SEM Investigation on the Micromorphology of Vessel Wall Sculptures*

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道管壁変異の微細形態の走査電子顕微鏡的研究*

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Introduction

The structure of the vessel wall is complicated by sculptures, such as perforation plates, pits, spiral thickenings and warts (or vestures)…, arising as normal features of the vessel wall[1]. To obtain an exact knowledge of the morphology of the sculptures, therefore, is very important for better understanding of the actual vessel wall structure.

Morphology of the sculptures of a vessel wall such as perforation plates, pits and spiral thickenings has been investigated in many species of Japanese hardwoods from various standpoints at a light microscopic level[2~14]. The micromorphology of them and other sculptures which cannot be clearly observed by light microscopy (LM) has been observed in a limited number of species by transmission electron microscopy (TEM)[15~20], but not systematically in many species compared with the sculptures of softwood tracheid wall until the advent of scanning electron microscopy (SEM) which has widely been applied in the observation of wood structure.

It was demonstrated by early SEM investigations[21~29] that SEM was an excellent tool for the observation on micromorphology of sculptures of wood cell wall, which are particularly complicated in their three-dimensional structure, because of the great depth of focus of the microscope. Subsequently, therefore, numerous valuable information regarding the sculptures of vessel wall using SEM has been reported to the present.

The three-dimensional structure of the perforation plates which is difficult to observe by LM and TEM has been clarified in different species by means of SEM [22,30~49], though the formation process of them has been investigated by LM[50,51], TEM[52~56] and SEM[32,39,46]. Micromorphology of the perforation plates has been observed in a wide variety of New Zealand woods by MEYLAN and BUTTERFIELD[43,44] and of Japanese woods by OHTANI and ISHIDA[47] using SEM. In particular, valuable information about microfibrillar webs[40,57] and combination perforation plates (and mismatching perforation plates)[42,43] obtained from SEM observation is worthy of notice. SEM micrograph of the microfibrillar webs in modern angiosperms has first been represented as seen in *Cercidiphyllum japonicum* by ISHIDA[22]. Occurrence and various textures of them in scalariform perforation plates in several species have been found by ISHIDA[36], MEYER and MUHAMMAD[57], MEYLAN and BUTTERFIELD[40] and BUTTERFIELD and MEYLAN[32]. Later SEM observations have confirmed that these webs are remnants of the former primary walls-middle lamella partition that survive the enzymatic breakdown process during perforation plate differentiation and that they occur in openings not only of scalariform perforation plates but also of multiple perforation plates except the scalariform in mature wood in some species[37,43,47,49]. Micromorphology of combination perforation plates (and mismatching perforation plates) has also been clearly illustrated by SEM micrographs, although these perforation plates have been found in several species by LM[58~60]. Various types of such perforation plates in different species have been reported by MEYLAN and BUTTERFIELD[42,43], OHTANI and ISHIDA[45,47], BUTTERFIELD and MEYLAN[34] and PARAMESWARAN and LIESE[48].

After thirty years of monumental work on vestured pits by BAILEY[61,62], early TEM observations[63~66] confirmed that the findings of BAILEY's investigation were substantially correct. According to the TEM[63~69] and later SEM observations[70~82], the extent of vesturing in pit chamber is frequently characteristic of a particular wood, and the size and shape of individual vestures vary not only among species but also within a species. Several attempts to categorize pit vestures (and vestured pits) into distinct types have been made[63,77,80,82]. Much attention on the relationship between vestures and warts in vessel wall has been paid by many investigators[19,20,63,73,77,79~88]. Similarities on both structures have been recognized on the basis of their occurrence[20,63,73,77,79,80,83,87,88], micromorphology[73,77,79], chemical nature[63,79,85] and formation process[84], although a difference in the formation process between both structures has been reported[19,86].

Fine structure of pit membranes in vessels has not been investigated in many species. On the basis of the evidences on the pit membrane in a limited number of species[89~110], the vessel pit membrane is described as a simple membrane without any visible openings consisting of the two primary walls of the adjacent cells and the intercellular layer[16,19]. And also it is well known that such pit membranes do not have a centrally thickened torus like many softwood pits[16]. However, BONNER and THOMAS[111] have reported that the newly matured intervessel pit membranes of *Liriodendron tulipifera* contain distinct openings and that with age the membranes become progressively occluded with incrustations which obstruct the small openings. The pit membranes with torus were first found in the intervascular pits of *Daphne odora* by the author[112]. From extensive SEM observation on the intervascular pit membranes in 187 species (109 genera, 47 families) of Japanese dicotyledonous woods by OHTANI and ISHIDA[113], 7 species belonging to *Daphne* and *Osmanthus* have been confirmed to invariably have the torus in their intervascular pit membranes.

From observations on the occurrence and morphology of spiral thickenings in a wide variety of species at a LM level[114~117], spiral thickenings have been considered to be an important diagnostic feature[1]. Fine structure of them in the vessels of *Tilia americana* has been investigated using TEM[16,93]. SEM observations on their micromorphology have been reported by PARHAM and KAUSTINEN[118], MILLER[119,120], OHTANI and ISHIDA[121], and MEYLAN and BUTTERFIELD[122]. The following three attempts have been made to classify spiral thickenings. The first separates them into three main types of unbranched, branched and swirled[118]. The second is based on the dominant helical direction, separating them into (1) S helix, (2) Z helix, (3) S and Z helix and (4) thickening forming no spiral[121]. The third is based on the prominence of the thickenings, separating them into (1) fine striations, (2) light helical thickenings sometimes merging with the vessel wall, (3) prominent helical thickenings and (4) very close prominent helical thickenings[122]. Extensive SEM observations on the occurrence and micromorphology of spiral thickenings in vessel wall have been carried out in a wide variety of Japanese woods by OHTANI and ISHIDA[121] and of New Zealand woods by MEYLAN and BUTTERFIELD[44,122], respectively.

Although warts in the tracheid wall in numerous softwood species have been investigated from various aspects[99,123~151], warts on the vessel wall have been mostly investigated in association with vestured pits and much attention has been paid to the relationship between warts and pit vestures as described above[19,20,63,73,77,79~88]. Therefore, the number of species examined is rather limited[18,63,70,73,77,79~88,97,152~156], although a survey on wart occurrence in many species has been carried out using LM[142,157]. Recently, extensive SEM observations on the occurrence of warts in vessel walls were reported on Japanese dicotyledonous woods of 221 species by the author[158].

The occurrence and morphology of trabeculae in vessels have been observed in many species belonging to *Vitis* etc. by LM[159~167]. Using SEM, valuable information on the micromorphology of them in the vessels in some species has been reported[168~172]. The SEM observations have confirmed the general similarity in their micromorphology between the trabeculae occurring in the various gymnosperm woods examined by KEITH[173] and those found in vessels. On the basis of SEM observation on the occurrence of them in New Zealand hardwoods[169], their distribution has been reported to be low and irregular.

The purpose of the present study is to show the characteristic features on micromorphology of vessel wall sculptures of Japanese dicotyledonous woods at a

SEM level. To obtain these information is of considerable importance in elucidating characteristic wood properties of individual species from the aspect of their wood structure at a SEM level. The present paper deals synthetically with the results obtained regarding vessel wall sculptures using SEM including the information in the earlier papers published by OHTANI[158,172] and OHTANI and ISHIDA[45~47,77,113,121]. Because the sculptures are very complicated in their three-dimensional structure, the micromorphology should be exactly illustrated by SEM micrographs showing details. However, they have already been published in earlier papers[45~47,77,113,121,158,172]. In the present paper, therefore, they are not shown to avoid overlapping. Readers should refer to papers[45~47,77,113,121,158,172].

Materials and Methods

The names of the species (223 species, 120 genera, 51 families) examined in the present study are listed in Table 1. The species named used mostly follow OHWI[174].

Table 1. List of species examined

Family	Species	Japanese name	No.*
Salicaceae	*Populus nigra* LINN. var. *italica* MUENCHH.	Seiyôhakoyanagi	1
	Populus sieboldii MIQ.	Yamanarashi	1
	Populus maximowiczii HENRY	Doroyanagi	1
	Salix bakko KIMURA	Bakkoyanagi	1
	Salix kinuyanagi KIMURA	Kinuyanagi	1
	Salix sachalinensis FR. SCHM.	Onoeyanagi	2
Myricaceae	*Myrica rubra* SIEB. et ZUCC.	Yamamomo	3
Juglandaceae	*Platycarya strobilacea* SIEB. et ZUCC.	Nogurumi	1
	Pterocarya rhoifolia SIEB. et ZUCC.	Sawagurumi	1
	Juglans ailanthifolia CARR.	Onigurumi	4
Betulaceae	*Carpinus tschonoskii* MAXIM.	Inushide	3
	Carpinus laxiflora (SIEB. et ZUCC.) BLUME	Akashide	2
	Carpinus japonica BLUME	Kumashide	2
	Carpinus cordata BLUME	Sawashiba	6
	Ostrya japonica SARG.	Asada	3
	Corylus sieboldiana BLUME	Tsunohashibami	1
	Betula maximowicziana REGEL	Udaikanba	5
	Betula platyphylla SUKATCHEV var. *japonica* (MIQ.) HARA	Shirakanba	3
	Betula ermanii CHAM.	Dakekanba	2
	Betula grossa SIEB. et ZUCC.	Yogusominebari	2
	Alnus firma SIEB. et ZUCC.	Yashabushi	1
	Alnus maximowiczii CALLIER	Miyamahannoki	1
	Alnus hirsuta TURCZ.	Keyamahannoki	3
	Alnus serrulatoides CALLIER	Kawarahannoki	1
	Alnus japonica (THUNB.) STEUD.	Hannoki	1
Fagaceae	*Fagus crenata* BLUME	Buna	6
	Fagus japonica MAXIM.	Inubuna	1
	Quercus acuta THUNB.	Akagashi	3

Table 1 (Continued)

Family	Species	Japanese name	No.*
	Quercus sessilifolia BLUME	Tsukubanegashi	3
	Quercus gilva BLUME	Ichiigashi	4
	Quercus myrsinaefolia BLUME	Shirakashi	2
	Quercus glauca THUNB.	Arakashi	3
	Quercus salicina BLUME	Urajirogashi	3
	Quercus phillyraeoides A. GRAY	Ubamegashi	2
	Quercus mongolica FISCHER	Mongorinara	1
	Quercus mongolica FISCHER var. *grosseserrata* (BLUME) REHD. et WILS.	Mizunara	3
	Quercus serrata THUNB.	Konara	2
	Quercus dentata THUNB.	Kashiwa	1
	Quercus variabilis BLUME	Abemaki	1
	Quercus acutissima CARRUTH.	Kunugi	1
	Castanea crenata SIEB. et ZUCC.	Kuri	2
	Castanopsis cuspidata (THUNB.) SCHOTTKY	Tsuburajii	3
	Castanopsis cuspidata (THUNB.) SCHOTTKY var. *Siebold* (MAKINO) NAKAI	Sudajii	3
	Pasania glabra (THUNB.) OERST.	Shiribukagashi	1
Ulmaceae	*Ulmus davidiana* PLANCH. var. *japonica* (REHD.) NAKAI	Harunire	4
	Ulmus laciniata (TRAUTV.) MAYR	Ohyô	1
	Zelkova serrata (THUNB.) MAKINO	Keyaki	2
	Celtis sinensis PERS. var. *japonica* (PLANCH.) NAKAI	Enoki	2
	Aphananthe aspera (THUNB.) PLANCH.	Mukunoki	1
Moraceae	*Morus bombycis* KOIDZ.	Yamaguwa	4
	Broussonetia papyrifera (LINN.) VENT.	Kajinoki	1
	Ficus pumila LINN.	Ôitabi	1
	Ficus erecta THUNB.	Inubiwa	1
	Ficus erecta THUNB. var. *yamadorii* MAKINO	Keinubiwa	1
Proteaceae	*Helicia cochinchinensis* LOUR.	Yamamogashi	2
Cercidiphyllaceae	*Cercidiphyllum japonicum* SIEB. et ZUCC.	Katsura	6
Berberidaceae	*Berberis thunbergii* DC.	Megi	2
	Nandina domestica THUNB.	Nanten	1
Magnoliaceae	*Michelia compressa* (MAXIM.) SARG.	Ogatamanoki	2
	Magnolia obovata THUNB.	Hônoki	5
	Magnolia salicifolia (SIEB. et ZUCC.) MAXIM.	Tamushiba	3
	Magnolia kobus DC. var. *borealis* SARG.	Kitakobushi	2
	Illicium religiosum SIEB. et ZUCC.	Shikimi	3
	Liriodendron tulipifera LINN.	Yurinoki	1
Lauraceae	*Cinnamomum camphora* (LINN.) SIEB.	Kusunoki	4
	Cinnamomum japonicum SIEB., ex NAKAI	Yabunikkei	2
	Machilus thunbergii SIEB. et ZUCC.	Tabunoki	3
	Lindera erythrocarpa MAKINO	Kanakuginoki	2
	Lindera umbellata THUNB.	Kuromoji	2
	Parabenzoin praecox (SIEB. et ZUCC.) NAKAI	Aburachan	2
	Neolitsea sericea (BLUME) KOIDZ.	Shirodamo	1

Table 1 (Continued)

Family	Species	Japanese name	No.*
	Neolitsea aciculata (BLUME) KOIDZ.	Inugashi	2
	Actinodaphne lancifolia (SIEB. et ZUCC.) MEISN.	Kagonoki	2
	Actinodaphne longifolia (BLUME) NAKAI	Baribarinoki	3
Saxifragaceae	*Hydrangea petiolaris* SIEB. et ZUCC.	Gotôzuru	1
	Hydrangea paniculata SIEB.	Noriutsugi	1
	Deutzia crenata SIEB. et ZUCC.	Utsugi	2
Hamamelidaceae	*Hamamelis japonica* SIEB. et ZUCC.	Mansaku	1
	Distylium racemosum SIEB. et ZUCC.	Isunoki	1
Rosaceae	*Prunus mume* SIEB. et ZUCC.	Ume	2
	Prunus persica (LINN.) BATSCH.	Momo	2
	Prunus apetala (SIEB. et ZUCC.) FRANCH et SAVAT.	Chôjizakura	1
	Prunus incisa THUNB.	Mamezakura	1
	Prunus pendula MAXIM. forma *ascendens* (MAKINO) OHWI	Edohigan	1
	Prunus jamasakura SIEB., ex KOIDZ.	Yamazakura	2
	Prunus sargentii REHDER	Ezoyamazakura	2
	Prunus maximowiczii RUPR.	Miyamazakura	2
	Prunus spinulosa SIEB. et ZUCC.	Rinboku	3
	Prunus ssiori FR. SCHM.	Shiurizakura	3
	Prunus grayana MAXIM.	Uwamizuzakura	1
	Prunus buergeriana MIQ.	Inuzakura	2
	Photinia glabra (THUNB.) MAXIM.	Kanamemochi	1
	Eriobotrya japonica (THUNB.) LINDL.	Biwa	1
	Malus sieboldii (REGEL) REHDER	Zumi	1
	Pourthiaea villosa (THUNB.) DECNE. var. *laevis* (THUNB.) STAPF	Kamatsuka	2
	Sorbus commixta HEDL.	Nanakamado	1
	Sorbus alnifolia (SIEB. et ZUCC.) C. KOCH	Azukinashi	8
	Sorbus japonica (DECNE.) HEDL.	Urajironoki	2
Leguminosae	*Albizia julibrissin* DURAZZ.	Nemunoki	3
	Acacia confusa MERR.	Sôshiju	1
	Gleditsia japonica MIQ.	Saikachi	1
	Caesalpinia japonica SIEB. et ZUCC.	Jaketsuibara	2
	Sophora japonica LINN.	Enju	1
	Maackia amurensis RUPR. et MAXIM. var. *buergeri* (MAXIM.) C. K. SCHN.	Inuenju	1
	Cladrastis platycarpa (MAXIM.) MAKINO	Fujiki	1
	Euchresta japonica HOOK. fil.	Miyamatobera	1
	Lespedeza bicolor TURCZ. forma *acutifolia* MATSUM.	Yamahagi	2
	Caragana chamlagu LAM.	Muresuzume	2
	Pueraria lobata (WILLD.) OHWI	Kuzu	2
	Wisteria floribunda (WILLD.) DC.	Fuji	2
	Millettia japonica (SIEB. et ZUCC.) A. GRAY	Natsufuji	2
	Robinia pseudo-acacia LINN.	Harienju	11
Rutaceae	*Zanthoxylum piperitum* (LINN.) DC.	Sanshô	2

Table 1 (Continued)

Family	Species	Japanese name	No.*
	Zanthoxylum ailanthoides SIEB. et ZUCC.	Karasuzanshô	2
	Phellodendron amurense RUPR.	Kihada	1
Simaroubaceae	*Ailanthus altissima* SWINGLE	Shinju	1
	Picrasma quassioides (D. DON) BENN.	Nigaki	1
Meliaceae	*Melia azedarach* LINN.	Sendan	1
	Cedrela sinensis JUSS.	Chanchin	1
Euphorbiaceae	*Daphniphyllum macropodum* MIQ.	Yuzuriha	2
	Daphniphyllum teijsmannii ZOLL.	Himeyuzuriha	2
	Mallotus japonicus (THUNB.) MUELL. ARG.	Akamegashiwa	2
	Aleurites cordata R. BR.	Aburagiri	2
	Sapium japonicum (SIEB. et ZUCC.) PAX et HOFFM.	Shiraki	2
Buxaceae	*Buxus microphylla* SIEB. et ZUCC. var. *japonica* (MUELL. ARG.) REHD. et WILS.	Tsuge	1
Anacardiaceae	*Rhus succedanea* LINN.	Haze	1
	Rhus verniciflua STOKES	Urushi	1
	Rhus sylvestris SIEB. et ZUCC.	Yamahaze	3
	Rhus trichocarpa MIQ.	Yamaurushi	3
	Rhus javanica LINN.	Nurude	2
Aquifoliaceae	*Ilex macropoda* MIQ.	Aohada	3
	Ilex micrococca MAXIM.	Tamamizuki	3
	Ilex sugerokii MAXIM. var. *longipedunculata* (MAXIM.) MAKINO	Ushikaba	1
	Ilex crenata THUNB.	Inutsuge	1
	Ilex pedunculosa MIQ.	Soyogo	1
	Ilex rotunda THUNB.	Kuroganemochi	3
	Ilex integra THUNB.	Mochinoki	2
	Ilex latifolia THUNB.	Tarayô	1
Celastraceae	*Celastrus orbiculatus* THUNB.	Tsuruumemodoki	2
	Euonymus sieboldianus BLUME	Mayumi	2
	Euonymus oxyphyllus MIQ.	Tsuribana	2
Staphyleaceae	*Euscaphis japonica* (THUNB.) KANITZ	Gonzui	2
Aceraceae	*Acer sieboldianum* MIQ.	Kohauchiwakaede	1
	Acer japonicum THUNB.	Hauchiwakaede	1
	Acer palmatum THUNB. var. *palmatum*	Irohamomiji	1
	Acer palmatum THUNB. var. *matsumurae* (KOIDZ.) MAKINO	Yamamomiji	3
	Acer mono MAXIM.	Itayakaede	4
	Acer miyabei MAXIM.	Kurobiitaya	1
	Acer distylum SIEB. et ZUCC.	Hitotsubakaede	1
	Acer ukurunduense TRAUTV. et MEY.	Ogarabana	1
	Acer carpinifolium SIEB. et ZUCC.	Chidorinoki	2
	Acer crataegifolium SIEB. et ZUCC.	Urikaede	2
	Acer rufinerve SIEB. et ZUCC.	Urihadakaede	3
	Acer cissifolium (SIEB. et ZUCC.) K. KOCH	Mitsudekaede	1
Hippocastanaceae	*Aesculus turbinata* BLUME	Tochinoki	2

Table 1 (Continued)

