COMPONENTS OF VASCULAR TISSUE IN THE CORM OF *ISOETES TAIWANENSIS*

by

Su-Hwa Tsai Chiang & Shu-Yu Chen*

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ABSTRACT

Three cell types, tracheid, sieve cell and parenchyma are recognized in the vascular tissue of the corm of *Isoetes taiwanensis* Devol. The cambium gives rise to several layers of phloem cells, alternating with several layers of xylem cells. The earliest cambial derivatives are phloem cells. Phloem is composed of sieve cells only with sieve areas uniformly distributed on both radial and transverse walls, whereas xylem consists of mainly the parenchyma and small amount of tracheids scattering among parenchyma. One, occasionally two tubular bridges (termed sieve trabeculae) lying radially across the cell lumen of sieve cell are recognized.

INTRODUCTION

The corm of the genus *Isoetes* has long been the subject of structural and developmental studies. The anatomical literature on the corm has been made as early as 1845 by Von Mohl, and has past through the investigations of many workers (Yang, Chiang and Devol, 1975, and their citation). The secondary vascular tissue of the corm, in fact, has received the greatest interest among the earlier workers (Russow, 1872; Scott and Hill, 1900; Stokey, 1909; Weber, 1922; West and Takeda,1915; Yang et al, 1975). Various interpretations on the pattern of the localization of xylem and phloem within the secondary vascular tissue has been presented by these workers. A rather detailed study on the distribution-pattern of cell types in the secondary vascular tissue of *I. howellii* was provided by Paolillo (1963).

Although occasional reports are made on results from electron microscopy (Kruatrachue and Evert, 1974; 1977), most of these studies refer to entirely on optical microscopical level. The improvement of the trasmission electron microscope (TEM) reveals the ultrastructure of various organelles, whereas the scanning electron microscope (SEM) shows and makes the outline as well as the entire intercellular association of the given tissue more evident. The previous reports have mentioned the general structure of the various cells in the vascular tissue of the corm of *I. taiwanensis* merely on the optical microscopic (O M) level (Chiang, 1976; Yang et al, 1975). The present report shows the peculiar distribution-pattern of cell types in the secondary vascular tissue of the corm of *I. taiwanensis* as seen under SEM; contrasts them with that observed under OM in our previous work, and other species by the earlier workers.

The most important purpose is to correct the previous descriptions concerning the wall thickening of tracheid.

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* (江蔡淑華和陳淑宇) , Department of Botany,National Taiwan University, Taipei, Taiwan, ROC

MATERIALS AND METHODS

Corm segments of *Isoetes taiwanensis* DeVol were obtained from greenhouse, fixed in FPA (formalin-propionic acid-50% ethanol), dehydrated in TBA (teriary butanol-ethanol) series, embedded in paraffin, sectioned with a rotary microtome at 20, 30 and 50 μm (Johansen, 1940). The sections were mounted on glass cover slips with albumin. After removing the paraffin they were coated with gold on the stubs. Photographs were taken with Hitachi S-550 SEM.

RESULTS

Primary vascular tissue:

There are two types of cells in the lacunated primary xylem core. They are parenchyma and tracheids. Most of the parenchyma are irregular in shape and some of them are crushed (Figs, 1,2,4,5). Nuclei are visible in some of them. The secondary thickening of the tracheid ranges from annular to helical, most of them are helical (Figs. 4,5). Some of the individual annular walls do not form a continuous ring but become interrupted or curved inward the cell lumen.

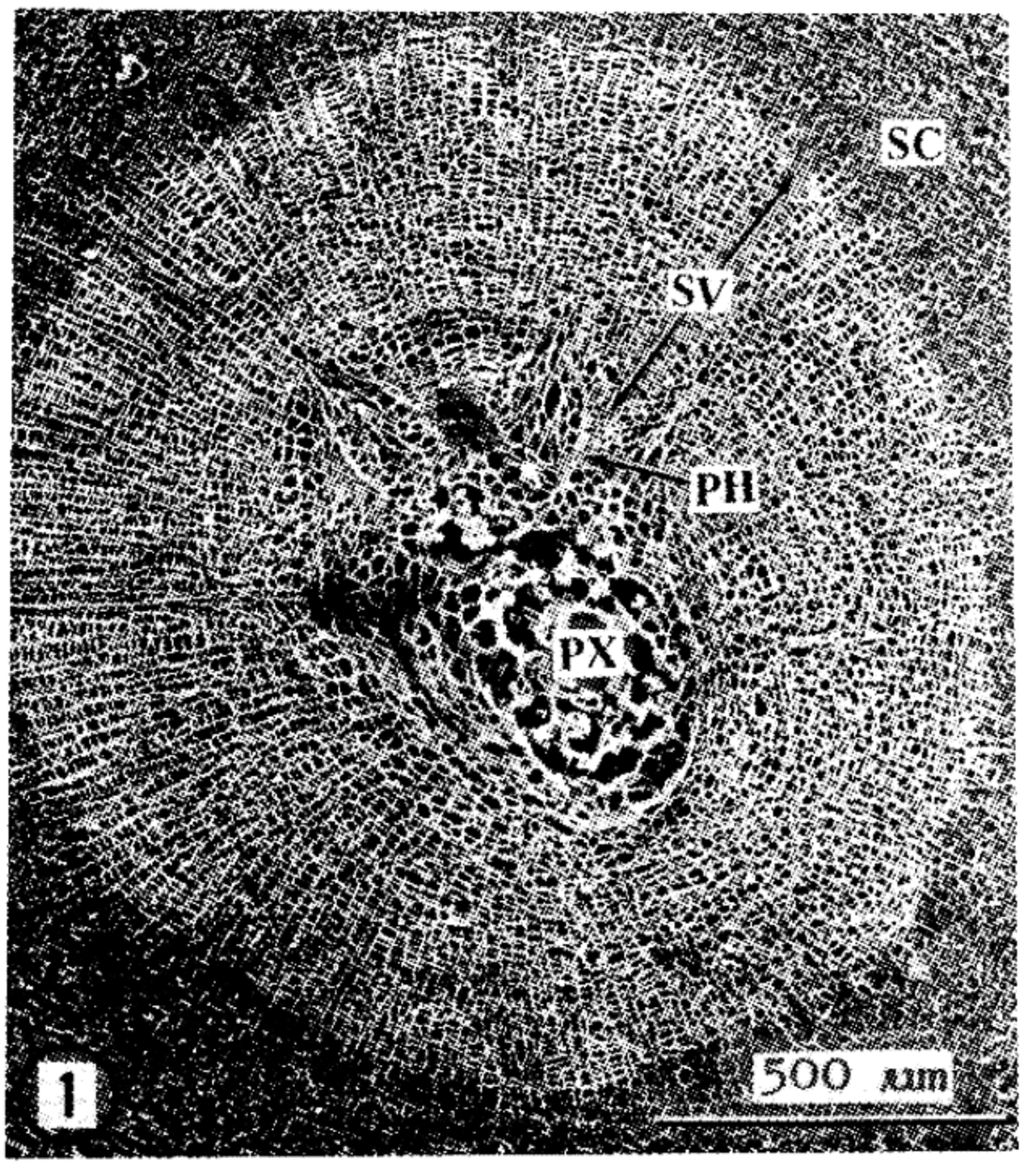
The primary phloem (phloem mantle) is interrupted by the leaf- or root-traces, and always appears as triangulate in transection (Figs. 1,2). It is composed of sieve cells only except the boundary region of this tissue ((Fig. 3). The occurrence and the morphology of the sieve area are almost the same as those in the secondary phloem except the cell size. The cell is smaller than that in the secondary phloem. The cell morphology will be described in the following section.

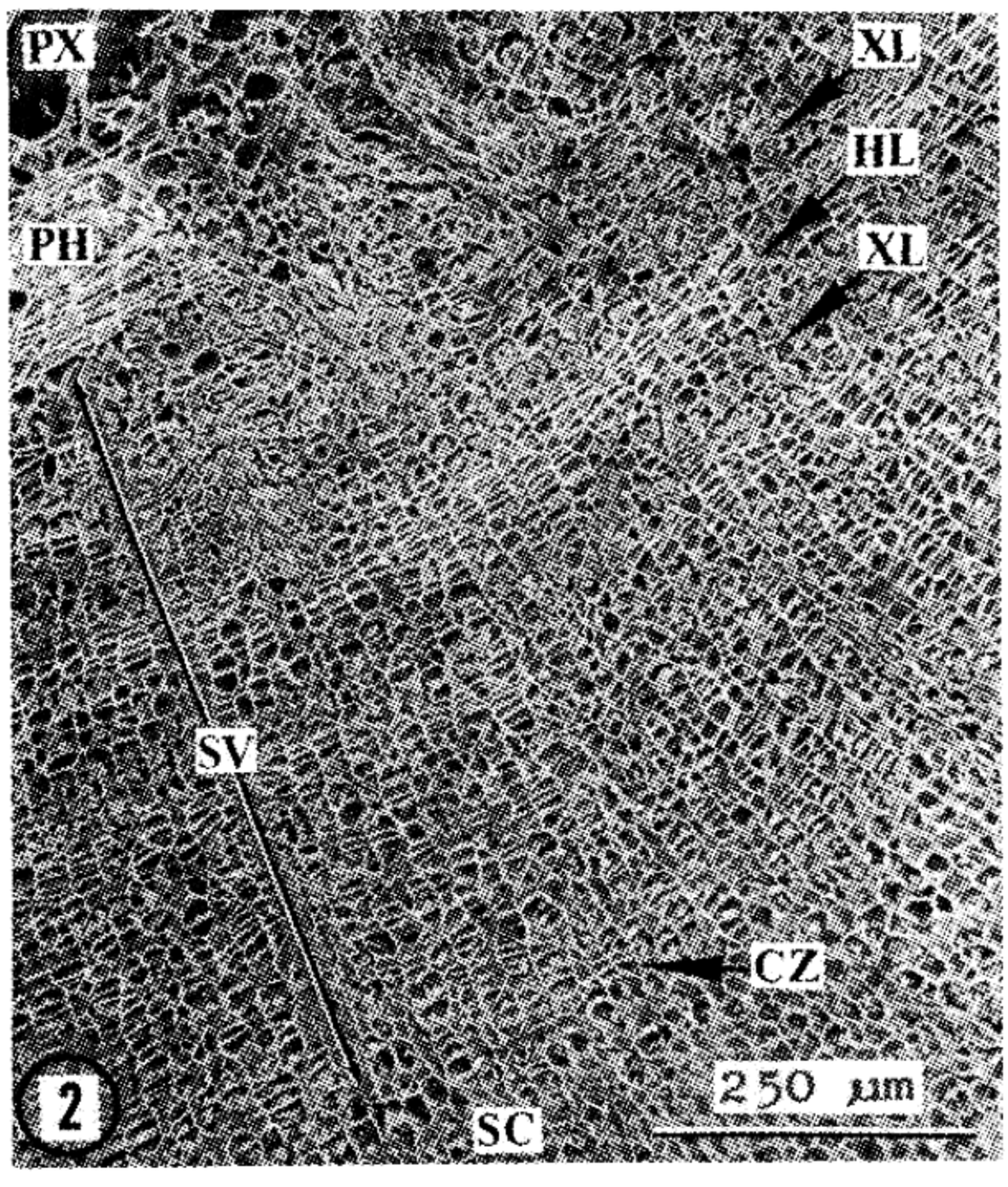
Seoondary vascular tissue:

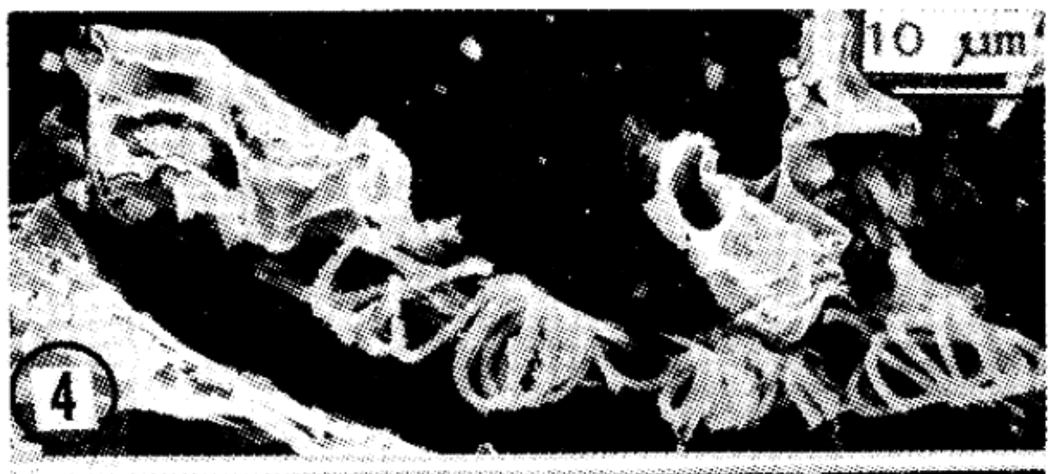
The cambium gives rise externally to the parenchyma only which form the secondary cortex (Figs. 6,7). The cortical parenchyma are filled with starch and appear to be more round as compared with the internal derivatives of the cambial calls (Figs. 8,9). The outline of the internal derivatives of cambium are flat in radial and transverse views, and are pentagonal or hexagonal in tangential view. They finally become secondary vascular tissue (prismatic layer). The early internal derivatives of the cambium are phloem cells. The cambium produces layers of phloem cells alternating with layers of xylem cells (Figs. 2,10,12). They are designated as phloem zone (or phloem layer) and xylem zone (or xylem layer) respectively in the present report. The alternating pattern of the phloem zone and the xylem zone is more conspicuous in larger corm.

