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**Study on the Pit of Wood Cells Using
Scanning Electron Microscopy***

Report 5. Vestured Pits in Japanese
Dicotyledonous Woods**

By

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走査型電子顕微鏡による木材細胞の壁孔に関する研究*

第5報** 本邦産双子葉植物の木部のベスチャード壁孔

大谷 諄*** 石田茂雄***

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Introduction

In 1933, BAILEY (1933) published the results of an extensive survey on "vestured pits" in dicotyledons using the optical microscopy. On the basis of the observations upon 2660 species, 979 genera, 152 families, and 33 orders, he

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came to the following conclusions. "The so-called sievelike appearance of the pits in the vessels of Leguminosae and of other families of dicotyledons is not due to perforations of the pit membranes, but to minute outgrowths from the free surfaces of the secondary wall. These processes are highly refractive, vary in number, shape, and size, and occur not only in the pit chambers but also on the inner surface of the secondary wall of vessels. They appear to be restricted to tracheary elements." BAILEY (1933) first used the term "vestured pits" to describe the pits which have these refractive processes. Thirty years after, the observations by BAILEY (1933) were confirmed by CÔTÉ and DAY (1962), SCHMID and MACHADO (1963) and WARDROP, INGLE and DAVIES (1963) using the electron microscopy. These electron microscopic studies revealed that the nature of vestured pitting reported by BAILEY (1933) was substantially correct. That is, vestures are outgrowths or deposits in the bordered pit chambers of tracheary elements in certain species of dicotyledonous woods.

It was already pointed out by BAILEY (1933) that pit vestures varied in shape remarkably. Although he did not classified the vestures into distinct types, he revealed several different types of vestures such as coralloid (coral-like), papillary, filamentous (branching and anastomosing) and massive. Subsequently, shape of vestures was also observed by the electron microscopy. Although CÔTÉ and DAY (1962) confirmed several types (coralloid, filamentous and massive) described by BAILEY (1933), they reported that papillary was merely an optical artefact. Furthermore, they described that it was difficult to categorize vestures because of great variation and overlapping of structural characteristics and that two broad types, i. e., branched and unbranched, could be suggested. SCHMID and MACHADO (1963) described that vestures varied according to number, size and form, and that they could be characterized into three by main structural types, i. e., simple (papilloid), coralloid, and distinctly branched. KANAZAWA (1968) studied vestured pits of 13 species belonging to Leguminosae and classified the shape of vestures into cylinder, coralloid and filamentous types. SCURFIELD, SILVA and INGLE (1970) examined the architecture of the internal (lumen) surfaces, and the pits in the walls, of the tracheary elements of 22 species distributed amongst the Gnetaceae and 16 angiosperm families, using SEM. They described that any classification of vestures on the basis of their morphology would have to include consideration of their form both in pit chambers and pit apertures. They distinguished the shape of vestures into several types such as filamentous (*Pentacme* type), bead-like (*Leptospermum* type), coralloid (*Gnetum* type) or foliate (*Gymnocladus* type).

It has been reported by many investigators that certain species having vestured pits in the vessel also have vestured pits not only in the tracheid but also in wood fiber. BAILEY (1933) showed bordered pit pair of adjacent fiber tracheids in *Eugenia dichotoma* DC. having papillary projections attached to the margins of both the inner and the outer apertures. YAMANAKA and HARADA (1968) reported that vestures were also present in the bordered pits of tracheids of *Parashorea plicata*. SCURFIELD, SILVA and INGLE (1970) found that vestured pits occurred

in the fibers of *Alstonia scholaris* and *Gonystylus macrophyllus*, and described that the occurrence of vestures was not necessarily associated with the conducting function of cells in which they occurred as suggested by BAILEY (1933). GREAVES (1973) found vested pits in fiber wall of *Eucalyptus maculate* and *Eucalyptus regnans*. BUTTERFIELD and MEYLAN (1974 a) and MEYLAN and BUTTERFIELD (1974) reported that 9 species belonging to 5 genera (*Persoonia*, *Leptospermum*, *Metrosideros*, *Lophomyrtus* and *Neomrytus*) of New Zealand woods had vestures in many of their fiber pits. MEYLAN and BUTTERFIELD (1973) found a trabecula with a vested pit in the vessel member of *Fuchsia excorticata* LINN. f. PARAMESWARAN and LIESE (1974) reported that the vested bordered pits occurred in the tracheids of *Gnetum*.

The resemblance between vestures and warts in vessels of hardwoods has been investigated by the electron microscopy. CÔTÉ and DAY (1962) reported that the structure described by BAILEY (1933) as vested walls corresponded to the warts and that vestures and warts were very similar in appearance in the electron microscope. They believed that vestures and warts were of a similar nature. WARDROP, INGLE and DAVIES (1963) and WARDROP (1965) pointed out that vestures and warts were similar in their structure. SCURFIELD and SILVA (1970) and SCURFIELD, SILVA and INGLE (1970) reported that no distinction could be made between warts and vestures on morphological or chemical grounds and that vestures were regarded as enlarged or conglomerate warts. SCHMID and MACHADO (1964), however, reported that vestures were formed by living protoplasm, whereas warts were the remnants of the dead protoplast.

In the first paper of this series (ISHIDA and OHTANI, 1970), authors reported brief observations of vested pits in black locust using SEM, as a preliminary study on "vested pits" of hardwoods. As a result, it was demonstrated that SEM was an excellent tool for the study of morphological variation of vested pits and that vestures varied considerably in their location, size, shape in pits on the vessel wall within a black locust (ISHIDA and OHTANI, 1970).

As described above, the location, size and shape of the vestures vary considerably in different dicotyledonous woods. In certain species and genera, the vestures are confined to the intervacular pits, whereas in others they occur as well in the half-bordered pit pairs or in the wood fibers (BAILEY, 1933; MEYLAN and BUTTERFIELD, 1974). In order to determine whether such differences are utilized as diagnostic criteria in the identification and classification of the woods or not, fundamental information is needed on the occurrence of vested pits and their morphological variation in each of different dicotyledonous woods. However, survey on morphological variation of vested pits in each species of different Japanese dicotyledonous woods has not been made. It is use of SEM that makes such study possible exactly and effectively.

The authors have studied for these years on the cell wall sculpturing in Japanese dicotyledonous woods as much as possible, using the SEM. In this paper, observations of vested pits in them are described. The dicotyledonous

woods examined contain all the important Japanese hardwoods and, in addition to them, several species having vestured pits were consciously collected, with reference to the list of families with vestured pits published by BAILEY (1933).

The objectives of this report are 1) to show occurrence and morphological variation of vestures in pits on the vessel wall in 20 species of Japanese dicotyledonous woods, 2) to attempt the classification of species having vestured pits on the basis of occurrence and morphological variation of vestures in pits on the vessel wall and 3) to point out the resemblance between vestures and warts.

Materials and Methods

The following species were selected for this study.

No.	Family	Botanical name	Japanese name
1.	Leguminosae	<i>Albizia julibrissin</i> DURAZZ.	Nemunoki
2.		<i>Acacia confusa</i> MERR.	Sôshiju
3.		<i>Gleditsia japonica</i> MIQ.	Saikachi
4.		<i>Caesalpinia japonica</i> SIEB. et ZUCC.	Jaketsuibara
5.		<i>Sophora japonica</i> LINN.	Enju
6.		<i>Maackia amurensis</i> RUPR. et MAXIM. var. <i>buergeri</i> (MAXIM.) C. K. SCHN.	Inuenju
7.		<i>Cladrastis platycarpa</i> (MAXIM.) MAKINO	Fujiki
8.		<i>Euchresta japonica</i> HOOK. fil.	Miyamatobera
9.		<i>Lespedeza bicolor</i> TURCZ. forma <i>acutifolia</i> MATSUM.	Yamahagi
10.		<i>Caragana chamlagu</i> LAM.	Muresuzume
11.		<i>Pueraria lobata</i> (WILLD.) OHWI	Kuzu
12.		<i>Wisteria floribunda</i> (WILLD.) DC.	Fuji
13.		<i>Millettia japonica</i> (SIEB. et ZUCC.) A. GRAY	Natsufuji
14.		<i>Robinia pseudo-acacia</i> LINN.	Harienju
15.	Thymelaeaceae	<i>Daphne odora</i> THUNB.	Jinchôge
16.		<i>Daphne kamtschatica</i> MAXIM. var. <i>jezoensis</i> (MAXIM.) OHWI	Naniwazu
17.	Lythraceae	<i>Lagerstroemia subcostata</i> KOEHNE	Shimasarusuberi
18.		<i>Lagerstroemia indica</i> LINN.	Sarusuberi
19.	Oleaceae	<i>Ligustrum japonicum</i> THUNB.	Nezumimochi
20.		<i>Ligustrum obtusifolium</i> SIEB. et ZUCC.	Ibotanoki

The above species were confirmed to have vestured pits, during the course of study on the cell wall sculpturing in Japanese dicotyledonous woods (212 species, 120 genera, 52 families) using SEM.

wood specimens were collected from living trees and/or obtained from the wood collection of the Department of Forest Products, Hokkaido University. Small blocks were taken from the sapwood of them. The longitudinal radial

and tangential surfaces to be observed were obtained by splitting and by cutting using razor blade. Specimens were finished in the form of ca. 7 mm × 7 mm × 1 mm and dried at room conditions. They were stuck on the brass standard stubs with electric conductive paint. The surfaces to be observed were coated with gold or carbon-gold in a high vacuum. Specimens were examined with the SEM (JSM-2).

