shown. Tangential view.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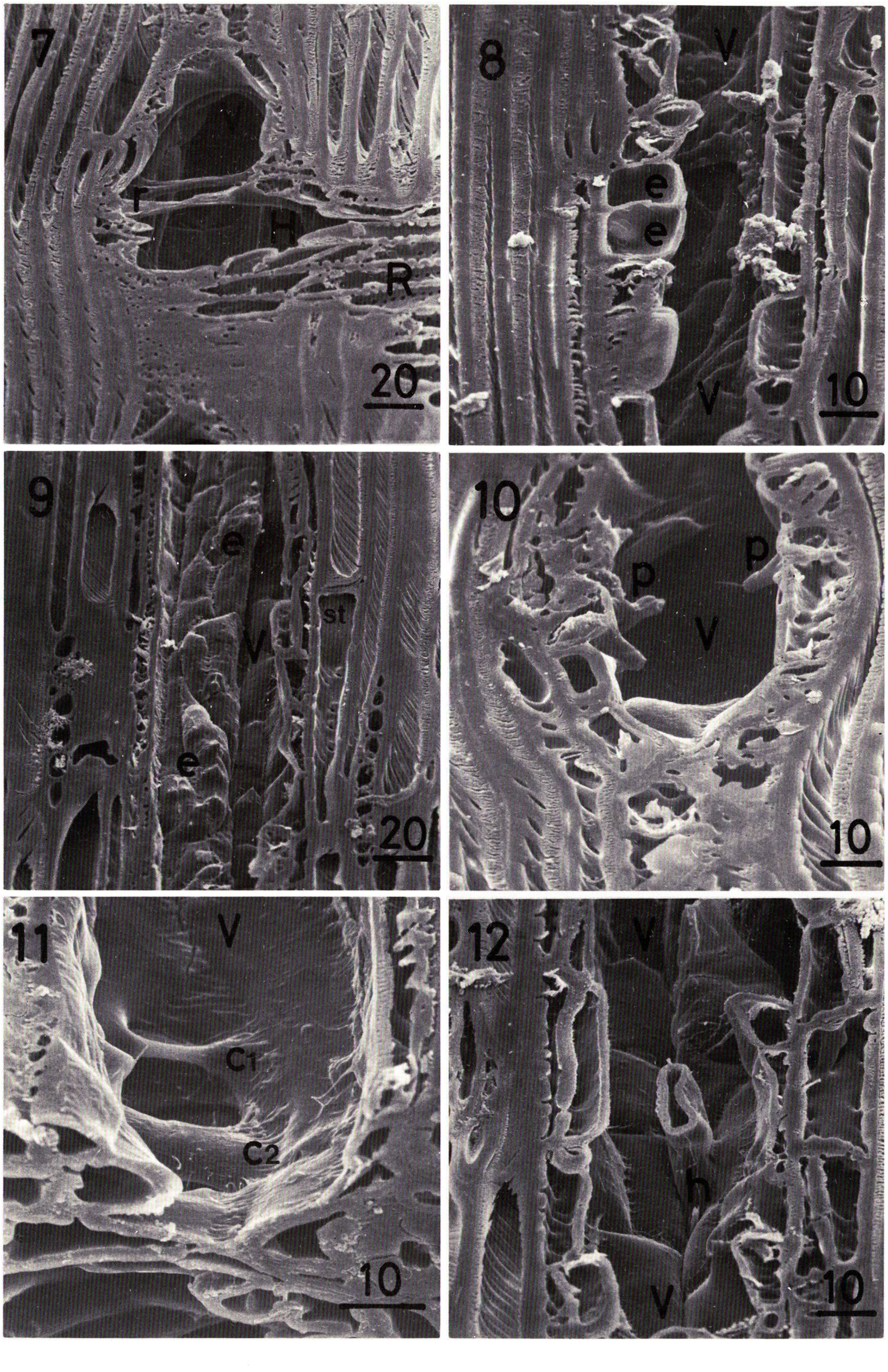