Cells in xylem zone:

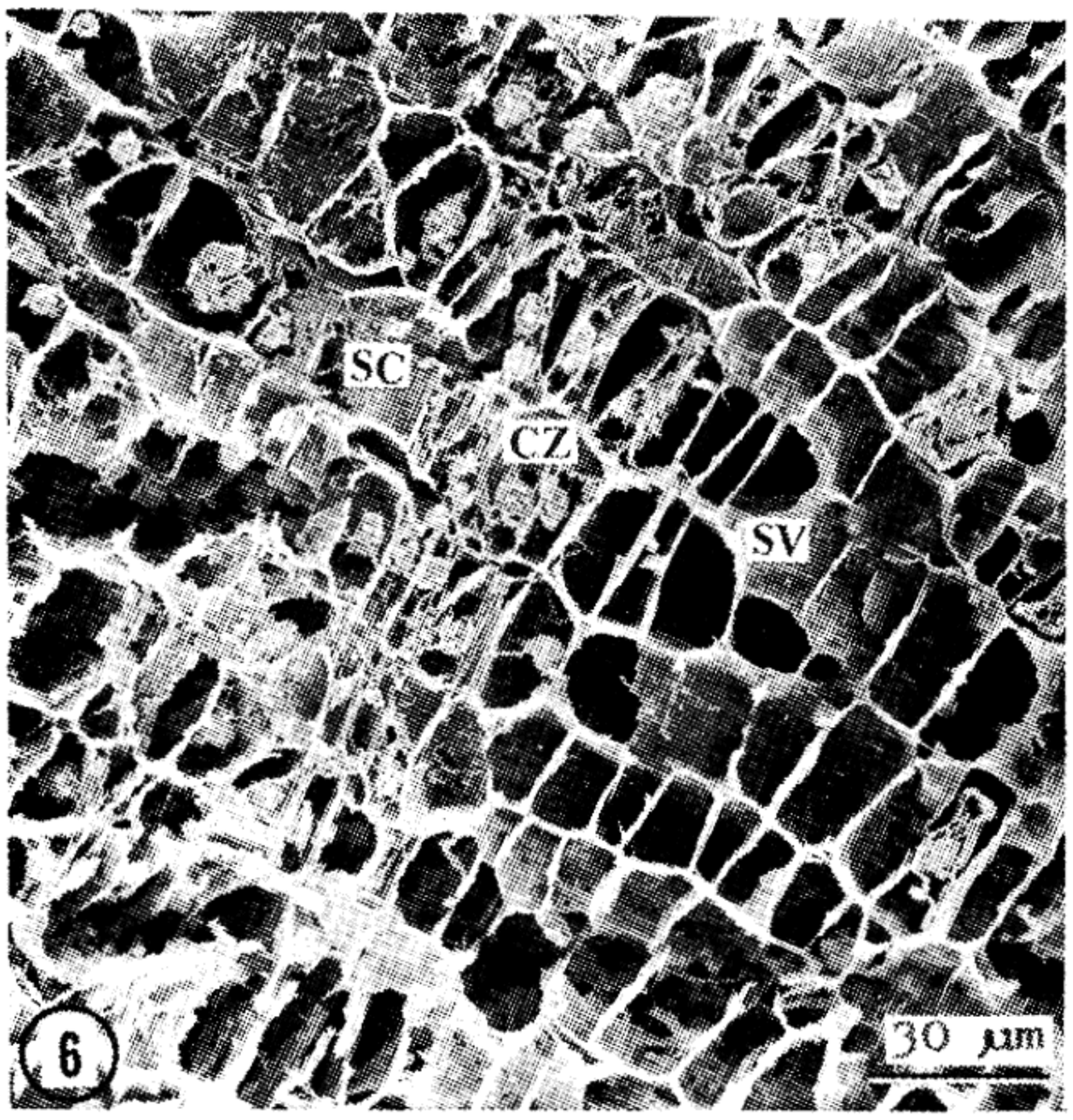
The xylem zone is composed of parenchyma and tracheids. The cell number of parenchyma is extensively more numerous that than of tracheid. The larger corms always contain more tracheids in the xylem zone than the small corms, some of which have no tracheids at all. The parenchyma are always larger than the tracheids in cell size. The nucleus is evident in parenchyma. The cell contents in parenchyma are scanty in some cells but denser in some others (Figs. 10,11,12). No tracheids have been seen located immediately next to the sieve cells. All the tracheids found are bordered with either parenchyma or tracheids. The tracheids are empty and highly variable in size, shape and the pattern of secondary thickening. Two kinds of the tracheids can be recognized according to the size and shape of the cell: (1) large and prismatic tracheid (Fig. 29-a,b,c); and (2) small and slender tracheid (Fig. 29-d). The large and

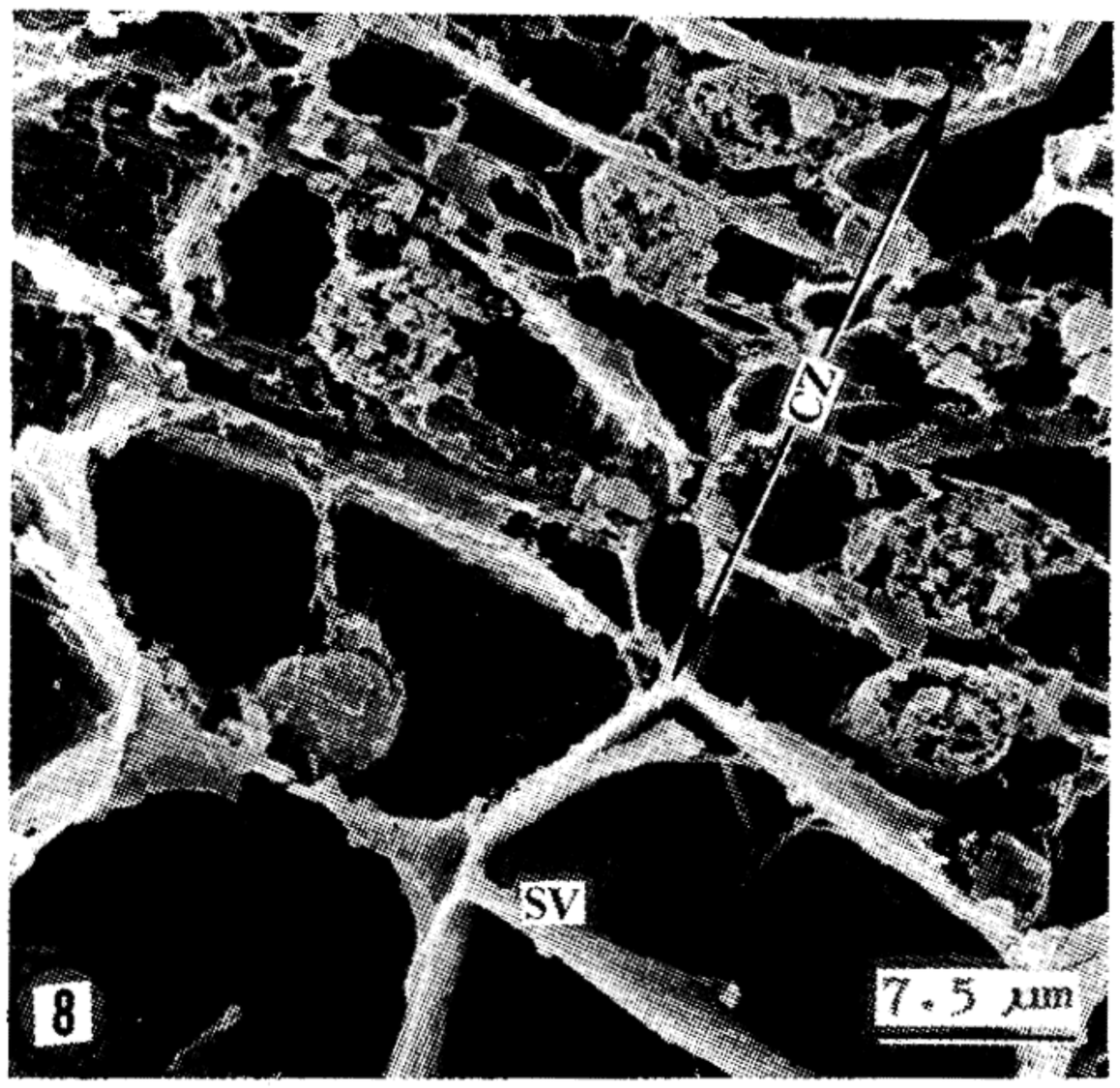


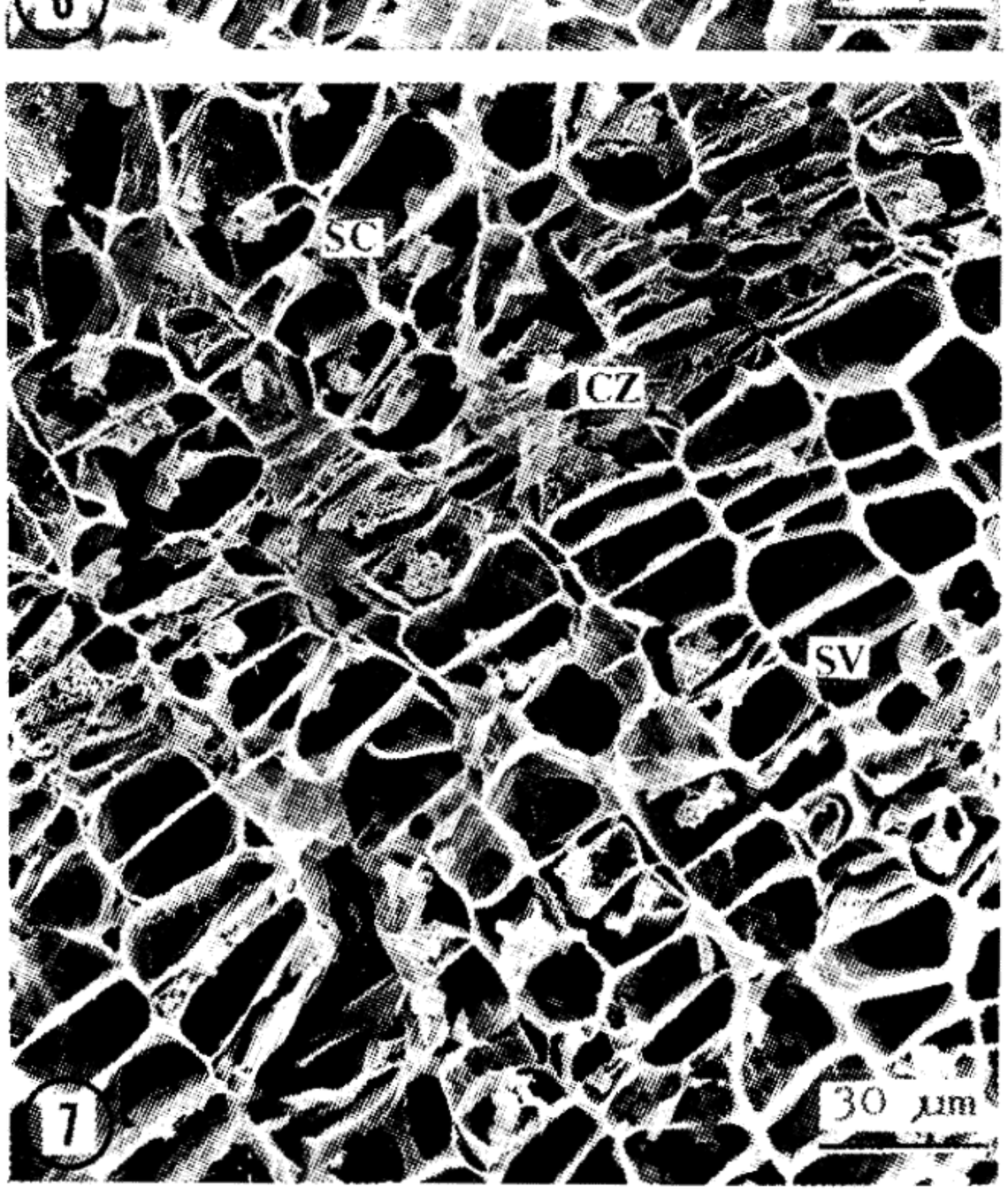


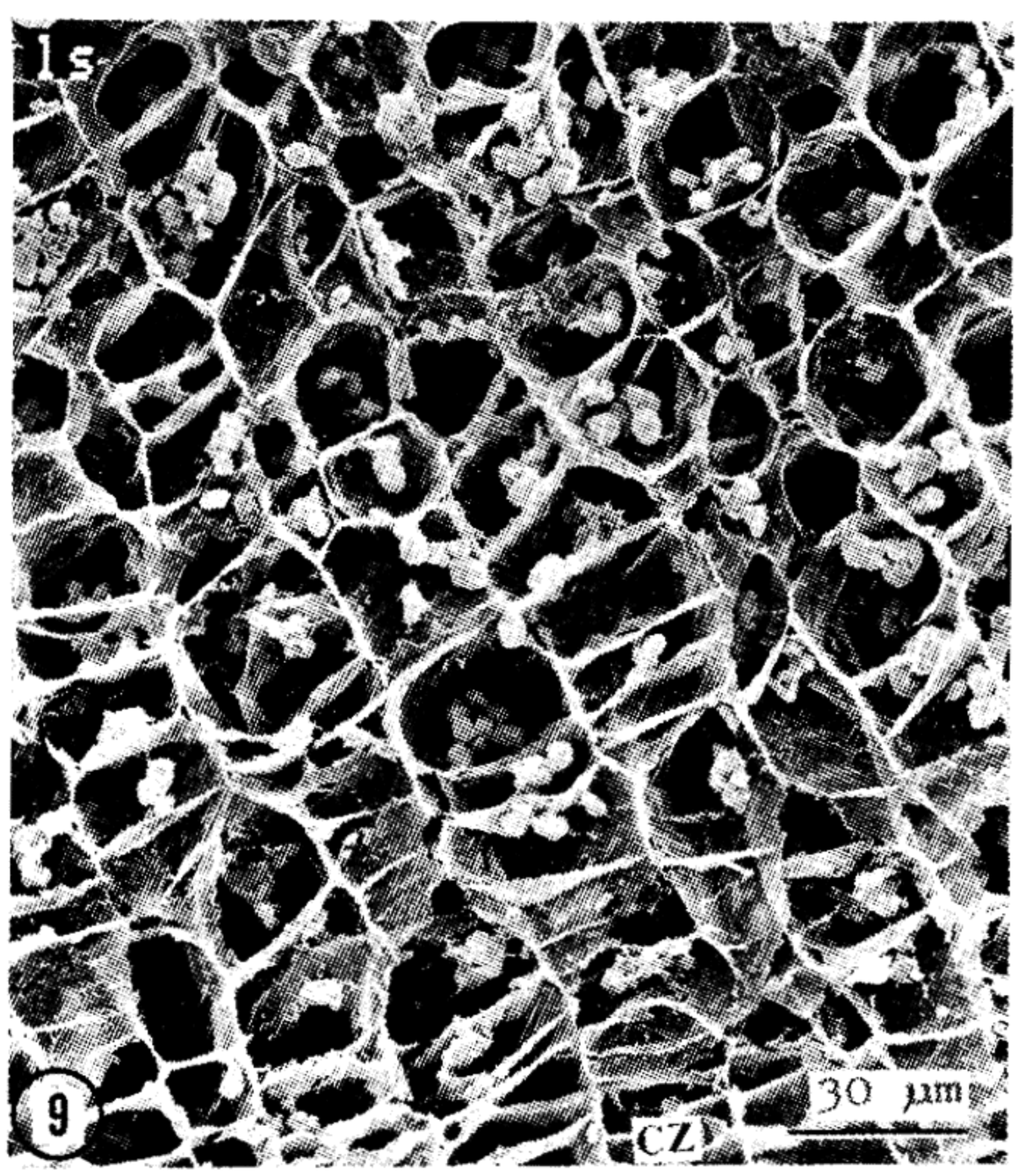


Figs. 1-5: Transections of corm
1, central region
2, secondary vascular tissue and its adjacent tissues; note the alternating pattern of phloem layer and xylem layer.
3, enlarge view of primary phloem (arrow-sieve area).
4,5, portion of primary xylem, note the helical and annular wall patterns.
HL-phloem layer; PH-primary phloem; PX-primary xylem; SC-secondary cortex; SV-secondary vascular tissue; XL-xylem layer.