Family	Species	Japanese name	No.*
Sapindaceae	*Sapindus mukorossi* GAERTN.	Mukuroji	2
Sabiaceae	*Meliosma rigida* SIEB. et ZUCC.	Yamabiwa	2
	Meliosma myriantha SIEB. et ZUCC.	Awabuki	2
Rhamnaceae	*Zizyphus jujuba* MILL. var. *inermis* (BUNGE) REHD.	Natsume	1
	Hovenia dulcis THUNB.	Kenponashi	3
Elaeocarpaceae	*Elaeocarpus japonicus* SIEB. et ZUCC.	Kobanmochi	2
Tiliaceae	*Tilia japonica* (MIQ.) SIMONKAI	Shinanoki	2
Malvaceae	*Hibiscus syriacus* LINN.	Mukuge	1
Sterculiaceae	*Firmiana simplex* (LINN.) W. F. WIGHT	Aogiri	1
Theaceae	*Camellia japonica* LINN.	Yabutsubaki	3
	Camellia japonica LINN. var. *hortensis* (MAKINO) MAKINO	Tsubaki	1
	Stewartia monadelpha SIEB. et ZUCC.	Himeshara	3
	Ternstroemia gymnanthera (WIGHT et ARN.) SPRAGUE	Mokkoku	2
	Cleyera japonica THUNB. (p. p., em. SIEB. et ZUCC.)	Sakaki	2
	Eurya japonica THUNB.	Hisakaki	2
Flacourtiaceae	*Idesia polycarpa* MAXIM.	Iigiri	3
Thymelaeaceae	*Daphne kiusiana* MIQ.	Koshônoki	2
	Daphne odora THUNB.	Jinchôge	3
	Daphne miyabeana MAKINO	Karasushikimi	2
	Daphne pseudo-mezereum A. GRAY	Onishibari	1
	Daphne kamtschatica MAXIM. var. *jezoensis* (MAXIM.) OHWI	Naniwazu	3
Lythraceae	*Lagerstroemia subcostata* KOENE	Shimasarusuberi	1
	Lagerstroemia indica LINN.	Sarusuberi	1
Araliaceae	*Aralia elata* (MIQ.) SEEMANN	Taranoki	1
	Dendropanax trifidus (THUNB.) MAKINO	Kakuremino	3
	Acanthopanax sciadophylloides FRANCH. et SAVAT.	Koshiabura	1
	Evodiopanax innovans (SIEB. et ZUCC.) NAKAI	Takanotsume	2
	Kalopanax pictus (THUNB.) NAKAI	Harigiri	3
Cornaceae	*Cornus controversa* HEMSLEY	Mizuki	3
	Cornus brachypoda C. A. MEY.	Kumanomizuki	2
	Cornus kousa BUERGER, ex HANCE	Yamabôshi	2
Clethraceae	*Clethra barbinervis* SIEB. et ZUCC.	Ryôbu	5
Ericaceae	*Pieris japonica* (THUNB.) D. DON	Asebi	1
	Lyonia ovalifolia (WALL.) DRUDE var. *elliptica* (SIEB. et ZUCC.) HAND.-MAZZ.	Nejiki	1
	Enkianthus cernuus (SIEB. et ZUCC.) MAKINO forma *rubens* (MAXIM.) OHWI	Benidôdan	2
	Vaccinium bracteatum THUNB.	Shashanbo	1
Myrsinaceae	*Myrsine seguinii* LÉV.	Taimintachibana	1
Ebenaceae	*Diospyros morrisiana* HANCE	Tokiwagaki	1
	Diospyros lotus LINN.	Mamegaki	1

Table 1 (Continued)

Family	Species	Japanese name	No.*
	Diospyros kaki THUNB.	Kakinoki	1
Symplocaceae	*Symplocos coreana* (LÉV.) OHWI	Tannasawafutagi	3
	Symplocos lancifolia SIEB. et ZUCC.	Shirobai	2
	Symplocos theophrastaefolia SIEB. et ZUCC.	Kanzaburônoki	3
	Symplocos glauca (THUNB.) KOIDZ.	Mimizubai	2
	Symplocos prunifolia SIEB. et ZUCC.	Kurobai	3
Styracaceae	*Styrax japonica* SIEB. et ZUCC.	Egonoki	2
	Styrax obassia SIEB. et ZUCC.	Hakuunboku	1
	Pterostyrax corymbosa SIEB et ZUCC.	Asagara	1
Oleaceae	*Ligustrum japonicum* THUNB.	Nezumimochi	2
	Ligustrum obtusifolium SIEB. et ZUCC.	Ibotanoki	1
	Osmanthus aurantiacus (MAKINO) NAKAI var. *thunbergii* (MAKINO) HONDA	Usugimokusei	1
	Osmanthus aurantiacus (MAKINO) NAKAI var. *aurantiacus*	Kinmokusei	2
	Osmanthus fragrans LOUR.	Ginmokusei	1
	Osmanthus heterophyllus (G. DON) P. S. GREEN	Hiiragi	4
	Osmanthus fortunei CARR.	Hiiragimokusei	2
	Osmanthus insularis KOIDZ.	Nataorenoki	3
	Osmanthus rigidus NAKAI	Ômokusei	1
	Syringa reticulata (BLUME) HARA	Hashidoi	3
	Fraxinus spaethiana LINGELSH.	Shioji	1
	Fraxinus mandshurica RUPR. var. *japonica* MAXIM.	Yachidamo	2
	Fraxinus japonica BLUME	Toneriko	1
	Fraxinus lanuginosa KOIDZ.	Aodamo	2
Verbenaceae	*Clerodendrom trichotomum* THUNB.	Kusagi	2
Scrophulariaceae	*Paulownia tomentosa* (THUNB.) STEUD.	Kiri	1
Bignoniaceae	*Catalpa ovata* G. DON	Kisasage	1
Caprifoliaceae	*Sambucus sieboldiana* BLUME, ex GRAEBN. var. *miquelii* (NAKAI) HARA	Ezoniwatoko	2
	Viburnum dilatatum THUNB.	Gamazumi	2
	Viburnum awabuki K. KOCH	Sangoju	1

* Number of sampling trees

Wood samples were obtained from living trees grown normally and/or the wood collections of the Department of Forest Products, Hokkaido University etc. Small blocks were taken from the outer sapwood. Various surfaces, mainly longitudinal radial and tangential surfaces, to be observed were obtained by splitting, and cutting using a single-edge razor blade. Final cuts were done with a new razor blade. Specimens were finished in the form of ca. 6 mm×6 mm×1 mm and dried at room conditions. They were stuck on the brass standard stub with electrically conductive paste. The surfaces to be observed were coated with carbon-gold while being rotated in a high vacuum evaporation unit. Observations were made with a JSM-2 SEM at 15～25 kV.

In addition to the SEM observations, observations on some items were also carried out with field emission SEM, TEM using direct carbon replica[175,176], polarizing microscope (PM) and LM.

Results and Discussion

1. Perforation plates

1.1. Micromorphology of perforation plates

According to the definition of IAWA[177], vessel perforations are distinguished into simple and multiple perforations, and three kinds of multiple perforation plates, i. e., scalariform, reticulate and ephedroid perforation plates, are defined in the glossary. However, the terms for various forms of the multiple perforation plates except the scalariform in past works are not consistent as pointed out by GRAY and DEZEEUW[35]. To avoid the confusion of the term, therefore, the multiple perforation plates examined were distinguished into scalariform perforation plates and multiple perforation plates except the scalariform in the present study. The term "multiple perforation plate" used in this paper is defined as the latter.

Simple perforation plates examined were divided into the following four types on the basis of the form of rim.

Type 1……Simple perforation plate having prominent bordered rim.
Type 2……Simple perforation plate having bordered rim.
Type 3……Simple perforation plate having non-bordered rim with blunt edge.
Type 4……Simple perforation plate having non-bordered rim with pointed edge.

Apart from these types of simple perforation plates, simple perforation plates with so-called vestures on their rim were found only in *Caragana chamlagu* having vestured pits. Such simple perforation plates have been found in 9 species (4 genera, 3 families) indigenous to New Zealand by KUČERA et al.[38] and in *Leptospermum crassipes* by BAAS[30].

Scalariform perforation plates examined were divided into the following three types on the basis of the number of bars within a scalariform perforation plate.

Type 1……Few-barred (1～20 bars) scalariform perforation plate.
Type 2……Intermediate-barred (21～40 bars) scalariform perforation plate.
Type 3……Many barred (over 41 bars) scalariform perforation plate.

According to the previous reports[178~180], scalariform perforation plates with 5 or few bars are placed in the "few" class, with 5～15 in the "intermediate" class, and over 15 in the "many" class. However, application of such a division was inadequate to the scalariform perforation plates observed in the present study, because the majority of them had bars over 15.

Various forms of multiple perforation plates were observed in the present study. Most of their forms corresponded with those reported already by several investigators[31,35,43,48,58,181]. Although they were difficult to divide into main types, they were divided into the following three types.

Type 1……Multiple perforation plate having many small slit-like or oval openings which are similar in shape and size.

Type 2……Multiple perforation plate having many slit-like or oval openings which are different each other in shape and size.

Type 3……Multiple perforation plate having several irregular openings in shape and size.

Besides three kinds of perforation plates described above, transitional forms between different typical kinds of perforation plates were always found in the species having more than one kind of them.

Microfibrillar webs[40,57] were observed in the openings in the lateral margin of some scalariform perforation plates in all the species having the plates of types 2 and 3. They were also commonly found in the last few openings at each end of long scalariform perforation plates. Complete microfibrillar webs[40,57], which are present in most or all regions of all openings of a scalariform perforation plate, were found in some plates in all the species having the plates of type 3 and in 6 species having the plates of type 2. The microfibrils forming a complete microfibrillar webs were mainly oriented perpendicularly to the bars (orthogonal microfibrillar webs[40,57]) in some plates and arranged in a reticulate fashion (reticulate microfibrillar webs[40,57]) in others. It should be noticed that the scalariform perforation plates with complete microfibrillar webs had promiment bordered bars and narrow openings between them as pointed out in the preceding papers[37,47].

It is well known that the openings in each half perforation plate in adjacent vessel members normally coincide exactly[31,37]. This fact was also confirmed in almost all perforation plates except particular ones in some species. The perforation plates in which openings between adjacent vessel members are not coincident have been referred to as combination perforation plates (a perforation plate consisting of different kinds of two half perforation plates in adjacent vessel members) and as mismatching perforation plates (a perforation plate consisting of the same kind of two half perforation plates in adjacent vessel members)[34,42,43]. Various forms of combination perforation plates, i. e., simple-to-scalariform, simple-to-multiple, and scalariform-to-multiple plates, were observed in different species. Simple-to-scalariform plates were found in *Idesia polycarpa* and *Sambucus sieboldiana* var. *miquelii* having both kinds of simple and scalariform perforation plates, and in *Fagus crenata* and *F. japonica* having three kinds of simple, scalariform and multiple perforation plates. Simple-to-multiple plates were found in the five species (*Helicia cochinchinensis, Pourthiaea villosa* var. *laevis, Sorbus commixta, S. alnifolia* and *S. japonica*) having both kinds of simple and multiple perforation plates and in *Fagus crenata* and *F. japonica*. Scalariform-to-multiple plates were found in *Fagus crenata* and *F. japonica*. In this connection, BUTTERFIELD and MEYLAN[34], and MEYLAN and BUTTERFIELD[43] have observed a wide range of combination plates (simple-to-scalariform, simple-to-part-scalariform, simple-to-reticulate, and scalariform-to-reticulate plates) in 22 different New Zealand woods belonging to 9 angiosperm families. MEYLAN and BUTTERFIELD[43] have suggested that it is possible that combination plates occur in most woods having more than one type of perforation plate. Mismatching perforation plates in simple and multiple plates were often observed in the 5 species (*Helicia cochinchinensis*, *Pourthiaea villosa* var. *laevis*, *Sorbus commixta*, *S. alnifolia* and *S. japonica*) having both kinds of simple and multiple perforation plates and in *Fagus crenata* and *F. japonica*. Most of scalariform and multiple perforation plates in *Fagus crenata* and *F, japonica* were mismatching plates. Three kinds of mismatching perforation plates were also rarely found in some species besides the species described just above.

1.2. Description on the micromorphological variation of perforation plates of the species

On the basis of the occurrence of various forms of perforation plates in each species, the species examined were divided into 6 groups (Table 2). In this paper, for convenience, three kinds of combination perforation plates, i. e., simple-to-scalariform, simple-to-multiple and scalariform-to-multiple, are entered into each category of scalariform, multiple and multiple perforation plates, respectively. And also three kinds of mismatching perforation plates, i. e., simple, scalariform and multiple, are regarded as simple, scalariform and multiple perforation plates, respectively.

Table 2. Grouping of species examined divided on the basis of the occurrence of perforation plate kind

Group No.	Number of species (genera, families)	Kind of perforation plates		
		Simple	Scalariform	Multiple
1	136 (71, 32)	○	—	—
2	46 (24, 15)	—	○	—
3	24 (15, 9)	○	○	—
4	9 (7, 5)	—	○	○
5	5 (3, 2)	○	—	○
6	3 (2, 2)	○	○	○

○ : Present
—: Absent

1) Species with exclusively simple perforation plates

136 species (71 genera, 32 families) belonged to this group. The species names are listed in Table 3. Although the simple perforation plates of type 1 were found in only 16 species among 136 species, those of types 2, 3 and 4 were found in most species. In most ring-porous woods, the simple perforation plates of type 4 were mostly present in the earlywood vessels and those of type 2 and/or 3 were present in the latewood vessels.

2) Species with exclusively scalariform perforation plates

46 species (24 genera, 15 families) belonged to this group. The species having exclusively or mostly scalariform perforation plates of types 1, 2 and 3 were 17, 19 and 10 in number, respectively. The species names are listed in Table 4.

Table 3. Species with exclusively simple perforation plates

Family	Species
Salicaceae	*Populus nigra* var. *italica*, *P. sieboldii*, *P. maximowiczii*, *Salix bakko*, *S. kinuyanagi*, *S. sachalinensis*
Juglandaceae	*Platycarya strobilacea*, *Pterocarya rhoifolia*, *Juglans ailanthifolia*
Betulaceae	*Ostrya japonica*
Fagaceae	*Quercus acuta*, *Q. sessilifolia*, *Q. gilva*, *Q. myrsinaefolia*, *Q. glauca*, *Q. salicina*, *Q. phillyraeoides*, *Q. mongolica*, *Q. mongolica* var. *grosseserrata*, *Q. serrata*, *Q. dentata*, *Q. variabilis*, *Q. acutissima*, *Pasania glabra*
Ulmaceae	*Ulmus davidiana* var. *japonica*, *U. laciniata*, *Zelkova serrata*, *Celtis sinensis* var. *japonica*, *Aphananthe aspera*
Moraceae	*Morus bombycis*, *Broussonetia papyrifera*, *Ficus pumila*, *F. erecta*, *F. erecta* var. *yamadorii*
Berberidaceae	*Berberis thunbergii*, *Nandina domestica*
Rosaceae	*Prunus mume*, *P. persica*, *P. apetala*, *P. incisa*, *P. pendula* forma *ascendens*, *P. jamasakura*, *P. sargentii*, *P. maximowiczii*, *P. spinulosa*, *P. ssiori*, *P. grayana*, *P. buergeriana*, *Photinia glabra*, *Eriobotrya japonica*, *Malus sieboldii*
Leguminosae	*Albizia julibrissin*, *Acacia confusa*, *Gleditsia japonica*, *Caesalpinia japonica*, *Sophora japonica*, *Maackia amurensis* var. *buergeri*, *Cladrastis platycarpa*, *Euchresta japonica*, *Lespedeza bicolor* forma *acutifolia*, *Caragana chamlagu*, *Pueraria lobata*, *Wisteria floribunda*, *Millettia japonica*, *Robinia pseudo-acacia*
Rutaceae	*Zanthoxylum piperitum*, *Z. ailanthoides*, *Phellodendron amurense*
Simaroubaceae	*Ailanthus altissima*, *Picrasma quassioides*
Meliaceae	*Melia azedarach*, *Cedrela sinensis*
Euphorbiaceae	*Mallotus japonicus*, *Aleurites cordata*, *Sapium japonicum*
Anacardiaceae	*Rhus succedanea*, *R. verniciflua*, *R. sylvestris*, *R. trichocarpa*, *R. javanica*
Celastraceae	*Celastrus orbiculatus*, *Euonymus sieboldianus*, *E. oxyphyllus*
Aceraceae	*Acer sieboldianum*, *A. japonicum*, *A. palmatum* var. *palmatum*, *A. palmatum* var. *matsumurae*, *A. mono*, *A. miyabei*, *A. distylum*, *A. ukurunduense*, *A. carpinifolium*, *A. crataegifolium*, *A. rufinerve*, *A. cissifolium*
Hippocastanaceae	*Aesculus turbinata*
Sapindaceae	*Sapindus mukorossi*
Rhamnaceae	*Zizyphus jujuba* var. *inermis*, *Hovenia dulcis*
Elaeocarpaceae	*Elaeocarpus japonicus*
Tiliaceae	*Tilia japonica*
Malvaceae	*Hibiscus syriacus*
Sterculiaceae	*Firmiana simplex*
Thymelaeaceae	*Daphne kiusiana*, *D. odora*, *D. miyabeana*, *D. pseudo-mezereum*, *D. kamtschatica* var. *jezoensis*
Lythraceae	*Lagerstroemia subcostata*, *L. indica*
Araliaceae	*Aralia elata*, *Dendropanax trifidus*, *Acanthopanax sciadophylloides*, *Evodiopanax innovans*, *Kalopanax pictus*

Table 3 (Continued)

Family	Species
Myrsinaceae	*Myrsine seguinii*
Ebenaceae	*Diospyros morrisiana, D. lotus, D. kaki*
Oleaceae	*Ligustrum japonicum, L. obtusifolium, Osmanthus aurantiacus* var. *thunbergii, O. aurantiacus* var. *aurantiacus, O. fragrans, O. heterophyllus, O. fortunei, O. insularis, O. rigidus, Syringa reticulata, Fraxinus spaethiana, F. mandshurica* var. *japonica, F. japonica, F. lanuginosa*
Verbenaceae	*Clerodendrom trichotomum*
Scrophulariaceae	*Paulownia tomentosa*
Bignoniaceae	*Catalpa ovata*

Table 4. Species with exclusively scalariform perforation plates

Family	Species	Type*
Betulaceae	*Carpinus cordata*	1
	Corylus sieboldiana	1
	Betula maximowicziana	1
	Betula platyphylla var. *japonica*	1
	Betula ermanii	1
	Betula grossa	1
	Alnus firma	2
	Alnus maximowiczii	2
	Alnus hirsuta	2
	Alnus serrulatoides	2
	Alnus japonica	2
Cercidiphyllaceae	*Cercidiphyllum japonicum*	2
Magnoliaceae	*Michelia compressa*	1
	Liriodendron tulipifera	1
Saxifragaceae	*Hydrangea petiolaris*	1
	Hydrangea paniculata	3
	Deutzia crenata	3
Hamamelidaceae	*Hamamelis japonica*	1
	Distylium racemosum	1
Buxaceae	*Buxus microphylla* var. *japonica*	1
Aquifoliaceae	*Ilex macropoda*	2
	Ilex micrococca	2
	Ilex sugerokii var. *longipedunculata*	2
	Ilex crenata	2
	Ilex pedunculosa	2
	Ilex rotunda	2
	Ilex integra	2
	Ilex latifolia	2
Staphyleaceae	*Euscaphis japonica*	2
Sabiaceae	*Meliosma rigida*	1
Theaceae	*Stewartia monadelpha*	1

Table 4 (Continued)

Family	Species	Type*
	Ternstroemia gymnanthera	2
	Cleyera japonica	3
Cornaceae	*Cornus controversa*	2
	Cornus brachypoda	2
	Cornus kousa	2
Clethraceae	*Clethra barbinervis*	3
Symplocaceae	*Symplocos coreana*	3
	Symplocos theophrastaefolia	3
	Symplocos glauca	3
	Symplocos prunifolia	3
Styracaceae	*Styrax japonica*	1
	Styrax obassia	1
	Pterostyrax corymbosa	1
Caprifoliaceae	*Viburnum dilatatum*	3
	Viburnum awabuki	3

* Type of scalariform perforation plates.
1……Few-barred (1–20 bars)
2……Intermediate-barred (21–40 bars)
3……Many-barred (over 41 bars)

Table 5. Species with both simple and scalariform perforation plates

Subgroup No.	Family	Species
1	Myricaceae	*Myrica rubra*
	Fagaceae	*Castanea crenata*
		Castanopsis cuspidata
		Castanopsis cuspidata var. *siebold*
	Ericaceae	*Pieris japonica*
2	Betulaceae	*Carpinus tschonoskii*
		Carpinus laxiflora
		Carpinus japonica
	Magnoliaceae	*Magnolia obovata*
		Magnolia salicifolia
		Magnolia kobus var. *borealis*
	Lauraceae	*Cinnamomum camphora*
		Cinnamomum japonicum
		Machilus thunbergii
		Lindera erythrocarpa
		Lindera umbellata
		Parabenzoin praecox
		Neolitsea sericea
		Neolitsea aciculata
		Actinodaphne lancifolia
		Actinodaphne longifolia
	Sabiaceae	*Meliosma myriantha*
	Flacourtiaceae	*Idesia polycarpa*
	Caprifoliaceae	*Sambucus sieboldiana* var. *miquelii*

3) Species with both simple and scalariform perforation plates

24 species (15 genera, 9 families) belonged to this group. The species names are listed in Table 5.

