THE ULTRASTRUCTURE OF PITS IN *PAULOWNIA TOMENTOSA*

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ABSTRACT

The pitting between various cell elements in *Paulownia tomentosa* was studied at the ultrastructural level. Plasmodesmata are more numerous in the pit membranes of ray parenchyma than in the longitudinal parenchyma. The edges of the pit borders in the latter are curved, while those of the former are more angular in shape. Numerous blind pits were found in ray parenchyma cells, but they occurred less frequently in fiber tracheids. The tylosis wall with a "compound middle lamella equivalent" layer arches over the half-bordered pit pair area, sometimes showing a recess at the half-bordered pit pair area. The pit membrane of all pitting types is a continuation of the compound middle lamella. Pit borders of vessel pits show a variety of forms and shapes. In bordered pit pairs, the S_1 of the pit border ends at the rim of the pit chamber.

Keywords: *Paulownia tomentosa*, simple pit pair, bordered pit pair, half-bordered pit pair, blind pit, tylosis wall.

INTRODUCTION

Paulownia tomentosa is one of nine species and two varieties of the genus grown natively in China. Because of its unique properties, the wood of this species has been studied and used extensively in China (Cheng 1983a, b). *Paulownia* is a ring to semi-ring porous wood composed of the vessel cells, fiber tracheids, fusiform and strand parenchyma, and ray cells. Vessels are mainly solitary and frequently occluded with tyloses. Two types of fiber tracheids have been reported (Cheng 1983a); type a fiber tracheids possess bordered pit pairs, with even thick cell walls all over the cell and pointed ends, while type b fiber tracheids are equipped with bordered pit pairs, thick walls at both pointed end areas but with thin walls swollen at the middle of the cell. Although the anatomical structure of *Paulownia* has been studied, no literature can be found on the structure of pits at the ultrastructural level.

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FIG. 1. End wall of two ray parenchyma cells. Note the absence of the secondary wall thickening and the presence of numerous plasmodesmata.

FIG. 2. Simple pit pairs between two ray parenchyma cells at the end wall area and characterized by a "nodular like" wall. Plasmodesmata present at the pit membrane and the unpitted area. Also note two "blind pits" leading to an intercellular space and also located at the end wall area (arrows).

FIG. 3. Two simple pit pairs between ray parenchyma cells. Plasmodesmata are present at the pit membrane. Also note the cell wall of the ray parenchyma cell at the fiber tracheid side is thinner than that at the interparenchyma wall.

FIG. 4. Simple pit pairs between two longitudinal parenchyma cells. The edge of the pit border is rounded-off on both sides of the pit pair.

FIG. 5. A simple pit pair between two longitudinal parenchyma cells. Note the extension of one of the pit borders and the "bordered pit like border" on the other side of the pit pair.