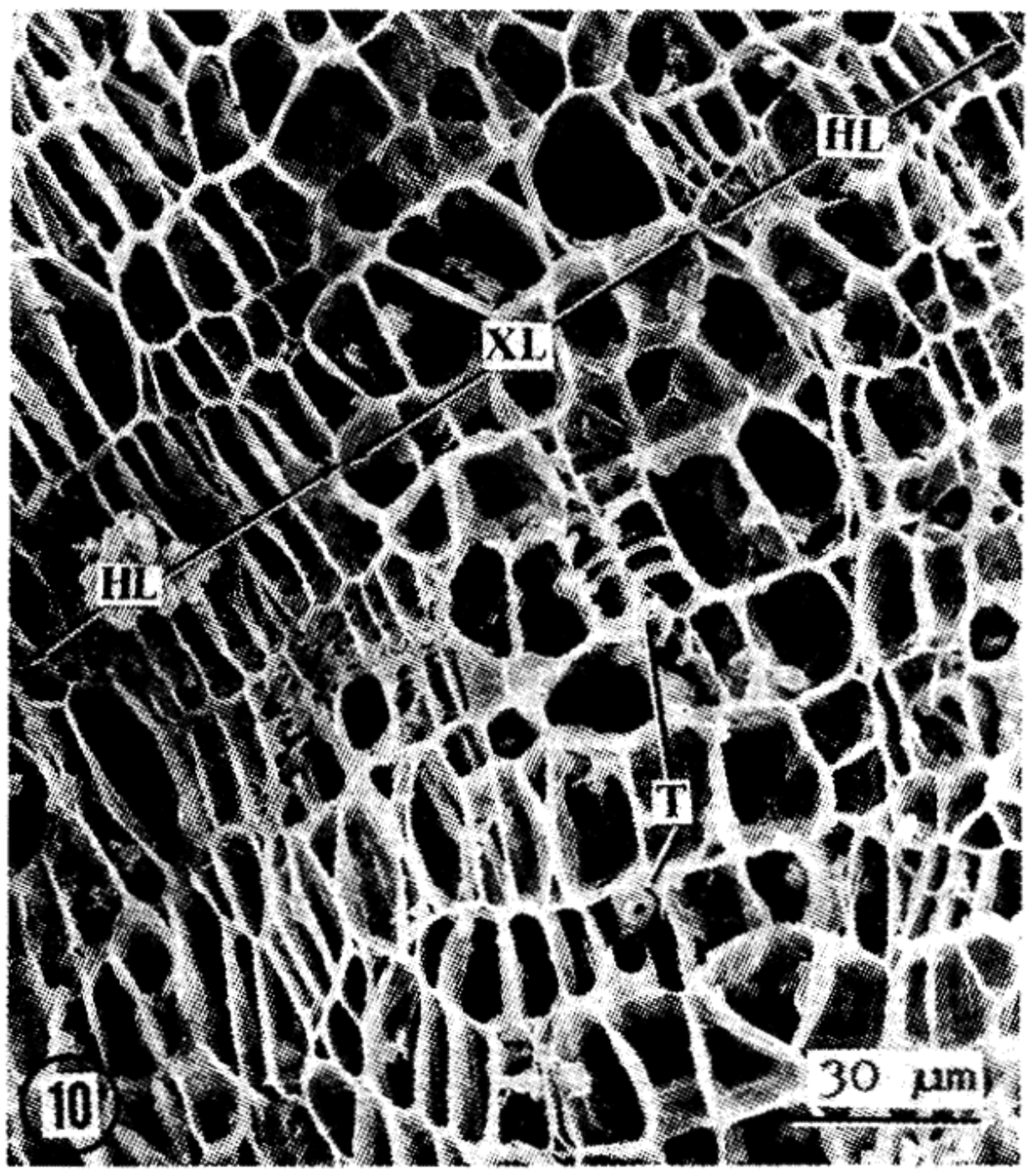


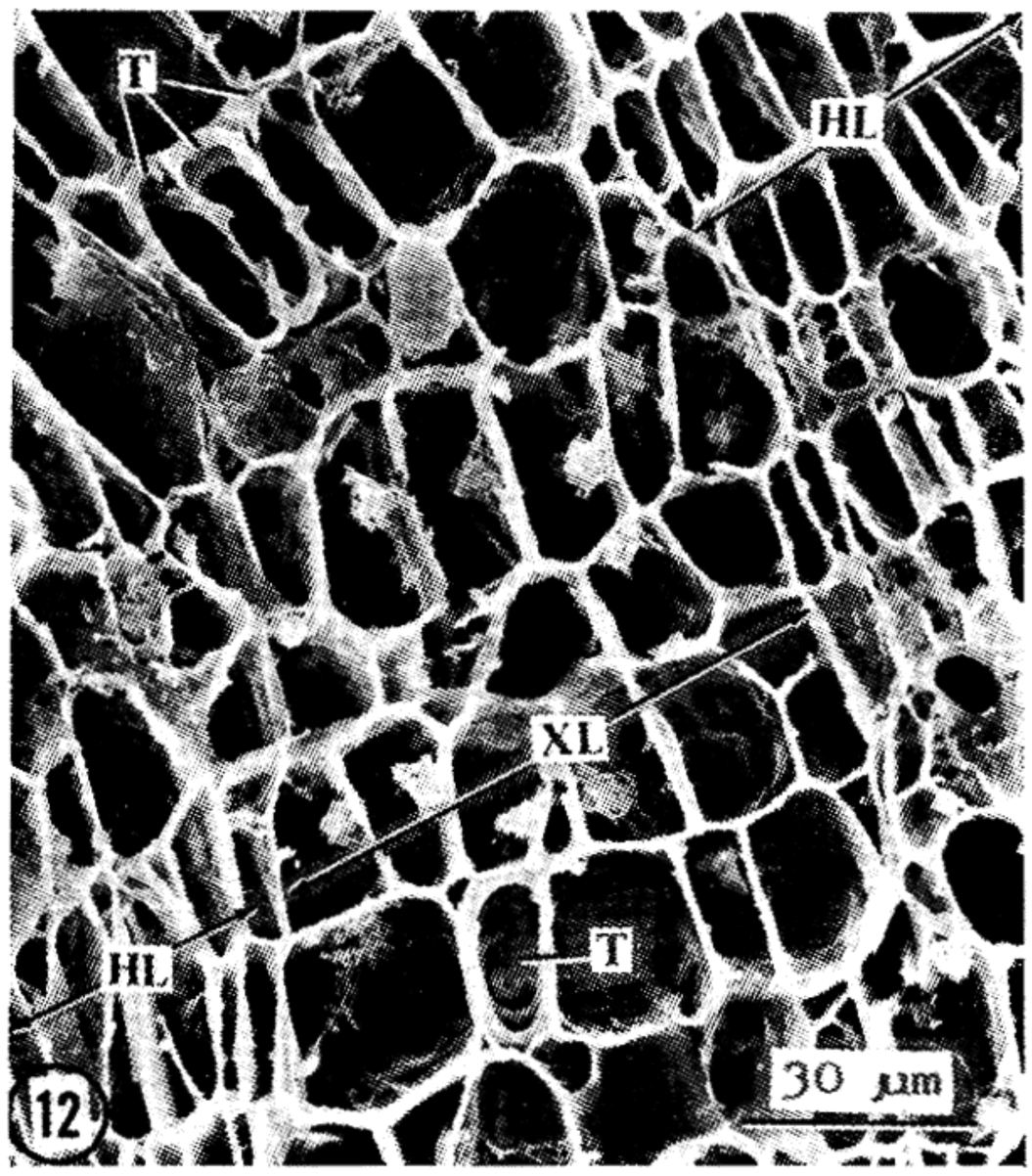


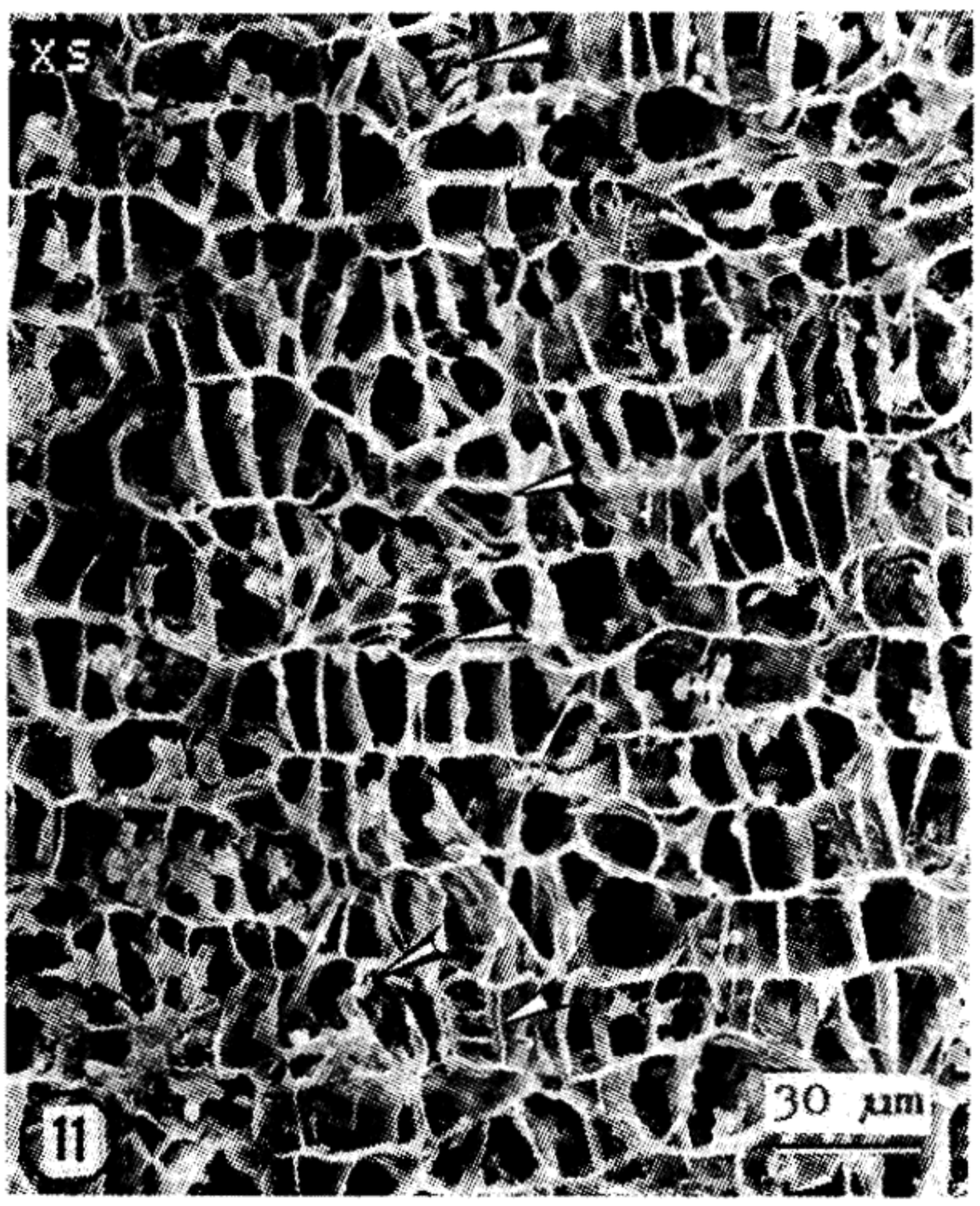




Figs. 6-8: Transections through the cambial zone.
Fig. 9: Longisection showing the cambial zone and its outward secondary cortical tissue.
CZ-cambial zone; SC-secondary cortex;
SV-secondary vascular tissue.