3, 1) Species with both kinds of the plates occurring regularly within an annual ring

5 species belonged to this subgroup. In *Pieris japonica*, the simple perforation plates of types 2 and 3 were present in the inner part of an annual ring, and the scalariform perforation plates of type 1 were present in the outer part. Although perforation plates in *Myrica rubra* were almost similar in their micromorphological variation to those in *Pieris japonica*, simple perforation plates were present in only few vessels at the beginning of an annual ring. In *Castanea crenata*, *Castanopsis cuspidata* and *C. cuspidata* var. *siebold*, the simple perforation plates of types 2, 3 and 4 were present in the earlywood vessels and in most latewood ones. The scalariform perforation plates of type 1 were rarely found in only small vessels in latewood.

3, 2) Species with both kinds of the plates occurring irregularly within an annual ring

19 species belonged to this subgroup. The occurrence of scalariform perforation plates in *Meliosma myriantha* was almost similar in their frequency to that of simple perforation plates. Scalariform perforation plates in this species were of type 1, and simple perforation plates were of type 2. In the remainder of the species belonging to this subgroup, the simple perforation plates of types 2, 3 and 4 were present in most vessels and the occurrence of scalariform perforation plates of type 1 had a tendency to be restricted to smaller vessels.

4) Species with both scalariform and multiple perforation plates

9 species (7 genera, 5 families) belonged to this group. The species names are listed in Table 6.

Table 6. Species with both scalariform and multiple perforation plates

Subgroup No.	Family	Species
1	Theaceae	*Camellia japonica*
		Camellia japonica var. *hortensis*
		Eurya japonca
	Ericaceae	*Lyonia ovalifolia* var. *elliptica*
		Enkianthus cernuus forma *rubens*
2	Magnoliaceae	*Illicium religiosum*
	Euphorbiaceae	*Daphniphyllum macropodum*
		Daphniphyllum teijsmannii
	Symplocaceae	*Symplocos lancifolia*

4, 1) Species with both kinds of the plates occurring regularly within an annual ring

5 species belonged to this subgroup. In *Camellia japonica* and *C. japonica* var. *hortensis*, the scalariform perforation plates of type 1 were present in the inner part of an annual ring, while the scalariform perforation plates of type 1 and the multiple perforation plates of types 1 and 2 were present in the outer part. In *Eurya japonica*, the scalariform perforation plates of type 3 were present in most vessels, and the multiple perforation plates of types 1 and 2 were present in the terminal zone of an annual ring. In *Lyonia ovalifolia* var. *elliptica* and *Enkianthus cernuus* forma *rubens*, the scalariform perforation plates of types 2 and 3 and the multiple perforation plates of type 2 were present in the inner part of an annual ring, and the multiple perforation plates of type 1 were exclusively present in the outer part.

4, 2) Species with both kinds of the plates occurring irregularly within an annual ring

In 4 species belonging to this subgroup, most perforation plates were scalariform and multiple perforation plates were rarely present. The scalariform perforation plates of type 3 were present in the 4 species. The multiple perforation plates of type 2 were exclusively present in *Illicium religiosum*, *Daphniphyllum macropodum* and *D. teijsmannii*, whereas those of types 1 and 2 were present in *Symplocos lancifolia*.

5) Species with both simple and multiple perforation plates

5 species (3 genera, 2 families) belonged to this group. The species names are listed in Table 7. In these species both kinds of perforation plates were irregularly present within an annual ring. Most perforation plates were simple, and multiple perforation plates were also present.

Both kinds of the plates occurred regardless of the diameter of the vessels in *Helicia cochinchinensis* and *Pourthiaea villosa* var. *laevis*, whereas the occurrence of multiple perforation plates were limited to some of smaller vessels in the 3 species belonging to *Sorbus*. The simple perforation plates of types 1 and 2 were present in *Helicia cochinchinensis*, whereas those of *Pourthiaea villosa* var. *laevis* were of type 1. Simple perforation plates in the 3 species of *Sorbus* were of types 1, 2 and 3. The multiple perforation plates of only type 3 were present in *Helicia*

Table 7. Species with both simple and multiple perforation plates

Family	Species
Proteaceae	*Helicia cochinchinensis*
Rosaceae	*Pourthiaea villosa* var. *laevis*
	Sorbus commixta
	Sorbus alnifolia
	Sorbus japonica

cochinchinensis, whereas those of types 1, 2 and 3 were present in *Pourthiaea villosa* var. *laevis* and in the 3 species of *Sorbus*. Although micromorphology of the multiple perforation plates in each of these species was very complicated, no differences were found among the 3 species belonging to *Sorbus*. It should be noticed that the perforation plates (multiple and simple) except typical simple perforation plates with smooth rim were mismatching or combination perforation plates in the 5 species.

6) Species with simple, scalariform and multiple perforation plates

Three kinds of perforation plates occurred regularly in association with the position of the vessels within an annual ring in the 3 species (2 genera, 2 families) belonging to this group (Table 8).

Table 8. Species with simple, scalariform and multiple perforation plates

Family	Species
Fagaceae	*Fagus crenata*
	Fagus japonica
Ericaceae	*Vaccinium bracteatum*

In *Fagus crenata* and *F. japonica*, the simple perforation plates of types 2 and 3 were present in the vessels in the inner part of an annual ring and the scalariform perforation plates of type 1 were present in some of the vessels in the outer part. Various forms of multiple perforation plates were present in others. These plates were of types 1, 2 and 3. In the 2 species most scalariform and multiple perforation plates were mismatching or combination plates. In *Vaccinium bracteatum*, the simple perforation plates of types 2 and 3 and the scalariform perforation plates of type 1 were present in the vessels of the inner part of an annual ring. The latter plates were also present in the outer part. The occurrence of multiple perforation plates were limited to the terminal zone. These plates were of types 1 and 2.

2. Pits

Although there are many aspects on the micromorphology of pits which should be observed using SEM, SEM observation was focused on vestured pits and intervascular pit membranes in the present study.

Because vestured pits are very complicated in three-dimensional structure, micromorphology of them is very difficult to be observed by the microscopes except SEM. On the other hand, the presence or absence of torus in the pit membranes was detected clearly using SEM, though fine structure of the pit membranes was not able to be exactly observed by SEM. Therefore, field emission SEM and TEM were applied to the observation of their fine structure.

2.1. Vestured pits

2.1.1. Definition of term "vestured pits" used in this paper

The term "vestured pits" was first used by BAILEY[61,62] to describe the bordered pits in dicotyledons which have minute projections arising from the pit border. He confirmed that these projections, i.e., vestures, also occurred on the inner surface of secondary wall of vessels as well the bordered pits in certain species[61,62]. On the other hand, "warts" were first found by KOBAYASHI and UTSUMI[135] and LIESE [136], on the inner surface and the inside of the pit chamber of tracheid wall of *Pinus* species. Therefore, it should be noticed that the terms "vestures" and "warts" are derived from the evidences of minute projections on the inner surface wall and the pit chamber wall in the vessels of angiosperms by LM and in the tracheids of gymnosperms by TEM, respectively.

According to the author's judgement on the basis of the observations on vestures and warts reported in the previous papers, morphological differences between "vestures" of angiosperms and "warts" of gymnosperms 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. Accordingly, the larger branched projections on the pit chamber wall and on the inner surface of the vessel wall have been termed "vestures", while the smaller unbranched ones on the inner surface of vessel wall which are almost similar in size and shape to warts on the tracheid wall of gymnosperms have been termed "warts".

In the 12 species examined in the present study (i.e., *Fagus crenata, F. japonica, Albizia julibrissin, Acacia confusa, Gleditsia japonica, Caesalpinia japonica, Sophora japonica, Maackia amurensis* var. *buergeri, Cladrastis platycarpa, Lespedeza bicolor* forma *acutifolia, Lagerstroemia subcostata* and *L. indica*), however, the larger branched projections and the smaller unbranched ones were impossible to be distinguished distinctly on the basis of the size and shape of them, because the two projections were present not only on the pit chamber wall within the same pit of vessel wall but also on the inner surface wall and furthermore various forms showing continuous transition from the larger branched projections to the smaller unbranched ones were invariably found both on the pit chamber wall within the same pit and on a limited inner surface of vessel wall. These facts have also been recognized in different species besides the species described just above[20,73,75,79,80,88]. Both projections were attacked in the same degree by some chemical treatments such as delignification et al, as reported in the previous papers[63,79]. Therefore, the two projections, i.e., vestures and warts, should be regarded as the same structure on the inner surface of the vessel wall including the surface of the vessel wall lining the pit cavity. Accordingly, in this paper the "vestures" are defined as all the projections on the inner surface of the vessel wall including the surface of the vessel wall lining the pit cavity and the "vestured pits" are defined as the pits having these projections, i.e., "vestures".

2.1.2. Micromorphology of vestured pits

Pit vestures varied remarkably in shape and size. As pointed out by CÔTÉ and DAY[63], categorizing pit vestures into distinct types was very difficult, because of variation and overlapping of characteristics in shape. Unbranched vestures were limited to small ones. They corresponded well with wart-like vestures described by SCURFIELD and SILVA[79]. Branched vestures varied remarkably in shape and size. Branched vestures tended to be more complicated in shape as they became larger in size. In many cases, larger vestures branched in several times from their base to tips and shape of them varied among species and genera. For example, "coraloid"[62] vestures were found in *Lagerstroemia subcostata* and *L. indica*, and "filamentous"[62] vestures were found only in *Pueraria lobata*.

Size of vestures was up to ca. 1 μ in diameter at base and up to ca. 3 μ in height. In many cases, vestures were larger in height than in width. When branches of vestures expanded widely, however, such vestures were larger in width than in height. Vestures with such branches occasionally reached ca. 5 μ in their maximum width.

Pit vestures showed a certain pattern in their size, shape and distribution within a pit associated with the extent of vesturing. Therefore, the vestured pits observed in the present study were divided into the following three types on the basis of the extent of vesturing within a pit chamber.

Type 1……Pits of slight vesturing. Several simple vestures arise from only the margin of the outer pit aperture on the pit chamber wall, or numerous smaller unbranched vestures arise from near the outer pit aperture on the pit chamber wall. Vestures are not present near the pit annulus on the pit chamber wall. Vestures do not occulude the outer aperture.

Type 2……Pits of moderate vesturing. Vestures mostly occulude the 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. Many smaller simple vestures always occur near the base of the larger branched vestures on the pit annulus side. Vestures are not present near the pit annulus on the pit chamber wall.

Type 3……Pits of remarkable vesturing. Vestures arise from the whole surface of pit chamber wall. 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 on the pit chamber wall. In many cases, all vestures project toward the pit membrane until they reach it. Tips of them are closely arranged parallel to the pit membrane. In such cases, therefore, pit chamber is almost occupied by the vestures.

2.1.3. Description of the micromorphological variation of vestured pits of the species

On the basis of the occurrence of vestures in pits in each species, the species examined were divided into 3 groups (Table 9).

Table 9. Grouping of species examined divided on the basis of the occurrence of vestures in pits

Group No.	Number of species (genera, families)	Occurrence of vestures in pits	
		Vestured pits	Non-vestured pits
1	17 (17, 6)	○	—
2	21 (10, 6)	○	○
3	185 (96, 48)	—	○

○: Present —: Absent

Table 10. Subgrouping of the species with exclusively vestured pits divided on the basis of the extent of vesturing in each pit kind

Subgroup No.	Species	Extent of vesturing in pit*			
		V-V pit	V-R pit	V-P pit	V-F pit
1	*Acacia confusa*2) *Lespedeza bicolor* forma *acutifolia*	3	3	3	3
2	*Albizia julibrissin*2) *Caesalpinia japonica*2) *Pueraria lobata*2)	2, 3	2	2	
3	*Gleditsia japonica* *Sophora japonica*2) *Maackia amurensis* var. *buergeri*2) *Cladrastis platycarpa*2) *Euchresta japonica*	2	2	2	2
4	*Caragana chamlagu* *Aleurites cordata*2) *Sapium japonicum*2) *Meliosma myriantha*1)2) *Zizyphus jujuba* var. *inermis* *Clethra barbinervis* *Enkianthus cernuus* forma *rubens*	1	1	1	1

1)……No V-V pits were found.
2)……No V-F pits were found.
* V-V pit……Intervascular pit
V-R pit……Vessel to ray parenchyma pit
V-P pit……Vessel to axial parenchyma pit
V-F pit……Vessel to wood fiber pit
1……Slight vesturing
2……Moderate vesturing
3……Remarkable vesturing

1) Species with exclusively vestured pits

17 species (17 genera, 6 families) belonged to this group. The extent of vesturing in each pit kind (i. e., V-V pits……Intervascular pits, V-R pits……Vessel to ray parenchyma pits, V-P pits……Vessel to axial parenchyma pits, V-F pits…… Vessel to wood fiber pits) in the vessel wall of the 17 species is shown in Table 10. The 17 species were divided into 4 subgroups (Table 10).

In *Acacia confusa* and *Lespedeza bicolor* forma *acutifolia* of the 1st subgroup, all the pits were the vestured pits of type 3 regardless of pit kind.

In *Albizia julibrissin, Caesalpinia japonica* and *Pueraria lobata* of the 2nd subgroup, V-V pits were the vestured pits of types 2 and 3, while V-R and V-P pits were the vestured pits of type 2. In *Albizia julibrissin*, vesturing in V-V pits was more remarkable in the vessels in the outer part than in the inner part of an annual ring. In *Caesalponia japonica* and *Pueraria lobata*, the extent of vesturing in V-V pits varied regardless of the vessel member diameter and its position within an annual ring.

In the 5 species of the 3rd subgroup, all the pits were the vestured pits of type 2.

In the 7 species of the 4th subgroup, all the pits were the vestured pits of type 1.

2) Species with vestured and non-vestured pits

21 species (10 genera, 6 families) belonged to this group. On the basis of the extent of vesturing in each pit kind, the 21 species were divided into 5 subgroups as shown in Table 11.

In *Lagerstroemia subcostata* and *L. indica* of the 1st subgroup, V-V pits were the vestured pits of type 3, while V-R and V-P pits varied remarkably in the extent of vesturing not only within a vessel member but also in the limited region of vessel wall. The extent of vesturing in V-R and V-P pits varied regardless of the vessel member diameter and its position within an annual ring. Vestured pits of them were those of types 1, 2 and 3, and non-vestured pits were also present.

In *Wisteria floribunda* and *Millettia japonica* of the 2nd subgroup, V-V pits were the vestured pits of type 2, while V-R and V-P pits varied considerably in the extent of vesturing. Non-vestured pits and the vestured pits of types 1 and 2 were found in each of V-R and V-P pits. The extent of vesturing varied regardless of the vessel member diameter and its position within an annual ring.

In *Robinia pseudo-acacia* of the 3rd subgroup, vestured pits in all the pit kinds were those of types 1 and 2, though non-vestured pits were also present in V-R and V-P pits. The extent of vesturing in V-V pits was more remarkable in the outer part than in the inner part of an annual ring, while that of V-R and V-P pits varied regardless of the vessel member diameter and its position within an annual ring.

In *Symplocos coreana* of the 4th subgroup, V-V pits were the vestured pits of type 1, while others were non-vestured pits and the vestured pits of type 1. In pits except V-V pits, pit vestures tended to be more densely developed in the

Table 11. Subgrouping of the species with vestured and non-vestured pits divided on the basis of the extent of vesturing in each pit kind

Subgroup No.	Species	Extent of vesturing in pit*			
		V-V pit	V-R pit	V-P pit	V-F pit
1	*Lagerstroemia subcostata*[2)] *Lagerstroemia indica*[2)]	3	0, 1, 2, 3	0, 1, 2, 3	
2	*Wisteria floribunda*[2)] *Millettia japonica*[2)]	2	0, 1, 2	0, 1, 2	
3	*Robinia pseudo-acacia*[2)]	1, 2	0, 1, 2	0, 1, 2	
4	*Symplocos coreana*	1	0, 1	0, 1	0, 1
5	*Fagus crenata* *Fagus japonica* *Quercus acuta*[1)] *Quercus sessilifolia*[1)] *Quercus gilva*[1)] *Quercus myrsinaefolia*[1)] *Quercus glauca*[1)] *Quercus salicina*[1)] *Quercus phillyraeoides*[1)] *Quercus variabilis*[1)] *Quercus acutissima*[1)] *Pasania glabra*[1)] *Eurya japonica*[1)] *Ligustrum japonicum* *Ligustrum obtusifolium*	0, 1	0, 1	0, 1	0, 1

1)……No V-V pits were found.
2)……No V-F pits were found.
* V-V pit……Intervascular pit
V-R pit……Vessel to ray parenchyma pit
V-P pit……Vessel to axial parenchyma pit
V-F pit……Vessel to wood fiber pit
0……Non-vestured pit
1……Slight vesturing
2……Moderate vesturing
3……Remarkable vesturing

outer part than in the inner part of an annual ring.

In the 15 species of the 5th subgroup, non-vestured and vestured pits were found in each of pit kinds. All the vestured pits of these species were those of type 1 regardless of pit kinds. In *Fagus crenata* and *F. japonica*, vestured pits were found in the vessels in the outer part of an annual ring, but not in those in the inner part. In *Quercus variabilis* and *Q. acutissima*, vestured pits were found in some of the vessels in the outer part of an annual ring. In *Quercus acuta*, *Q. sessilifolia*, *Q. gilva*, *Q. myrsinaefolia*, *Q. glauca*, *Q. salicina*, *Q. phillyraeoides* and *Pasania glabra*, vestured pits tended to be found in the smaller vessel members. In *Eurya japonica*, occurrence of pit vestures varied regardless of the vessel member diameter and its position within an annual ring. In *Ligustrum japonicum* and *L. obtusifolium*, the extent of vesturing tended to be more remarkable in the outer part than in the inner part of an annual ring.

3) Species with exclusively non-vestured pits

185 species (96 genera, 48 families) except the species listed in Tables 10 and 11 belonged to this group.

2. 2. Pit membrane

2. 2. 1. Micromorphology of pit membrane

The vessel pit membrane is described as a membrane, without torus and any visible openings, consisting of two primary walls of the adjacent cells and the intercellular layer[1,16]. However, this description is based on mainly TEM observations on a limited number of species[89~110]. Therefore, a further observation on the pit membranes in a wide variety of angiosperm species was considered to be needed. Microfibrillar orientation in the pit membrane was not always exactly detected by SEM observation due to thickness of C–Au coating layer on the surface of specimens used in the present study. However, the presence or absence of torus in the intervascular pit membranes was clearly able to be confirmed using SEM. Therefore, the presence or absence of torus in them was mainly observed. Of the 223 species examined in the present study, intervascular pits were present in 197 species (110 genera, 50 families).

2. 2. 2. Description on the intervascular pit membrane of the species

1) Species having the intervascular pit membrane with torus

10 species (2 genera, 2 families) were confirmed to invariably have the torus in their intervascular pit membranes (Table 12). The pit membranes with torus were invariably found in the 3 species which belong to subsection *Daphnanthoides* of the 5 species examined of section *Daphne* of *Daphne*, and in all of the 7 species examined of *Osmanthus*. According to OHWI[174], *Daphne kiusiana*, *D. miyabeana*, *D. pseudo-mezereum* and *D. kamtschatica* var. *jezoensis*, and *Osmanthus aurantiacus* var. *thunbergii*, *O. fragrans*, *O. heterophyllus*, *O. fortunei*, *O. insularis* and *O.*

Table 12. Species having intervascular pit membranes with torus

Family	Genus	Species
Thymelaeaceae	*Daphne*	*D. kiusiana*
		D. odora
		D. miyabeana
Oleaceae	*Osmanthus*	*O. aurantiacus* var. *thunbergii*
		O. aurantiacus var. *aurantiacus*
		O. fragrans
		O. heterophyllus
		O, fortunei
		O. insularis
		O. rigidus

rigidus are described as the species belonging to *Daphne* and *Osmanthus* indigenous to Japan, respectively. Of the 4 species of *Daphne*, *Daphne kiusiana* and *D. miyabeana* belong to subsection *Daphnanthoides*[182]. Therefore, the presence of the torus in the intervascular pit membranes is a characteristic feature in the species belonging to subsection *Daphnanthoides* of *Daphne* and *Osmanthus* indigenous to Japan.

2) Species having the intervascular pit membrane without torus

Of the 197 species (110 genera, 50 families) having intervascular pits, 187 species (109 genera, 50 families) except the 10 species described just above were confirmed to invariably have the intervascular pit membranes without torus.