Results and Discussion

1. Occurrence and morphological variation of vestures in pits on the vessel wall

Woods of 212 species belonging to 120 genera, 52 families were examined for the presence of vested pits. Vested pits were found in the vessels of only 3 families (Leguminosae, Lythraceae and Oleaceae) and in the fiber tracheids of only one family (Thymelaeaceae). The occurrence of vested pits in the vessels in the Oleaceae and in the fiber tracheids in the Thymelaeaceae is not recorded in the list of families with vested pits published by BAILEY (1933).

Families and genera examined where vested pits were not found are as follows: Salicaceae (*Populus*, *Salix*), Myricaceae (*Myrica*), Juglandaceae (*Platycarya*, *Juglans*), Betulaceae (*Carpinus*, *Ostrya*, *Corylus*, *Betula*, *Alnus*), Fagaceae (*Fagus*, *Quercus*, *Castanea*, *Castanopsis*, *Pasania*), Ulmaceae (*Ulmus*, *Zelkova*, *Celtis*, *Aphananthe*), Moraceae (*Morus*, *Broussonetia*, *Ficus*), Proteaceae (*Helicia*), Trochodendraceae (*Trochodendron*), Cercidiphyllaceae (*Cercidiphyllum*), Berberidaceae (*Berberis*), Magnoliaceae (*Michelia*, *Magnolia*, *Illicium*, *Liriodendron*), Lauraceae (*Cinnamomum*, *Machilus*, *Lindera*, *Parabenzoin*, *Neolitsea*, *Actinodaphne*), Saxifragaceae (*Hydrangea*, *Deutzia*), Hamamelidaceae (*Hamamelis*, *Distylium*), Rosaceae (*Prunus*, *Photinia*, *Eriobotrya*, *Malus*, *Pourthiaea*, *Sorbus*), Rutaceae (*Zanthoxylum*, *Phellodendron*), Simaroubaceae (*Ailanthus*, *Picrasma*), Meliaceae (*Melia*, *Cedrela*), Euphorbiaceae (*Daphniphyllum*, *Mallotus*, *Aleurites*, *Sapium*), Buxaceae (*Buxus*), Anacardiaceae (*Rhus*), Aquifoliaceae (*Ilex*), Celastraceae (*Celastrus*, *Euonymus*), Staphyleaceae (*Euscaphis*), Aceraceae (*Acer*), Hippocastanaceae (*Aesculus*), Sapindaceae (*Sapindus*), Sabiaceae (*Meliosma*), Rhamnaceae (*Zizyphus*, *Hovenia*), Elaeocarpaceae (*Elaeocarpus*), Tiliaceae (*Tilia*), Malvaceae (*Hibiscus*), Sterculiaceae (*Firmiana*), Theaceae (*Camellia*, *Stewartia*, *Ternstroemia*, *Cleyera*, *Eurya*), Flacourtiaceae (*Idesia*), Araliaceae (*Aralia*, *Dendropanax*, *Acanthopanax*, *Evodiopanax*, *Kalopanax*), Cornaceae (*Cornus*), Clethraceae (*Clethra*), Ericaceae (*Leucothoe*, *Pieris*, *Lyonia*, *Enkianthus*, *Vaccinium*), Myrsinaceae (*Myrsine*), Ebenaceae (*Diospyros*), Symplocaceae (*Symplocos*), Styracaceae (*Styrax*, *Pterostyrax*), Oleaceae (*Osmanthus*, *Syringa*, *Fraxinus*), Verbenaceae (*Clerodendrum*), Scrophulariaceae (*Paulownia*), Bignoniaceae (*Catalpa*), Caprifoliaceae (*Sambucus*, *Viburnum*).

It is well known that vested pits occur most commonly in the vessels of some of the more specialized families of dicotyledonous woods, particularly in Leguminosae (KOLLMANN and CÔTÉ, 1968). Occurrence and morphological variation of vestures (i. e., the presence or absence of vestures, localization of vestures

within a pit, and the shape and size of vestures) in pits on the vessel wall of the different species having vested pits, however, have scarcely been studied. Information on the morphological variation of vestures is especially important, not only to determine the value of vested pits in the identification and classification of woods, but also to elucidate the nature of vestures themselves.

Differences of occurrence and morphological variation of vestures in the pits on the vessel wall were found between species. In many cases, morphology of vestures varied according to pit types (i. e., intervacular pits, vessel-ray parenchyma pits, vessel-axial parenchyma pits and vessel-wood fiber pits) on the vessel wall within a species. Therefore, the results obtained are separately described on each pit type.

1-1. Intervascular pits

In all species examined belonging to Leguminosae and Lythraceae, all the intervacular pits were found to be vested pits. Vestures of *Lespedeza bicolor*, *Acacia confusa*, *Lagerstroemia subcostata* and *Lagerstroemia indica* were most remarkable in their development among the species examined in the present study. The vestures of these four species almost filled the entire pit chamber. Vestures in the intervacular pits of *Lespedeza bicolor* were bead-like in appearance when they were viewed from the pit membrane side (Photos 1 and 2). Photo 3 (*Lespedeza bicolor*) and photo 4 (*Acacia confusa*) show the outer surface of the vessel wall obtained from the split specimens. In *Lespedeza bicolor* and *Acacia confusa*, it was often found that some vestures were attached to the pit membranes as shown in Photos 3 and 4. In this connection, WARDROP, INGLE and DAVIES (1963) have reported that vestures of *Eugenia* appear to arise from the pit membrane. On the other hand, HARADA (1968) has found that some vestures of *Parashorea* are closely attached to the pit membrane as if the vestures seem to arise from the pit membrane. However, he has described that it cannot be judged whether the vestures arise from the pit membrane or not, because vestures arising from the pit border can be also considered to have stopped in their growth on the pit membrane. YAMANAKA and HARADA (1968) have reported that vested pits in certain species of Dipterocarpaceae are filled up with resinous substances. In the present study it was also often observed that amorphous substances were deposited on the inner surface of the vessel wall and also within pits of *Lespedeza bicolor* and *Acacia confusa*. Therefore, it should be reasonable to consider that the vestures which are attached to the pit membrane do not arise from the pit membrane but from the pit chamber wall and the tips of the vestures are attached strongly to the pit membrane with amorphous substances such as resinous substances. Vestures (labelled V) of five pits at the right in Photo 3 are removed at their bases from the pit chamber wall during the specimen preparation and the tips of them are attached to the pit membranes. It can be assumed from shape of these vestures that vestures fill the entire pit chamber. Small projections (arrows) on the pit membranes in Photo 3 correspond well to those in *Alistonia scholaris*, which have

already been found by SCURFIELD, SILVA and INGLE (1970). They have described that the occurrence of simple vestures or warts on the surface of the pit chamber floor is a unique feature of the pit of *Alistonia scholaris*. From Photos 1, 2 and 3, vestures of *Lespedeza bicolor* are considered to correspond to "mats of fine texture" of vestures within the pit chamber described by BAILEY (1933). Photo 5 shows vestures viewed from the outer surface of the vessel wall of *Acacia confusa*. Vestures fill the entire pit chamber in Photo 5 but not in Photo 4. From Photos 4 and 5, it can be seen that some larger vestures are complicated in shape and each of them branches in several times from base to tip. Vestures arising from the pit chamber wall near the pit annulus are smaller in size and some of them are unbranched (arrows in Photos 4 and 5).

Vestures of the intervascular pits of *Lagerstroemia subcostata* and *Lagerstroemia indica* belonging to Lythraceae were found to be quite similar each other in their morphology. Vestures in these species were bead-like in appearance when they were viewed from the pit membrane side (Photo 6). Photos 7 and 8 show a complementary pair of the split surfaces of the vessel walls. Each pit labelled by the same figures in the two photographs forms a vested intervascular pit pair. It can be clearly seen from the pair photos that the tips of vestures are not attached to the pit membranes although the vestures almost fill the entire pit chamber. Irregular narrow opening oriented nearly at a right angle to the longitudinal axis of the vessel is found in each pit (Photos 6, 7 and 8). This opening is a common feature in the vested intervascular pit of the two species. In Photos 9 and 10, shape and size of vestures, and their location within a pit can be clearly confirmed. That is, vestures arise obviously from the pit chamber wall to pit chamber, and they become smaller in size and less complicated in shape from the margin of the outer pit aperture toward the pit annulus on the pit chamber wall. Shape of these vestures corresponds to "coralloid" type described by BAILEY (1933).