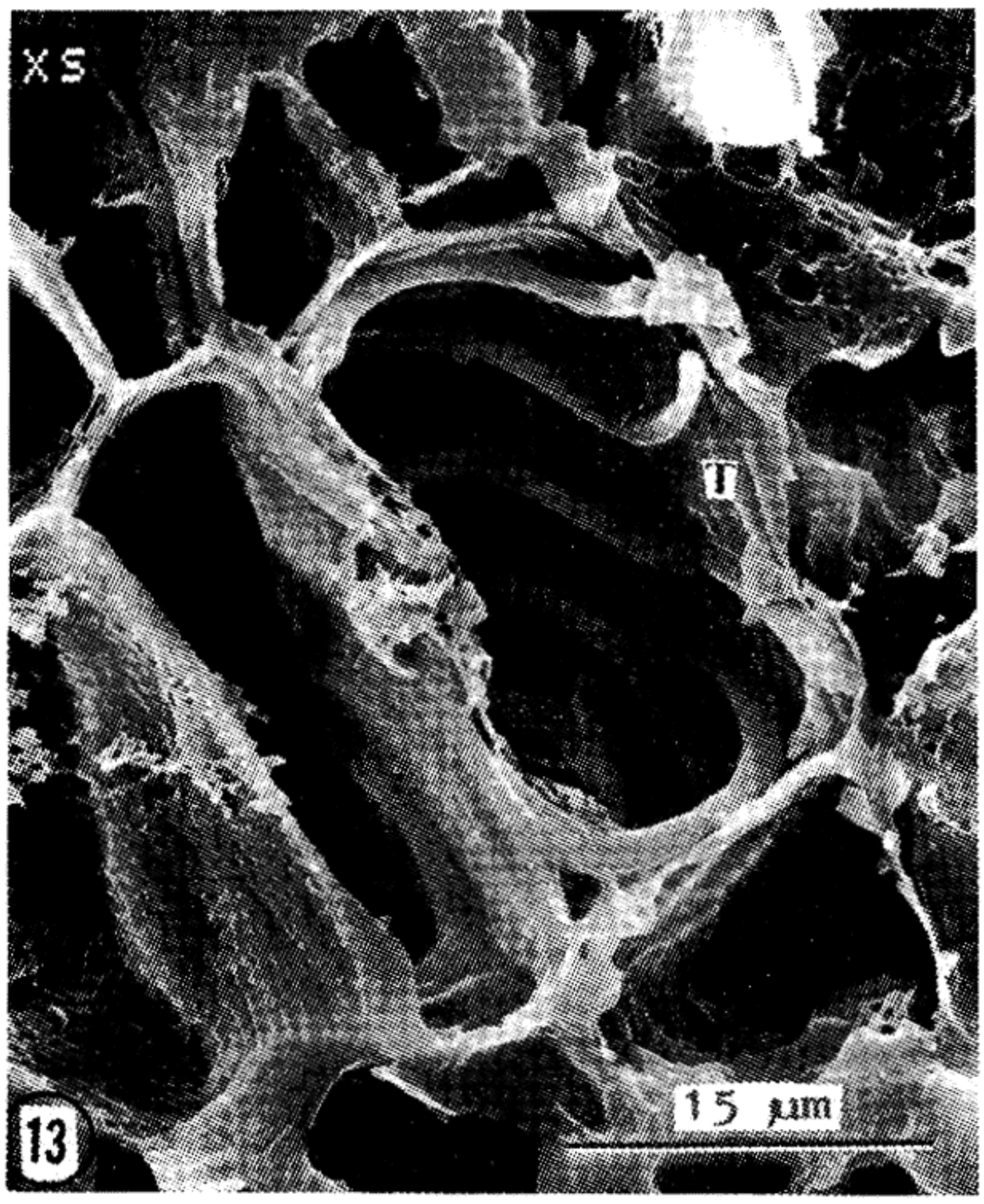


Fig. 10: Longisection of secondary vascular tissue, showing the alternating pattern of phloem layer and xylem layer.

Figs. 11-13: Transection.

11, xylem layer; tracheids scattering among the parenchyma.

12, showing the same pattern as 11.

13, isolated large prismatic tracheid with flat square outline in sectional view, and the helical secondary wall thickening.

HL-phloem layer; T-tracheid; XL-xylem layer.

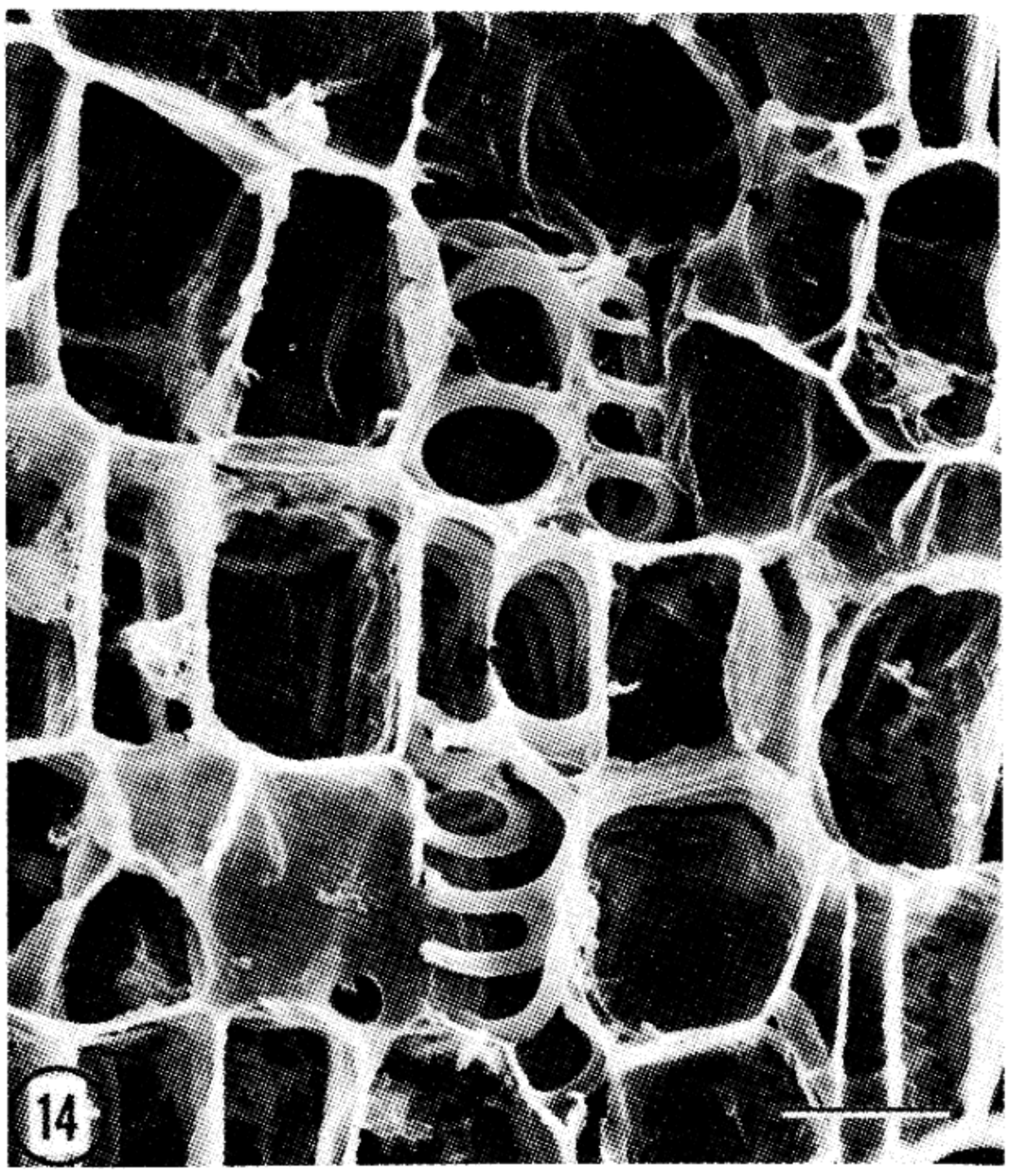
prismatic (Lap) tracheid occurs either solitary (Figs. 12-lower T, 13, 19) or several in group (Figs. 12-upper T,18). But the small and slender (SmS) tracheid always occurs in pair or twin pattern (Figs. 10, 14, 15, 16). The entire size of pairing SmS tracheids is almost the same as the cells bordering it (Figs. 10, 14, 15). It is probable that the pairing SmS tracheids have a common initial cell. Some tracheid initials divide into two cells before the deposition of secondary wall.

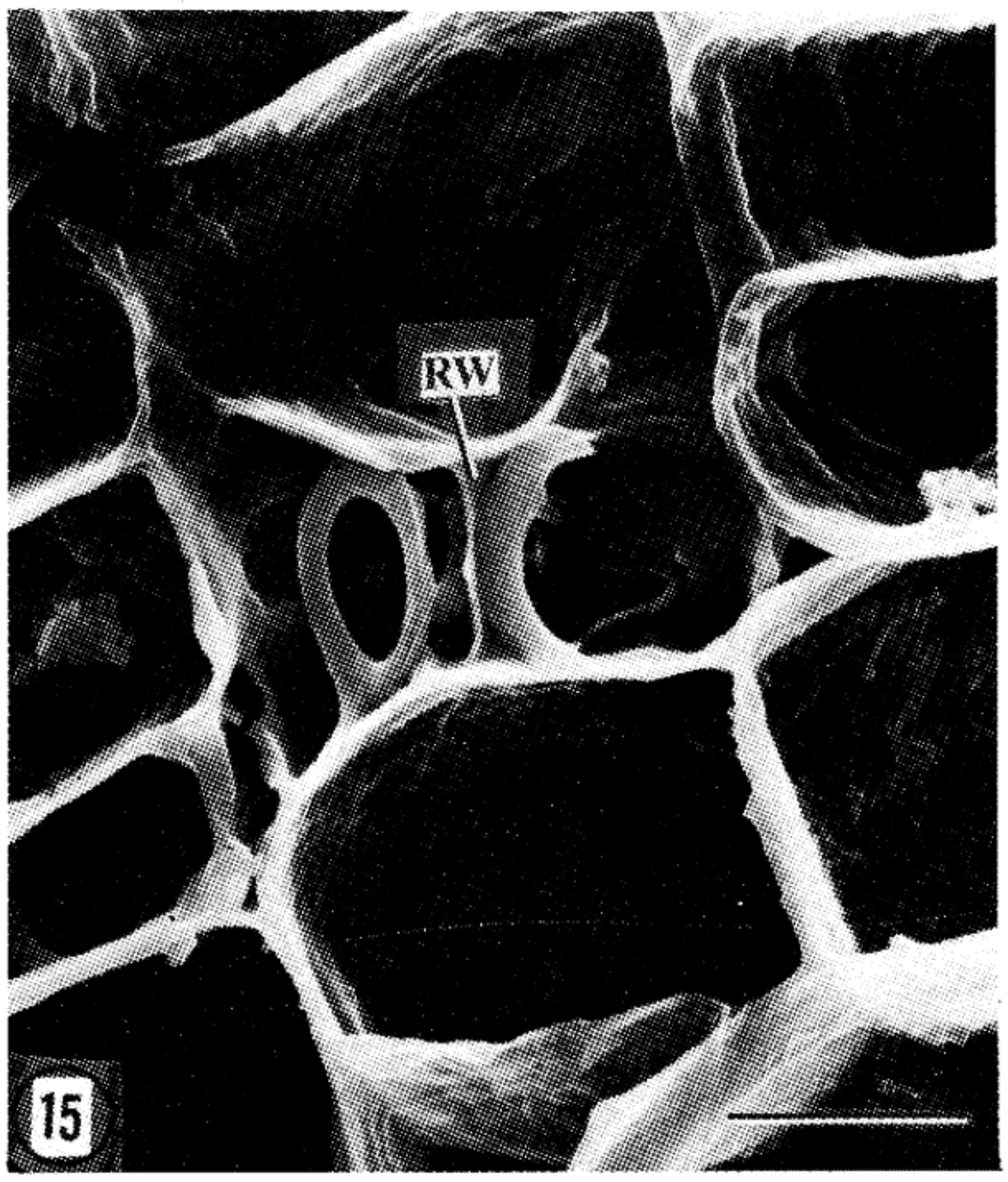
The examples of the wide variety of secondary wall thickening occurring in tracheids are shown in Fig. 29. Although there is a slightly structural diversity it is also apparent that basically all annular and helical, modified or intermediate of these two patterns. In annular type, most of the single annular rings are continuous (Figs. 29-d, 15, 16, 17), but the discontinuous annular rings (interrupted type) are also seen (Figs. 29-c, 14). Formation of the bridge between two annular rings and branching helical thickening are commonly observed (Figs. 13, 14). Although all the patterns of the secondary wall thickenings described above are found in both LaP and SmS tracheids. Majority of the Lap tracheids exhibit either annular or helical types (Figs. 12, 13, 18, 19), whereas most SmS tracheids have annular thickenings (Figs. 14, 15, 16, 17). The annular rings as well as the helices in Lap tracheids are more or less square in shape. Secondary thickenings are nearly parallel to the cell surface (Figs. 13, 18, 19). But the annular rings in SmS tracheids always have more rounded shape (Figs. 14, 15, 16, 17).

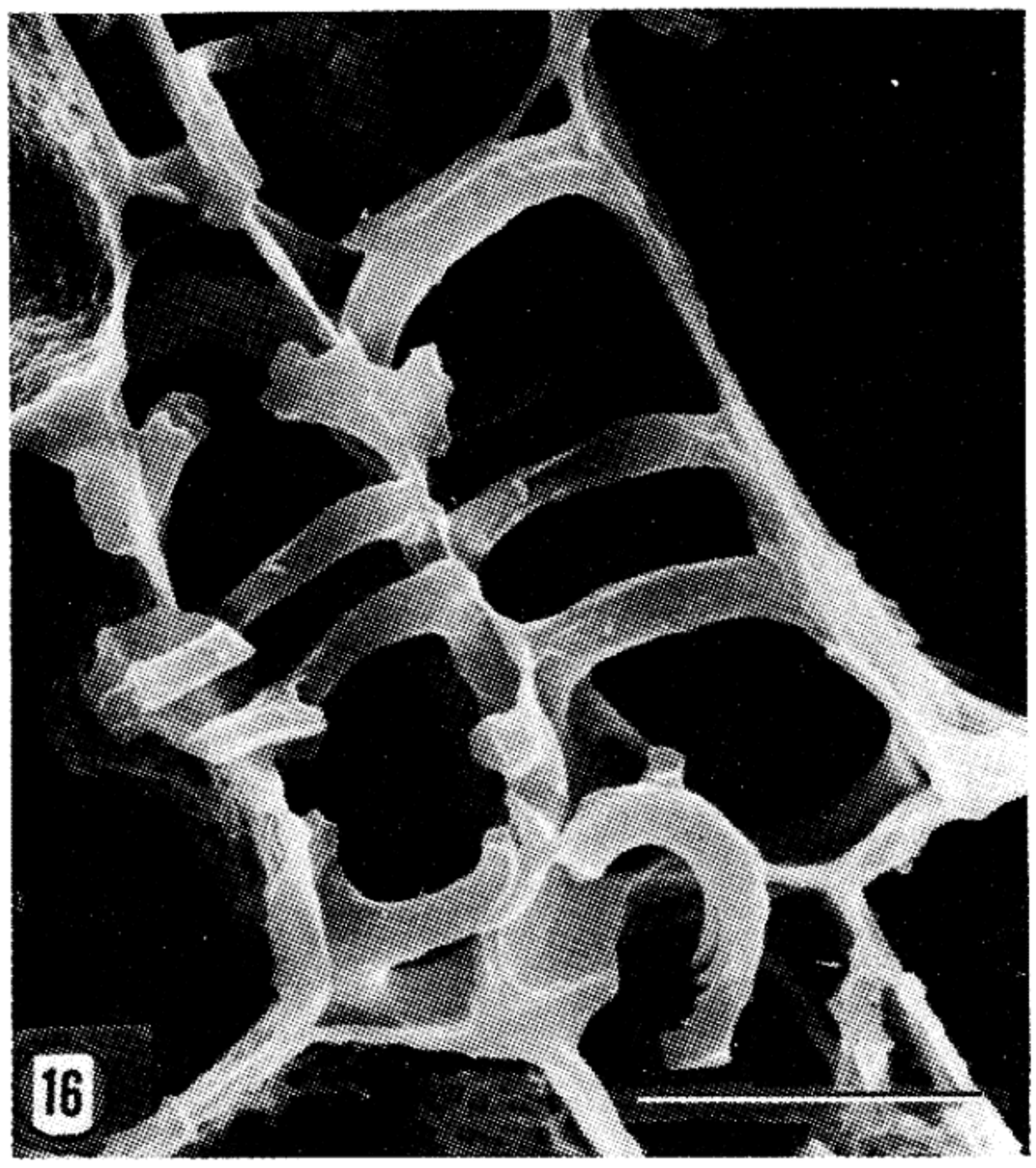
The relationship between cell shape, cell orientation, and the pattern of wall thickening can also be demonstrated in Fig. 29. The aligning axis of secondary wall thickenings in SmS tracheid is either perpendicular or parallel to the corm axis (Figs. 14, 15, 16, 17), whereas that of the Lap tracheid remains parallel (Figs. 13, 18, 19). As mentioned above, SmS tracheids are in pairing or twin patten. Two sister tracheids in the same twin tracheids have the same type of wall thickening, and show the same orientation in their annular axis.