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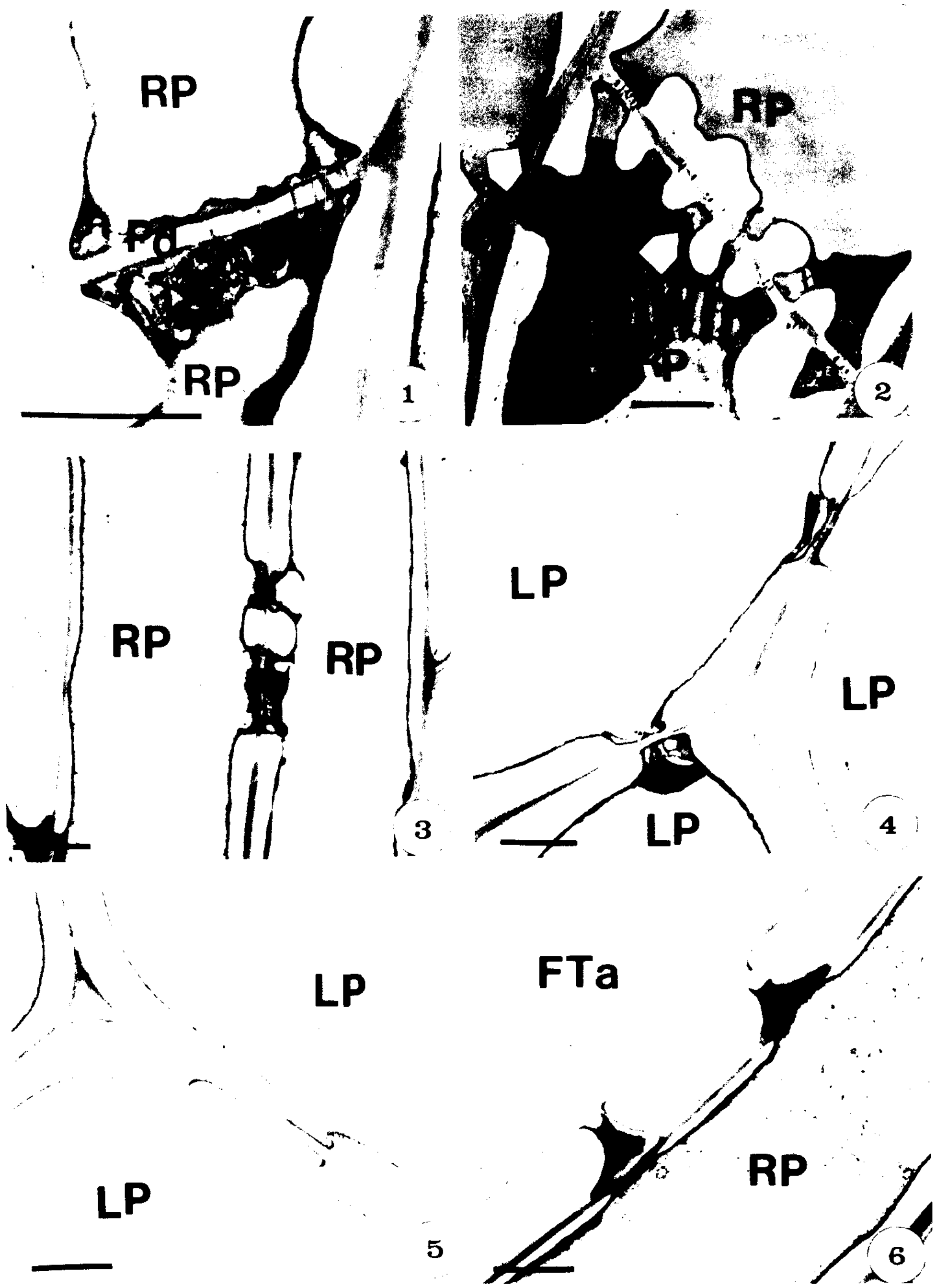

FIG. 6. Two half-bordered pit pairs between a fiber tracheid (Type a) and a ray parenchyma cell. The extension of the pit border on the ray parenchyma cell side is noticed.

Abbreviations.—FT_a—Type a fiber tracheid; FT_b—Type b fiber tracheid; LP—Longitudinal parenchyma cell; Pd—Plasmodesmata; RP—Ray parenchyma cell; V—Vessel. Black scale bar on each figure is equal to 2 μm.

Because of the importance of pitting in the permeability of wood (Cronshaw 1960; Bonner and Thomas 1972; Kininmonth 1972; Thomas 1976), a better understanding of the structure of the pits in this unique and important species would be valuable. The main objectives of this study were to reveal the fine structure of pits in cross-sectional view and to enhance our knowledge of hardwood pitting between various cell types.

MATERIALS AND METHODS

Five match-size sticks of the heartwood *Paulownia tomentosa* were prepared and stained with 1% OsO_4 solution for 6 hours. An extra-low viscosity embedding medium solution (Oliveira et al. 1983) was used for specimen embedding. A vacuum was applied during dehydration with acetone to the embedding stage in order to increase the penetration of the solution. Cross sections, 500–900 Å in thickness, were cut with a diamond knife and mounted on uncoated 200 mesh grids. Observations and micrographs were made with a Philips 300 Transmission Electronic Microscope using 60 K volts.

OBSERVATIONS AND DISCUSSION

Simple pit pairs

Simple pit pairs exist between adjacent ray parenchyma cells (Figs. 1–3) and between adjacent longitudinal parenchyma cells (Figs. 4 and 5). Plasmodesmata are numerous in the pit membrane of the simple pits both at the pitted and unpitted areas, especially at the end wall areas of the ray parenchyma cells. These fine channels may be present with less frequency (Fig. 4) or absent (Fig. 5) in the pit membrane of the longitudinal parenchyma cells. The lack of plasmodesmata in longitudinal parenchyma cells was also reported by Wheeler (1982) in red maple. The pit membrane of the simple pit pairs in parenchyma cells, both in ray and longitudinal parenchyma, of *Paulownia tomentosa* shows the same thickness and electron density as the compound middle lamella of the adjacent cell wall. The continuation of the pit membrane and the compound middle lamella were also reported in *Amburana* by Schmid (1965) and in *Quercus* by Wheeler and Thomas (1981).