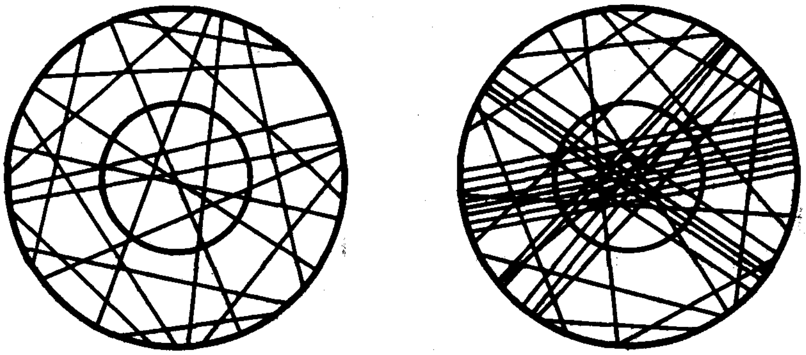
No openings were detected in the pit membranes in the 185 of 187 species having the intervascular pit membrane without torus. However, the openings that were distinctly detected at magnification of 10,000 times using SEM were occasionally present in the intervascular pit membranes in the 2 species (*Daphne pseudo-mezereum* and *D. kamtschatica* var. *jezoensis*) belonging to subsection *Pseudo-mezereum* of *Daphne*.

2.2.3. Fine structure of the pit membrane with torus

Fine structure of the intervascular pit membranes with torus in the 3 species belonging to subsection *Daphnanthoides* of *Daphne* and the 7 species of *Osmanthus* was examined by means of field emission SEM and TEM using direct carbon replica[175,176].

Solvent-dried intervascular pit membranes without extraneous materials[111] had a common feature within the species belonging to each of subsection *Daphnanthoides* and *Osmanthus*. In the 3 species belonging to subsection *Daphnanthoides*, the torus was incrusted with amorphous substances and the margo consisted of randomly oriented microfibrils. Openings in the margo were occasionally present in these species. In the 7 species belonging to *Osmanthus*, the torus was incrusted with amorphous substances, similar to that in subsection *Daphnanthoides*, but margo had a structure which consisted of both dominant randomly oriented microfibrils and radiating ones. In many cases, the radiating microfibrils were oriented in several directions, but sometimes they were oriented in all or in only limited directions. They were intermingled with the randomly oriented microfibrils. Openings in the margo were also occasionally present in the these species, as in subsection *Daphnanthoides*.

The amorphous substances of the torus in all the species belonging to subsection *Daphnanthoides* and *Osmanthus*, were almost removed by the treatment with sodium chlorite. In the subsection *Daphnanthoides*, the torus treated with this reagent showed a structure consisting of randomly oriented microfibrils continued from the margo. In the pit membrane treated there was no distinction between torus and margo because thickening of the central part disappeared. On the other hand, in the *Osmanthus*, the torus treated showed a structure which consisted of both randomly oriented microfibrils and radiating ones continued from the margo.



A B

Fig. 1. Diagramatic representation of the intervascular pit membrane structure in *Daphnanthoides* (A, left) and *Osmanthus* (B, right).

In most cases, the radiating microfibrils in the torus were densely arranged parallel with each other in several directions and a crossed texture was found, thus showing a slight thickening in the central part of the pit membrane.

Fig. 1 shows a diagrammatic representation of the fine structure of intervascular pit membrane in subsection *Daphnanthoides* and in *Osmanthus.*

3. Spiral thickenings

3. 1. Micromorphology of spiral thickenings

The spiral thickenings varied remarkably in their micromorphology (i. e., the helical direction, helical winding angle to the long axis of the vessel member, interval between ridges, magnitude of branching, and width, height and shape of ridge.) not only among the species but also within the same species as described in the previous reports[1,118,122,183].

It was found in the present study that categorizing the spiral thickenings occurred within the same species into distinct types on the basis of micromorphology of the spiral thickenings except their helical direction was most difficult, because of complication of variations of their micromorphology within the same species in many cases. In order to describe the observations briefly and precisely, therefore, outer appearance of the spiral thickenings was divided into the four types as follows, on the basis of the dominant helical direction of the spiral thickenings within a vessel member.

Type 1……All the spiral thickenings within a vessel member are "S" in their helical direction ("S" spiral thickenings)

Type 2……All the spiral thickenings within a vessel member are "Z" in their helical direction ("Z" spiral thickenings)

Type 3……Spiral thickenings within a vessel member are not constant in their helical direction ("SZ" spiral thickenings)

Type 4……Localized thickenings are present in a limited region of the inner surface wall within a vessel member and do not extend so long as they form spiral to the vessel member axis (Thickenings forming no spiral)

The spiral thickenings of type 1, i. e., "S" spiral thickenings, were found in the 122 of the 141 species having spiral thickenings. This fact corresponded well with the general description that the spiral thickenings are usually oriented in an "S" helix[1,122].

The spiral thickenings of type 2, i. e., "Z" spiral thickenings, were found in the 44 species. The occurrence of them was restricted to the species belonging to certain genera. Especially, the species belonging to *Sorbus, Berberis, Ligustrum* and *Osmanthus* were characterised by the presence of "Z" spiral thickenings.

The spiral thickenings of type 3 that are not constant in their helical direction within a vessel member were found in the 37 species. Even in the species in which their occurrence is the highest in frequency, the spiral thickenings of the other types were dominantly present. The occurrence of them was relatively high in their frequency in *Carpinus cordata, Ostrya japonica, Acer mono, Morus bombycis* and *Robinia pseudo-acacia.* In this connection, PARHAM and KAUSTINEN[118] have reported that swirled spiral thickenings are distinct in *Acer saccharum* and in some vessels of *Carpinus caroliniana* near the cell tips. MEYLAN and BUTTERFIELD[122] have pointed out that the "swirling" phenomenon is frequently associated with the cell tips though it is not entirely confined to them. This tendency of their occurrence was also confirmed by the present study.

The spiral thickenings of type 4, i. e., localized thickenings forming no spiral, were found in the 81 species. They were present in all of the 70 species having spiral thickenings in some vessel members, because they were found as the transitional forms between typical spiral thickenings and smooth inner surface wall. Because the spiral thickenings of type 4 do not exhibit "spiral" in their appearance, it may be inadequate for them to be entered into the category of the spiral thickenings. For the reason described just above, however, they should be considered as the modification of normal spiral thickenings.

3.2. Description on the micromorphological variation of spiral thickenings of the species

On the basis of the occurrence of spiral thickenings in each species, the species examined were divided into 3 groups (Table 13).

Table 13. Grouping of species examined divided on the basis of the occurrence of spiral thickenings

Group No.	Number of species (genera, families)	Occurrence of spiral thickenings	
		Vessel member with spiral thickenings	Vessel member without spiral thickenings
1	71 (32, 19)	○	—
2	70 (47, 27)	○	○
3	82 (46, 27)	—	○

○ : Present —: Absent

1) Species with spiral thickenings in all the vessel members

71 species (32 genera, 19 families) belonged to this group. The species names are listed in Table 14. On the basis of the occurrence of types of spiral thickenings, these species were divided into 8 subgroups as shown in Table 14.

In the 20 species of the 1st subgroup, the spiral thickenings of type 1 were present in all the vessel members in each species.

In the 9 species of the 2nd subgroup, the spiral thickenings of type 2 were present in all the vessel members in each species.

In the 13 species of the 3rd subgroup, the spiral thickenings of types 1 and 2 were present. In *Nandina domestica*, *Sorbus commixta* and the 5 species belonging to *Daphne*, the spiral thickenings of type 1 were present in only larger vessel members in the inner part of an annual ring and spiral thickenings of type 2

Table 14. Subgrouping of species with spiral thickenings in all the vessel members divided on the basis of the occurrence of spiral thickening types

Subgroup No.	Species	Types of spiral thickenings*
1	*Helicia cochinchinensis, Michelia compressa, Illicium religiosum, Euchresta japonica, Caragana chamlagu, Ilex macropoda, I. micrococca, I. sugerokii* var. *longipedunculata, I. crenata, I. pedunculosa, I. rotunda, I. latifolia, Euonymus sieboldianus, E. oxyphyllus, Tilia japonica, Vaccinium bracteatum, Symplocos theophrastaefolia, S. glauca, S. lancifolia, S. prunifolia*	1
2	*Ligustrum japonicum, L. obtusifolium, Osmanthus aurantiacus* var. *thunbergii, O. aurantiacus* var. *aurantiacus, O. fragrans, O. heterophyllus, O. fortunei, O. insularis, O. rigidus*	2
3	*Nandina domestica, Prunus mume, Photinia glabra, Eriobotrya japonica, Malus sieboldii, Sorbus commixta, Ternstroemia gymnanthera, Daphne kiusiana, D. odora, D. miyabeana, D. pseudomezereum, D. kamtschatica* var. *jezoensis, Pieris japonica*	1, 2
4	*Carpinus cordata, Ostrya japonica, Ilex integra, Elaeocarpus japonicus, Cleyera japonica*	1, 3
5	*Deutzia crenata, Camellia japonica, C. japonica* var. *hortensis, Syringa reticulata, Viburnum dilatatum, V. awabuki*	1, 4
6	*Prunus apetala, P. incisa, P. pendula* forma *ascendens, P. jamasakura, P. sargentii, P. maximowiczii, P. spinulosa, P. ssiori, P. grayana, P. buergeriana, Sorbus alnifolia, S. japonica, Aesculus turbinata*	1, 2, 3
7	*Pourthiaea villosa* var. *laevis*	1, 2, 4
8	*Acer sieboldianum, A. japonicum, A. mono, A. miyabei*	1, 3, 4

* 1……"S" spiral thickenings
2……"Z" spiral thickenings
3……"SZ" spiral thickenings
4……Thickenings forming no spiral

were present in others. Those of the latter type were predominant in their occurrence. In the remainder, the spiral thickenings of both types were present regardless of the vessel member diameter and its position within an annual ring. The spiral thickenings of type 1 were found in most vessel members in *Prunus mume*, whereas remarkable difference between both types was not found in frequency of their occurrence in the other species.

In the 5 species of the 4th subgroup, the spiral thickenings of types 1 and 3 were present. In all of them, both types were irregularly present within an annual ring and the spiral thickenings of type 1 were predominant in their occurrence. In *Ilex integra*, *Elaeocarpus japonicus* and *Cleyera japonica*, the spiral thickenings of type 3 were rarely found.

In 6 species of the 5th subgroup, the spiral thickenings of types 1 and 4 were present. In *Camellia japonica* and *C. japonica* var. *hortensis*, the thickenings of type 4 were present in most vessel members and the spiral thickenings of both types were present regardless of the vessel member diameter and its position within an annual ring. In the remainder, the thickenings of type 4 were present only in vessel members in the inner part of an annual ring and the spiral thickenings of type 1 were present in others. Those of the latter type were predominant in their occurrence.

In the 13 species of the 6th subgroup, the spiral thickenings of types 1, 2 and 3 were present. In *Sorbus alnifolia* and *S. japonica*, the spiral thickenings of type 1 were present in only the vessel members in the inner part of an annual ring and the spiral thickenings of types 2 and 3 were present in others. The spiral thickenings of type 2 tended to be present in the outer part and were predominant in their occurrence than the other types. In the remainder, three types were present regardless of the vessel member diameter and its position within an annual ring. In the 10 species belonging to *Prunus*, the spiral thickenings of type 1 were predominant in their occurrence than the other types. In *Aesculus turbinata*, remarkable difference between the spiral thickenings of types 1 and 2 was not found in their occurrence and the spiral thickenings of type 3 were rarely found.

In only one species, *Pourthiaea villosa* var. *laevis*, of the 7th subgroup, the spiral thickenings of types 1, 2 and 4 were present regardless of the vessel member diameter and its position within an annual ring. Although difference between the spiral thickenings of types 1 and 2 was not found in their occurrence, the two types were predominant in their occurrence than the thickenings of type 4.

In the 4 species belonging to *Acer* of the 8th subgroup, the spiral thickenings of types 1, 3 and 4 were present regardless of the vessel member diameter and its position within an annual ring. Although the spiral thickenings of type 1 were present in most vessel members, the spiral thickenings of types 3 and 4 were also present in others.

2) Species with spiral thickenings in some vessel members

In 70 species (47 genera, 27 families) belonged to this group. The species names are listed in Table 15. On the basis of the occurrence of types of spiral

Table 15. Subgrouping of species with spiral thickenings in some vessel members divided on the basis of the occurrence of spiral thickening types

Subgroup No.	Species	Types of spiral thickenings*
1	*Quercus mongolica*, *Q. mongolica* var. *grosseserrata*, *Q. serrata*, *Euscaphis japonica*, *Eurya japonica*, *Clethra barbinervis*, *Lyonia ovalifolia* var. *elliptica*, *Myrsine seguinii*, *Sambucus sieboldiana* var. *miquelii*	4
2	*Carpinus tschonoskii*, *C. japonica*, *Ulmus davidiana* var. *japonica*, *U. laciniata*, *Zelkova serrata*, *Celtis sinensis* var. *japonica*, *Aphananthe aspera*, *Magnolia obovata*, *M. salicifolia*, *M. kobus* var. *borealis*, *Cinnamomum camphora*, *C. japonicum*, *Machilus thunbergii*, *Lindera erythrocarpa*, *L. umbellata*, *Parabenzoin praecox*, *Neolitsea sericea*, *N. aciculata*, *Actinodaphne lancifolia*, *A. longifolia*, *Cladrastis platycarpa*, *Wisteria floribunda*, *Millettia japonica*, *Phellodendron amurense*, *Rhus verniciflua*, *R. trichocarpa*, *R. javanica*, *Celastrus orbiculatus*, *Acer palmatum* var. *matsumurae*, *A. distylum*, *A. carpinifolium*, *A. crataegifolium*, *A. rufinerve*, *A. cissifolium*, *Hibiscus syriacus*, *Firmiana simplex*, *Stewartia monadelpha*, *Catalpa ovata*	1, 4
3	*Berberis thunbergii*	2, 4
4	*Platycarya strobilacea*, *Ficus pumila*, *F. erecta*, *F. erecta* var. *yamadorii*, *Prunus persica*, *Albizia julibrissin*, *Caesalpinia japonica*	1, 2, 4
5	*Carpinus laxiflora*, *Corylus sieboldiana*, *Morus bombycis*, *Broussonetia papyrifera*, *Gleditsia japonica*, *Sophora japonica*, *Maackia amurensis* var. *buergeri*, *Robinia pseudo-acacia*, *Ailanthus altissima*, *Melia azedarach*, *Cedrela sinensis*, *Acer palmatum* var. *palmatum*, *A. ukurunduense*, *Sapindus mukorossi*, *Paulownia tomentosa*	1, 3, 4

* 1……"S" spiral thickenings
2……"Z" spiral thickenings
3……"SZ" spiral thickenings
4……Thickenings forming no spiral

thickenings, these species were divided into 5 subgroups as shown in Table 15.

In the species with typical spiral thickenings in some vessel members, the thickenings of type 4, i.e., localized thickenings forming no spiral, were always present because they were found as the transitional forms between typical spiral thickenings and smooth inner surface wall.

In the 9 species of the 1st subgroup, only the thickenings of type 4 were present. In *Quercus mongolica*, *Q. mongolica* var. *grosseserrata* and *Q. serrata*, the thickenings of type 4 were present in some vessel members in the outer part of an annual ring. In *Euscaphis japonica*, *Clethra barbinervis*, *Myrsine seguinii* and *Sambucus sieboldiana* var. *miquelii*, they were occasionally present regardless of the vessel member diameter and its position within an annual ring. In *Eurya japonica* and *Lyonia ovalifolia* var. *elliptica*, they were limited to some vessel members in terminal zone of an annual ring.

In the 38 species of the 2nd subgroup, the thickenings of types 1 and 4 were present. In the 3 species of *Magnolia*, *Stewartia monadelpha*, and the 6 species of *Acer*, the thickenings of types 1 and 4 were present regardless of the vessel member diameter and its position within an annual ring. In the remainder, no spiral thickenings were found in the larger vessel members in diameter and the thickenings of both types were present in only smaller vessel members.

In only one species, *Berberis thunbergii*, of the 3rd subgroup, the thickenings of types 2 and 4 were present. Spiral thickenings were not present in the larger vessel members in the inner part of an annual ring and the thickenings of both types were present in others.

In the 7 species of the 4th subgroup, the thickenings of types 1, 2 and 4 were present. In *Platycarya strobilacea* and *Albizia julibrissin*, spiral thickenings were not found in larger vessel members in the inner part of an annual ring and the thickenings of types 1, 2 and 4 were present in others. The spiral thickenings of type 2 were predominant in their occurrence in *Albizia julibrissin*, whereas remarkable difference among three types was not found in their occurrence in *Platycarya strobilacea*. In the 3 species of *Ficus* and *Caesalpinia japonica*, vessel members with the thickenings were irregularly present within an annual ring. In the 3 species of *Ficus* the thickenings of type 2 were predominant in their occurrence, whereas in *Caesalpinia japonica* remarkable difference among three types was not found in their occurrence. In *Prunus persica*, spiral thickenings were not present in larger vessel members in the inner part of an annual ring and the thickenings of the three types were present in others. The thickenings of types 1, 2 and 4 were irregularly present within an annual ring and the spiral thickenings of type 1 were predominant in their occurrence.

In the 15 species of the 5th subgroup, the thickenings of types 1, 3 and 4 were present. In the 13 species except the 2 species of *Acer*, spiral thickenings were not present in larger vessel members and the thickenings of types 1, 3 and 4 were present in others. In the 2 species belonging to *Acer*, the thickenings of types 1, 3 and 4 were present regardless of the vessel member diameter and its position within an annual ring. In all the species belonging to this subgroup, the spiral thickenings of type 1 were predominant in their occurrence than the other types. In *Robinia pseudo-acacia* and *Morus bombycis*, the spiral thickenings of type 3 were often found compared with other species.

3) Species without spiral thickenings in all the vessel members

82 species (46 genera, 27 families) belonged to this group. The species names are listed in Table 16.

In the present study, the vessel members in which the occurrence of spiral thickenings were restricted to only their tips were regarded as those without the spiral thickenings, because it was very difficult to confirm exhaustively their presence.

Table 16. Species without spiral thickenings

Family	Species
Salicaceae	*Populus nigra* var. *italica*, *P. sieboldii*, *P. maximowiczii*, *Salix bakko*, *S. kinuyanagi*, *S. sachalinensis*
Myricaceae	*Myrica rubra*
Juglandaceae	*Pterocarya rhoifolia*, *Juglans ailanthifolia*
Betulaceae	*Betula maximowicziana*, *B. platyphylla* var. *japonica*, *B. ermanii*, *B. grossa*, *Alnus firma*, *A. maximowiczii*, *A. hirsuta*, *A. serrulatoides*, *A. japonica*
Fagaceae	*Fagus crenata*, *F. japonica*, *Quercus acuta*, *Q. sessilifolia*, *Q. gilva*, *Q. myrsinaefolia*, *Q. glauca*, *Q. salicina*, *Q. phillyraeoides*, *Q. dentata*, *Q. variabilis*, *Q. acutissima*, *Castanea crenata*, *Castanopsis cuspidata*, *C. cuspidata* var. *siebold*, *Pasania glabra*
Cercidiphyllaceae	*Cercidiphyllum japonicum*
Magnoliaceae	*Liriodendron tulipifera*
Saxifragaceae	*Hydrangea petiolaris*, *H. paniculata*
Hamamelidaceae	*Hamamelis japonica*, *Distylium racemosum*
Leguminosae	*Acacia confusa*, *Lespedeza bicolor* forma *acutifolia*, *Pueraria lobata*
Rutaceae	*Zanthoxylum piperitum*, *Z. ailanthoides*
Simaroubaceae	*Picrasma quassioides*
Euphorbiaceae	*Daphniphyllum macropodum*, *D. teijsmannii*, *Mallotus japonicus*, *Aleurites cordata*, *Sapium japonicum*
Buxaceae	*Buxus microphylla* var. *japonica*
Anacardiaceae	*Rhus succedanea*, *R. sylvestris*
Sabiaceae	*Meliosma rigida*, *M. myriantha*
Rhamnaceae	*Zizyphus jujuba* var. *inermis*, *Hovenia dulcis*
Flacourtiaceae	*Idesia polycarpa*
Lythraceae	*Lagerstroemia subcostata*, *L. indica*
Araliaceae	*Aralia elata*, *Dendropanax trifidus*, *Acanthopanax sciadophylloides*, *Evodiopanax innovans*, *Kalopanax pictus*
Cornaceae	*Cornus controversa*, *C. brachypoda*, *C. kousa*
Ericaceae	*Enkianthus cernuus* forma *rubens*
Ebenaceae	*Diospyros morrisiana*, *D. lotus*, *D. kaki*
Symplocaceae	*Symplocos coreana*
Styracaceae	*Styrax japonica*, *S. obassia*, *Pterostyrax corymbosa*
Oleaceae	*Fraxinus spaethiana*, *F. mandshurica* var. *japonica*, *F. japonica*, *F. lanuginosa*
Verbenaceae	*Clerodendrom trichotomum*

4. Vestures

This chapter deals with the vestures on the inner surface of vessel wall except the pit region.