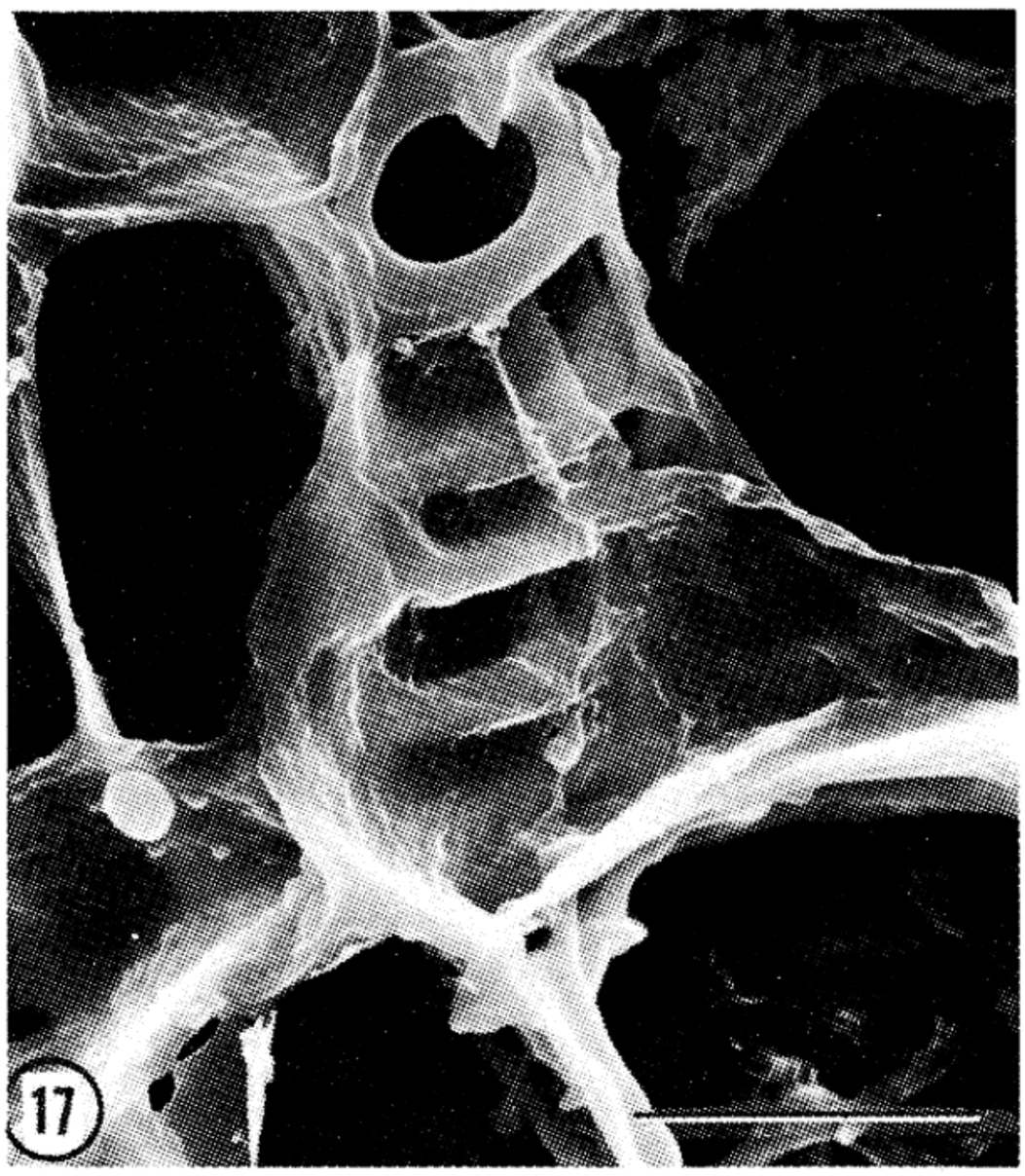
Cells in phloem zone

The first derivatives produced by the cambium are the phloem zone which consists of no parenchyma except its boundary region. All the cells in this zone are sieve cells (Figs. 10, 12, 20). The sieve cells can be identified the presence of distinct sieve areas. Most of the sieve pores occur in cluster pattern sometimes solitary (Figs. 20-28). The size of a single sieve pore usually ranges from 0.5 to 2 μm in diameter. The sieve areas are uniformly distributed on the radial and transverse walls (Figs. 22-28). Sieve pores are absent in both outer and inner tangential walls, they are smooth in appearance. The arrangement and the number of sieve pores on transverse wall resemble those on the radial wall. Many sieve cells are found to have a tubular bridge structure lying across the cell lumen from one tangential wall to another tangential wall (Figs. 20, 21, 22 ,24, 26, 27). This tubular bridges is designated as sieve trabecula in the present report. Majority of the sieve trabeculae are seated at the middle part of the cell lumen (Figs. 22, 26, 27), whereas some of them are found to be in the periphery (Fig. 24). The number of sieve trabecula in an individual sieve cell is one occasionally two. Several granular structure are always seen within the sieve trabecula (Figs. 22, 27). The sieve trabecula appears to bulge slightly at its both ends where the sieve trabecula becomes continuous with the inner surface of tangential wall of sieve cell. The width of the sieve trabecula is approximately 0.8μm at its middle part. Based on the presence of granular particles and the mode of connection with wall surface, the sieve trabecula seems to merely be a portion of the remnant of cell contents of the sieve cell.