Vestures of *Albizia julibrissin*, *Pueraria lobata* and *Caesalpinia japonica* are not as remarkable in their development as in four species described just above. In *Albizia julibrissin*, several larger branched vestures always arise from the pit chamber wall near the margin of the outer pit aperture (Photo 11). These vestures have laterally wide-spreading branches. In many cases, these individual vestures are larger in width than in height. Photos 12 and 13 show vestures which are more remarkable in their development than in Photo 11. In such cases, outer pit aperture is almost occluded by vestures. Branches of vestures are very complicated in appearance and are anastomosed (Photo 13). Although the morphology of each vesture within a pit chamber varies considerably, vestures become smaller in size and less complicated in shape toward the pit annulus. No vestures are found on the pit chamber wall near the pit annulus even in the pits in which vestures are most remarkable in their development in this species. In *Pueraria lobata*, shape and development of vestures vary considerably. These examples are shown in Photos 14-16. Branched vestures were found to arise from the

margin of the outer pit aperture regardless of the degree of the development. Although the outer pit aperture is not occluded by vestures in Photo 14, in many cases vestures occluded the outer pit aperture. They were net-like in appearance when they were viewed from the pit membrane side (Photos 15 and 16). It can be seen in Photos 15 and 16 that several vestures with anastomosing branches arise from the margin of the outer pit aperture on the pit chamber wall. Shape of these vestures corresponds to "filamentous" type described by BAILEY (1933). Vestures of *Caesalpinia japonica* also vary considerably in their development. As the present authors have already pointed out in vested intervacular pits of *Robinia pseudo-acacia* (ISHIDA and OHTANI, 1970), there were also little differences in vestures morphology among pits within a given vessel element of these two species. Vestures almost occlude the outer pit aperture in Photo 17, but not in Photo 18. In any case, at least some branched vestures arise from the margin of the outer pit aperture on the pit chamber wall.

In *Gleditsia japonica*, *Sophora japonica*, *Maackia amurensis*, *Cladrastis platycarpa*, *Euchresta japonica*, *Wisteria floribunda*, *Millettia japonica* and *Robinia pseudo-acacia*, larger, branched vestures always arise from the pit chamber wall near the margin of the outer pit aperture, but they do not necessarily occlude the outer pit aperture. Typical examples of each species are shown in Photos 19 (*Wisteria floribunda*), 20 (*Robinia pseudo-acacia*), 21 (*Sophora japonica*), 22 (*Maackia amurensis*) and 23 (*Cladrastis platycarpa*). There are little differences in morphology of vestures among these species. It is a common feature in these species that each larger branched vesture does not anastomose the branches of the other and many smaller unbranched vestures always occur near the base of the larger branched vestures on the pit annulus side and also no vestures are found on the pit chamber wall somewhat widely near the pit annulus.

In *Caragana chamlagu* simple vestures arise from the margin of the pit aperture to the center of it (Photo 24). Even in a surface view of the lumen side, these vestures can be clearly seen (Photo 25) because the pit border is thin at the margin of aperture. The shape of them corresponds well to "massive" or "tooth-like" described by BAILEY (1933).

In two species (*Ligustrum japonicum* and *Ligustrum obtusifolium*) examined belonging to Oleaceae, vested and non-vested pits were found (Photos 26 and 27). In many vested pits, vestures are simple in shape. Forked vestures, however, were also found.

In two species (*Daphne odora* and *Daphne kamtshatica*) examined belonging to Thymelaeaceae*, all the pits were non-vested (Photo 28).

* In *Daphne odora* THUNB. and *Daphne kamtshatica* MAXIM. var. *jezoensis* (MAXIM.) OHWI, vessels usually together with tracheids are arranged in flame-shaped or dendritic groups in cross section. Vessel elements and tracheids are easily distinguished from the fiber-tracheids, because tracheids and small vessel elements generally show the most conspicuous spiral thickenings among the three elements (HAMAYA, 1959). Small vessel elements, however, were very difficult to be distin-

gushed from the tracheids. Therefore, the term "vessel element" of the two species is used in this paper, including tracheid.

1-2. Vessel-ray parenchyma pits

In 11 species examined belonging to *Leguminosae* except *Wisteria floribunda*, *Millettia japonica* and *Robinia pseudo-acacia*, all the vessel-ray parenchyma pits were vestured. In these species except *Pueraria lobata* and *Caesalpinia japonica*, morphology of vestures was quite similar to that of intervascular pits in each species. Some examples of these species are shown in Photos 29 (*Lespedeza bicolor*), 30 (*Cladrastis platycarpa*) and 31 (*Caragana chamlagu*). In *Pueraria lobata* and *Caesalpinia japonica*, vestures in vessel-ray parenchyma pits were less in their development than in the intervascular pits. Pit vestures do not occlude the outer pit aperture as shown in Photo 32 (compare Photo 32 and Photos 14-16).

In *Wisteria floribunda*, *Millettia japonica*, *Robinia pseudo-acacia*, *Lagerstroemia subcostata*, *Lagerstroemia indica*, *Ligustrum japonicum* and *Ligustrum obtusifolium*, vestured and non-vestured pits were found. In *Lagerstroemia subcostata* and *Lagerstroemia indica*, vestures of the intervascular pits were most remarkable in their development among those of all species examined as described above, while the vessel-ray parenchyma pits having no vestures were often observed. Occurrence of vestures within a vessel-ray parenchyma pit varies remarkably not only within a vessel element but also in the limited area of vessel wall. Vestures fill the entire pit chamber (A in Photos 33 and 34), arise partially from the pit border (B in the photos), or are absent (C in the photos). In *Wisteria floribunda*, *Millettia japonica* and *Robinia pseudo-acacia*, vestures of the vessel-ray parenchyma pits were not remarkable in their development than those of the intervascular pits (Photo 35). Some vessel-ray parenchyma pits of these three species were also non-vestured. In *Ligustrum japonicum* and *Ligustrum obtusifolium*, many vessel-ray parenchyma pits were non-vestured. Vestured pits, however, were rarely found. Vestures are simple in shape and arise partially from the edge of pit border near the margin of pit aperture (arrows in Photo 36).

In *Daphne odora* and *Daphne kamtshatica*, all the vessel-ray parenchyma pits were non-vestured (Photo 37).

1-3. Vessel-axial parenchyma pits

Morphology of vestures in vessel-axial parenchyma pits of all the species examined was quite similar to that of vessel-ray parenchyma pits in each species. Some examples of these pits are shown in Photos 38 (*Lespedeza bicolor*), 39 (*Cladrastis platycarpa*), 40 (*Caragana chamlagu*), 41 (*Lagerstroemia subcostata*), 42 (*Millettia japonica*), 43 (*Ligustrum obtusifolium*) and 44 (*Daphne kamtshatica*).

1-4. Vessel-wood fiber pits.

Vasicentric parenchyma was usually found around the vessel of all the species examined belonging to *Leguminosae* and *Lythraceae*. Therefore, the vessels are scarcely contiguous to wood fibers in these species. Very rarely, however, vessel-wood fiber pits were found in *Gleditsia japonica*, *Euchresta japonica*, *Lespedeza*

bicolor and *Caragana chamlagu*. All these pits were vested. Morphology of their vestures is quite similar to that of the intervascular pits in each species. An example of the vessel-wood fiber pit in *Lespedeza bicolor* is shown in Photo 45.

In *Ligustrum japonicum* and *Ligustrum obtusifolium*, vested and non-vested pits were found in the vessel-wood fiber pits like in the other pit types. Morphology of vestures is quite similar to that of the other pit types (Photos 46 and 47).

In *Daphne odora* and *Daphne kamtschatica*, vested pits did not found in the vessel-wood fiber pits like in the other pit types (Photo 48).

Although it is well known that certain species having vested pits in the vessel also have vested pits not only in the tracheid but also in the wood fiber, no vested pits were found in the other cell elements except the vessel in 18 species examined in the present study except *Daphne odora* and *Daphne kamtschatica*. In *Daphne odora* and *Daphne kamtschatica*, all the pits on the vessel

Table 1. Presence or absence of vestures in the pit type on the vessel wall of the species examined

Species	V-V pit	V-R pit	V-P pit	V-F pit
1. <i>Albizia julibrissin</i> DURAZZ.	○	○	○	*
2. <i>Acacia confusa</i> MERR.	○	○	○	*
3. <i>Gleditsia japonica</i> MIQ.	○	○	○	○
4. <i>Caesalpinia japonica</i> SIEB. et ZUCC.	○	○	○	*
5. <i>Sophora japonica</i> LINN.	○	○	○	*
6. <i>Maackia amurensis</i> RUPR. et MAXIM. var. <i>buergeri</i> (MAXIM.) C. K. SCHN.	○	○	○	*
7. <i>Cladrastis platycarpa</i> (MAXIM.) MAKINO	○	○	○	*
8. <i>Euchresta japonica</i> HOOK. fil.	○	○	○	○
9. <i>Lespedeza bicolor</i> TURCZ. forma <i>acutifolia</i> MATSUM.	○	○	○	○
10. <i>Caragana chamlagu</i> LAM.	○	○	○	○
11. <i>Pueraria lobata</i> (WILLD.) OHWI	○	○	○	*
12. <i>Wisteria floribunda</i> (WILLD.) DC.	○	○×	○×	*
13. <i>Millettia japonica</i> (SIEB. et ZUCC.) A. GRAY	○	○×	○×	*
14. <i>Robinia pseudo-acacia</i> LINN.	○	○×	○×	*
15. <i>Daphne odora</i> THUNB.**	×	×	×	×
16. <i>Daphne kamtschatica</i> MAXIM. var. <i>jezoensis</i> (MAXIM.) OHWI**	×	×	×	×
17. <i>Lagerstroemia subcostata</i> KOEHNE	○	○×	○×	*
18. <i>Lagerstroemia indica</i> LINN.	○	○×	○×	*
19. <i>Ligustrum japonicum</i> THUNB.	○×	○×	○×	○×
20. <i>Ligustrum obtusifolium</i> SIEB. et ZUCC.	○×	○×	○×	○×

○: Vested pit ×: Non-vested pit

V-V pit: Intersvascular pit V-R pit: Vessel-ray parenchyma pit

V-P pit: Vessel-axial parenchyma pit V-F pit: Vessel-wood fiber pit

*: No V-F pits were found.