4.1. Micromorphology of vestures

The shape, size and distribution of vestures were variable in many of the species with vestures in the inner surface except the pit region of the vessel wall. The shape of vestures was able to be divided into main two categories: unbranched and branched. Unbranched vestures corresponded well with the warts described in the previous reports[63,73,79~82,97,155]. They were similar in shape to the warts of softwood tracheids[145]. They were found in all of the species with vestures. They were hemispherical, conical, rod-like and massive etc. in shape. Although hemispherical and conical vestures were present in all the species with vestures, rod-like and massive ones were present in certain species. Branched vestures were restricted in their occurrence to the following species; *Fagus crenata*, *F. japonica*, *Albizia julibrissin*, *Acacia confusa*, *Gleditsia japonica*, *Caesalpinia japonica*, *Sophora japonica*, *Maackia amurensis* var. *buergeri*, *Cladrastis platycarpa*, *Lespedeza bicolor* forma *acutifolia*, *Lagerstroemia subcostata* and *L. indica*. Unbranched vestures were also always present in these species. Continuity in shape and size between simple unbranched vestures and complicated branched ones were always recognized in the species with branched ones.

The size (i. e., diameter at the base) of vestures ranged from 50 to 700 nm. These values were almost the same as the warts in the softwood tracheids[145]. Only small vestures of 50~200 nm were present in *Enkianthus cernuus* forma *rubens*. Vestures bigger than 500 nm were often found in *Fagus crenata* and *F. japonica*, but numerous smaller ones were also present as already reported[18,97]. The height of unbranched vestures ranged from 50 to 400 nm in many species. However, vestures in *Fagus crenata* occasionally reached to 750 nm in height. In general, branched vestures were bigger in height than unbranched ones. Some branched vestures in *Caesalpinia japonica* were bigger than 1 μ in height.

In many of the species with vestures, distribution of vestures varied among vessel members within the same species. Accordingly, vesture distribution was divided into the following two types on the basis of the difference of the distribution on the entire inner surface wall except the pit region within a vessel member regardless of their shape and size.

Type 1……Vestures are sparsely or locally present.

Type 2……Vestures are densely present.

4. 2. Description on the micromorphological variation of vestures of the species

The species examined were divided into 3 groups by the presence or absence of the vessel members with vestures (Table 17).

Table 17. Grouping of species examined divided on the basis of the occurrence of vestures

Group No.	Number of species (genera, families)	Occurrence of vestures	
		Vessel member with vestures	Vessel member without vestures
1	20 (15, 10)	○	—
2	25 (9, 4)	○	○
3	178 (101, 47)	—	○

○ : Present —: Absent

1) Species with vestures on the inner surface wall of all the vessel members

20 species (15 genera, 10 families) belonged to this group. The species names are listed in Table 18.

On the basis of the difference of vesture distribution on the inner surface wall, these species were divided into 2 subgroups as shown in Table 18.

In the 7 species (6 genera, 5 families) of the 1st subgroup, only the vessel members with the vestures of type 2 were present.

In the 13 species (9 genera, 5 families) of the 2nd subgroup, the vessel members with the vestures of types 1 and 2 were present. In *Albizia julibrissin*, *Lespedeza bicolor* forma *acutifolia* and *Symplocos coreana*, the vessel members with the vestures of type 1 were present in the inner part of an annual ring and those of type 2 were present in the outer part. In the remainder, distribution of vestures varied regardless of the vessel member diameter and its position within an annual ring.

Table 18. Subgrouping of species with vestures in all the vessel members divided on the basis of vesture distribution

Subgroup No.	Species	Types of vesture distribution*
1	*Aleurites cordata* *Sapium japonicum* *Zizyphus jujuba* var. *inermis* *Eurya japonica* *Lagerstroemia subcostata* *Lagerstroemia indica* *Enkianthus cernuus* forma *rubens*	2
2	*Quercus acuta* *Quercus sessilifolia* *Quercus myrsinaefolia* *Quercus glauca* *Quercus salicina* *Pasania glabra* *Albizia julibrissin* *Acacia confusa* *Caesalpinia japonica* *Lespedeza bicolor* forma *acutifolia* *Meliosma myriantha* *Clethra barbinervis* *Symplocos coreana*	1, 2

* 1……Vestures are sparsely or locally present
2……Vestures are densely present

2) Species with vestures on the inner surface wall of some vessel members

25 species (9 genera, 4 families) belonged to this group. The species names are listed in Table 19. On the basis of the difference of vesture distribution on the inner surface wall of vessel members, these species were divided into 2 subgroups as shown in Table 19.

Table 19. Subgrouping of species with vestures in some vessel members divided on the basis of vesture distribution

Subgroup No.	Species	Types of vesture distribution*
1	*Fagus crenata* *Fagus japonica* *Quercus gilva* *Quercus phillyraeoides* *Quercus variabilis* *Quercus acutissima* *Acer japonicum*	0, 1, 2
2	*Castanopsis cuspidata* *Castanopsis cuspidata* var. *siebold* *Liriodendron tulipifera* *Gleditsia japonica* *Sophora japonica* *Maackia amurensis* var. *buergeri* *Cladrastis platycarpa* *Acer sieboldianum* *Acer palmatum* var. *palmatum* *Acer palmatum* var. *matsumurae* *Acer mono* *Acer miyabei* *Acer distylum* *Acer ukurunduense* *Acer carpinifolium* *Acer crataegifolium* *Acer rufinerve* *Acer cissifolium*	0, 1

* 0……Vestures are not or scarcely present
1……Vestures are sparsely or locally present
2……Vestures are densely present

In the 7 species (3 genera, 2 families) of the 1st subgroup, the vestures of types 1 and 2 were found in some vessel members. In *Fagus crenata*, *F. japonica*, *Quercus variabilis* and *Q. acutissima*, vestures were more densely distributed in the outer part of an annual ring than in the inner part. In the remainder, vesture distribution varied regardless of the vessel member diameter and its position within an annual ring.

In the 18 species (7 genera, 4 families) of the 2nd subgroup, the vestures of type 1 were found in some vessel members. In *Castanopsis cuspidata* and *C. cuspidata* var. *siebold*, the vessel members with the vestures of type 1 were rarely found in the outer part of an annual ring. In *Liriodendron tulipifera*, the vessel members of type 1 were present in the terminal zone. In *Gleditsia japonica*, *Sophora japonica*, *Maackia amurensis* var. *buergeri* and *Cladrastis platycarpa* belonging to Leguminosae, branched and unbranched vestures were occasionally found to arise on some of the spiral thickenings of the vessel members in the outer part of an annual ring. Vestures adhering to the spiral thickenings have been also found in three species having vestured pits indigenous to New Zealand[44,122]. In the 11 species belonging to *Acer*, vessel members with the vestures of type 1 occurred irregularly within an annual ring.

3) Species without vestures on the inner surface wall of all the vessel members

178 species (101 genera, 47 families) except the species listed in Tables 18 and 19 belonged to this group.

5. Trabeculae

Trabeculae were found in the vessel members of the 11 species (11 genera, 8 families) listed in Table 20.

Table 20. Species in which trabeculae were found in vessel members

Family	Genus	Species
Salicaceae	*Salix*	*S. bakko*
Ulmaceae	*Ulmus*	*U. davidiana* var. *japonica*
Lauraceae	*Neolitsea*	*N. aciculata*
Rosaceae	*Prunus*	*P. buergeriana*
	Pourthiaea	*P. villosa* var. *laevis*
	Sorbus	*S. commixta*
Celastraceae	*Celastrus*	*C. orbiculatus*
	Euonymus	*E. sieboldianus*
Thymelaeaceae	*Daphne*	*D. kiusiana*
Araliaceae	*Acanthopanax*	*A. sciadophylloides*
Caprifoliaceae	*Sambucus*	*S. sieboldiana* var. *miquelii*

The trabeculae were bar- and spool-like structures extending radially across the lumen of the vessel member from one tangential wall to the other. They showed an increase in diameter toward their bases contacting the tangential wall as reported in the vessel members[168,170] and in the softwood tracheids[173]. However, deviations from the typical rod- and spool-like trabeculae were also rarely found.

The typical trabeculae consisted of a central core and a shell of cell wall substance enclosing it. The central core of trabeculae was connected with the intercellular layer of the tangential wall and the cell wall enclosing the core had a structural continuity with the tangential wall.

It was found from the SEM and PM observations that the dominant direction of microfibrillar orientation in the secondary wall enclosing the central core was parallel to the long axis of the trabeculae except for the basis. This structure of trabeculae corresponded well with that in softwood tracheids[173].

The occurrence of trabeculae varied among the species in which they were found. Moreover, trabeculae were present in the wood samples from only one tree of the same species, but not in them from the others. As pointed out by BUTTERFIELD and MEYLAN[169], therefore, the presence of the trabeculae cannot be considered to be a normal feature in wood structure.

6. Characteristic features on the micromorphology of vessel wall sculptures in the species examined

The results obtained on micromorphological features on the perforation plates, pits, spiral thickenings and vestures in each of the species examined are summarized in Table 21. Observations on the trabeculae are not shown in Table 21, because their occurrence cannot be considered to be a characteristic feature of the species in which they were found as already described.

The figures in Table 21 indicate the following features in each of the vessel wall sculptures.

A. Perforation plates
- 1…Simple perforation plates are exclusively present.
- 2…Scalariform perforation plates are exclusively present.
  - 2-1…Few-barred scalariform perforation plates are exclusively (or mostly) present.
  - 2-2…Intermediate-barred scalariform perforation plates are exclusively (or mostly) present.
  - 2-3…Many-barred scalariform perforation plates are exclusively (or mostly) present.
- 3…Both kinds of simple and scalariform perforation plates are present.
- 4…Both kinds of scalariform and multiple perforation plates are present.
- 5…Both kinds of simple and multiple perforation plates are present.
- 6…Three kinds of simple, scalariform and multiple perforation plates are present.

B. Pits

B. 1. Vestures
- 1…Vestured pits are exclusively present.
  - 1-1…Slight vesturing
  - 1-2…Moderate vesturing
  - 1-3…Remarkable vesturing
- 2…Vestured and non-vestured pits are present.
  - 2-1…Slight vesturing in the vestured pits.
  - 2-2…Moderate vesturing in the vestured pits.
  - 2-3…Remarkable vesturing in the vestured pits.
- 3…Non-vestured pits are exclusively present.

B. 2. Pit membranes
- 1…Pit membranes with torus are exclusively present.
- 2…Pit membranes without torus are exclusively present.
- –…Intervascular pits are absent.

C. Spiral thickenings
- 1…Spiral thickenings are present in all the vessel members
  - 1-1…"S" spiral thickenings are present.
  - 1-2…"Z" spiral thickenings are present.

1-3…"SZ" spiral thickenings are present.

1-4…Thickenings forming no spiral are present.

2…Spiral thickenings are present in some vessel members.

2-1…"S" spiral thickenings are present in the vessel members with spiral thickenings.

2-2…"Z" spiral thickenings are present in the vessel members with spiral thickenings.

2-3…"SZ" spiral thickenings are present in the vessel members with spiral thickenings.

2-4…Thickenings forming no spiral are present in the vessel members with spiral thickenings.

3…Spiral thickenings are absent in all the vessel members.

D. Vestures

1…Vestures are present in all the vessel members.

1-1…Vestures are sparsely or locally present.

1-2…Vestures are densely present.

2…Vestures are present in some vessel members.

2-1…Vestures are sparsely or locally present in the vessel members with vestures.

2-2…Vestures are densely present in the vessel members with vestures.

3…Vestures are not or scarcely present in all the vessel members.

Wood samples examined were collected from more than one sampling tree in each of as many species as possible, but not in all the species examined (Table 1). The wood samples from different trees of the same species revealed common micromorphological features of vessel wall sculptures. Therefore, it is reasonable to conclude that micromorphological features of vessel wall sculptures indicated in Table 21 show characteristic features of each of the species examined. The results in the table are considered to provide fundamental information helpful for the elucidation of characteristic wood properties in individual species from their vessel wall structure.

Sculptures observed in the present study varied considerably in their micromorphology not only among the different species but also in the same species. In order to describe the observations briefly and precisely, they were divided into several kinds and types on the basis of certain criteria. The characteristic features in each of the species examined are shown in Table 21. Therefore, detailed observations on differences within micromorphological features described in the same categories and patterns of micromorphological variation of vessel wall sculptures within a species are not sufficiently shown in Table 21. However, common characteristic features of the micromorphology of the vessel wall sculptures including these observations among the species were recognized as follows, within the range of the species examined, although this problem cannot be discussed sufficiently because of the limitation of number of the species examined.

Table 21. Characteristic features on micromorphology of vessel wall sculptures in the species examined

Family	Genus	Species	Perforation plates	Pits		Spiral thickenings	Vestures
				Vestures	Pit membranes		
Salicaceae	*Populus*	*P. nigra* var. *italica*	1	3	2	3	3
		P. sieboldii	1	3	2	3	3
		P. maximowiczii	1	3	2	3	3
	Salix	*S. bakko*	1	3	2	3	3
		S. kinuyanagi	1	3	2	3	3
		S. sachalinensis	1	3	2	3	3
Myricaceae	*Myrica*	*M. rubra*	3	3	2	3	3
Juglandaceae	*Platycarya*	*P. strobilacea*	1	3	2	2–1, 2, 4	3
	Pterocarya	*P. rhoifolia*	1	3	2	3	3
	Juglans	*J. ailanthifolia*	1	3	2	3	3
Betulaceae	*Carpinus*	*C. tschonoskii*	3	3	2	2–1, 4	3
		C. laxiflora	3	3	2	2–1, 3, 4	3
		C. japonica	3	3	2	2–1, 4	3
		C. cordata	2–1	3	2	1–1, 3	3
	Ostrya	*O. japonica*	1	3	2	1–1, 3	3
	Corylus	*C. sieboldiana*	2–1	3	2	2–1, 3, 4	3
	Betula	*B. maximowicziana*	2–1	3	2	3	3
		B. platyphylla var. *japonica*	2–1	3	2	3	3
		B. ermanii	2–1	3	2	3	3
		B. grossa	2–1	3	2	3	3
	Alnus	*A. firma*	2–2	3	2	3	3
		A. maximowiczii	2–2	3	2	3	3
		A. hirsuta	2–2	3	2	3	3
		A. serrulatoides	2–2	3	2	3	3
		A. japonica	2–2	3	2	3	3
Fagaceae	*Fagus*	*F. crenata*	6	2–1	2	3	2–1, 2
		F. japonica	6	2–1	2	3	2–1, 2
	Quercus	*Q. acuta*	1	2–1	—	3	1–1, 2
		Q. sessilifolia	1	2–1	—	3	1–1, 2
		Q. gilva	1	2–1	—	3	2–1, 2
		Q. myrsinaefolia	1	2–1	—	3	1–1, 2

		Q. glauca	1	2–1	—	3	1–1, 2
		Q. salicina	1	2–1	—	3	1–1, 2
		Q. phillyraeoides	1	2–1	—	3	2–1, 2
		Q. mongolica	1	3	2	2–4	3
		Q. mongolica var. *grosseserrata*	1	3	2	2–4	3
		Q. serrata	1	3	2	2–4	3
		Q. dentata	1	3	2	3	3
		Q. variabilis	1	2–1	—	3	2–1, 2
		Q. acutissima	1	2–1	—	3	2–1, 2
	Castanea	*C. crenata*	3	3	2	3	3
	Castanopsis	*C. cuspidata*	3	3	2	3	2–1
		C. cuspidata var. *siebold*	3	3	2	3	2–1
	Pasania	*P. glabra*	1	2–1	—	3	1–1, 2
Ulmaceae	*Ulmus*	*U. davidiana* var. *japonica*	1	3	2	2–1, 4	3
		U. laciniata	1	3	2	2–1, 4	3
	Zelkova	*Z. serrata*	1	3	2	2–1, 4	3
	Celtis	*C. sinensis* var. *japonica*	1	3	2	2–1, 4	3
	Aphananthe	*A. aspera*	1	3	2	2–1, 4	3
Moraceae	*Morus*	*M. bombycis*	1	3	2	2–1, 3, 4	3
	Broussonetia	*B. papyrifera*	1	3	2	2–1, 3, 4	3
	Ficus	*F. pumila*	1	3	2	2–1, 2, 4	3
		F. erecta	1	3	2	2–1, 2, 4	3
		F. erecta var. *yamadorii*	1	3	2	2–1, 2, 4	3
Proteaceae	*Helicia*	*H. cochinchinensis*	5	3	2	1–1	3
Cercidiphyllaceae	*Cercidiphyllum*	*C. japonicum*	2–2	3	2	3	3
Berberidaceae	*Berberis*	*B. thunbergii*	1	3	2	2–2, 4	3
	Nandina	*N. domestica*	1	3	2	1–1, 2	3
Magnoliaceae	*Michelia*	*M. compressa*	2–1	3	2	1–1	3
	Magnolia	*M. obovata*	3	3	2	2–1, 4	3
		M. salicifolia	3	3	2	2–1, 4	3
		M. kobus var. *borealis*	3	3	2	2–1, 4	3
	Illicium	*I. religiosum*	4	3	—	1–1	3
	Liriodendron	*L. tulipifera*	2–1	3	2	3	2–1
Lauraceae	*Cinnamomum*	*C. camphora*	3	3	2	2–1, 4	3
		C. japonicum	3	3	2	2–1, 4	3
	Machilus	*M. thunbergii*	3	3	2	2–1, 4	3

Table 21 (Continued)

Family	Genus	Species	Perforation plates	Pits		Spiral thickenings	Vestures
				Vestures	Pit membranes		
	Lindera	*L. erythrocarpa*	3	3	2	2–1, 4	3
		L. umbellata	3	3	2	2–1, 4	3
	Parabenzoin	*P. praecox*	3	3	2	2–1, 4	3
	Neolitsea	*N. sericea*	3	3	2	2–1, 4	3
		N. aciculata	3	3	2	2–1, 4	3
	Actinodaphne	*A. lancifolia*	3	3	2	2–1, 4	3
		A. longifolia	3	3	2	2–1, 4	3
Saxifragaceae	*Hydrangea*	*H. petiolaris*	2–1	3	2	3	3
		H. paniculata	2–3	3	2	3	3
	Deutzia	*D. crenata*	2–3	3	2	1–1, 4	3
Hamamelidaceae	*Hamamelis*	*H. japonica*	2–1	3	2	3	3
	Distylium	*D. racemosum*	2–1	3	2	3	3
Rosaceae	*Prunus*	*P. mume*	1	3	2	1–1, 2	3
		P. persica	1	3	2	2–1, 2, 4	3
		P. apetala	1	3	2	1–1, 2, 3	3
		P. incisa	1	3	2	1–1, 2, 3	3
		P. pendula forma *ascendens*	1	3	2	1–1, 2, 3	3
		P. jamasakura	1	3	2	1–1, 2, 3	3
		P. sargentii	1	3	2	1–1, 2, 3	3
		P. maximowiczii	1	3	2	1–1, 2, 3	3
		P. spinulosa	1	3	2	1–1, 2, 3	3
		P. ssiori	1	3	2	1–1, 2, 3	3
		P. grayana	1	3	2	1–1, 2, 3	3
		P. buergeriana	1	3	2	1–1, 2, 3	3
	Photinia	*P. glabra*	1	3	—	1–1, 2	3
	Eriobotrya	*E. japonica*	1	3	—	1–1, 2	3
	Malus	*M. sieboldii*	1	3	—	1–1, 2	3
	Pourthiaea	*P. villosa* var. *laevis*	5	3	2	1–1, 2, 4	3
	Sorbus	*S. commixta*	5	3	2	1–1, 2	3
		S. alnifolia	5	3	2	1–1, 2, 3	3
		S. japonica	5	3	2	1–1, 2, 3	3
Leguminosae	*Albizia*	*A. julibrissin*	1	1–2, 3	2	2–1, 2, 4	1–1, 2