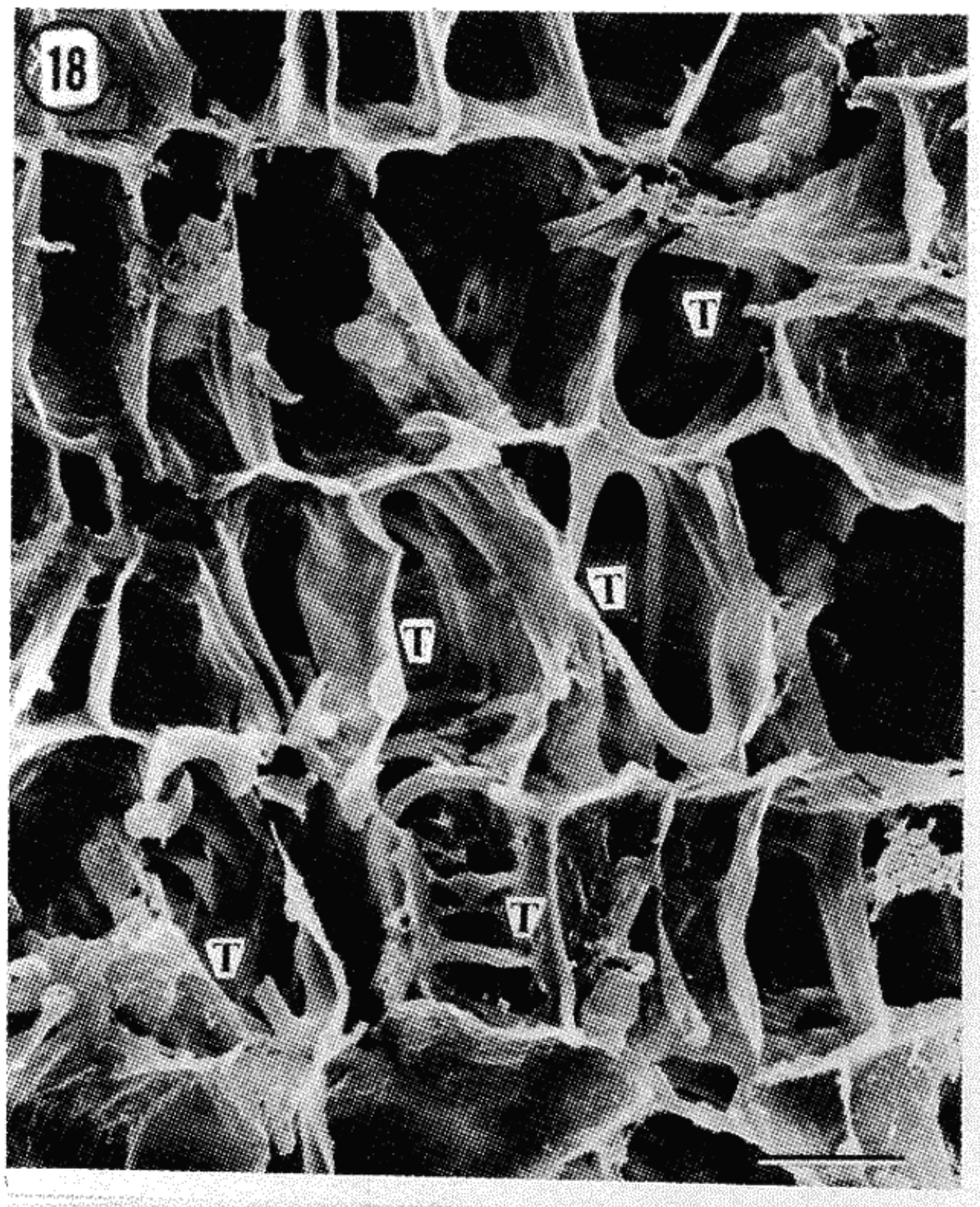


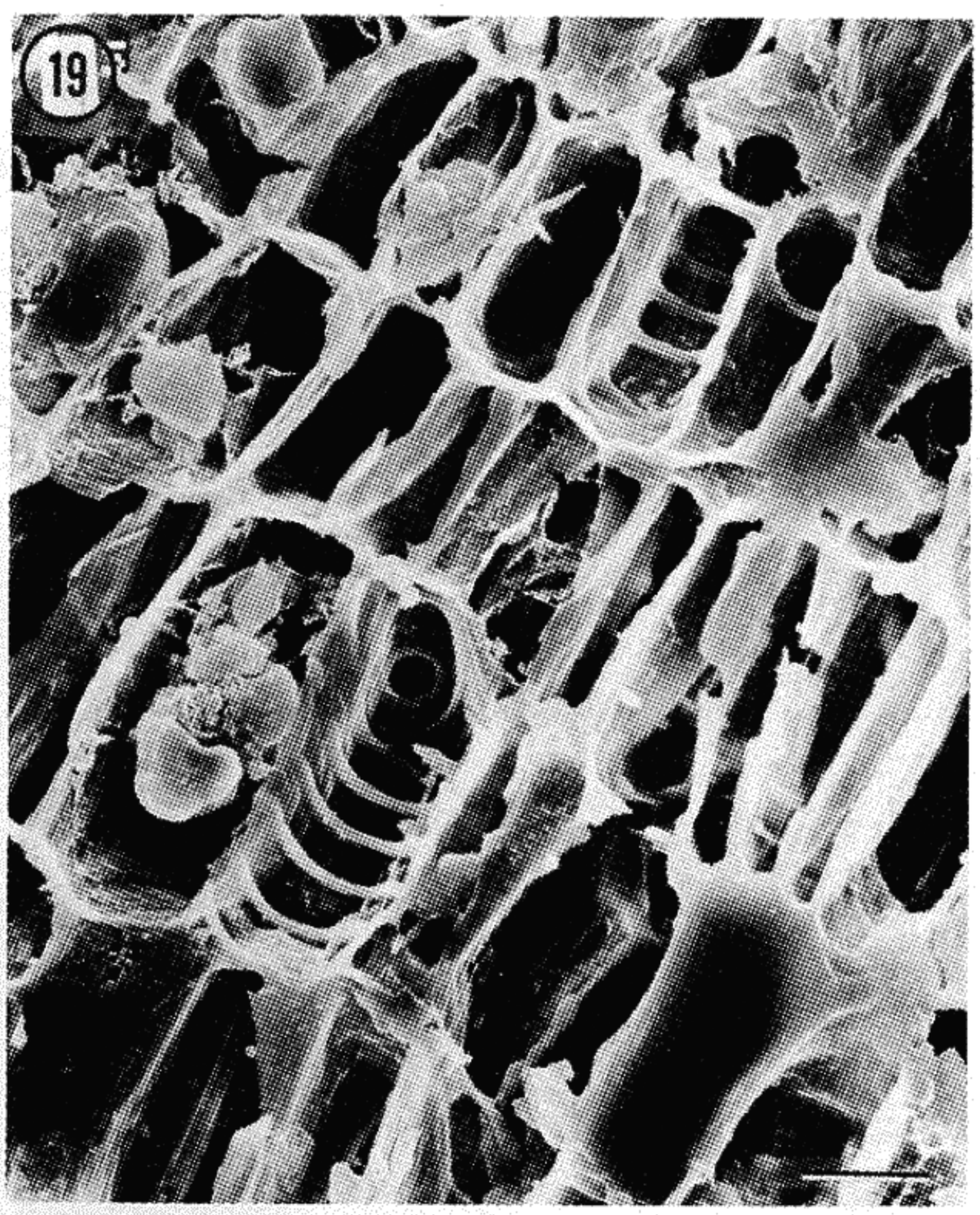


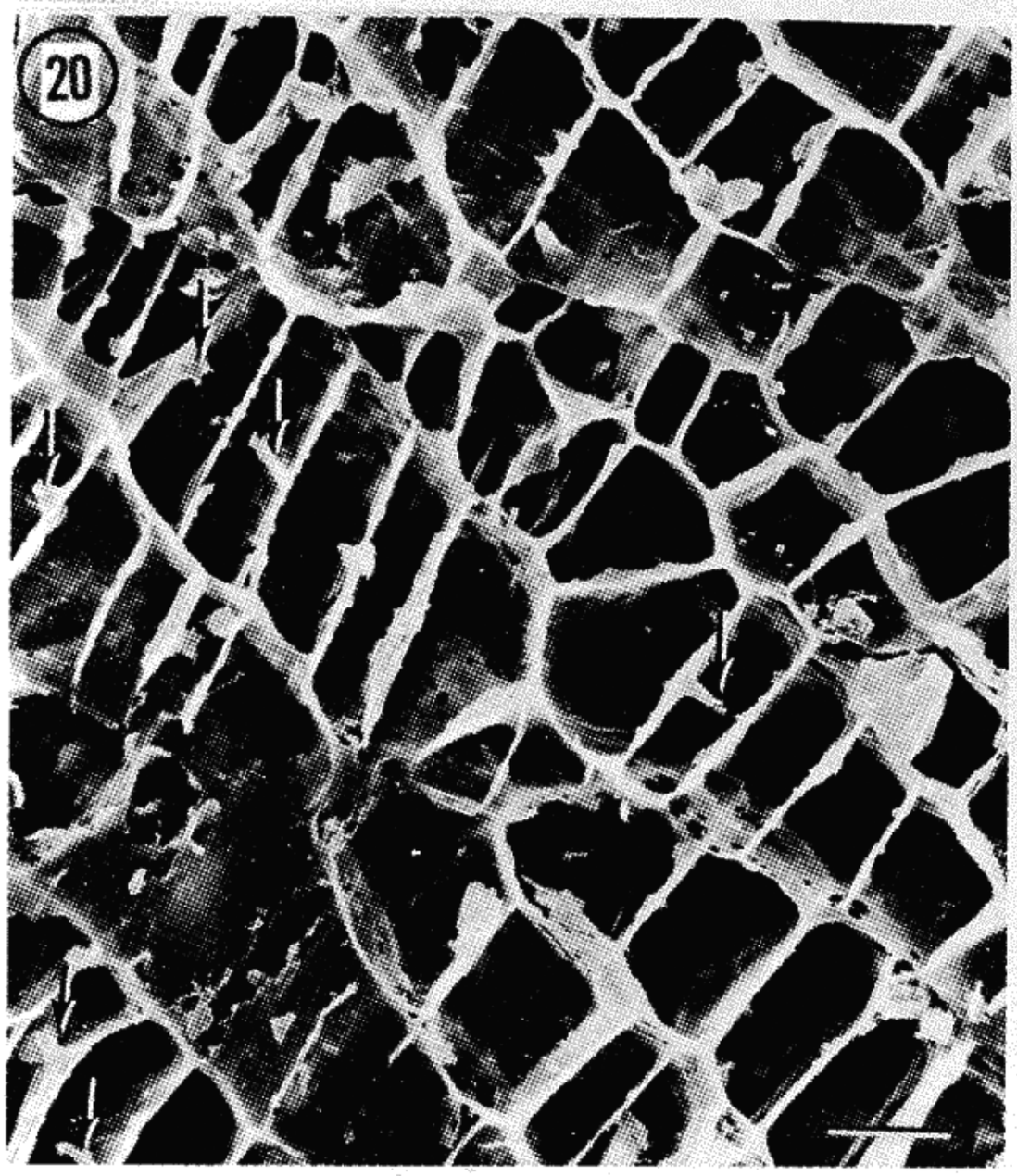


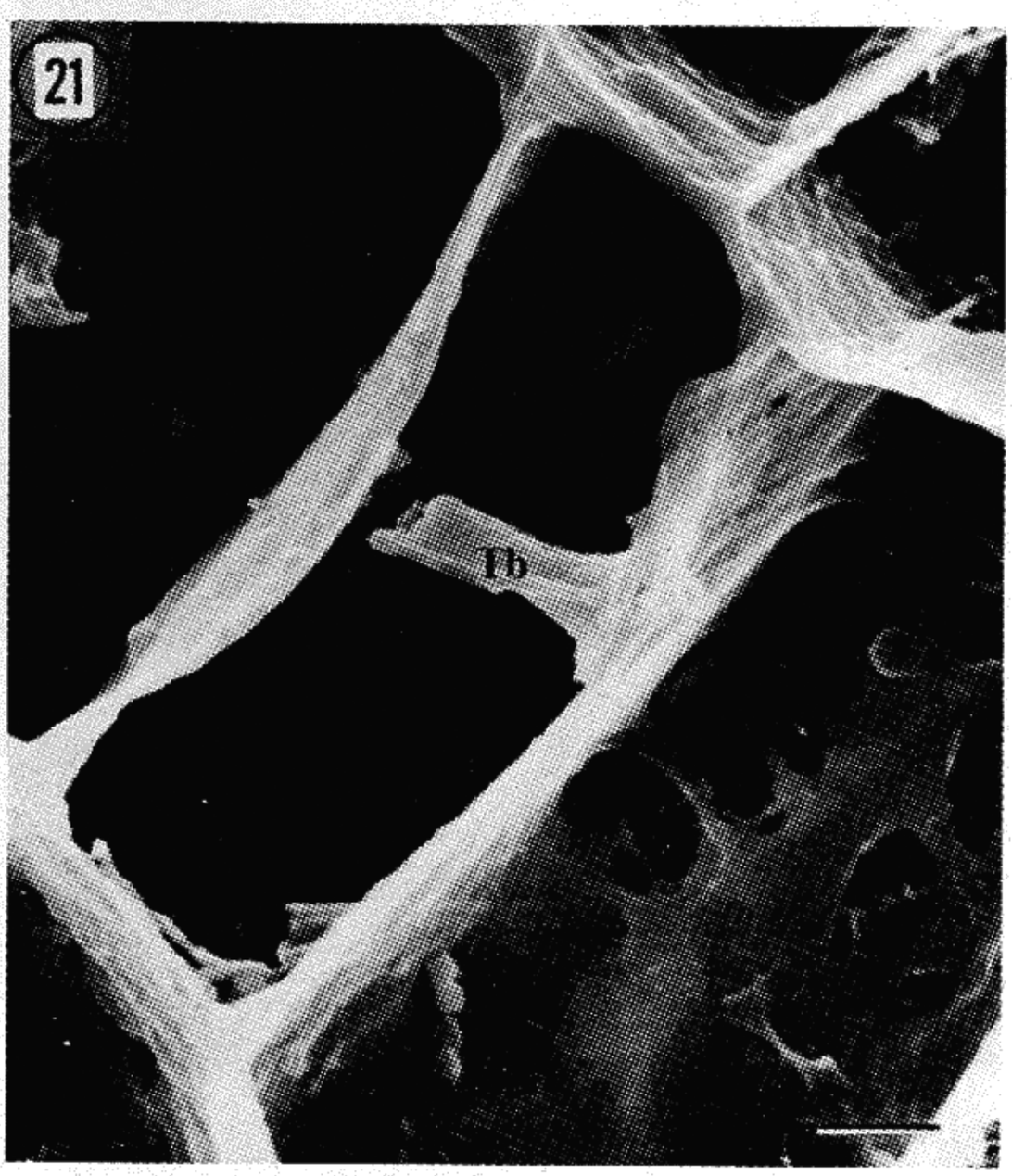
Figs. 14-15: Transection through the xylem layer, showing the orientation of pairing tracheid RW-radial wall,. bar=10 μm.

Figs. 16-17: Longisection through the xylem layer, pairing tracheid in 16, bar=10 μm.