** : Although all the pits on the vessel wall are non-vested, all the pits on the fiber tracheid wall are vested.

wall were non-vestured, while all the pits on the fiber tracheid wall were vestured. There were little differences in vestures morphology between two species. Vestures in the former were merely less in their development than those in the latter. Distinct differences in morphology of vestures among the pits types (i. e., fiber tracheid-vessel pits, fiber tracheid-ray parenchyma pits, fiber tracheid-axial parenchyma pits and inter-fiber tracheid pits) on the fiber tracheid wall could not be found (Photos 49 and 50). Vestures arise from the edge of pit border near the margin of pit aperture and are simple in shape.

The above-described observations on occurrence of vestures in pits on the vessel wall of the species examined can be summarized as in Table 1. Furthermore, the species examined in the present study are divided into 7 groups as indicated in Table 2, on the basis of degree of vestures development in the pit types on the vessel wall. As shown in Tables 1 and 2, occurrence and morphological variation of vestures in pits on the vessel wall indicate common pattern in two species belonging to the same genus in each of Thymelaeaceae, Lythraceae

Table 2. Classification of species examined on the basis of the degree of the vestures development in the pit type

Type	V-V pit	V-R pit	V-P pit	V-F pit	Species
1	+	+	+	+	<i>Albizia julibrissin</i> DURAZZ.* <i>Acacia confusa</i> MERR.* <i>Lespedeza bicolor</i> TURCZ. forma <i>acutifolia</i> MATSUM.
2	++	+	+	*	<i>Caesalpinia japonica</i> SIEB. et ZUCC. <i>Pueraria lobata</i> (WILLD.) OHWI
3	+	+	+	+	<i>Gleditsia japonica</i> MIQ. <i>Sophora japonica</i> LINN.* <i>Maackia amurensis</i> RUPR. et MAXIM. var. <i>buergeri</i> (MAXIM.) C. K. SCHN.* <i>Cladrastis platycarpa</i> (MAXIM.) MAKINO* <i>Euchresta japonica</i> HOOK. fil. <i>Caragana chamlagu</i> LAM.
4	+	+++-	+++-	*	<i>Lagerstroemia subcostata</i> KOEHNE <i>Lagerstroemia indica</i> LINN.
5	+	+--	+--	*	<i>Wisteria floribunda</i> (WILLD.) DC. <i>Millettia japonica</i> (SIEB. et ZUCC.) A. GRAY <i>Robinia pseudo-acacia</i> LINN.
6	+--	+--	+--	+--	<i>Ligustrum japonicum</i> THUNB. <i>Ligustrum obtusifolium</i> SIEB. et ZUCC.
7	-	-	-	-	<i>Daphne odora</i> THUNB.** <i>Daphne kamtschatica</i> MAXIM. var. <i>jezoensis</i> (MAXIM.) OHWI**

++: Vestured pit. Vestures are remarkable in their development.

+: Vestured pit. Vestures are not remarkable in their development.

-: Non-vestured pit

*: No V-F pits were found.

** : Although all the pits on the vessel wall are non-vestured, all the pits on the fiber tracheid wall are vestured.

and Oleaceae, but not in several species from different genera belonging to Leguminosae. Therefore, this fact suggests that occurrence and morphological variation of vestures in pits on the vessel wall can be regarded as a common feature within a genus but not within a family.

2. Shape of vestures

It has already been reported by some investigators that vestures vary remarkably in shape in the different species (BAILEY, 1933; CÔTÉ and DAY, 1962; SCURFIELD, SILVA and INGLE, 1970; MEYLAN and BUTTERFIELD, 1974). Even in the limited number of species examined in the present study, vestures were found to vary remarkably in shape. As CÔTÉ and DAY (1962) have already pointed out, it was also found in the present study that categorizing vestures into distinct types was most difficult, because of variation and overlapping of characteristics in shape. On the basis of many SEM microphotographs recorded in the present study, shape of vestures can be classified into 15 types as shown in Fig. 1.

Types of vestures shown in Fig. 1 are interpreted as follows.

- Type 1 Very small unbranched vesture. Dot- or conical-shaped.
 Type 2 Small unbranched vesture. Massive in shape. This type of vesture corresponds to "massive" described by BAILEY (1933).
 Type 3 Small unbranched vesture. Rod-shaped.
 Type 4 Small branched vesture. Forked in shape.
 Type 5 Small branched vesture. Irregular in shape.
 Type 6 Middle branched vesture. Irregular massive in shape.

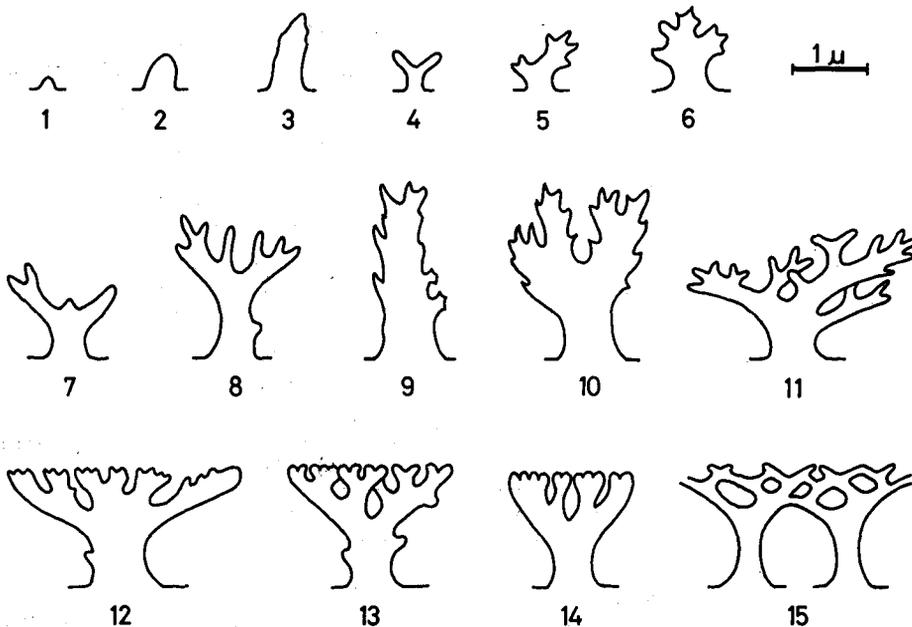


Fig. 1. Types of vestures

- Type 7 Middle branched vesture.
- Type 8 Middle branched vesture. Typical branched vesture with many branches.
- Type 9 Middle branched vesture. Rod-shaped vesture with many small branches.
- Type 10 Large branched vesture. Branched rod-shaped vesture with many small projections.
- Type 11 Large branched vesture. Vesture branches in several times from base to tips. Branches of vesture expand widely.
- Type 12 Large branched vesture. Branches of vesture expand widely. Branches are thicker than those of type 11 and have small projections.
- Type 13 Large branched vesture. Vesture branches in several times from base to tips. Branched fine tips of vesture are closely arranged parallel to the pit membrane. Vesture is bead-like in appearance when it is viewed from the pit membrane side.
- Type 14 Large branched vesture. Coralloid in shape. This type of vesture corresponds to "coralloid" described by BAILEY (1933). Branched fine tips of vesture are closely arranged parallel to the pit membrane. Vesture is bead-like in appearance when it is viewed from the pit membrane side.
- Type 15 Large branched vesture. Branching and anastomosing vesture. This type of vesture corresponds to "filamentous" described by BAILEY (1933). Vesture is net-like in appearance when it is viewed from the pit membrane side.

Vestures of types 1, 4 and 5 are found in many vested pits, regardless of the degree of vestures development in the pits. Vestures of types 2 and 3 are found in the vested pits, in which vestures are little in their development. Vestures of types 6 and 7 are found in the vested pits, in which vestures are moderate or remarkable in their development. Vestures of types 8-11 are found in the vested pits, in which vestures are moderate in their development. Vestures of types 12-15 are found in the vested pits, in which vestures are remarkable in their development.

In many cases, one vested pit does not consist of only vestures of one type but the combination of vestures of several types. For example, a vested intervascular pit of *Wisteria floribunda* (Photo 19) consists of many vestures of types 1, 4, 5, 6, 7, 8, 9 and 10.

Size of vestures is up to ca. $1\ \mu$ in diameter at their base and up to ca. $3\ \mu$ in height. In many types, each vesture is larger in height than in width. When branches of vestures expand widely such as types 11 and 12, however, such vestures are larger in width than in height. Vestures with such branches occasionally reach ca. $5\ \mu$ in their max. width.