	Acacia	*A. confusa*	1	1–3	2	3	1–1, 2
	Gleditsia	*G. japonica*	1	1–2	2	2–1, 3, 4	2–1
	Caesalpinia	*C. japonica*	1	1–2, 3	2	2–1, 2, 4	1–1, 2
	Sophora	*S. japonica*	1	1–2	2	2–1, 3, 4	2–1
	Maackia	*M. amurensis* var. *buergeri*	1	1–2	2	2–1, 3, 4	2–1
	Cladrastis	*C. platycarpa*	1	1–2	2	2–1, 4	2–1
	Euchresta	*E. japonica*	1	1–2	2	1–1	3
	Lespedeza	*L. bicolor* forma *acutifolia*	1	1–3	2	3	1–1, 2
	Caragana	*C. chamlagu*	1	1–1	2	1–1	3
	Pueraria	*P. lobata*	1	1–2, 3	2	3	3
	Wisteria	*W. floribunda*	1	2–1, 2	2	2–1, 4	3
	Millettia	*M. japonica*	1	2–1, 2	2	2–1, 4	3
	Robinia	*R. pseudo-acacia*	1	2–1, 2	2	2–1, 3, 4	3
Rutaceae	*Zanthoxylum*	*Z. piperitum*	1	3	2	3	3
		Z. ailanthoides	1	3	2	3	3
	Phellodendron	*P. amurense*	1	3	2	2–1, 4	3
Simaroubaceae	*Ailanthus*	*A. altissima*	1	3	2	2–1, 3, 4	3
	Picrasma	*P. quassioides*	1	3	2	3	3
Meliaceae	*Melia*	*M. azedarach*	1	3	2	2–1, 3, 4	3
	Cedrela	*C. sinensis*	1	3	2	2–1, 3, 4	3
Euphorbiaceae	*Daphniphyllum*	*D. macropodum*	4	3	—	3	3
		D. teijsmannii	4	3	—	3	3
	Mallotus	*M. japonicus*	1	3	2	3	3
	Aleurites	*A. cordata*	1	1–1	2	3	1–2
	Sapium	*S. japonicum*	1	1–1	2	3	1–2
Buxaceae	*Buxus*	*B. microphylla* var. *japonica*	2–1	3	2	3	3
Anacardiaceae	*Rhus*	*R. succedanea*	1	3	2	3	3
		R. verniciflua	1	3	2	2–1, 4	3
		R. sylvestris	1	3	2	3	3
		R. trichocarpa	1	3	2	2–1, 4	3
		R. javanica	1	3	2	2–1, 4	3
Aquifoliaceae	*Ilex*	*I. macropoda*	2–2	3	2	1–1	3
		I. micrococca	2–2	3	2	1–1	3
		I. sugerokii var. *longipedunculata*	2–2	3	2	1–1	3
		I. crenata	2–2	3	2	1–1	3
		I. pedunculosa	2–2	3	2	1–1	3

Table 21 (Continued)

Family	Genus	Species	Perforation plates	Pits: Vestures	Pits: Pit membranes	Spiral thickenings	Vestures
		I. rotunda	2–2	3	2	1–1	3
		I. integra	2–2	3	2	1–1, 3	3
		I. latifolia	2–2	3	2	1–1	3
Celastraceae	*Celastrus*	*C. orbiculatus*	1	3	2	2–1, 4	3
	Euonymus	*E. siebolianus*	1	3	2	1–1	3
		E. oxyphyllus	1	3	2	1–1	3
Staphyleaceae	*Euscaphis*	*E. japonica*	2–2	3	2	2–4	3
Aceraceae	*Acer*	*A. sieboldianum*	1	3	2	1–1, 3, 4	2–1
		A. japonicum	1	3	2	1–1, 3, 4	2–1, 2
		A. palmatum var. *palmatum*	1	3	2	2–1, 3, 4	2–1
		A. palmatum var. *matsumurae*	1	3	2	2–1, 4	2–1
		A. mono	1	3	2	1–1, 3, 4	2–1
		A. miyabei	1	3	2	1–1, 3, 4	2–1
		A. distylum	1	3	2	2–1, 4	2–1
		A. ukurunduense	1	3	2	2–1, 3, 4	2–1
		A. carpinifolium	1	3	2	2–1, 4	2–1
		A. crataegifolium	1	3	2	2–1, 4	2–1
		A. rufinerve	1	3	2	2–1, 4	2–1
		A. cissifolium	1	3	2	2–1, 4	2–1
Hippocastanaceae	*Aesculus*	*A. turbinata*	1	3	2	1–1, 2, 3	3
Sapindaceae	*Sapindus*	*S. mukorossi*	1	3	2	2–1, 3, 4	3
Sabiaceae	*Meliosma*	*M. rigida*	2–1	3	—	3	3
		M. myriantha	3	1–1	—	3	1–1, 2
Rhamnaceae	*Zizyphus*	*Z. jujuba* var. *inermis*	1	1–1	2	3	1–2
	Hovenia	*H. dulcis*	1	3	2	3	3
Elaeocarpaceae	*Elaeocarpus*	*E. japonicus*	1	3	2	1–1, 3	3
Tiliaceae	*Tilia*	*T. japonica*	1	3	2	1–1	3
Malvaceae	*Hobiscus*	*H. syriacus*	1	3	2	2–1, 4	3
Sterculiaceae	*Firmiana*	*F. simplex*	1	3	2	2–1, 4	3
Theaceae	*Camellia*	*C. japonica*	4	3	2	1–1, 4	3
		C. japonica var. *hortensis*	4	3	2	1–1, 4	3
	Stewartia	*S. monadelpha*	2–1	3	—	2–1, 4	3

	Ternstroemia	*T. gymnanthera*	2–2	3	—	1–1, 2	3
	Cleyera	*C. japonica*	2–3	3	—	1–1, 3	3
	Eurya	*E. japonica*	4	2–1	—	2–4	1–2
Flacourtiaceae	*Idesia*	*I. polycarpa*	3	3	2	3	3
Thymelaeaceae	*Daphne*	*D. kiusiana*	1	3	1	1–1, 2	3
		D. odora	1	3	1	1–1, 2	3
		D. miyabeana	1	3	1	1–1, 2	3
		D. pseudo-mezereum	1	3	2	1–1, 2	3
		D. kamtschatica var. *jezoensis*	1	3	2	1–1, 2	3
Lythraceae	*Lagerstroemia*	*L. subcostata*	1	2–1, 2, 3	2	3	1–2
		L. indica	1	2–1, 2, 3	2	3	1–2
Araliaceae	*Aralia*	*A. elata*	1	3	2	3	3
	Dendropanax	*D. trifidus*	1	3	2	3	3
	Acanthopanax	*A. sciadophylloides*	1	3	2	3	3
	Evodiopanax	*E. innovans*	1	3	2	3	3
	Kalopanax	*K. pictus*	1	3	2	3	3
Cornaceae	*Cornus*	*C. controversa*	2–2	3	2	3	3
		C. brachypoda	2–2	3	2	3	3
		C. kousa	2–2	3	2	3	3
Clethraceae	*Clethra*	*C. barbinervis*	2–3	1–1	2	2–4	1–1, 2
Ericaceae	*Pieris*	*P. japonica*	3	3	2	1–1, 2	3
	Lyonia	*L. ovalifolia* var. *elliptica*	4	3	2	2–4	3
	Enkianthus	*E. cernuus* forma *rubens*	4	1–1	2	3	1–2
	Vaccinium	*V. bracteatum*	6	3	2	1–1	3
Myrsinaceae	*Myrsine*	*M. seguinii*	1	3	2	2–4	3
Ebenaceae	*Diospyros*	*D. morrisiana*	1	3	2	3	3
		D. lotus	1	3	2	3	3
		D. kaki	1	3	2	3	3
Symplocaceae	*Symplocos*	*S. coreana*	2–3	2–1	2	3	1–1, 2
		S. lancifolia	2–3	3	—	1–1	3
		S. theophrastaefolia	2–3	3	—	1–1	3
		S. glauca	4	3	—	1–1	3
		S. prunifolia	2–3	3	—	1–1	3
Styracaceae	*Styrax*	*S. japonica*	2–1	3	2	3	3
		S. obassia	2–1	3	2	3	3
	Pterostyrax	*P. corymbosa*	2–1	3	2	3	3

Table 21 (Continued)

Family	Genus	Species	Perforation plates	Pits		Spiral thickenings	Vestures
				Vestures	Pit membranes		
Oleaceae	*Ligustrum*	*L. japonicum*	1	2–1	2	1–2	3
		L. obtusifolium	1	2–1	2	1–2	3
	Osmanthus	*O. aurantiacus* var. *thunbergii*	1	3	1	1–2	3
		O. aurantiacus var. *aurantiacus*	1	3	1	1–2	3
		O. fragrans	1	3	1	1–2	3
		O. heterophyllus	1	3	1	1–2	3
		O. fortunei	1	3	1	1–2	3
		O. insularis	1	3	1	1–2	3
		O. rigidus	1	3	1	1–2	3
	Syringa	*S. reticulata*	1	3	2	1–1, 4	3
	Fraxinus	*F. spaethiana*	1	3	2	3	3
		F. mandshurica var. *japonica*	1	3	2	3	3
		F. japonica	1	3	2	3	3
		F. lanuginosa	1	3	2	3	3
Verbenaceae	*Clerodendrom*	*C. trichotomum*	1	3	2	3	3
Scrophulariaceae	*Paulownia*	*P. tomentosa*	1	3	2	2–1, 3, 4	3
Bignoniaceae	*Catalpa*	*C. ovata*	1	3	2	2–1, 4	3
Caprifoliaceae	*Sambucus*	*S. sieboldiana* var. *miquelii*	3	3	2	2–4	3
	Viburnum	*V. dilatatum*	2–3	3	2	1–1, 4	3
		V. awabuki	2–3	3	2	1–1, 4	3

Characteristic features of the sculptures were consistent within each of 10 families (Salicaceae, Ulmaceae, Lauraceae, Hamamelidaceae, Meliaceae, Lythraceae, Araliaceae, Cornaceae, Ebenaceae and Styracaceae), but not within each of 24 families (Juglandaceae, Betulaceae, Fagaceae, Moraceae, Berberidaceae, Magnoliaceae, Saxifragaceae, Rosaceae, Leguminosae, Rutaceae, Simaroubaceae, Euphorbiaceae, Anacardiaceae, Aquifoliaceae, Celastraceae, Aceraceae, Sabiaceae, Rhamnaceae, Theaceae, Thymelaeaceae, Ericaceae, Symplocaceae, Oleaceae and Caprifoliaceae). In the 24 families, their features was consistent within each of 14 genera (*Betula, Alnus, Fagus, Castanopsis, Ficus, Magnolia, Zanthoxylum, Daphniphyllum, Euonymus, Camellia, Ligustrum, Osmanthus, Fraxinus* and *Viburnum*), but not within each of 10 genera (*Carpinus, Quercus, Prunus, Sorbus, Rhus, Ilex, Acer, Meliosma, Daphne* and *Symplocos*). Special considerations on micromorphological features of the sculptures should be paid in the species belonging to each of these 10 genera. Classification of the species within *Quercus, Prunus, Sorbus, Ilex, Acer, Daphne* and *Symplocos* follows KITAMURA and MURATA[184,185].

In the 4 species belonging to *Carpinus*, common features were found in the pits and vestures, but not in the perforation plates and spiral thickenings. Both simple and scalariform perforation plates were present in *C. tschonoskii, C. laxiflora* and *C. japonica*, whereas few-barred scalariform perforation plates were exclusively present in *C. cordata*. Spiral thickenings were present in some vessel members in *C. tschonoskii, C. laxiflora* and *C. japonica*, whereas they were present in all the vessel members in *C. cordata*. Although "S" spiral thickenings and thickenings forming no spiral were found in the former, "SZ" spiral thickenings were also found in *C. laxiflora*. In the latter, "S" and "SZ" spiral thickenings and thickenings forming no spiral were found.

Common features in all of the sculptures were not found even within the species belonging to each of subgenera *Cyclobalanopsis* and *Lepidobalanus* of *Quercus*. In the 6 species (*Q. acuta, Q. sessilifolia, Q. gilva, Q. myrsinaefolia, Q. glauca* and *Q. salicina*) belonging to subgenus *Cyclobalanopsis*, common features were found in the sculptures with the exception of vestures. Vestures were present in some vessel members in *Q. gilva*, whereas they were present in all the vessel members in the other species. In each of the latter, they were sparsely present in some vessel members and were densely present in others. In *Q. variabilis* and *Q. acutissima* of section *Cerris* and *Q. phillyraeoides* of section *Ilex* belonging to subgenus *Lepidobalanus*, common features were found in all the sculptures. In the 4 species (*Q. mongolica, Q. mongolica* var. *grosseserrata, Q. serrata* and *Q. dentata*) belonging to section *Prinus* of subgenus *Lepidobalanus*, common features were found in the sculptures with the exception of spirial thickenings. Spiral thickenings were not found in *Q. dentata*, whereas they were found in some vessel members in the others. They showed thickenings forming no spiral in each of the latter.

In the 12 species belonging to *Prunus*, common features were in the sculptures except spiral thickenings. Spiral thickenings were present in all the vessel members in *P. mume* of subgenus *Prunus*, *P. apetala*, *P. incisa*, *P. pendula* forma *ascendens*, *P. jamasakura*, *P. sargentii* and *P. maximowiczii* of subgenus *Cerasus*, *P. spinulosa* of subgenus *Laurocerasus*, and *P. ssiori*, *P. grayana* and *P. buergeriana* of subgenus *Padus*, whereas they were present in some vessel members in *P. persica* of subgenus *Amygdalus*. Although "S" and "Z" spiral thickenings were present in all of the species examined belonging to subgenera *Prunus*, *Cerasus*, *Laurocerasus* and *Padus*, "SZ" spiral thickenings were also present in the 10 species belonging to subgenera *Cerasus*, *Laurocerasus* and *Padus*. On the other hand, "S" and "Z" spiral thickenings and thickenings forming no spiral were present in *P. persica* of subgenus *Amygdalus*.

In the 3 species belonging to *Sorbus*, common features were found in the sculptures except spiral thickenings. Although spiral thickenings were present in all the vessel members in the 3 species, the micromorphology was different between sections. That is, they showed "S" and "Z" spiral in *S. commixta* of section *Sorbus*, whereas they showed "S", "Z" and "SZ" spiral in *S. alnifolia* and *S. japonica* of section *Micromeles*.

In the 5 species belonging to *Rhus*, common features were found in the sculptures except spiral thickenings. Spiral thickenings were not present in *R. succedanea* and *R. sylvestris*, whereas they were present in some vessel members in *R. verniciflua*, *R. trichocarpa* and *R. javanica*. "S" spiral thickenings and thickenings forming no spiral were present in the 3 species.

In the 8 species belonging to *Ilex*, common features were found in the sculptures except spiral thickenings. In *I. macropoda* of section *Prinoides* and *I. micrococca* of section *Prinos* belonging to subgenus *Prinos*, common features were found in all the sculptures. Of the 6 species belonging to subgenus *Ilex*, common features were found in all the sculptures in the 4 species (*I. sugerokii* var. *longipedunculata*, *I. crenata*, *I. pedunculosa* and *I. rotunda*) of section *Lioprinus*. In *I. integra* and *I. latifolia* of section *Ilex*, however, the micromorphology of spiral thickenings was different. Only "S" spiral thickenings were present in *I. latifolia*, whereas "S" and "SZ" spiral thickenings were present in *I. integra*.

In the 12 species belonging to *Acer*, common features were found in perforation plates and pits, but not in spiral thickenings and vestures. In *A. mono* and *A. miyabei* of section *Palmata*, common features were found in all the sculptures. And also, in *A. carpinifolium* of section *Carpinifolia*, *A. crataegifolium* and *A. rufinerve* of section *Macrantha* and *A. cissifolium* of section *Cissifolia*, common features were found in all the sculptures. Among the species belonging to each of sections *Palmata* and *Spicata*, however, common features were not found in all the sculptures. Among the 4 species examined of section *Palmata*, common features were found in the perforation plates and pits, but not in the spiral thickenings and vestures. Spiral thickenings were present in all the vessel members in *A. sieboldianum* and *A. japonicum*, whereas they were present in some vessel members in *A. palmatum* var. *palmatum* and *A. palmatum* var. *matsumurae*. Although "S" spiral thickenings and thickenings forming no spiral were present in the 4 species, "SZ" spiral thickenings were also present in *A. sieboldianum*, *A. japonicum* and *A. palmatum* var. *palmatum*. Vestures were present in some vessel members in the 4 species. They were sparsely present in *A. siebolianum*, *A. palmatum* var. *palmatum* and *A. palmatum* var. *matsumurae*, whereas they were sparsely or densely present in *A. japonicum*. Between *A. distylum* and *A. ukurunduense* of section *Spicata*, micromorphology of spiral thickenings was different. Spiral thickenings were present in some vessel members in the two species. "S" spiral thickenings and thickenings forming no spiral were present in the two species, and "SZ" spiral thickenings in addition to the two types were also present in *A. ukurunduense*.

Between the 2 species (*M. rigida* and *M. myriantha*) belonging to *Meliosma*, different features were found in the perforation plates, pit vestures and vestures on the inner surface wall. In *M. rigida*, few-barred scalariform perforation plates were exclusively present and vestures were not present both in pits and on the inner surface wall. On the other hand, in *M. myriantha*, simple and few-barred scalariform perforation plates were present and vestured pits of slight vesturing were always present. Vestures on the inner surface wall were present in all the vessel members and they were sparsely or densely present.

In the 5 species belonging to *Daphne*, common features were found in the sculptures except intervascular pit membranes. Torus was always present in the intervascular pit membranes in *D. kiusiana*, *D. odora* and *D. miyabeana* belonging to subsection *Daphnanthoides* of section *Daphne*, but not in those in *D. pseudomezereum* and *D. kamtschatica* var. *jezoensis* belonging to subsection *Pseudomezereum* of section *Daphne*.

Between *S. coreana* of section *Palura* and the 4 species (*S. theophrastaefolia*, *S. glauca*, *S. lancifolia* and *S. prunifolia*) of section *Lodhra* belonging to *Symplocos*, remarkable differences were found in the sculptures except perforation plates. Among the 4 species of section *Lodhra*, common features were found in the sculptures except perforation plates. Although scalariform and multiple perforation plates were present in *S. lancifolia*, scalariform perforation plates were exclusively present in the others.

As described above, when common features were not found within species belonging to the same genus, differences on the micromorphological features of the sculptures were often found among the subgenera, sections and subsections within the same genus. Moreover, micromorphology of the sculptures revealed common features in the species belonging to each of the 3 subgenera (*Cerasus*, *Padus* and *Prinos*), 5 sections (*Cerris*, *Micromeles*, *Lioprinus*, *Macrantha* and *Palmata*) and 2 subsections (*Daphnanthoides* and *Pseudomezereum*).

These facts described just above suggest that the micromorphological features of the vessel wall sculptures shown in the present study have taxonomic significance and, therefore, provide useful information as diagnostic criteria for wood identification, one of the major application of wood anatomy, on the basis of micromorphology at a SEM level. Especially, many unique characteristic features of micromorphology of vessel wall sculptures in certain species, such as perforation plates in the species belonging to *Fagus, Helicia, Pourthiaea* and *Sorbus* etc., vestured pits in the species belonging to the genera of Leguminosae and *Lagerstroemia* etc., pit membranes with torus in the species belonging to subsection *Daphnanthoides* and *Osmanthus,* spiral thickenings in the species belonging to *Sorbus, Acer, Osmanthus* and *Magnolia* etc. and vestures on the inner surface wall in the species belonging to *Fagus, Lagerstroemia* and several genera of Leguminosae, are considered to be valuable in themselves as diagnostic criteria for wood identification.

Wood identification on the basis of the micromorphology at a SEM level is considered to have many advantages compared with that at a LM level. In addition to the information on the vessel wall sculptures obtained in the present study, information about other micromorphological features which can be utilized as diagnostic criteria for wood identification should be accumulated in a wide variety of species for the preparation of the key table at a SEM level. Therefore, further investigations at a SEM level for the purpose of wood identification are necessary.

Summary and Conclusion

Micromorphology of vessel wall sculptures was observed in 223 species, 120 genera, 51 families of Japanese dicotyledonous woods using SEM. The present SEM observation revealed the micromorphology of vessel wall sculptures in many species which have not yet been recorded and also confirmed the known information obtained mainly from LM observation.

In order to describe the observations obtained in the present study on the micromorphology of the sculptures briefly and precisely, each of sculptures was divided into several kinds and types on the basis of certain criteria in their micromorphology. Based on the occurrence of these kinds and types of each sculpture within a species, the species examined were classified into several groups and the micromorphological variation in each of the species was described.

Perforation plates were divided into three kinds ; i. e., simple, scalariform and multiple perforation plates. Based on the occurrence of these kinds within a species, the species examined were classified into the following 6 groups: (1) 136 species (71 genera, 32 families) having exclusively simple perforation plates, (2) 46 species (24 genera, 15 families) having exclusively scalariform perforation plates, (3) 24 species (15 genera, 9 families) having simple and scalariform perforation plates, (4) 9 species (7 genera, 5 families) having scalariform and multiple perforation plates, (5) 5 species (3 genera, 2 families) having simple and multiple perforation plates, (6) 3 species (2 genera, 2 families) having simple, scalariform and multiple perforation plates.