The pit borders of simple pit pairs between two ray parenchyma cells show a typical structure with parallel square-edged pit borders on both sides of the pit canal (Fig. 3). In contrast, the edges of the pit border in longitudinal parenchyma simple pits are rounded on both sides of the pit border (Fig. 4). Frequently, the

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FIG. 7. A half-bordered pit pair between a fiber tracheid (Type a) and a longitudinal parenchyma cell. The S_1 layer ends at the rim of the pit chamber (arrow).

FIG. 8. A half-bordered pit between a ray parenchyma cell and a fiber tracheid (Type b) at the middle swollen part of the fiber tracheid. Note the extension of the pit border on the ray parenchyma cell side.

FIG. 9. A "bilateral compound pitting" between a longitudinal parenchyma cell and a vessel cell. A double recess of the pit border in the vessel is observed (arrow).

FIG. 10. A half-bordered pit pair between a ray parenchyma cell and a vessel cell. A tylosis wall (black arrow) with a "compound middle lamella equivalent" (CMLE) layer is arching at the pitting area. A sub-fine layer (small arrow) locates outside of the CMLE adjacent to the vessel side.

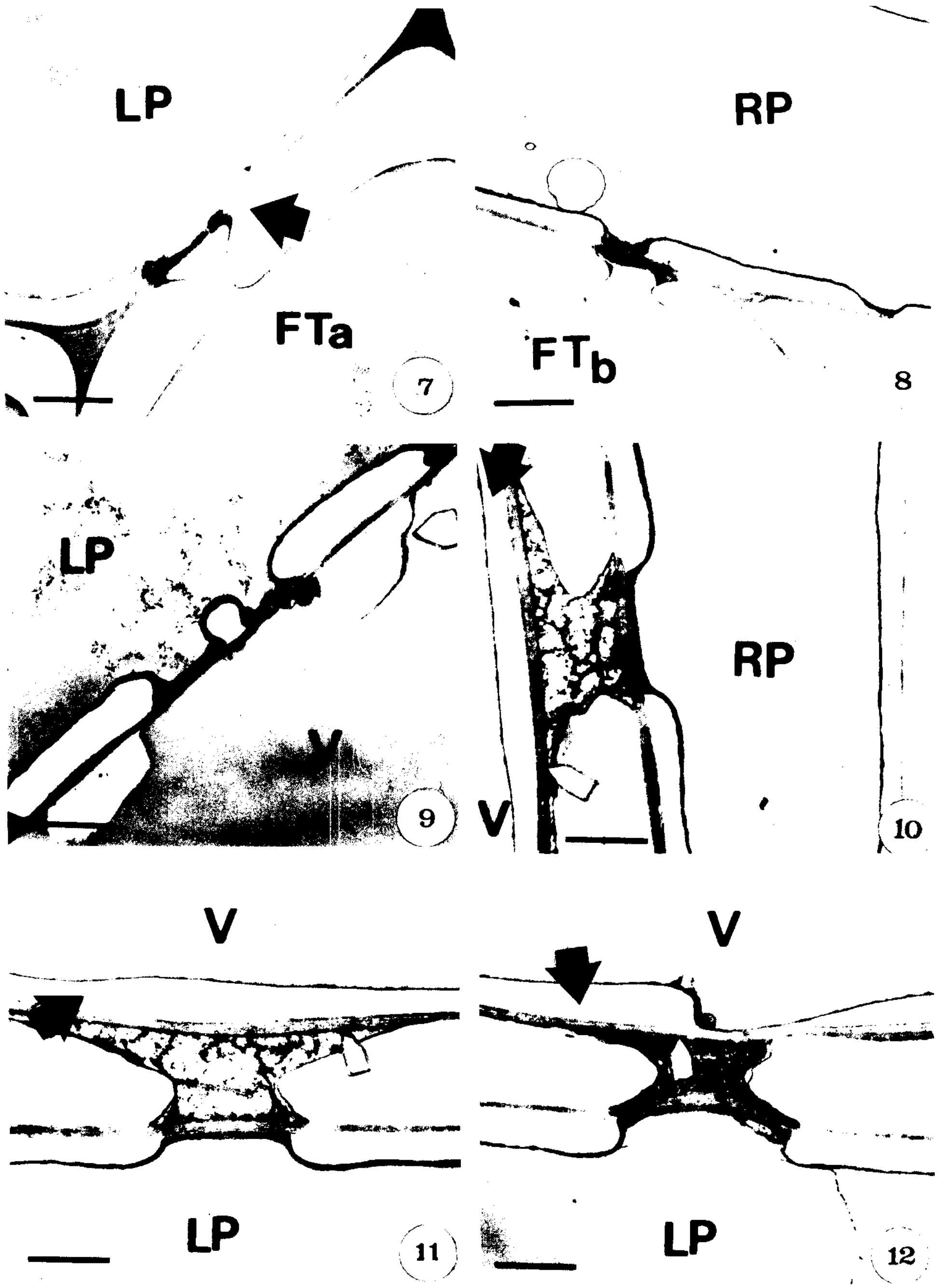

FIG. 11. A half-bordered pit pair between a longitudinal parenchyma cell and a vessel cell. A tylosis wall (large arrow) is arching at the pitting area. A sub-fine layer (small arrow) on the CMLE is also present.

FIG. 12. A half-bordered pit pair between a longitudinal parenchyma cell and a vessel cell. A tylosis wall (black arrow) with a wall recess arching at the pitting area. A sub-fine layer (small arrow) within the CMLE is also detectable in this picture.

pit borders of the simple pits of longitudinal cells do not match (Fig. 5). An extension of the pit borders from one of the longitudinal parenchyma cells was observed in Fig. 5. This extension of the pit border from the parenchyma was also observed in the half-bordered pit pairs.

Half-bordered pit pairs