Occurrence of types of vestures shown in Fig. 1 in species examined is shown

Table 3. Occurrence of vestures types in the species examined

Species	Types of vestures														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1. <i>Albizia julibrissin</i> DURAZZ.	○			○	○	○	○		○			○			
2. <i>Acacia confusa</i> MERR.	○			○	○	○	○						○		
3. <i>Gleditsia japonica</i> MIQ.	○			○	○	○	○	○	○	○	○				
4. <i>Caesalpinia japonica</i> SIEB. et ZUCC.	○			○	○	○	○	○	○	○	○				
5. <i>Sophora japonica</i> LINN.	○			○	○	○	○	○	○	○	○				
6. <i>Maackia amurensis</i> RUPR. et MAXIM. var. <i>buergeri</i> (MAXIM.) C. K. SCHN.	○			○	○	○	○	○	○	○	○				
7. <i>Cladrastis platycarpa</i> (MAXIM.) MAKINO	○			○	○	○	○	○	○	○	○				
8. <i>Euchresta japonica</i> HOOK. fil.	○			○	○	○	○		○						
9. <i>Lespedeza bicolor</i> TURCZ. forma <i>acutifolia</i> MATSUM.	○			○	○	○	○						○		
10. <i>Caragana chamlagu</i> LAM.	○	○	○	○	○										○
11. <i>Pueraria lobata</i> (WILLD.) OHWI	○			○	○	○	○								
12. <i>Wisteria floribunda</i> (WILLD.) DC.	○			○	○	○	○	○	○	○					
13. <i>Millettia japonica</i> (SIEB. et ZUCC.) A. GRAY	○			○	○	○	○	○	○	○	○				
14. <i>Robinia pseudo-acacia</i> LINN.	○			○	○	○	○	○	○	○					
15. <i>Daphne odora</i> THUNB.	○	○		○	○										
16. <i>Daphne kamtschatica</i> MAXIM. var. <i>jezoensis</i> (MAXIM.) OHWI	○	○	○	○	○										
17. <i>Lagerstroemia subcostata</i> KOEHNE	○			○	○									○	
18. <i>Lagerstroemia indica</i> LINN.	○			○	○									○	
19. <i>Ligustrum japonicum</i> THUNB.	○	○	○	○	○										
20. <i>Ligustrum obtusifolium</i> SIEB. et ZUCC.	○	○	○	○	○										

○: Present

in Table 3. Vestures of types 1, 4 and 5 were found in the vested pits of all species examined. Vestures of types 2 and 3 were found in the vested pits on the vessel wall of *Caragana chamlagu*, *Ligustrum japonicum* and *Ligustrum obtusifolium* and on the fiber tracheid wall of *Daphne odora* and *Daphne kamshatica*. Vestures of types 6 and 7 were found in the vested pits on the vessel wall of all species examined belonging to Leguminosae except *Caragana chamlagu*. Vestures of types 8, 9 and 10 were found in vested pits of many species belonging to Leguminosae. Vestures of type 11 were found in vested pits of only 4 species (*Gleditsia japonica*, *Sophora japonica*, *Maackia amurensis* and *Cladrastis platycarpa*) belonging to Leguminosae. Vestures of types 12, 13, 14 and 15, large in size and complicated in shape, were found in only limited species, respectively. Vestures of type 12 were found in the vested pits of only *Albizia julibrissin*. Vestures of type 13 were found in the vested pits of two species (*Acacia confusa* and *Lepedeza bicolor*). Vestures of type 14 were found in the vested pits of two species (*Lagerstroemia subcostata* and *Lagerstroemia indica*) belonging to Lythraceae. Vestures of type 15 were found in the intervascular pits of *Pueraria lobata*.

Occurrence of vestures types in shape shows a certain pattern within a genus, as shown in *Daphne*, *Lagerstroemia* and *Ligustrum*. Therefore, this fact suggests that shape of vestures can be also regarded as a common feature within a genus. Especially, as the vestures of characteristic shape such as types of 12–15 are found in only limited species and genera, they can be utilized as diagnostic criteria for the identification of these species.

3. Distribution of vestures within a vested pit

Vestures show a certain pattern in their distribution within a pit associated with degree of their development. Location of vestures occurrence on the pit chamber wall tends to become wider from the margin of the outer pit aperture toward the pit annulus, as vestures are more remarkable in their development. When vestures are little in their development, they arise from only the margin of the outer pit aperture on the pit chamber wall. In such a case, several simple vestures project from the margin of the outer pit aperture toward the center of it (Photos 24, 25, 26, 40 and 43). When vestures are moderate in their development, that is, vestures occlude outer pit aperture but not occupy the entire pit chamber, larger branched vestures arise from the margin of the outer pit aperture. They project toward the pit membrane and, in many cases, branches of them expand widely in the pit chamber (Photos 11, 21, 22 and 23). In this case, many small simple vestures always occur near the base of larger branched vestures on the pit annulus side. When the vestures are most remarkable in their development, vestures arise from the all pit chamber wall extending from the margin of the outer pit aperture to the pit annulus (Photos 2, 5 and 6). Vestures arising from the marginal zone of the outer pit aperture are larger in size and more complicated in shape, and they become smaller in size and less complicated in shape toward the pit annulus. Small unbranched vestures always occur near

the pit annulus. All vestures project toward the pit membrane until they reach the pit membrane. Tips of them are closely arranged parallel to the pit membrane. In such cases, therefore, pit chamber is almost occupied by vestures.

4. Projections on the inner (lumen) surface of the vessel wall

In species having vested pits in which vestures are remarkable in their development, i. e., in *Albizia julibrissin*, *Acacia confusa*, *Caesalpinia japonica*, *Lespedeza bicolor*, *Lagerstroemia subcostata* and *Lagerstroemia indica*, projections were always found on the inner (lumen) surface of the vessel wall. In *Albizia julibrissin*, branched and unbranched projections are irregularly distributed on the inner surface of the vessel wall (Photo 51). Projections on the inner surface of *Acacia confusa* are similar to those of *Lespedeza bicolor* in their shape, size and distribution. Although small unbranched projections are almost uniformly distributed on the inner surface in these two species, projections arising from the marginal zone of the inner pit aperture vary considerably in their development. When the projections are remarkable in their development, they completely obscure the outline of the inner pit apertures (Photo 52). These projections aggregate and are larger in size compared with unbranched ones which are almost uniformly distributed on the inner surface of the vessel wall except pit regions. In this connection, it has already been pointed out by BAILEY (1933) that vestures project more or less into the lumen of the vessel. YAMANAKA and HARADA (1968) have reported that vested pits of *Pentacme contorta* and *Dryobalanops aromatica* have vestures which overflow into the vessel lumen from the pit chamber. SCURFIELD, SILVA and INGLE (1970) have also reported that spreading of vestures beyond pit apertures is the usual feature in species of *Eucalyptus* and *Acacia*. BUTTERFIELD and MEYLAN (1974, a) have reported that vestures of almost all the vessel pits of *Persoonia toru* A. CUNN. line the pit canals and completely occlude most of the pit apertures, forming prominent mounds often extending over the vessel walls well beyond the limits of the pit apertures. In *Acacia confusa* and *Lespedeza bicolor*, larger aggregated projections were also irregularly distributed on the vessel wall except pit apertures (Photo 53). Photo 54 shows the transitional area between larger aggregated projections and smaller uniformly distributed ones. It can be seen in this photograph that the smaller uniformly distributed projections successively change into the larger aggregated ones in their shape and size. Although the former is unbranched, the latter is branched and anastomosed (Photo 55).

Projections on the inner surface of the vessel wall of *Caesalpinia japonica* were found to be unique in their shape, size and distribution. The projections vary remarkably in their shape, size and distribution. Photos 56 and 57 show the difference of their development between the vessel elements. Branched and unbranched projections are scattered in Photo 56, while both projections are densely distributed in Photo 57. Larger branched projections tend to be irregularly aggregated (Photo 58). They, however, were often found to be aggregated in the depressions such as cell corner or near the rim of simple perforation

plates. Photo 59 shows a part of Photo 58. Some of these projections branch in several times from base to tip (Photo 60).

In *Lagerstroemia subcostata* and *Lagerstroemia indica*, small unbranched projections are uniformly distributed on the inner surface of the vessel wall (Photo 61). Larger aggregated projections were not found near the inner pit apertures.

Except the above described 6 species (*Albizia julibrissin*, *Acacia confusa*, *Caesalpinia japonica*, *Lespedeza bicolor*, *Lagerstroemia subcostata* and *Lagerstroemia indica*), no projections were found on the inner surface of the vessel wall in the other species (Photo 62). It should be noticed that vestures of these species are less in their development than those of the 6 species having the projections on the inner surface of the vessel wall.

The following several observations are noticeable :

1) In species examined in the present study having spiral thickening on the vessel wall, no projections were usually found on the inner surface of the vessel wall. In *Sophora japonica*, *Gleditsia japonica* and *Cladrastis platycarpa*, however, it was found that projections arise from the spiral thickenings occasionally (Photos 63 and 64). These projections resemble in shape and size the vestures in each species. They are branched and unbranched, and arise not from the top but from the sides of the spiral thickenings. Such spiral thickenings appear to be of T-shape in their cross sectional view.

2) When spiral thickening meets pit aperture, in some cases, the end of spiral thickening enters into the pit chamber from the pit aperture and branches at the tip like vestures in appearance (arrows in Photo 65). Such facts were found in *Sophora japonica*, *Gleditsia japonica* and *Maackia amurensis*. In Photo 66, a part of spiral thickening is separated from the vessel wall together with the branched end (arrow in the photo). That is, this photograph shows that branched end is continuous to the spiral thickening. This fact suggests resemblance in nature between vestures and spiral thickenings.

3) Similarity in basic architecture between pits and perforations has been illustrated by some investigators (BUTTERFIELD and MEYLAN, 1971; ISHIDA and OHTANI, 1974; MEYLAN and BUTTERFIELD, 1972; OHTANI and ISHIDA, 1973). Perforations are often overarched by prominent border of secondary wall material in a similar way to that found in bordered pits. Therefore, it is supposed that vestures-like projections also occur on the perforation rim in the species having vested pits. Recently, BUTTERFIELD and MEYLAN (1974), MEYLAN and BUTTERFIELD (1975) have reported that vestures occasionally occur in the corners of the scalariform perforation plate openings in *Neomyrtus pedunculata*. Perforation plates of all the species examined in the present study were simple and no vestures-like projections were found on the rim of simple perforation except that of *Caragana chamlagu*. Vestures-like projections were often observed on the rim of simple perforation of *Caragana chamlagu* (Photo 67). These projections are very similar in shape and size to pit vestures of the same species.