Observations on pits were focussed on vestured pits and intervascular pit membranes. Resemblance between vestures and warts was first pointed out. Judging from the shape, size and distribution of the two projections on the pit chamber wall and on the inner surface wall of the vessels in species having both projections, it was concluded that vestures and warts were of the same structure. In this

paper, therefore, the "vestures" were defined as all the projections on the inner surface of vessel wall including the surface of vessel wall lining the pit cavity, and the "vestured pits" were defined as pits having these projections, i. e., "vestures". Based on the presence or absence of vestured pits within a species, the species examined were classified into the following 3 groups: (1) 17 species (17 genera, 6 families) having exclusively vestured pits, (2) 21 species (10 genera, 6 families) having vestured and non-vestured pits, (3) 185 species (95 genera, 48 families) having exclusively non-vestured pits. Vestured pits were divided into three types from the difference of the extent of vesturing within a pit. Based on the occurrence of these types within a species, the species belonging to each of the first and the second groups were divided into 4 and 5 subgroups, respectively.

The 3 species belonging to subsection *Daphnanthoides* (*Daphne*) and the 7 species belonging to *Osmanthus* were found to invariably have the intervascular pit membranes with torus. The 187 species (109 genera, 50 families) of 197 species (110 genera, 50 families) having the intervascular pits were found to invariably have the intervascular pit membranes without torus. Although the fine structure of the pit membranes with torus was different between the 3 species of subsection *Daphnanthoides* and the 7 species of *Osmanthus*, they revealed common features within the subsection *Daphnanthoides* and *Osmanthus*, respectively.

Based on the occurrence of spiral thickenings within a species, the species examined were classified into the following 3 groups: (1) 71 species (32 genera, 1 families) having spiral thickenings in all the vessel members (2) 70 species (47 genera, 27 families) having spiral thickenings in some vessel members, (3) 82 species (46 genera, 27 families) having no spiral thickenings in all the vessel members. Spiral thickenings were divided into four types from the helical direction within a vessel member. Based on the occurrence of these types within a species, the species belonging to each of the first and the second groups were divided into 8 and 5 subgroups, respectively.

Based on the occurrence of vestures on the inner surface of vessel wall, the species examined were classified into the following 3 groups: (1) 20 species (15 genera, 10 families) having vestures in all the vessel members, (2) 25 species (9 genera, 4 families) having vestures in some vessel members, (3) 178 species (101 genera, 47 families) having no vestures in all the vessel members. Vesture distribution was divided into two types from the difference of vesture distribution within a vessel member. Based on the occurrence of these types within a species, the species belonging to each of the first and the second groups were divided into 2 and 2 subgroups, respectively.

The occurrence of trabeculae was found in 11 species (11 genera, 8 families). The occurrence of them cannot be considered to have any taxonomic significance, because of the irregularity in their occurrence.

Micromorphological characteristic features on perforation plates, pits, spiral thickenings and vestures in the species examined were summarized in a table (Table 21). On the basis of the results obtained in the present study shown in

Table 21, the micromorphology of vessel wall sculptures was discussed with respect to common characteristic features among the species. As a result, it was concluded that the micromorphological features of vessel wall sculptures obtained in the present study had a taxonomic significance. Therefore, the results in the table are considered to be helpful for the elucidation of characteristic wood properties of individual species from the aspect of their vessel wall structure. Furthermore, the results obtained in the present study provide fundamental information not only for wood identification by micromorphology at a SEM level, but also for systematic investigation on the ultrastructure of vessel wall using EM.

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References

1) PANSHIN, A. J. and DE ZEEUW, C.: Textbook of wood technology, Vol. 1, 3rd. ed., McGraw Hill Book Co., New York, (1970).
2) INOKUMA, T., SHIMAJI, K. and SUDO, S.: The wood anatomical characters of Styracaceae in Japan, (in Japanese), Bull. Tokyo Univ. For., **45**, 181–201, (1953).
3) KANEHIRA, R.: Anatomical characters and identification of the important woods of the Japanese empire, (in Japanese), Gov. Res. Inst., Taihoku, Formosa, (1926).
4) KANESHI, C.: Die Untersuchung über die Grundlage der Holzidentifizierungsmethode, IV. Mitteilung: (1) Die Verbreitung und Anordnung der Tracheiden, (II) Die Wandstruktur der Holzelemente, besonders Tüpfelung, spiralige Verdickung, usw., (in Japanese), J. Jap. For Soc., **13** (4), 243–264, (1931).
5) KANESHI, C.: Die Untersuchung über die Grundlage der Holzidentifizierungsmethode, V. Mitteilung: Die Gestalte der Gefässe, Tracheiden und Libriformfassern, (in Japanese), J. Jap. For. Soc., **14** (2), 19–60, (1932).
6) SEKIYA, F.: On the primitive vessel members of some dicotyledonous wood, (in Japanese), J. Jap. For. Soc., **19** (3), 253–259, (1937).
7) SEKIYA, F. and MURATA, F.: Notes on the ray and parenchyma types in some dicotyledonous wood of scalariform type of vessel, (in Japanese), J. Jap. For. Soc., **21** (7), 378–384, (1939).
8) SHIMAJI, K.: Anatomical studies on the wood of some *Fagus* species, Bull. Tokyo Univ. For., **42**, 181–193, (1952).
9) SHIMAJI, K.: Anatomical studies on the wood of Japanese *Quercus*, II. On the subgenus *Cyclobalanopsis* (Kashi group), Bull. Tokyo Univ. For., **47**, 125–143, (1954).
10) SHIMAJI, K.: Anatomical studies on the wood of the Japanese *Pasania*, *Castanea* and *Castanopsis* (with a key to the 22 Japanese representative species of Fagaceae), Bull. Tokyo Univ. For., **55**, 81–91, (1959).

11) SHIMAJI, K.: Anatomical studies on the phylogenetic interrelationship of the genera in the Fagaceae, Bull. Tokyo Univ. For., **57**, 1–64, (1962).
12) SUDO, S.: Identification of Japanese hardwoods, (in Japanese), Bull. Gov. For. Exp. Sta., **118**, 1–138, (1959).
13) TABATA, H.: Vessel element of Japanese birches as viewed from ecology and evolution, Phys. and Ecol., **12**, 7–16, (1964).
14) WATARI, S.: Studies in the wood anatomy of several species of *Meliosma*, (in Japanese), Misc. Rep. Res. Inst. Nat. Res., **17** (**18**), 25–32, (1950).
15) BERLYN, G. P.: Recent advances in wood anatomy —The cell walls in secondary xylem—, For. Prod. J., **16** (**10**), 467–476, (1964).
16) CÔTÉ, W. A. JR.: The structure of wood and the wood cell wall, in "Principles of wood science and technology, I. Solid wood", KOLLMANN, F. F. P. and CÔTÉ, W. A. JR. ed., Springer-Verlag, New York, (1968).
17) CÔTÉ, W. A. JR. and DE ZEEUW, C.: Trends in literature on wood structure, 1955–62, For. Prod. J., **22** (4), 203–212, (1962).
18) HARADA, H.: Ultrastructure of angiosperm vessels and ray parenchyma, in "Cellular ultrastructure of woody plants", CÔTÉ, W. A. Jr., ed., Syracuse Univ. Press, New York, (1965).
19) SCHMID, R.: The fine structure of pits in hardwoods, in "Cellular ultrastructure of woody plants", CÔTE, W. A. Jr., ed., Syracuse Univ. Press, New York, (1965).
20) WARDROP, A. B.: The structure and formation of the cell wall in xylem, in "The formation of wood in forest trees", ZIMMERMANN, M. H., ed., Academic Press, New York, (1964).
21) FINDLAY, G. W. D. and LEVY, J. F.: Scanning electron microscopy as an aid to the study of wood anatomy and decay, J. Inst. Wood Sci., **4** (5), 57–63, (1969).
22) ISHIDA, S.: An observation on wood structure using scanning electron microscopy, (in Japanese), Reprint of address given to Jap. Wood Res. Soc., (1969).
23) ISHIDA, S. and OHTANI, J.: Study of tyloses by the scanning electron microscopy, Report I. Some preliminary observations of tyloses, mainly in Harunire (*Ulmus* sp.), Res. Bull. Coll. Exp. For., Hokkaido Univ., **26** (1), 1–9, (1968).
24) ISHIDA, S. and OHTANI, J.: An observation on stem anatomy of *Sasa kurilensis* using scanning electron microscopy, (in Japanese), Proc. Hokkaido Branch Jap. For. Soc., **17**, 14–15, (1968).
25) ISHIDA, S. and OHTANI, J.: Study of tyloses using the scanning electron microscope, Scanning Electron Microscopy, IITRI, Chicago, 198–203, (1969).
26) ISHIDA, S., OHTANI, J. and FUJIKAWA, S.: Scanning electron microscopy applied to a study of the wood structure, (in Japanese), Proc. Hokkaido Branch Jap. Wood Res. Soc., **1**, 5–8, (1968).
27) RESCH, A. and BLASCHKE, R.: Über die Anwendung des Raster-Elektronenmikroskopes in der Holzanatomie, Planta, **78** (1), 85–88, (1968).
28) SCURFIELD, G. and SILVA, S. R.: Scanning electron microscopy applied to a study of the structure and properties of wood, Scanning Electron Microscopy, IITRI, Chicago, 185–196, (1969).
29) SCURFIELD, G. and SILVA, S. R.: The structure of reaction wood as indicated by scanning electron microscopy, Aust. J. Bot., **17**, 391–402, (1969).
30) BAAS, P.: The peculiar wood structure of *Leptospermum crassipes* LEHM. (Myrtaceae), IAWA Bull., **1977** (2), 25–30, (1979).
31) BUTTERFIELD, B. G. and MEYLAN, B. A.: Perforation plates: observations using scanning electron microscopy, N. Z. J. For. Sci., **1** (1), 116–124, (1971).

32) BUTTERFIELD, B. G. and MEYLAN, B. A.: Scalariform perforation plate development in *Laurelia novae-zelandiae* A. CUNN.: a scanning electron microscope study, Aust. J. Bot., **20**, 253–259, (1972).

33) BUTTERFIELD, B. G. and MEYLAN, B. A.: Vestured scalariform perforation plate openings in *Neomyrtus pedunculata*, Aust. J. Bot., **22**, 425–427, (1974).

34) BUTTERFIELD, B. G. and MEYLAN, B. A.: Simple to scalariform combination perforation plates in *Vitex lucens* KIRK (Verbenaceae) and *Brachyglottis repanda* J. R. et G. FORST. (Compositae), IAWA Bull., **1975** (3), 39–42, (1975).

35) GRAY, R. L. and DE ZEEUW, C. H.: Terminology for multiperforate plates in vessel elements, IAWA Bull., **2**, 22–27, (1974).

36) ISHIDA, S.: Research on wood structure by scanning electron microscopy II, (in Japanese), Wood Ind., **25** (12), 560–564, (1970).

37) ISHIDA, S. and OHTANI, J.: An observation of the scalariform perforation plate of the vessel in some hardwoods, using scanning electron microscopy, Res. Bull. Coll. Exp. For., Hokkaido Univ., **31** (1), 79–86, (1974).

38) KUČERA, L. J., MEYLAN, B. A. and BUTTERFIELD, B. G.: Vestured simple perforation plates, IAWA Bull., **1**, 3–6, (1977).

39) MEYLAN, B. A. and BUTTERFIELD, B. G.: Perforation plate development in *Knightia excelsa* R. BR.: a scanning electron microscope study, Aust. J. Bot., **20**, 79–86, (1972).

40) MEYLAN, B. A. and BUTTERFIELD, B. G.: Scalariform perforation plates: observations using scanning electron microscopy, Wood and Fiber, **4**, 225–233, (1972).

41) MEYLAN, B. A. and BUTTERFIELD, B. G.: Three-dimensional structure of wood, Chapman and Hall Ltd., London, (1972).

42) MEYLAN, B. A. and BUTTERFIELD, B. G.: Unusual perforation plates.: observations using scanning electron microscopy, Micron, **4**, 47–59, (1973).

43) MEYLAN, B. A. and BUTTERFIELD, B. G.: Occurrence of simple, multiple and combination perforation plates in the vessels of New Zealand woods, N. Z. J. Bot., **13**, 1–18, (1975).

44) MEYLAN, B. A. and BUTTERFIELD, B. G.: The structure of New Zealand woods, DSIR Bull. **222**, N. Z. Dept. Sci. Ind. Res., Wellington, (1978).

45) OHTANI, J. and ISHIDA, S.: An observation of the sculptures of the vessel wall of *Fagus crenata* BL. using scanning electron microscopy, Res. Bull. Coll. Exp. For., Hokkaido Univ., **30** (1), 125–144, (1973).

46) OHTANI, J. and ISHIDA, S : An observation on perforation plate differentiation in *Fagus crenata* BL., using scanning electron microscopy, Res. Bull. Coll. Exp. For., Hokkaido Univ., **33** (1), 115–126, (1976).

47) OHTANI, J. and ISHIDA, S.: An observation on the perforation plates in Japanese dicotyledonous woods using scanning electron microscopy, Res. Bull. Coll. Exp. For., Hokkaido Univ., **35** (1), 65–98, (1978).

48) PARAMESWARAN, N. and LIESE, W.: Scanning electron microscopy of multiperforate perforation plates, Holzforsch., **27**, 181–186, (1973).

49) PARHAM, R. A.: On the substructure of scalariform perforation plates, Wood and Fiber, **4** (4), 342–346, (1973).

50) ESAU, K. and HEWITT, W. M. B.: Structure of end walls in differentiating vessels, Hilgardia, **13**, 229–244, (1940).

51) PRIESTLEY, J. H., SCOTT, L. I. and MALLINS, M. E.: Vessel development in the angiosperm, Proc. Leeds Phil. Lit. Soc., **3**, 42–54, (1935).

52) MURMANIS, L. L.: Breakdown of end walls in differentiating vessels of secondary xylem in *Quercus rubra* L., Ann. Bot., **42**, 679–682, (1978).

53) NIEDERMEYER, W.: Auflösung der Endwände in differenzierenden Gefäßzellen, Ber. Dtsch. Bot. Ges., **86**, 529–536, (1973).

54) SASSEN, M. M. A.: Breakdown of the plant cell wall during the cell-fusion process, Acta Bot. Neerl., **14**, 165–196, (1965).

55) THOMAS, R. J. and BONNER, L. D.: The ultrastructure of intercellular passageways in vessels of yellow-poplar (*Liriodendron tulipifera* L.) Part II: scalariform perforation plates, Wood and Fiber, **6** (3), 193–199, (1974).

56) YATA, S., ITOH, T. and KISHIMA, T.: Formation of perforation plates and bordered pits in differentiating vessel elements, Wood Res., **50**, 1–11, (1970).

57) MEYER, R. W. and MUHAMMAD, A. F.: Scalariform perforation plate fine structure, Wood and Fiber, **3**, 139–145, (1971).

58) GOTTWARD, H. and PARAMESWARAN, N.: Vielfache Gefäßdurchbrechungen in der Familie Dipterocarpaceae, Z. Bot., **52**, 321–334, (1964).

59) MÜLLER-STOLL, W. R. and SÜSS, H.: Über außergewöhnlich gestaltete vielfache Gefäßdurchbrechungen bei *Aeschynomene virginica* (L) B. S. P. (Papilionaceae), Ber. Dtsch. Bot. Ges., **82**, 613–619, (1969).

60) THOMPSON, W. P.: The relationships of the different types of angiospermic vessels, Ann. Bot., **37**, 183–192, (1923).

61) BAILEY, I. W.: Preliminary notes on cribriform and vestured pits, Trop. Woods, **31**, 46–48, (1932).

62) BAILEY, I. W.: The cambium and its derivative tissures, VIII. Structure, distribution, and diagnostic significance of vestured pits in dicotyledons, J. Arnold Arb., **14**, 259–273, (1933).

63) CÔTÉ, W. A. JR. and DAY, A. C.: Vestured pits —fine structure and apparent relationship with warts, Tappi, **45** (12), 906–910, (1962).

64) HARADA, H.: On the ultrastructure of lauan wood under the electron microscope, (in Japanese), Wood Ind, **23** (12), 550–554, (1968).

65) KANAZAWA, K.: Electronmicroscopic investigation on the vestured pit, (in Japanese), Bull. Fac. Agr., Shizuoka Univ., **18**, 75–83, (1968).

66) SCHMID, R. and MACHADO, R. D.: Über den Feinbau der 'verzierten' Tüpfel bei der Gattung *Plathymenia*, Holz Roh Werkst., 21, 41–47, (1963).

67) YAMABAYASHI, N., SUDO, S. and KANAZAWA, K.: Electron microscopic investigation of vestured pit (I), On some species of Legminosae in Japan, (in Japanese), Trans: 64th meet. Jap. For. Soc., 304–305, (1955).

68) YAMABAYASHI, N., OKAZAKI, H. and KANAZAWA, K.: Electron microscopic investigation of vestured pit (II), On the morphology of vestured pit of Legminosae in Japan, (in Japanese), Trans. Chûbu Branch Jap. For. Soc., 34–35, (1956).

69) YAMANAKA, K. and HARADA, H.: The ultrastructure of vessel wall in certain species of Dipterocarpaceae wood, (in Japanese), Bull. Kyoto Univ. For., **40**, 293–300, (1968).

70) BAAS, P. and ZWEYPFENNING, R. C. V. J.: Wood anatomy of the Lythraceae, Acta Bot. Neerl., **28** (2/3), 117–155, (1979).

71) BRIDGWATER, S. D. and BAAS, P.: Wood anatomy of Punicaceae, IAWA Bull., **1978** (1), 3–6, (1978).

72) CASSENS, D. L.: Vestured pits in the new world *Pithecellobium* (*sensu lato*), IAWA Bull., **1**, 59–64, (1980).

73) GREAVES, H.: Comparative morphology of selected sapwood species using the scanning electron microscope, Holzforsch., **27** (3), 80–88, (1973).

74) ISHIDA, S. and OHTANI, J.: Study on the pit of wood cells using scanning electron microscopy, Report I. An observation of the vestured pit in black locust, *Robinia pseudo-*

acacia LINN., Res. Bull. Coll. Exp. For., Hokkaido Univ., **27** (2), 347–354, (1970).

75) MEYLAN, B. A. and BUTTERFIELD, B. G.: Occurrence of vestured pits in the vessels and fibers of New Zealand woods, N. Z. J. Bot., **12**, 13–18, (1975).

76) MILLER, R. B.: Vestured pits in Boraginaceae, IAWA Bull. **3**, 43–48, (1977).

77) OHTANI, J. and ISHIDA, S.: Study on the pit of wood cells using scanning electron microscopy, Report 5. Vestured pits in Japanese dicotyledonous woods, Res. Bull. Coll. Exp. For., Hokkaido Univ., **33** (2), 407–436, (1976).

78) SCHMID, R. and LIESE, W.: Zur Feinstruktur der Gefäßtüpfel von *Cercidium praecox* und *C. australe*, Ber. Dtsch, Bot. Ges., **85**, 623–630, (1972).

79) SCURFIELD, G. and SILVA, S. R.: The vestured pits of *Eucalyptus regnans* F. MUELL.: a study using scanning electron microscopy, Bot. J. Linn. Soc., **63**, 313–320, (1970).

80) SCURFIELD, G., SILVA, S. R. and INGLE, H. D.: Vessel wall structure: an investigation using scanning electron microscopy, Aust, J. Bot., **18**, 301–312, (1970).

81) VLIET, G. J. C. M. VAN.: Wood anatomy of Crypteroniaceae sensu lato, J. Microscopy, **104** (1), 65–82, (1975).

82) VLIET, G. J. C. M. VAN.: Vestured pits of Combretaceae and allied families, Acta Bot. Neerl., **27** (5/6), 273–285, (1978).

83) BUTTERFIELD, B. G. and MEYLAN, B. A.: Vestured vessel and fiber pits in *Persoonia toru* A. CUNN. (Proteaceae), IAWA Bull., **1974** (1), 10–15, (1974).

84) MORI, N., FUJITA, M., HARADA, H. and SAIKI, H.: On the formation of vestured pit in *Robinia pseudo-acacia* LINN., (in Japanese), Rep. Summ. 29th Meet. Jap. Wood Res. Soc., 46, (1979).

85) MORI, N., FUJITA, M., HARADA, H. and SAIKI, H.: Investigation on chemical component of vestured pit using ultrathin sections, (in Japanese), Rep. Summ. 30th Meet. Jap. Wood Res. Soc., 55, (1980).

86) SCHMID, R. and MACHADO, R. D.: Zur Entstehung und Feinstruktur skulpturierter Hoftüpfel bei Leguminosen, Planta, **60**, 612–626, (1964).

87) WARDROP, A. B.: Morphological factors involved in the pulping and beating of wood fibers, Svensk Papperstid., **65**, 66–83, (1963).

88) WARDROP, A. B., INGLE, H. D. and DAVIES, G. W.: Nature of vestured pits in angiosperms, Nature, **197**, 202–203, (1963).

89) BOSSHARD, H.: Elektronenmikroskopische Untersuchungen im Holz von *Fraxinus excelsior*, Ber. Schweiz. Bot. Ges., **62**, 482–508, (1952).