The shape of half-bordered pit pairs between parenchyma cells and tracheary elements depends upon the types of cells they join and the forms of pit borders on the tracheary element. The typical form of half-bordered pit pairs, with a dome-shaped pit chamber, is illustrated in Figs. 6 and 7. The pit apertures of type a fiber tracheids (Figs. 6 and 7) are narrower than those of type b fiber tracheids (Fig. 8). The difference of pit aperture width may be attributed to the cell-wall thickness. A "bilateral compound pitting" was found between a longitudinal parenchyma cell and a vessel cell (Fig. 9). This type of pit consists of two simple pits on the parenchyma side and one bordered pit on the vessel side. The shapes of the half-bordered pit pairs in parenchyma-vessel pit, mainly due to the forms of pit borders on the vessel side, exhibit a variety of shapes and forms. The pit borders of the vessel cells may show a single dome shape arching (Figs. 10–12), or a double arching structure (Fig. 13, arrow) or no arching at all (Fig. 9 and lower part of Fig. 13) or even recess twice (Fig. 13, arrow). The extension of the pit borders of parenchyma cells, both ray and longitudinal, in the half-bordered pit pair seems to be a general feature of the *Paulownia.*

The pit membrane of half-bordered pit pairs shows a continuation of the compound middle lamella as those in the simple pits but lacking of plasmodesma. In some cases, the pit membrane of half-bordered pit pairs bulges out from the parenchyma side to the tracheary cell side (Figs. 6 and 12). The phenomenon of bulge of the pit membrane may have arisen because of the pressure difference between a living parenchyma and a dead tissue cell in the sapwood region.

Some vessel elements are occluded with tyloses. A so-called "compound middle lamella equivalent" (CMLE) (Koran and Côté 1965) layer is located between the tylosis wall and the vessel wall (Figs. 10–12). This CMLE layer with a sub-fine layer (small arrows) adjacent to the vessel side also extends over the area of the half-bordered pit pairs. These sub-fine layers are mainly situated at the half-bordered pit area and disappear where the CMLE joined with the vessel wall. The function of this sub-layer in the CMLE is still unknown. A recess, resembling a pitting area, is found in the tylosis wall at the half-bordered pit region (Fig. 12). Pits on the tylosis in *Robina pseudoacacia* heartwood were reported by Koran