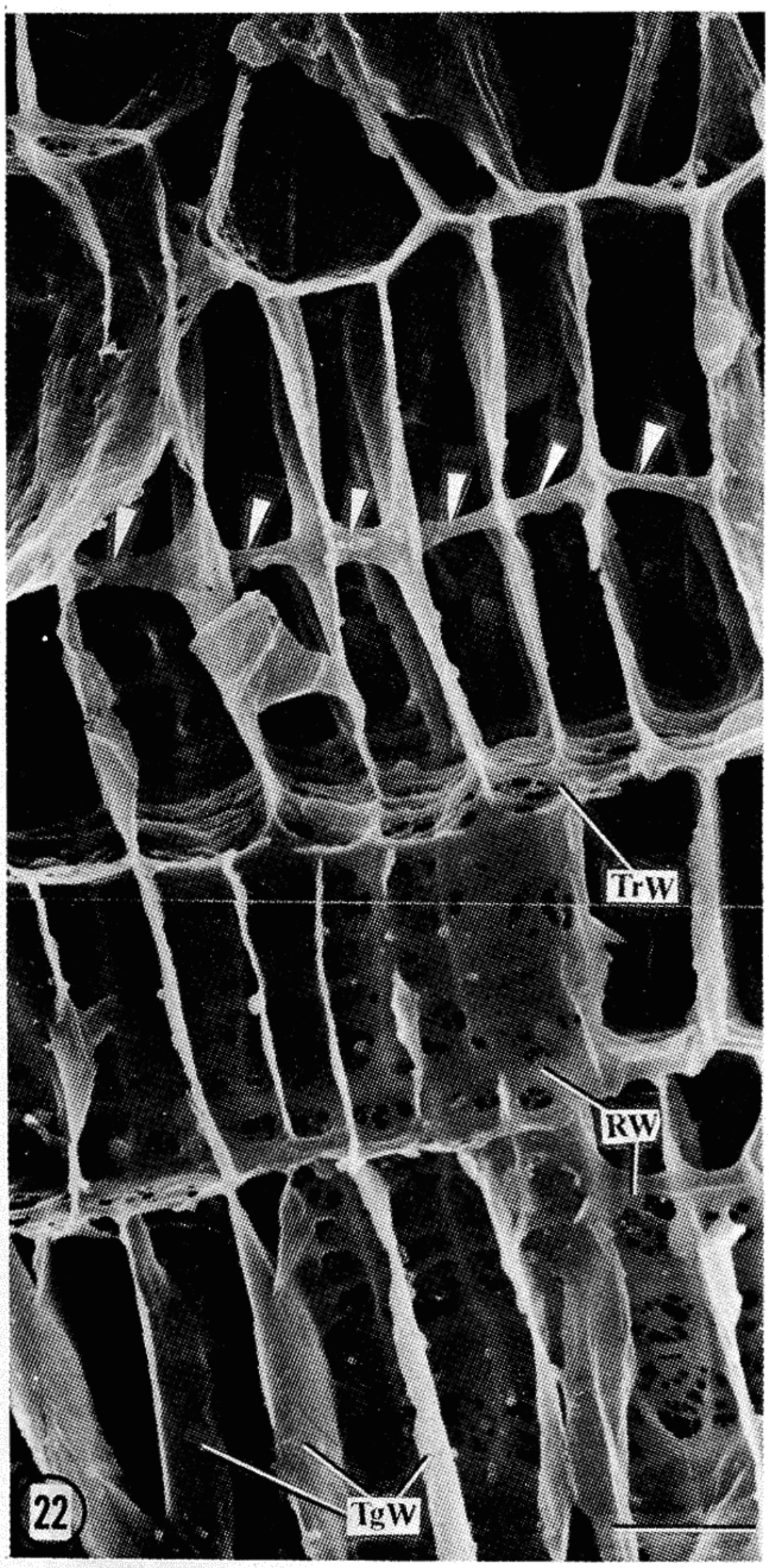


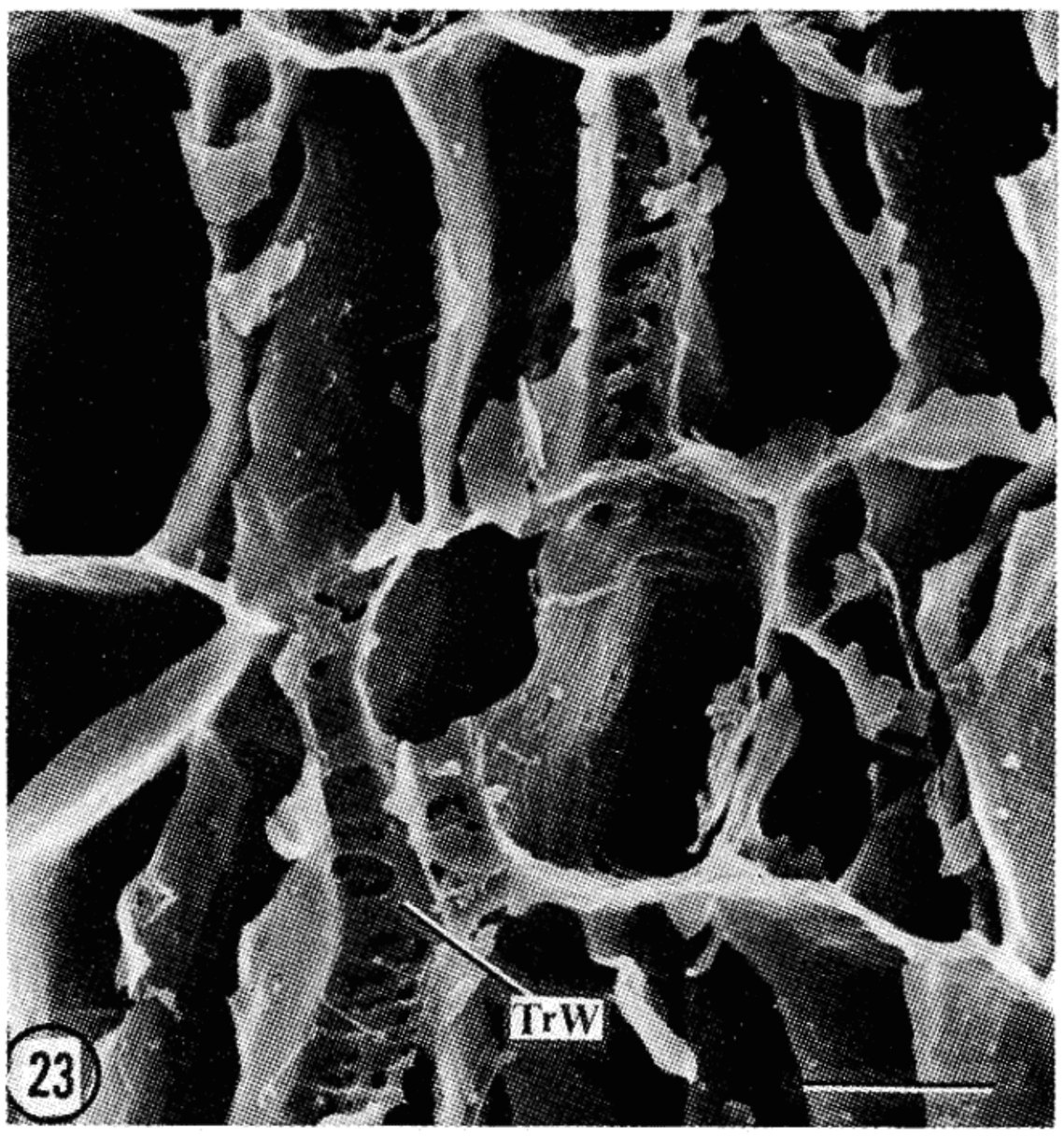


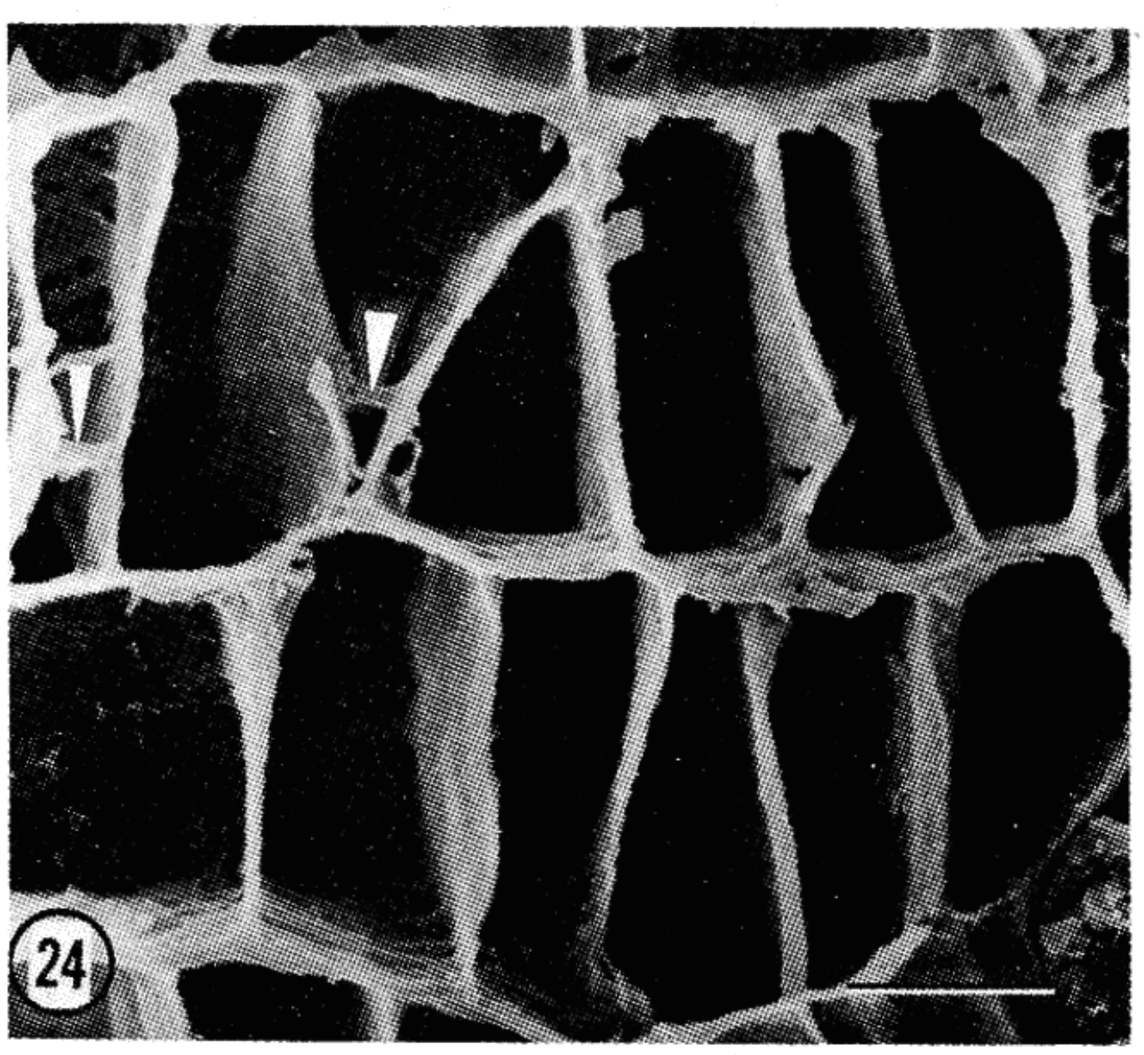




Figs. 18, 19: Transection through the xylem layer
Figs. 20, 21: Transection through the phlem layer, arrows in 20 showing the sieve trabeculae.
T-tracheid; Tb-sieve trabecula, bar =10 μm.