5. Resemblance between vestures and warts

The term "vestured pit" was first used by BAILEY (1933) to describe the bordered pits in dicotyledons which have minute projections arising from the pit border. He confirmed that these projections also occurred on the inner surface of secondary walls of vessels as well as the bordered pits. On the other hand, "warts" were first found by KOBAYASHI and UTSUMI (1951), and by LIESE (1951), on the inner surface and on the inside of the pit chamber of tracheid wall of *Pinus* species (LIESE, 1965). Subsequently many workers revealed the presence of this structure in tracheids in the other gymnosperms. Therefore, the terms "vestures" and "warts" are derived from the expression of minute projections on the inner surface and the pit chamber wall of the vessel wall of angiosperm and of the tracheid wall of gymnosperm, respectively.

Judging from observations on vestures and warts reported until now, the morphological differences between "vestures" of angiosperm and "warts" of gymnosperm are mainly recognized in their size and shape. In general, the vestures are larger in size and more complicated in shape compared with the warts. Therefore, the smaller unbranched projections on the inner (lumen) surface of the vessel wall and wood fiber wall which are almost similar in size and shape to warts on the inner surface of the tracheid wall of gymnosperm have been called as "warts" even in angiosperm. However, "warts" have been examined less intensively in angiosperms than in gymnosperms (OHTANI and ISHIDA, 1973; PARHAM and BAIRD, 1974).

According to such conception, smaller unbranched projections which are uniformly distributed on the inner surface of the vessel wall of *Acacia confusa*, *Lespedeza bicolor*, *Lagerstroemia subcostata* and *Lagerstroemia indica*, correspond to so-called warts. Larger branched projections which occlude the inner pit apertures or are aggregated irregularly on the inner surface of the vessel wall of *Lespedeza bicolor* and *Acacia confusa* differ from the so-called warts judging from their shape and size. They should be preferably considered to correspond to vestures. However, these two sorts of projections, i. e., the smaller unbranched projections and the larger branched ones, cannot be clearly distinguished on the basis of their size and shape because the former successively changes into the latter in size and shape at the area where the both projections meet. In this connection, SCURFIELD, SILVA and INGLE (1970) have reported that spreading of vestures beyond pit apertures in *Acacia* makes it difficult to make any clear distinction between vestures and warts. GREAVES (1973) has observed that the vestures develop extensively across the pit structure on the inner wall of vessel in *Eucalyptus regnans*, and has pointed out an analogy between warts and vestures. Furthermore, branched projections on the inner surface of the vessel wall of *Albizia julibrissin* and *Caesalpinia japonica*, and larger branched projections aggregated irregularly on the inner surface of the vessel wall of *Caesalpinia japonica* cannot be also called as "warts". They should be rather considered to be vestures. As these larger branched projections, however, exist together with the

smaller unbranched ones and the transitional projections between both ones also occur, both projections cannot be clearly distinguished.

As shown in the present study, projections arising from the pit chamber wall, i. e., pit vestures, vary remarkably in size and shape even within a pit. Smaller unbranched vestures on the pit chamber wall found in all the species examined correspond to "warts" according to their shape and size. As recognized with regard to projections on the inner surface of the vessel wall, continuous transition from smaller unbranched vestures (i. e., warts-like) to typical larger branched vestures is also found on the pit chamber wall. Furthermore, as shown in Fig. 1 and Table 3, smaller simple vestures were found in more species compared with larger complicated ones. Especially, vestures of types 1, 4 and 5 in Fig. 1 were found in all the species examined. In other words, these vestures are considered to indicate general morphological features of vestures in size and shape. Therefore, the conception that vestures are larger in size and more complicated in shape compared with warts, is not necessarily correct.

These facts as described above suggest that all the projections on the inner surface of the vessel wall including pit chamber wall are essentially the same structure even if they vary considerably in shape, size and distribution.

It has already been pointed out by CÔTÉ and DAY (1962), SCURFIELD and SILVA (1970) and SCURFIELD, SILVA and INGLE (1970) that vestures and so-called warts are similar in chemical nature. In addition, the preliminary observation by the present authors suggested the similarity of the two structures in some of their chemical natures. In *Albizia julibrissin*, *Lespedeza bicolor*, *Acacia confusa*, *Caesalpinia japonica* and *Lagerstroemia subcostata*, which have always projections on the inner surface of the vessel wall, the morphological change of the two structures, i. e., vestures and projections on the inner surface of the vessel wall, after being subjected to one of the following chemical treatments was observed using SEM. 1) Alcohol-benzene (24 hr.). 2) Sodium chlorite-acetic acid (5 hr. at 80°C) (THOMAS, 1968). 3) Hydrogen peroxide-acetic acid (1.5 hr. at 90°C). Vestures and projections on the inner surface of the vessel wall remained intact after the treatment of 1). Although CÔTÉ and DAY (1962) have reported that neither the vestures nor the warts appear to be badly degraded by the treatment of acidified sodium chlorite at 75°C for four hours, both structures were degraded considerably by the treatment of 2) in the present study. They were almost dissolved by the treatment of 3). Both two structures were attacked in the same degree in either case of the two treatments. Although further study is needed to elucidate their chemical nature, these results suggest the similarity of two structures in some chemical natures.

Special consideration needs to be given to the larger branched projections on the inner surface of the vessel wall, such as aggregated projections of *Acacia confusa*, *Caesalpinia japonica* (Photos 58, 59 and 60), *Lespedeza bicolor* (Photos 53, 54 and 55) and projections on the spiral thickenings of *Sophora japonica* (Photos 63 and 64), *Gleditsia japonica* and *Cladrastis platycarpa*. The location,

shape and size of them, as well as vestures, invite speculation as to their formation. It is well known that vestures and so-called warts are formed at the latest stage of the cell wall thickening. In the latest stage of vessel differentiation, the cytoplasm is confined to a narrow peripheral zone which is bounded on the outside by the plasma membrane and on the inside by the vacuolar membrane. The plasma membrane is in close contact with the inner surface of the vessel wall. The components of the cytoplasm of the vessel at the latest stage are ER, dictyosome, mitochondrion and so on, which are considered to be concerned in the formation of vestures and warts (CRONSHAW, 1965; WARDROP, 1965). Distribution, shape and size of all the projections on the inner surface of the vessel wall (including the vestures), are considered to be mainly determined by the distribution of these cytoplasmic components and the period until their disorganization. It is easily assumed that the cytoplasmic components, which are concerned in the formation of the projections, are concentrated and the activity of the protoplast is prolonged in the depressions of the vessel wall such as pit chamber, cell corner and so on compared with elsewhere on the vessel wall. Such conditions will bring about the occurrence of larger branched projections, aggregated in the depressions of the vessel wall. In addition, it is true that complicated configuration of the region of cell wall where the projections will be formed is also included in this condition. Such conception is supported by the evidence that concentrated and larger warts occur at the tracheid corner of certain species of softwoods (LIESE, 1965; OHTANI and FUJIKAWA, 1971).

Although further investigation on chemical natures and origin of vestures and so-called warts is necessary, it is the strong contention of the authors that vestures and so-called warts of vessel are very similar in appearance, nature and origin. That is, all the projections on the inner surface of the vessel wall including the surface of the vessel wall lining the pit cavity should be regarded as of the same structure.

Summary and Conclusions

1) Occurrence and morphological variation of vestures in pits on the vessel wall were observed upon 20 species, 17 genera, 4 families of Japanese dicotyledonous woods using SEM. Differences of occurrence and morphological variation of vestures in the pits on the vessel wall were found between species. In many cases, morphology of vestures varied according to pit types (i. e., intervacular pits, vessel-ray parenchyma pits, vessel-axial parenchyma pits and vessel-wood fiber pits) on the vessel wall within a species. Occurrence of vestures in pit types on the vessel wall of the species examined is shown in Table 1. Furthermore, 20 species examined were divided into 7 groups, on the basis of degree of development of vestures in pit types on the vessel wall (Table 2). In 18 species except *Daphne odora* and *Daphne kamtshatica*, no vested pits were found in the cells except the vessel. In *Daphne odora* and *Daphne kamtshatica*, however, all the pits on the vessel wall were non-vestured, while all the pits on the fiber

tracheid were vested. These evidences suggest that vested pits can be obviously utilized as diagnostic criteria in the identification and classification of dicotyledonous woods, although further survey on many species is necessary.

2) Even in the limited number of species examined in the present study, vestures varied remarkably in shape and size. Categorizing pit vestures into distinct types was very difficult, because of variation and overlapping of characteristics in shape. An attempt categorizing vestures into 15 types was made on the basis of SEM microphotographs recorded in the present study (Fig. 1).

3) Vestures showed a certain pattern in their distribution within a pit associated with degree of their development. Location of vestures occurrence on the pit chamber wall becomes wider from marginal zone of outer pit aperture to pit annulus, as pit vestures are more remarkable in their development. And also, vestures become smaller in size and less complicated in shape from marginal zone of outer pit aperture to pit annulus.