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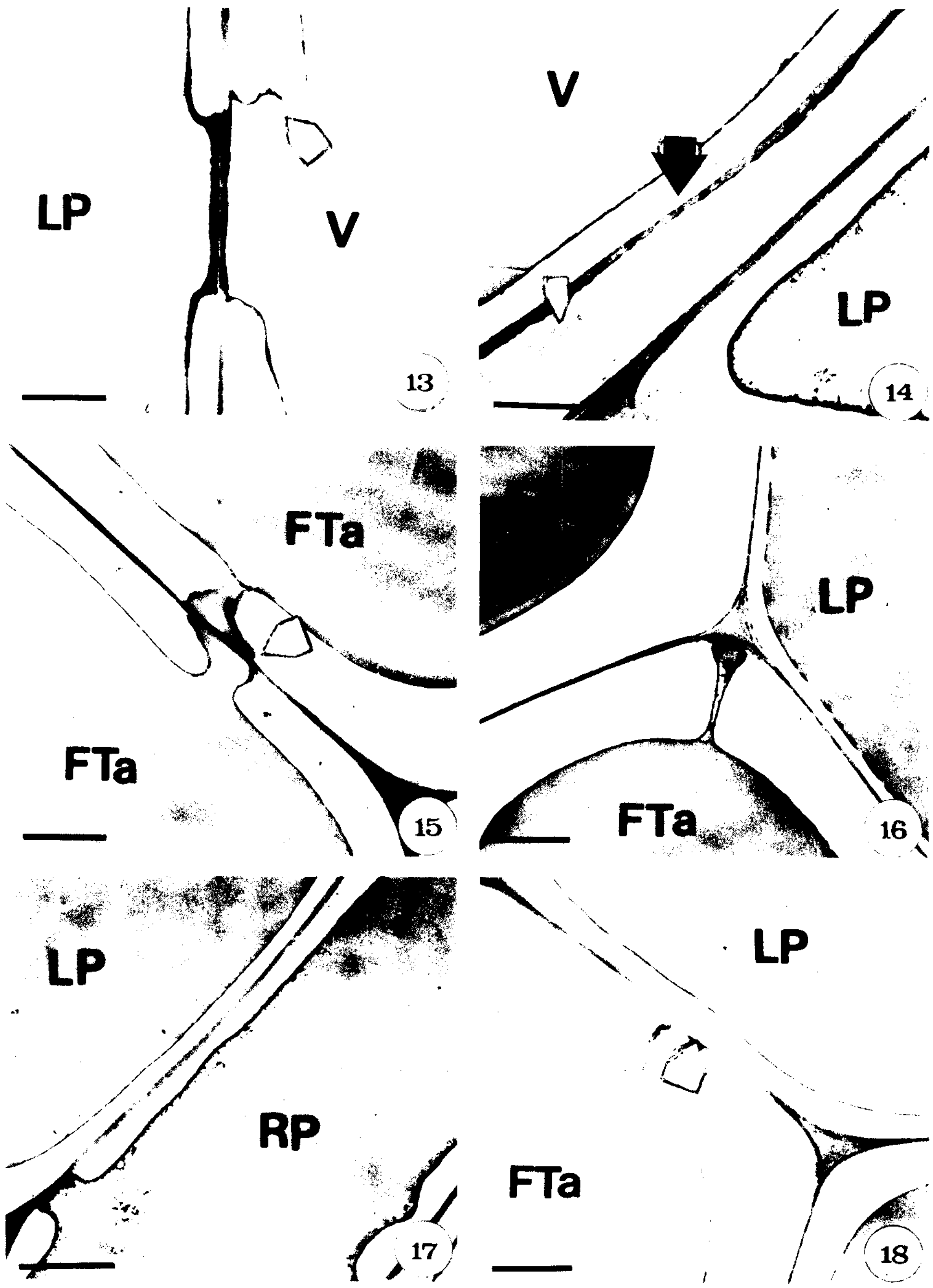
FIG. 13. A "half-bordered pit pair" between a longitudinal parenchyma cell and a vessel cell. Note the extension of the pit border on the longitudinal parenchyma and a double arching pit border on the vessel cell (arrow).