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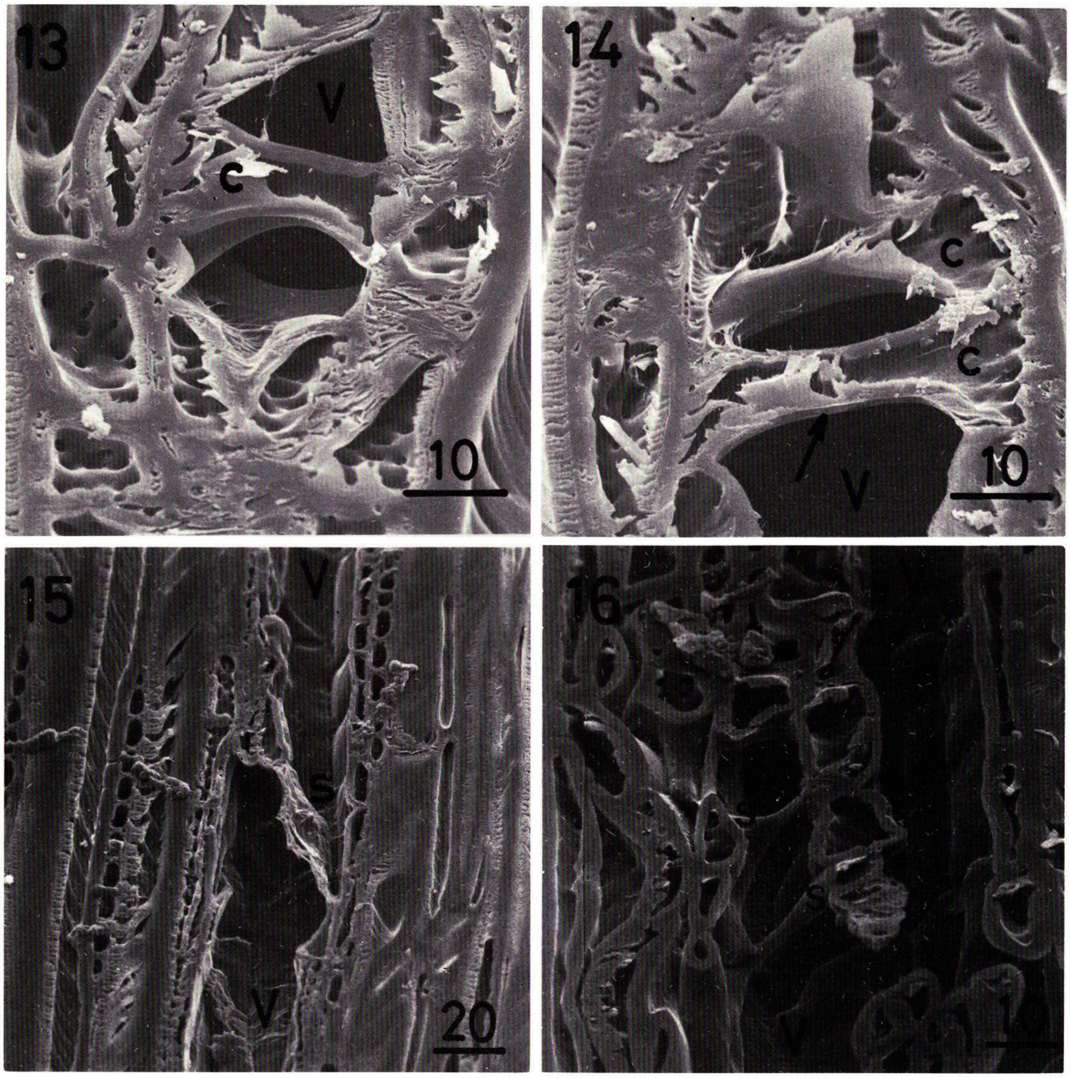
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