4) Projections are always present on the inner surface of the vessel wall in the species having vested pits in which vestures are remarkable in their development, i. e., in *Albizia julibrissin*, *Acacia confusa*, *Caesalpinia japonica*, *Lespedeza bicolor*, *Lagerstroemia subcostata* and *Lagerstroemia indica*. In *Albizia julibrissin*, small unbranched projections are irregularly distributed together with branched ones. In *Caesalpinia japonica*, projections vary remarkably in their distribution, shape and size. In *Acacia confusa* and *Lespedeza bicolor*, smaller unbranched projections are uniformly distributed, while larger branched projections frequently obscure the inner pit apertures and are irregularly aggregated on the inner surface of the vessel wall except the pit region. In *Lagerstroemia subcostata* and *Lagerstroemia indica*, smaller unbranched projections are uniformly distributed. In the species except the above described species, no projections are found on the inner surface of the vessel wall. The following observations are noticeable. 1) In *Sophora japonica*, *Gleditsia japonica* and *Cladrastis platycarpa*, vestures-like projections arise occasionally from the spiral thickenings on the vessel wall. 2) In *Sophora japonica*, *Gleditsia japonica* and *Maackia amurensis*, when the spiral thickening meets the pit aperture, in some cases the tip of it enters from the pit aperture into the pit chamber and branches like vestures in appearance. 3) In *Caragana chamlagu*, vestures-like projections are often found to arise from the rim of simple perforation. 4) Judging from the shape, size and distribution of the vestures and the projections on the inner surface of the vessel wall shown in the present study, and in addition, considering chemical nature, origin and formation process of the two structures, vestures and so-called warts are considered to be substantially of the same nature. Therefore, the two structures should be regarded as of the same structure on the inner surface of the vessel wall including the surface of the vessel wall lining the pit cavity.

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要 約

本邦産双子葉植物 (4科, 17属, 20種) の2次木部の道管壁における壁孔内のベスチャー (Vestures) の出現とそれらの形態変動および道管壁内表面の突起物の形態が, 走査型電子顕微鏡を用いて観察された。得られた結果を要約すれば, 次の通りである。

1. 供試樹種の道管壁における壁孔のベスチャーの出現およびそれらの形態変動の差異が, 樹種間で認められた (Photo 1~50)。同一樹種内でのベスチャーの出現およびそれらの形態変動は, 道管壁の壁孔の種類 (即ち, 道管相互壁孔, 道管・放射柔細胞間壁孔, 道管・軸方向柔細胞間壁孔, 道管・木部繊維間壁孔) により差異が認められた。Table 1は, 供試樹種について道管壁の壁孔のベスチャーの出現状況を道管壁の壁孔の種類別に示したものである。また, Table 2は, 供試樹種について道管壁の壁孔のベスチャーの発達程度を道管壁の壁孔の種類別に示したものである。Table 2に示されているように, 道管壁の壁孔におけるベスチャーの形態の変動傾向により, 本研究で観察された20樹種は7グループに分けることが出来る。Table 1およびTable 2より明らかなように, 道管壁の壁孔のベスチャーの出現およびそれらの形態変動の傾向は, 同じ属に属する樹種では同じパターンを示したが, 同一科内では属

が異なれば同じパターンを示さない例が認められた。即ち、ベスチャーの出現およびそれらの形態変動の傾向は、属の1つの特徴であることが推定される。したがって、本研究で得られた観察結果は、ベスチャード壁孔は双子葉植物の材部の識別および分類のための指標となりうることを示唆している。

2. 本研究で観察された限られた樹種においてさえ、個々のベスチャーの形および大きさは極めて変化にとんでいる。個々のベスチャーの形には微妙な変形が、また、個々のベスチャー間にはそれらの形の部分的な重複が認められるので、ベスチャーの形を明確ないくつかのタイプに分けることはむづかしい。しかし、本研究で記録された多くの SEM 写真をもとにして、ベスチャーの形を便宜上 15 のタイプに区別してみた (Fig. 1)。

3. 1 ベスチャード壁孔内でのベスチャーの分布様式は、ベスチャーの発達程度と関連して一定のパターンを示す。即ち、ベスチャーの発達が著しくない場合、形の単純な比較的小さなベスチャーが外孔口周縁の pit chamber wall (壁孔縁の壁孔室に面している部分) のみから外孔口の中心に向かって生じる。ベスチャーの発達が著しくなるにしたがい、それらの発生個所は壁孔環の方へ広がる。枝分れした大きなベスチャーは外孔口周縁の pit chamber wall から生じ外孔口を閉塞するように発達している。そして、壁孔環の方へゆくにしたがいベスチャーは小さくなりそれらの形は単純になる。ベスチャーの発達が最も著しい場合、ベスチャーは外孔口周縁部から壁孔環付近にいたる全 pit chamber wall から生じる。また、すべてのベスチャーは壁孔壁にむかって壁孔壁に達するまで発達し、壁孔室全体をみたくことになる。

4. ベスチャーの発達の顕著なベスチャード壁孔を有する樹種 (ネムノキ, ソーシジュ, ジャケツイバラ, ヤマハギ, シマサルスベリ, サルスベリ) の道管壁内表面には常に突起物が存在する。ネムノキの道管壁内表面には、小さな枝分れしない突起物と比較的大きな枝分れした突起物が混在する (Photo 51)。ジャケツイバラの道管壁内表面の突起物の存在状態はきわめて特異である。即ち、それらの分布、形、大きさは非常に変化にとんでいる (Photo 56~60)。ソウシジュ, ヤマハギの道管壁内表面には、小さな枝分れしない突起物と比較的大きな枝分れした突起物が存在する。前者はほぼ均一に分布しているが、後者は密集し群をなして不規則に分布している (Photo 53~55)。また、密集した比較的大きな枝分れした突起物は内孔口付近にしばしば認められ、内孔口を閉塞する場合がある (Photo 52)。シマサルスベリ, サルスベリの道管壁内表面には、小さな枝分れしない突起物がほぼ均一に分布している (Photo 61)。上記 6 樹種以外の樹種の道管壁内表面には、突起物は殆んど存在しない (Photo 62)。

道管壁内表面の突起物と関連して、次のいくつかの興味あることが観察された。

i. エンジュ, サイカチ, フジキの小道管のらせん肥厚からベスチャーと同じ形態の突起物が生じている場合がある (Photo 63, 64)。

ii. エンジュ, サイカチ, イヌエンジュの小道管のらせん肥厚が壁孔口と出会う場合、それらのらせん肥厚が壁孔口から壁孔室内に入りこみ、その先端がベスチャーのように枝分れし

ていることがしばしばある (Photo 65, 66)。

iii. ムレスズメの道管要素間の単せん孔のせん孔縁には、しばしばベスチャーと同じ形の突起物が存在する (Photo 67)。

5. 本研究で観察されたベスチャーと道管壁内表面の突起物の形、大きさ、分布をもとにし、さらに、両者の化学的性質、起源、形成過程をも考えあわせると、ベスチャーといわゆるいぼ状突起 (Warts) は本来同じ性質の突起物であることが推定される。即ち、双子葉植物の木部における道管壁の壁孔内にあるベスチャーと道管壁内表面にあるいわゆるいぼ状突起は、壁孔腔に面している道管壁内表面をも含めて、道管壁内表面の同一突起物として取扱われるべきものであろう。

Explanation of photographs

- Photo 1.** *Lespedeza bicolor* TURCZ. forma *acutifolia* MATSUM. Vestured intervacular pits in the wall of a vessel element viewed from the outer surface.
- Photo 2.** *Lespedeza bicolor* TURCZ. forma *acutifolia* MATSUM. Enlarged view of the vestured intervacular pits shown in Photo 1.
- Photo 3.** *Lespedeza bicolor* TURCZ. forma *acutifolia* MATSUM. Vestures (labelled V) of the five intervacular pits at the right in this photograph are removed at their base from pit chamber wall and tips of them are attached to the pit membranes. Small projections (arrows) are found on the pit membranes.
- Photo 4.** *Acacia confusa* MERR. Pit vestures are cut during specimen preparation and tips of them (labelled V) are attached to the pit membranes. Small unbranched vestures (arrows) are found on the pit chamber wall near the pit annulus.
- Photo 5.** *Acacia confusa* MERR. Vestured intervacular pits in the wall of a vessel element viewed from the outer surface. Small unbranched vestures (arrows) are found on the pit chamber wall near the pit annulus.
- Photo 6.** *Lagerstroemia subcostata* KOEHNE A vestured intervacular pit in the wall of a vessel element viewed from the outer surface.
- Photos 7 and 8.** *Lagerstroemia subcostata* KOEHNE A complementary pair of split surfaces of adjacent vessel elements. Each pit labelled by the same figures forms a vestured intervacular pit pair.
- Photo 9.** *Lagerstroemia subcostata* KOEHNE Split vessel wall showing pit vestures of intervacular pits. The outer part of vessel wall is removed.
- Photo 10.** *Lagerstroemia subcostata* KOEHNE Split vessel wall showing pit vestures of intervacular pits. The inner part of vessel wall is removed.
- Photo 11.** *Albizia julibrissin* DURAZZ. Vestured intervacular pits in the wall of a vessel element viewed from the outer surface.
- Photo 12.** *Albizia julibrissin* DURAZZ. Vestured intervacular pits in the wall of a vessel element viewed from the outer surface.
- Photo 13.** *Albizia julibrissin* DURAZZ. A part of vestured intervacular pit in the wall of a vessel element viewed from the outer surface.
- Photo 14.** *Pueraria lobata* (WILLD.) OHWI Vestured intervacular pits in the wall of a vessel element viewed from the outer surface.
- Photo 15.** *Pueraria lobata* (WILLD.) OHWI Vestured intervacular pits in the wall of a vessel element viewed from the outer surface.
- Photo 16.** *Pueraria lobata* (WILLD.) OHWI Vestured intervacular pits in the wall of a vessel element viewed from the outer surface.
- Photo 17.** *Caesalpinia japonica* SIEB. et ZUCC. Vestured intervacular pits in the wall of a vessel element viewed from the outer surface.
- Photo 18.** *Caesalpinia japonica* SIEB. et ZUCC. Vestured intervacular pits in the wall of a vessel element viewed from the outer surface.