FIG. 14. A tri-layer cell wall that is composed of a tylosis wall (black arrow), a vessel wall, and a longitudinal parenchyma cell wall between a vessel and a longitudinal parenchyma cell. A gap filled with cytoplasmic residue between a tylosis wall and a vessel wall is observed. Also note a layer on the vessel wall at S_3 layer position with different electron density (small arrow).

FIG. 15. A bordered pit pair between the two fiber tracheids (Type a). Note the S_1 layer end at the rim of the pit chamber (arrow).

FIG. 16. A "blind pit" on the fiber tracheid (Type a) cell wall that leads to the cell corner space



among two fiber tracheids and a longitudinal parenchyma cell. Also note that the thickness of the cell wall of the longitudinal parenchyma is equivalent to the S_1 layer of the secondary wall on the fiber tracheid.

FIG. 17. A "blind pit" on the ray parenchyma cell wall leading to a longitudinal parenchyma cell.

FIG. 18. A "blind pit" on the fiber tracheid (Type a) cell wall that leads to a longitudinal parenchyma cell. The S_1 layer of the secondary wall remains at the "pit membrane equivalent" area (arrow).

and Côté (1965). At this tylosis pit recess area, the "pit membrane" is obviously a continuation of the CMLE. The CMLE layer is similar to that of the compound middle lamella of the regular cell wall in terms of electron density, and thickness of the layer, except that an additional subfine layer exists on the side of the CMLE to the vessel wall. The walls of the vessel cell at S_3 position, which is adjacent to the CMLE, show different electron densities (Figs. 10–12, 14). Whether this layer is formed during the formation of the tylosis wall or as a result of impregnation of new wall material into the existing vessel wall is not known.

Bordered pit pairs

A bordered pit pair between two type a fiber tracheids with a dome-shaped pit chamber is shown in Fig. 15. The uneven matched pit borders as indicated in Fig. 15 are found frequently in *Paulownia.* The S_1 layer of the secondary wall of the fiber tracheid ends at the rim of the pit chamber as well can be observed in the half-bordered pit pairs (Figs. 7, 10, and 16). The absence of the S_1 layer in the over-arching portion of the pit border was also reported by Harada (1963 and 1965) in *Fagus crenata* fiber tracheids, by Fengel (1966) in *Fagus sylvatica* fiber tracheids and vessels, Yang (1978) in *Betula alleghanensis* fiber tracheids and vessels, Wheeler and Thomas (1981) in *Quercus falcata* vasicentric tracheids and fiber tracheids and Wheeler (1982) in *Acer rubrum* fibers. In contrast, some published micrographs of *Fagus crenata* (Kishi et al. 1981) and *Ligustrum lucidum* (Parameswaran and Vidal Gomes 1981) showed that the S_1 layer is a part of the pit border. This discrepancy may be due to the sectioning planes through the pit as explained by Kishi et al. (1981). However, the S_1 layer is a common feature of the pit border in softwood bordered pit pairs (Jutte and Spit 1963; Wardrop and Harada 1965; Harada and Côté 1967; Murmanis and Sachs 1969; Imamura and Harada 1973). Whether the absence of the S_1 layer is a unique feature of the above-mentioned species or a common characteristic of the hardwood pit border remains to be determined.

Neither the forms nor the pad-like structure that is an uncommon structure on the hardwood pit membrane could be detected in *Paulownia.* However, this uncommon "thickening" feature was reported by Parameswaran and Liese (1981) in *Ligustrum,* and by Ohtari and Ishida (1978) in dicotyledonous woods. Aspirated pits occur commonly in softwood bordered pit pairs in heartwood region. However, there is no aspirated pit that could be observed in *Paulownia,* although an unusual pit aspiration had been reported by Thomas (1972) in some angiosperms.

Blind pits

A blind pit is defined as a pit, either simple or bordered, without a complementary pit on the other side of the adjacent cell. In this species, the blind pits are found more frequently in ray parenchyma cells than in fiber tracheids. The blind pits may lead to intercellular space (Fig. 2), or to the cell corner (Fig. 16), or to the cell-wall areas (Figs. 17 and 18). Also, they may frequently be found in the end wall area of ray parenchyma (Fig. 2). Blind pits were also observed by Schmid (1965) in *Amburana acreana* and by Wheeler and Thomas (1981) in *Quercus falcata,* but were not seen by Wheeler (1982) in *Acer rubrum.* No blind pits are detected in the longitudinal parenchyma and vessel cells of *Paulownia.*

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