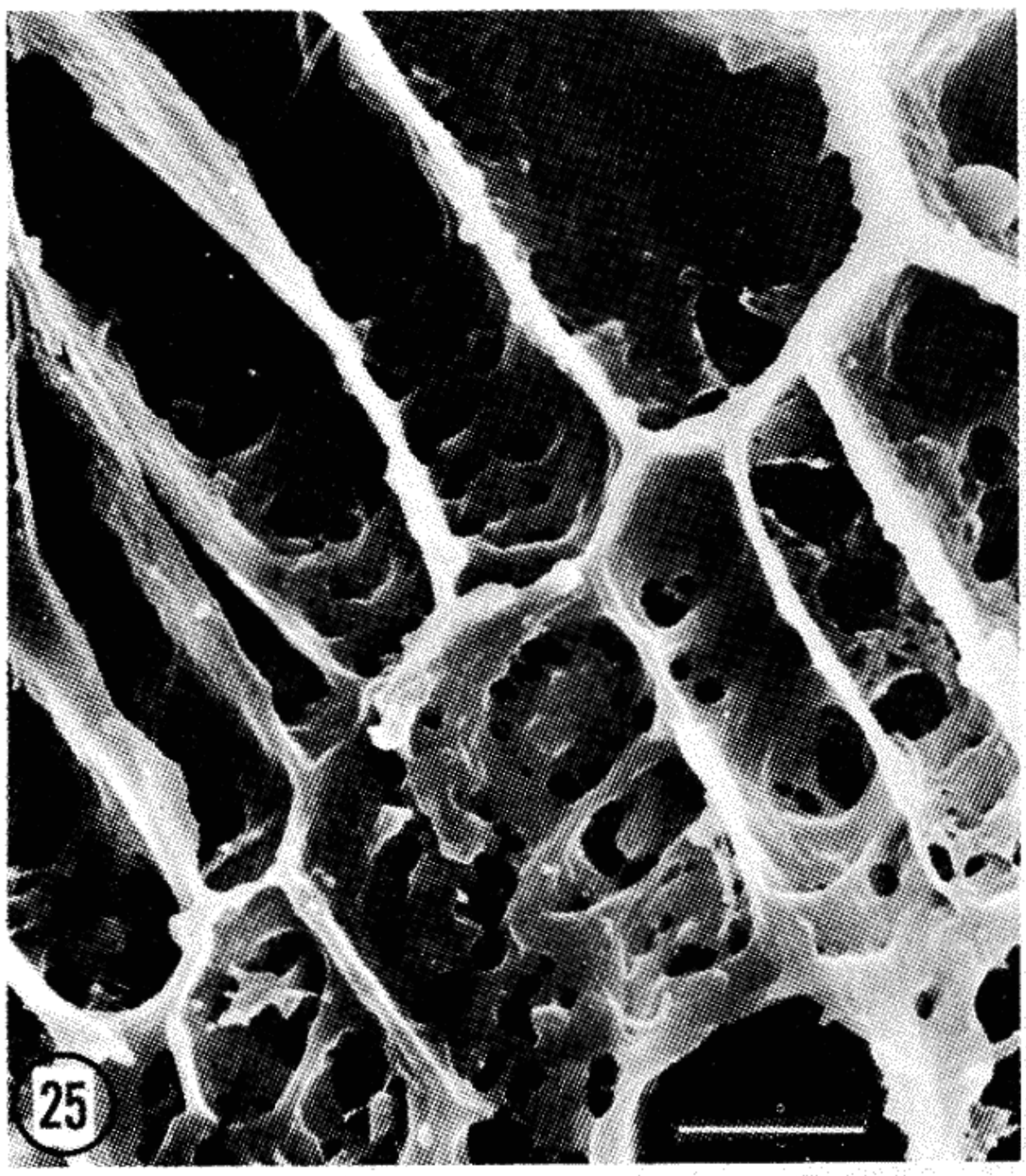


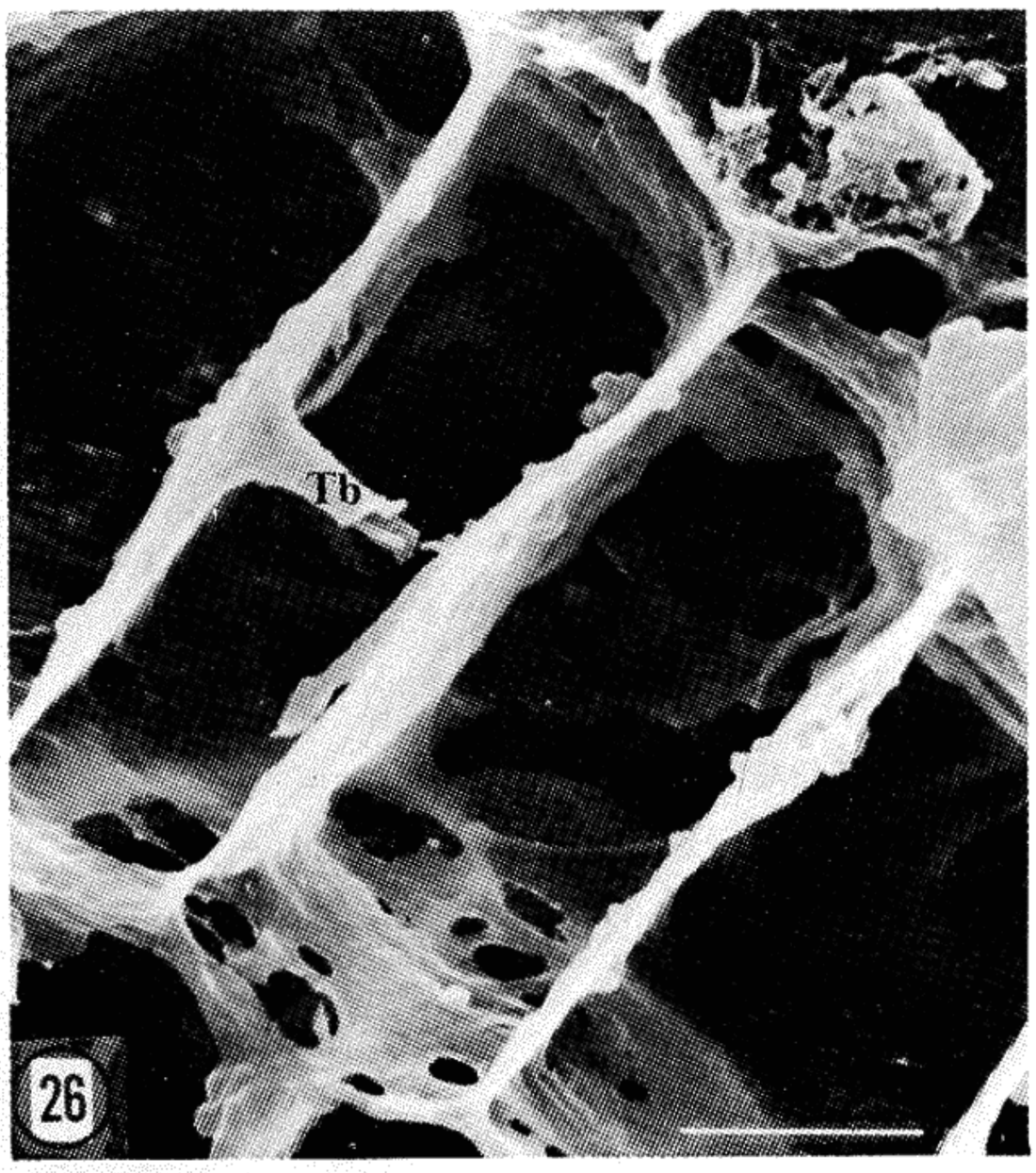


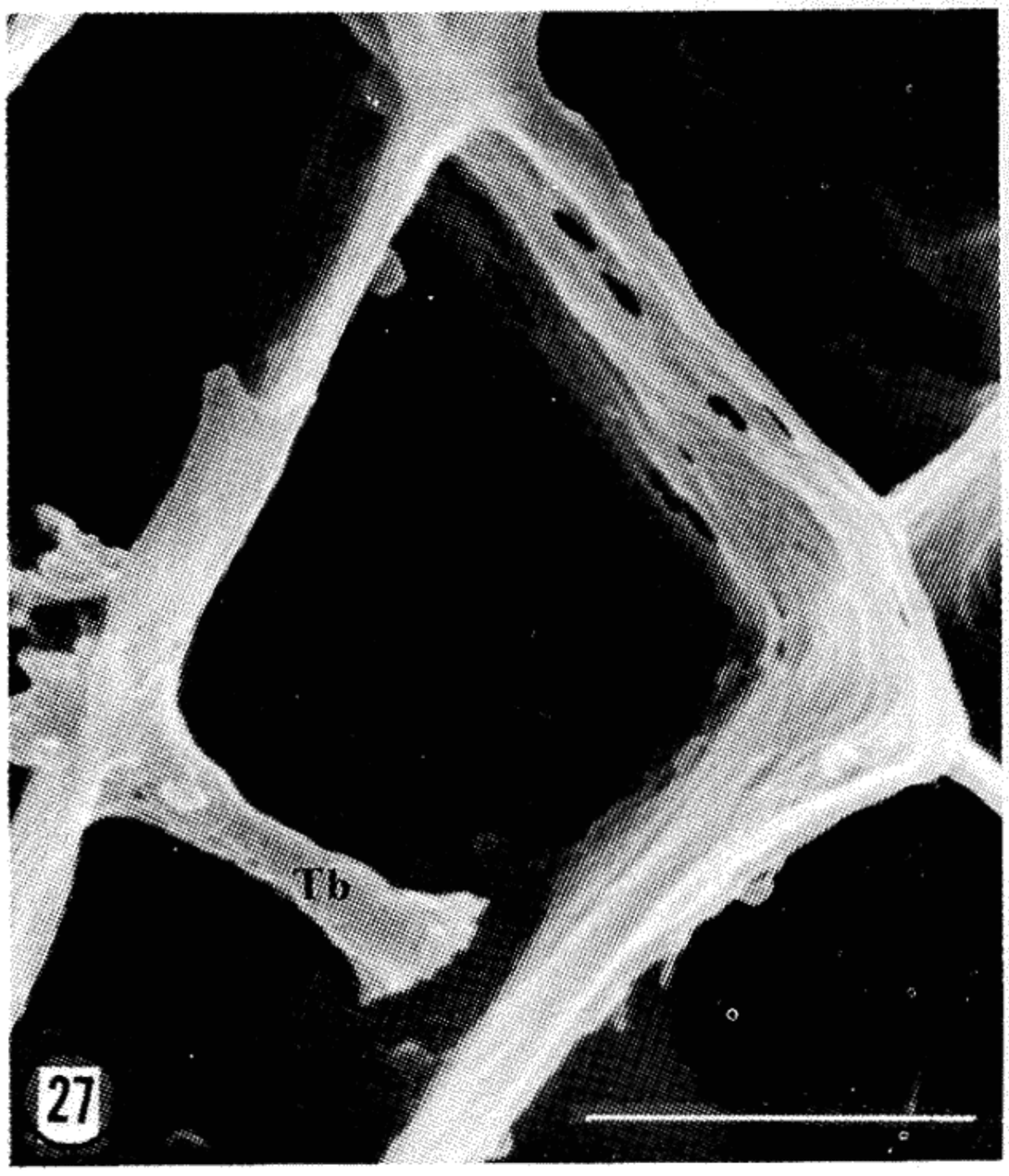


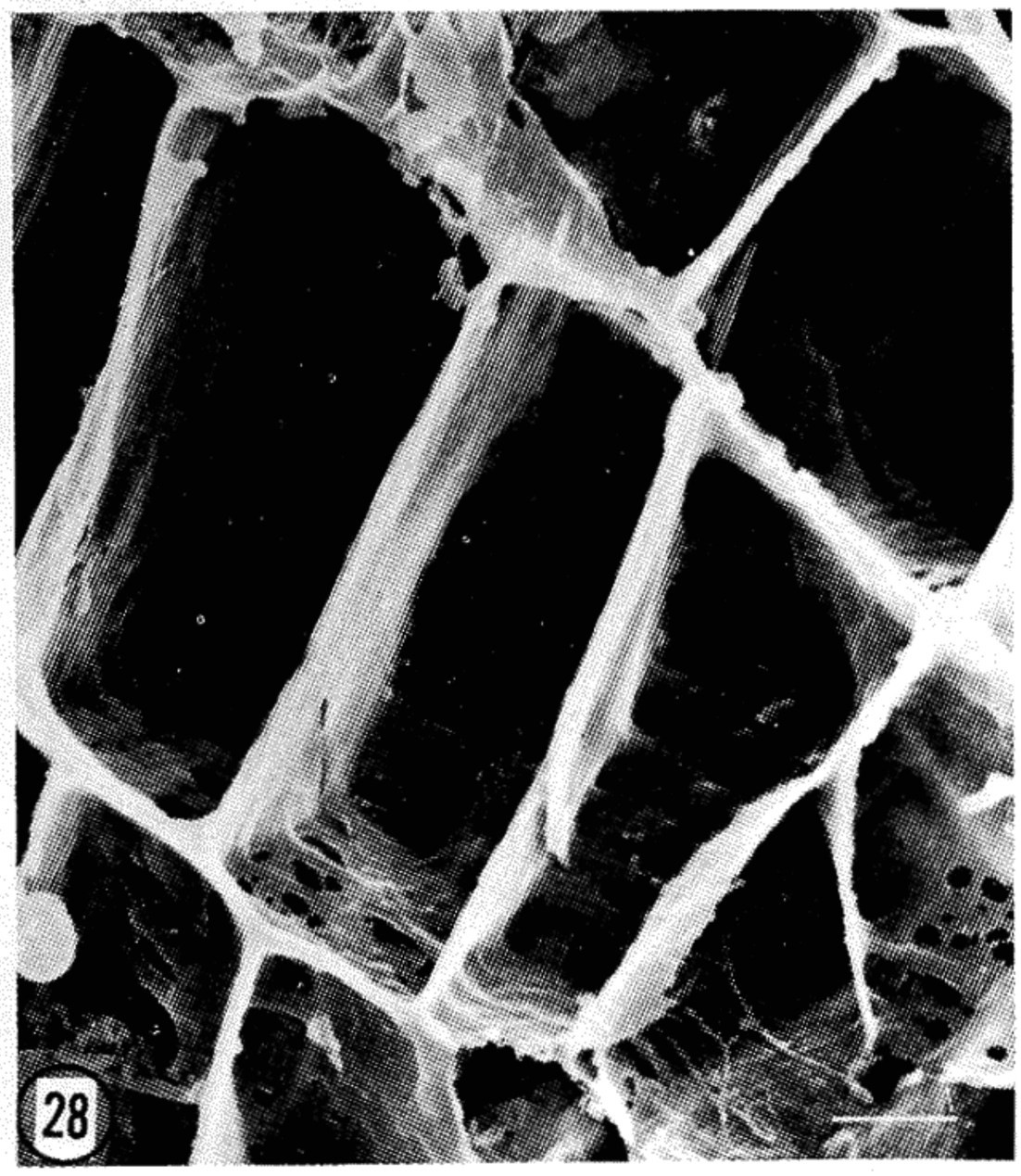
Figs. 22-24: Phloem layer in longisection(22)and transection (23, 24). Note a series of six sieve cells all with sieve trabeculae (arrows) across the cell lumen radially; and the absence of sieve areas on tangential walls.

RW-radial wall; TgW-tangential wall; TrW-transverse wall, bar=10 μm.









Figs. 25-28: Sieve cells in longisection(25), and transection(26-28). Tb-sieve trabecula, bar=5 μm.

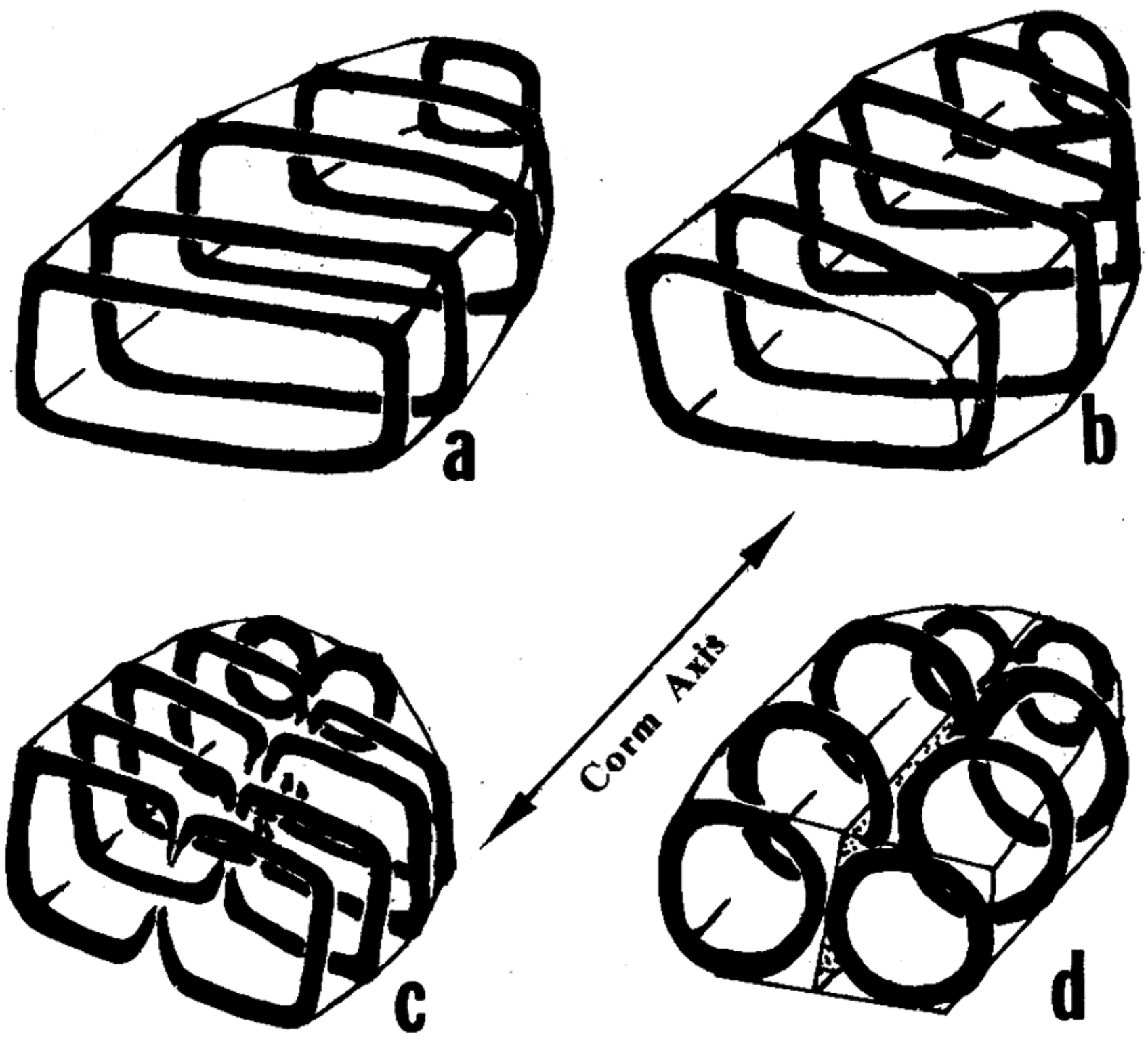


Fig. 29: Diagrams showing the basic wall pattetns in tracheary element in secondary vascular tissue.
a, annular in large prismatic tracheid.
b, helical in large prismatic tracheid.
c, discontinuous annular in intermediate type of a and d
d, annular in small slender tracheid.

DISCUSSION

The histology of the secondary vascular tissue in the genus *Isoetes* has received various interpretations by the earlier workers(Paolillo, 1963; Scott and Hill, 1900; Stokey, 1909; Von Mohl, 1845; West and Takeda, 1915). The cell types in the secondary vascular tissue discribed in these investigations are still limited as parenchyma, sieve cells and annular or helical tracheids. Recent studies by the present workers have demonstrated the presence of the tracheid having one-band secondary wall thickening scattered among the sieve cells (Chiang, 1976; Yang et al, 1975). It is now necessary to make a very important correction concerning the tracheid of one-band wall. The one-band secondary wall thickening is now examined to be the sieve trabecula lying across the cell lumen. The sieve trabecula is suggested to be the remnant of cell contents in the sieve cell. The nature as well as the detailed structure of the sieve trabecula, as a matter of fact, needs further examination, especially TEM survey. However, the sieve trabecula is so easy to be observed that we have taken it for the one band wall thickening of tracheid. The principal purpose of the present report is to correct and supplement the previous descriptions which were made merely based on OM examination (Chiang, 1976; Yang et al, 1975).

The arrangement of the tissues and cell types in *I. taiwanensis* resembles that observed in *I. howellii* (Paolillo, 1963). The xylem zone are formed alternating with the phloem zone. As mentioned by Kruatrachue and Evert (1977) and Paolillo (1963), the xylem zone designated in the present report always lacks tracheary elements, especially in the young corm. It is also true that the same result is shown in the present species. Paolillo (1963) described this tissue as the parenchyma layers. The absence of the tracheary elements in the aquatic species is rather common in other vascular plants. The xylem zone and phloem zone in this plant can be recognized easily in a larger corm simply by the size of cell. The sieve cells do not scatter among the parenchyma. Therefore the xylem zone used here seems to not against a fair terminology.

It is interesting to note the presence of the twin tracheids. The wall thickening pattern, alignment of the wall thickening, the size and the shape of two sister tracheids in one set of twin-tracheids are the same. Consequently, it is suggested that they probably originate from a common initial cell though the ontogeny of sister tracheids has not been clearly studied. The fact that entire size of two sister-tracheids (one set of twin tracheids) is almost the same as that of their continuous parenchyma can also support this view.

The recognization of sieve elments in both primary and secondary vascular tissue seems to be more difficult under OM (Stokey, 1909; Weber, 1922). The presence of the sieve cells in the leaf and corm of *I. muricata* has been observed under TEM (Kruatrachue and Evert, 1974, 1977). Several techniques for callose detection have been used in recognization of sieve elements. Some workers have demonstrated the presence of callose in some cells of the cambial derivatives (Esau, Cheadle and Gifford, 1953; Lamoureux, 1961). Besides, the recent investigations also indicate that there are sieve cells in this tissue (Kruatrachue and Evert, 1977; Paolallo, 1963; Yang et al, 1975). The SEM presentation in *I.taiwanensis* clearly reveals the conspicuous difference between parenchyma and sieve cells, especially the wall structure. Although the detailed structure can not be observed on SEM it is evident that the distributional pattern of sieve pores in this species somewhat differs from that in *I. muricata* in which the sieve pores ocour in all walls (Kruatrachue and Evert, 1977). A further careful exam-

ination under TEM is necessary in order to understand development and cellular structure of sieve trabecula and sieve cell.

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構成臺灣水韭球莖維管組織之細胞

江蔡淑華　陳淑宇
國立臺灣大學植物學系

中 文 摘 要

臺灣水韭球莖內之維管組織、由管胞、篩胞和薄壁細胞三種細胞所組成。由形成層產生的維管組織排列特殊，靱皮區和木質區交互而排。形成層最初產生者爲靱皮區細胞。靱皮區內只具篩胞，而木質區內則多爲薄壁細胞，只有少數管胞滲雜其間。篩域均勻地分佈於篩胞之徑線切面和橫切面之細胞壁上，篩胞內常可看到一道（偶有二道）管狀細絃（命名爲篩絃）由兩切線縱切面壁貫串細胞腔。