- Photo 19.** *Wisteria floribunda* (WILLD.) DC. A vested intervascular pit in the wall of a vessel element viewed from the outer surface.
- Photo 20.** *Robinia pseudo-acacia* LINN. A part of vested intervascular pit in the wall of a vessel element viewed from the outer surface.
- Photo 21.** *Sophora japonica* LINN. Vested intervascular pits in the wall of a vessel element viewed from the outer surface.
- Photo 22.** *Maackia amurensis* RUPR. et MAXIM. var. *buengeri* (MAXIM.) C. K. SCHN. Vested intervascular pits in the wall of a vessel element viewed from the outer surface.
- Photo 23.** *Cladrastis platycarpa* (MAXIM.) MAKINO Vested intervascular pits in the wall of a vessel element viewed from the outer surface.
- Photo 24.** *Caragana chamlagu* LAM. Vested intervascular pits in the wall of a vessel element viewed from the outer surface.
- Photo 25.** *Caragana chamlagu* LAM. Vested intervascular pits in the wall of a vessel element viewed from the lumen side.
- Photo 26.** *Ligustrum obtusifolium* SIEB. et ZUCC. Vested intervascular pits in the wall of a vessel element viewed from the outer surface.
- Photo 27.** *Ligustrum obtusifolium* SIEB. et ZUCC. Non-vested intervascular pits in the wall of a vessel element viewed from the outer surface.
- Photo 28.** *Daphne kamtschatica* MAXIM. var. *jezoensis* (MAXIM.) OHWI Non-vested intervascular pits in the wall of a vessel element viewed from the outer surface.
- Photo 29.** *Lespedeza bicolor* TURCZ. forma *acutifolia* MATSUM. Vested vessel-ray parenchyma pits in the wall of a vessel element viewed from the outer surface.
- Photo 30.** *Cladrastis platycarpa* (MAXIM.) MAKINO Vested vessel-ray parenchyma pits in the wall of a vessel element viewed from the outer surface.
- Photo 31.** *Caragana chamlagu* LAM. Vested vessel-ray parenchyma pits in the wall of a vessel element viewed from the outer surface.
- Photo 32.** *Pueraria lobata* (WILLD.) OHWI Vested vessel-ray parenchyma pits in the wall of a vessel element viewed from the outer surface.
- Photo 33.** *Lagerstroemia subcostata* KOEHNE Vessel-ray parenchyma pits in the wall of a vessel element viewed from the lumen side. The pits are vested (A), partially vested (B) or non-vested (C).
- Photo 34.** *Lagerstroemia subcostata* KOEHNE Vessel-ray parenchyma pits in the wall of a vessel element viewed from the outer surface. The pits are vested (A), partially vested (B) or non-vested (C).
- Photo 35.** *Millettia japonica* (SIEB. et ZUCC.) A. GRAY Vessel-ray parenchyma pits in the wall of a vessel element viewed from the outer surface. The pits are vested or non-vested.
- Photo 36.** *Ligustrum obtusifolium* SIEB. et ZUCC. Vessel-ray parenchyma pits in the wall of a vessel element viewed from the outer surface. The pits are partially vested (arrows) or non-vested.

- Photo 37.** *Daphne kamtshatica* MAXIM. var. *jezoensis* (MAXIM.) OHWI Non-vestured vessel-ray parenchyma pits in the wall of a vessel element viewed from the outer surface.
- Photo 38.** *Lespedeza bicolor* TURCZ. forma *acutifolia* MATSUM. Vestured vessel-axial parenchyma pits in the wall of a vessel element viewed from the outer surface.
- Photo 39.** *Cladrastis platycarpa* (MAXIM.) MAKINO Vestured vessel-axial parenchyma pits in the wall of a vessel element viewed from the outer surface.
- Photo 40.** *Caragana chamlagu* LAM. Vestured vessel-axial parenchyma pits in the wall of a vessel element viewed from the outer surface.
- Photo 41.** *Lagerstroemia subcostata* KOEHNE Vessel-axial parenchyma pits in the wall of a vessel element viewed from the outer surface. The pits are vestured or non-vestured.
- Photo 42.** *Millettia japonica* (SIEB. et ZUCC.) A. GRAY Vessel-axial parenchyma pits in the wall of a vessel element viewed from the outer surface. The pits are vestured or non-vestured.
- Photo 43.** *Ligustrum obtusifolium* SIEB. et ZUCC. Vessel-axial parenchyma pits in the wall of a vessel element viewed from the lumen side. The pits are partially vestured or non-vestured.
- Photo 44.** *Daphne kamtshatica* MAXIM. var. *jezoensis* (MAXIM.) OHWI A non-vestured pit in the wall of a vessel element viewed from the outer surface.
- Photo 45.** *Lespedeza bicolor* TURCZ. forma *acutifolia* MATSUM. A vestured vessel-wood fiber pit in the wall of a vessel element viewed from the outer surface.
- Photo 46.** *Ligustrum obtusifolium* SIEB. et ZUCC. Vestured vessel-wood fiber pits in the wall of a vessel element viewed from the outer surface.
- Photo 47.** *Ligustrum obtusifolium* SIEB. et ZUCC. Non-vestured vessel-wood fiber pits in the wall of a vessel element viewed from the outer surface.
- Photo 48.** *Daphne kamtshatica* MAXIM. var. *jezoensis* (MAXIM.) OHWI Non-vestured vessel-wood fiber pits in the wall of a vessel element viewed from the outer surface.
- Photo 49.** *Daphne kamtshatica* MAXIM. var. *jezoensis* (MAXIM.) OHWI A vestured fiber tracheid-vessel pit in the wall of a fiber tracheid viewed from the lumen side.
- Photo 50.** *Daphne kamtshatica* MAXIM. var. *jezoensis* (MAXIM.) OHWI Vestured fiber tracheid-axial parenchyma pits in the wall of a fiber tracheid viewed from the lumen side.
- Photo 51.** *Albizia julibrissin* DURAZZ. Inner surface of a vessel element. Branched and unbranched projections are irregularly distributed.
- Photo 52.** *Acacia confusa* MERR. Inner surface of a vessel element. Small unbranched projections are almost uniformly distributed on the inner surface, while larger branched projections obscure the inner pit apertures.
- Photo 53.** *Lespedeza bicolor* TURCZ. forma *acutifolia* MATSUM. Inner surface of a vessel element showing aggregated projections on the wall except pit apertures.

- Photo 54.** *Lespedeza bicolor* TURCZ. forma *acutifolia* MATSUM. A part of photo 53 showing the transitional area between larger aggregated projections and smaller uniformly distributed ones on the wall of a vessel element.
- Photo 55.** *Lespedeza bicolor* TURCZ. forma *acutifolia* MATSUM. A part of photo 53. Surface view of aggregated projections on the wall of a vessel element.
- Photo 56.** *Caesalpinia japonica* SIEB. et ZUCC. Inner surface of a vessel element. Branched and unbranched projections are scattered.
- Photo 57.** *Caesalpinia japonica* SIEB. et ZUCC. Inner surface of a vessel element. Branched and unbranched projections are densely distributed.
- Photo 58.** *Caesalpinia japonica* SIEB. et ZUCC. Inner surface of a vessel element showing crowded projections near the simple perforation. R: perforation rim.
- Photo 59.** *Caesalpinia japonica* SIEB. et ZUCC. A part of photo 58. Branched and unbranched projections on the inner surface of a vessel element.
- Photo 60.** *Caesalpinia japonica* SIEB. et ZUCC. Branched projections on the inner surface of a vessel element.
- Photo 61.** *Lagerstroemia subcostata* KOEHNE Inner surface of a vessel element. Small unbranched projections are uniformly distributed on the inner surface of the vessel wall.
- Photo 62.** *Millettia japonica* (SIEB. et ZUCC.) A. GRAY Inner surface of a vessel element. No projections are found on the inner surface of the vessel wall.
- Photo 63.** *Sophora japonica* LINN. Inner surface of a vessel element showing projections arising from spiral thickenings.
- Photo 64.** *Sophora japonica* LINN. A part of photo 63. Enlarged view of the projections arising from spiral thickenings.
- Photo 65.** *Sophora japonica* LINN. Inner surface of a vessel element. Spiral thickenings (arrows) enter into the pit chambers from the pit apertures and branch in the pit chambers.
- Photo 66.** *Sophora japonica* LINN. Inner surface of a vessel element. Spiral thickening is separated from the vessel wall together with the branched part (arrowed).
- Photo 67.** *Caragana chamlagu* LAM. Inner surface of a vessel. Vestures-like projections arising from the rim (R in the photo) of a simple perforation.