90) BUTTERFIELD, B. G. and MEYLAN, B. A.: Intervessel pit membranes in *Knightia excelsa* R. BR., IAWA Bull., **1972** (4), 3–9, (1972).

91) CÔTÉ, W. A. JR.: Electron microscope studies of pit membrane structure, For. Prod. J., 8, 296–301, (1958).

92) CÔTÉ, W. A. JR.: Structural factors affecting the permeability of wood, J. Polym. Sci., Part C, **2**, 231–242, (1963).

93) CÔTÉ, W. A. JR.: Wood ultrastructure, an atlas of electron micrographs, Univ. Washington Press, Seatle, Washington, (1967).

94) CRONSHAW, J.: The fine structure of the pits of *Eucalyptus regnans* (F. MUELL.) and their relation to the movement of liquids into the wood, Aust. J. Bot., 8, 51–57, (1960).

95) FENGEL, D.: Elektronenmikroskopische Beiträge zum Feinbau des Buchenholzes (*Fagus sylvatica* L.), III. Die Feinstruktur der Tüpfel im Buchenholz, Holz Roh Werkst., **24** (6), 245–253, (1966).

96) HARADA, H.: Electron-microscopic investigation on the pit of "Buna" (*Fagus crenata* BLUME)-and "Nara" (*Quercus crispula* BLUME)-wood, (in Japanese), Wood Ind., **9**, 375–379, (1954).

97) HARADA, H.: Electron microscopy of ultrathin sections of beech wood (*Fagus crenata* BLUME), J. Jap. Wood Res. Soc., **8**, 252–258, (1962).

98) HARADA, H.: Cell wall organization of wood, (in Japanese), J. Soc.Mat. Sci., Jap. **24** (**264**), 792–797, (1975).

99) HARADA, H., MIYAZAKI, Y. and WAKASHIMA, T: Electronmicroscopic investigation on the cell wall structure of wood, (in Japanese), Bull. Gov. For. Exp. Sta., **104**, 1–115, (1958).

100) JAYME, G. and AZZOLA, F. K.: Textur und Topochemie der Tüpfel und Tüpfelschließhäute von Buchenholzzellen (*Fagus sylvatica* L.), Holz Roh Werkst., **23** (5), 41–49, (1965).

101) KININMONTH, J. A.: Permeability and fine structure of certain hardwoods and effects on drying, II. Differences in fine structure of *Nothofagus fusca* sapwood and heartwood, Holzforsch., **26** (1), 32–38, (1972).

102) LIESE, W.: Der Feinbau der Hoftüpfel bei den Laubhölzern, Holz Roh Werkst., **15**, 449–453, (1957).

103) MIA, A. J.: Study of cell walls in angiospermous plants using light and electron microscopes, Wood Sci., **2** (1), 1–10, (1969).

104) SCHMID, R. and MACHADO, R. D.: Entwicklung und Feinstruktur der Tüpfelmembranen im Laubholz, Ber. Dtsch. Bot. Ges., **77** (**9**), 385–387, (1964).

105) SCHMID, R. and MACHADO, R. D.: Pit membranes in hardwoods —fine structure and development, Protoplasma, **66**, 185–204, (1968).

106) SIAU, J. F.: Flow in wood, Syracuse Univ. Press, New York, (1971).

107) THOMAS, R. J.: Bordered pit aspiration in angiosperms, Wood and Fiber, **3** (4), 236–237, (1972).

108) THOMAS, R. J.: Anatomical features affecting liquid penetrability in three hardwood species, Wood and Fiber, **7**(4), 256–263, (1976).

109) WALTER, C. S. and CÔTE, W. A. JR.: The distribution of pentachlorophenol in the microstructure of basswood, Holzforsch., **14** (6), 183–189, (1960).

110) YANG, K. C.: The fine structure of pits in yellow birch (*Betula alleghaniensis* BRITTON), IAWA Bull., **4**, 71–77, (1978).

111) BONNER, L. D. and THOMAS, R. J.: The ultrastructure of intercellular passageways in vessels in yellow poplar (*Liriodendron tulipifera* L.) Part I: vessel pitting, Wood Sci. Technol., **6**, 196–203, (1972).

112) OHTANI, J.: An observation of vestured pits using scanning electron microscopy, (in Japanese), Rep. Summ. 24th Meet. Jap. Wood Res. Soc., 46, (1970).

113) OHTANI, J. and ISHIDA, S.: Pit membrane with torus in dicotyledonous woods, Mokuzai Gakkaishi, **24** (**9**), 673–675, (1978).

114) GREGUSS, P.: Holzanatomie der europäischen Laubhölzer und Strächer, Akadémiai Kiado, Budapest, (1959).

115) METCALFE, C. R. and CHALK, L.: Anatomy of the dicotyledons, Vols I and II, Clarendon Press, Oxford, (1950).

116) YAMABAYASHI, N.: Identification of corean woods, (in Japanese), Yôkendo Ltd., Tokyo, (1938).

117) YAMABAYASHI, N.: Wood histology, (in Japanese), Morikita Shuppan Co., Tokyo, (1964).

118) PARHAM, R. A. and KAUSTINEN, H.: On the morphology of spiral thickenings, IAWA Bull., **2**, 8–14, (1973),

119) MILLER, R. B.: Reticulate thickenings in some species of *Juglans*, Am. J. Bot., **63** (**6**), 898–901, (1976).

120) MILLER, R. B.: Wood anatomy and identification of species of *Juglans*, Bot. Gaz., **137** (**4**), 368–377, (1976).

121) OHTANI, J. and ISHIDA, S.: An observation on the spiral thickenings in the vessel members in Japanese dicotyledonous woods using scanning electron microscopy, Res. Bull. Coll. Exp. For., Hokkaido Univ., **35** (2), 433–464, (1978).

122) MEYLAN, B. A. and BUTTERFIELD, B. G.: Occurrence of helical thickenings in the vessels of New Zealand woods, New Phytol., **81**, 139–146, (1978).

123) BAIRD, W. M., JOHNSON, M. A. and PARHAM, R. A.: Development and composition of the warty layer in balsam fir, II. Composition, Wood and Fiber, **6**, 211–222, (1974).

124) BAIRD, W. M., PARHAM, R. A. and JOHNSON, M. A.: Development and composition of the warty layer in barsam fir, I. Development, Wood and fiber, **6**, 114–125, (1974).

125) CÔTÉ, W. A. JR. and DAY, A. C.: Wood ultrastructure of the southern yellow pines, SUNY Coll. For, Tech. Pub. 95, Syracuse, New York, (1969).

126) CRONSHAW, J.: The formation of the warts structure in tracheids of *Pinus radiata*, Protoplasma, **2**, 233–242, (1965).

127) CRONSHAW, J., DAVIES, G. W. and WARDROP, A. B.: A note on the wart structure of conifer tracheids, Holzforsch., **15** (3), 75–78, (1961).

128) FREY-WYSSLING, A., MÜHLETHALER, K. and BOSSHARD, H. H.: Das Elektronenmikroskop im Dienste der Bestimmung von Pinusarten, Holz Roh Werkst., **13**, 245–249, (1955).

129) FREY-WYSSLING, A., MÜHLETHALER, K. and BOSSHARD, H. H.: Nachtrg zu: Das Elektronenmikroskop im Dienste der Bestimmung von Pinusarten, Holz Roh Werkst., **14**, 161–162, (1956).

130) HARADA, H.: Electron-microscopic investigation on the wart-like (particle) structure of conifer tracheids, (in Japanese), J. Jap. For. Soc., **35** (2), 393–396, (1953).

131) HARADA, H.: Electron-microscopic investigation of the wartlike structure of conifer tracheids (II), (in Japanese), J. Jap. Wood Res. Soc., **1**(2), 85–89, (1955).

132) HARADA, H.: The electron microscopic investigation of wood —On the fine structure of the wart-like structure and the pit membrane—, (in Japanese), Trans. 65th Meet. Jap. For. Soc., 1–8, (1956).

133) HARADA, H. and MIYAZAKI, Y.: The electron microscopic observation of the cell wall of conifer tracheids, (in Japanese), J. Jap. For. Soc., **34** (11), 350–352, (1952).

134) JURBERGS, K. A.: Warts in selected species of pine, J. Polym. Sci., Part C, **11**, 1–12, (1965).

135) KOBAYASHI, K. and UTSUMI, N.: Electron microscopy of conifer tracheids, (in Japanese), Committee Note on Electron Microscopy, **56**, 93–95, (1951).

136) LIESE, W.: Demonstration elektronenmikroskopischer Aufnahmen von Nadelholztüpfeln, Ber. Dtsch. Bot. Ges., **64**, 31–32, (1951).

137) LIESE, W.: Zur systematischen Bedeutung der submikroskopischen Warzenstruktur bei der Gattung *Pinus* L., Holz Roh Werkst., **14**, 417–424, (1956).

138) LIESE, W.: Elektronenmikroskopische Beobachtungen über die Warzenstruktur bei den Koniferen, Electron Microscopy, Proc. Stockholm Conf., 276–279, (1956).

139) LIESE, W.: Beitrag zur Warzenstruktur der Koniferentracheiden unter besonderer Berücksichtigung der Cupressaceae, Ber. Dtsch. Bot. Ges., **70**, 21–30, (1957).

140) LIESE, W.: Tertiary wall and warty layer in wood cells, J. Polym. Sci., Part C, **2**, 213–219, (1963).

141) LIESE, W.: Über den Abbau verholzter Zellwände durch Moderfäulepilze, Holz Roh Werkst., **22**, 289–295, (1964).

142) LIESE, W.: The warty layer, in "Cellular ultrastructure of woody plants", CÔTÉ, W. A. JR., ed., Syracuse Univ. Press, New York, (1965).

143) LIESE, W.: Elektronenmikroskopie des Holz, in Handbuch der Mikroskopie in der Technik, Band V. Mikroskopie des Holzes und des Papiers, Teil I. Mikroskopie des Rohholzes

und der Rinden, Hugo FREUND, W. ed., Umachau Verlag, 109–170, (1970).

144) LIESE, W. and JOHANN, I.: Elektronenmikroskopische Beobachtungen über eine besondere Feinstruktur der verholzten Zellwand bei einigen Konifern, Planta, **44**, 268–285, (1954).

145) OHTANI, J. and FUJIKAWA, S.: Study of warty layer by the scanning electron microscopy, I. The variation of warts on the tracheid wall with an annual ring of coniferous woods, J. Jap. Wood Res. Soc., **17** (3), 89–95, (1971).

146) TAKIYA, K., HARADA, H. and SAIKI, H.: The formation of the wart structure in conifer tracheid, (in Japanese), Bull. Kyoto Univ. For., **48**, 187–191, (1976).

147) TSOUMIS, G.: Electron microscopic observations relate the warty layer to extractives in wood, Tappi **48** (8), 451–455, (1965).

148) UEMURA, T.: A few electron micrographs of wood, (in Japanese). Sci. Bull. Fac. Agr. Kyushu Univ., **13**, 225–229, (1951).

149) VERHOFF, S. and KNIGGE, W.: Untersuchungen über Größe, Anzahl und Verteilung der Warzen auf der Radialwand der Tracheiden der Tanne (*Abies alba* M.), Holz Roh Werkst., **34**, 175–180, (1976).

150) WARDROP, A. B. and DAVIES, G. W.: Wart structure of gymnosperm tracheids, Nature, **194**, 497–498, (1962).

151) WARDROP, A. B., LIESE, W. and DAVIES, G. W.: The nature of the wart structure in conifer tracheids, Holzforsch., **13**, 115–120, (1959).

152) CÔTÉ, W. A. JR. and MARTON, R.: Brightness of high yield pulps, IV. Electron microscopy of white birch heartwood, Tappi, **45** (1), 46–53, (1962).

153) JAYME, G. and AZZOLA, F. K.: Zur chemischen Resistenz der Warzenschicht von Holzfasern, Holzforsch., **20** (3), 101–103, (1966).

154) KOLLMANN, F. F. P. and SACHS, I. B.: The effects of elevated temperature on certain wood cells, Wood Sci. Technol., **1**, 14–25, (1967).

155) PARHAM, R. A. and BAIRD, W. M.: Warts in the evolution of angiosperm wood, Wood Sci. Technol., 8 (**1**), 1–10, (1974).

156) SACHS, I. B., WARD, J. C. and BULGRIN, E. H.: Heartwood stain in red oak, Holz Roh Werkst., **24** (**10**) 489–497, (1966).

157) LIESE, W.: Zur Struktur der Tertiärwand bei den Laubhölzern, Naturwiss., **44**, 240–241, (1957).

158) OHTAHI, J.: Study of warty layer by the scanning electron microscopy, II. Occurrence of warts in vessel members and wood fibers of Japanese dicotyledonous woods, Res. Bull. Coll. Exp. For., Hokkaido Univ., **36** (3), 585–608, (1979).

159) BODE, H. R.: Über die Entwicklungsgeschichte der intracellulären Stäbe im Cambium, Ein Beitrag zum Problem der Reisigkrankheit des Weinstocks, Gartenbauwiss., **11**, 272–288, Koder (1938).

160) FUESS, J. and SCHNEIDERS, E.: Über Wirkungen und Schäden der Maifröste 1934 an 5BB-Reben, Gartenbauwiss., **9**, 353–363, (1935).

161) KROEMER, K. and MOOG, H.: Bericht über die Tätigkeit der Wissenschaftlichen Abteilung der Rebenveredlungsstation Geisenheim a. Rh, Landw. Jb., **82** (4), 684–685, (1936).

162) KROEMER, K., MOOG, H. and TROOST, G.: Bericht über die Tätigkeit der Wissenschaftlichen Abteilung der Rebenveredlungsstation Geisenheim a. Rh. im Jahre 1935, Landw. Jb., **83** (6), 851–852, (1936).

163) MÜLLER, C.: Ueber die Balken in den Holzelementen der Coniferen, Ber. Dtsch. Bot. Ges., **8**, 17–46, (1890).

164) MÜLLER-STOLL, W. R.: Über intrazelluläre Stabbildungen (Trabeculae) im Holz als anatomische Eigenart bei Gehölzen exponierter Gebirgslagen, Die Kulturpflanze, **13**, 763–799, (1969).

165) OCHS, G.: Der heutige Stand der Reisigkrankheitsforschung, Angew. Bot., **29**, 152–159, (1955).

166) RAATZ, W.: Die Stabbildungen im secundären Holzkörper der Bäume und die Initialentheorie, Jahrb. f. w. Bot. **23**, 567–636, (1892).

167) SCHNEIDERS, E.: Über die Zellstäbe und ihre phytopathologische Bedeutungen, Gartenbauwiss., **11**, 237–250, (1938).

168) BUTTERFIELD, B. G. and MEYLAN, B. A.: Trabeculae in a hardwood, IAWA Bull., **1972** (1), 3–9, (1972).

169) BUTTERFIELD, B. G. and MEYLAN, B. A.: Observations of trabeculae in New Zealand hardwoods, Wood Sci., Technol., **13**, 59–65, (1979).

170) MEYLAN, B. A. and BUTTERFIELD, B. G.: Scanning electron micrographs of New Zealand woods, 2. *Knightia excelsa* R. BR., N. Z.J. Bot., **11** (2), 201–212, (1973).

171) MEYLAN, B. A. and BUTTERFIELD, B. G.: A trabecula with a vestured pit, IAWA Bull., **3**, 12–14, (1973).

172) OHTANI, J.: An observation of the trabeculae in some dicotyledonous woods using scanning electron microscopy, Res. Bull. Coll. Exp. For., Hokkaido Univ., **34** (**1**), 69–78, (1977).

173) KEITH, C. T.: Observations on the anatomy and fine structure of the trabeculae of Sanio, IAWA Bull., **3**, 3–11, (1971).

174) OHWI, J.: Flora of Japan, (in Japanese), Revised Ed., Shibundo, Tokyo, (1972).

175) CÔTÉ, W. A. JR., KÓRÁN, Z. and DAY, A. C.: Replica techniques for electron microscopy of wood and paper, Tappi, **47**, 477–484, (1964).

176) HAYAT, M. A.: Principles and techniques of electron microscopy, Biological applications, Vol. 2, Van Nostrand Reinhold Co., New York, (1972).

177) COMMITTEE ON NOMENCLATURE, INTERNATIONAL ASSOCIATION OF WOOD ANATOMISTS: Multilingual Glossary of terms used in wood anatomy, Verlagsanstalt Buchdruckerei Konkordia Winterthur, (1964).

178) FROST, F. H.: Specialization in secondary xylem of dicotyledons, II. Evolution of end wall of vessel segment, Bot. Gaz., **90**, 67–94, (1930).

179) HALL, J. W.: The comparative anatomy and phylogeny of the Betulaceae, Bot. Gaz., **113** (3), 235–270, (1952).

180) STERN, W. L.: Comparative anatomy of xylem and phylogeny of Lauraceae, Trop. Woods, **100**, 1–73, (1954).

181) CHALK, L.: Multiperforate plates in vessels, with special reference to the Bignoniaceae, Forestry, **7**, 16–25, (1933).

182) HAMAYA, T.: Dendrological studies of the Japanese and some foreign genera of the Thymelaeaceae —Anatomical and phylogenetic studies—, Bull. Tokyo Univ. For., **55**, 1–80, (1959).

183) BAAS, P.: The wood anatomical range in *Ilex* (Aquifoliaceae) and its ecological and phylogenetic significance, Blumea, **21**, 193–258, (1973).

184) KITAMURA, S. and MURATA, G.: Coloured illustrations of woody plants of Japan, (in Japanese), Vol. 1, Hoikusha Publishing Co., Osaka, (1971).

185) KITAMURA, S. and MURATA, G.: Coloured illustrations of woody plants of Japan, (in Japanese), Vol. 2, Hoikusha Publishing Co., Osaka, (1979).

摘　　要

本研究は本邦産広葉樹材の道管壁変異の微細形態の樹種的特徴を走査電子顕微鏡（以下，SEM と略記）レベルで明らかにする目的で行われた。道管壁には，せん孔板・壁孔・らせん肥

厚・ベスチャー(または，いぼ状突起)・トラベキュレーなどの特異な構造，すなわち，細胞壁変異が存在しており，これらの存在が道管壁構造を非常に複雑にしている。本邦産広葉樹材の道管壁変異の微細形態や道管壁自体の微細構造についての今まで得られている知見は，限られた樹種についてのものであり十分であるとは言えない。したがって，多数の樹種についての道管壁変異の微細形態の知見は，道管壁構造解明上極めて重要である。

本研究では，SEM の特性に着目し SEM を効果的に用いることにより他の手法では観察が困難である複雑な立体構造を有する道管壁変異の微細形態が広範かつ詳細に観察された。

供試樹種は，51 科 120 属 223 種の本邦産主要広葉樹（本邦に植栽された外国原産樹種を少数含む）である (Table 1)。供試材は原則として正常に生育した生立木の胸高付近から採取された辺材外方部であるが，それらの一部は北海道大学農学部林産学科所蔵の材鑑その他から得られた。検鏡用試料は常法により作製され，SEM (JSM-2) により観察が行われた。

SEM 観察により得られた道管壁変異の多様な微細形態は，それらの実態をそこなうことなくいくつかの種類・タイプに区別・単純化され，樹種内に認められるこれらの種類・タイプをもとにして供試樹種の道管壁変異の樹種的特徴が示された。

1. せん孔板

観察されたせん孔板は，単せん孔板・階段せん孔板・多孔せん孔板（階段せん孔板以外の多孔せん孔板）の 3 種類に分けられた。さらに，単せん孔板はせん孔縁の形状により 4 タイプに，階段せん孔板はバーの数により 3 タイプに，また，多孔せん孔板はせん孔の形・大きさ・数などにより 3 タイプにそれぞれ分けられた。また，SEM 観察により明確に可視化された Microfibrillar webs や特異な形態を示す Combination perforation plate や Mismatching perforation plate の微細形態の観察結果が述べられた。

次に，樹種内に認められるせん孔板の種類をもとにして，供試樹種は次の 6 グループに分けられた (Table 2)。1) 単せん孔板のみを有する 136 樹種 (71 属 32 科)，2) 階段せん孔板のみを有する 46 樹種 (24 属 15 科)，3) 単せん孔板と階段せん孔板を有する 24 樹種 (15 属 9 科)，4) 階段せん孔板と多孔せん孔板を有する 9 樹種 (7 属 5 科)，5) 単せん孔板と多孔せん孔板を有する 5 樹種 (3 属 2 科)，6) 単せん孔板，階段せん孔板および多孔せん孔板を有する 3 樹種 (2 属 2 科)。それぞれのグループに属する樹種名は Table 3～8 に示されている。これらのグループ別にせん孔板の微細形態の樹種的特徴が述べられた。

2. 壁　孔

壁孔については，ベスチャード壁孔と道管相互壁孔の壁孔壁が観察された。

2.1. ベスチャード壁孔

まず，“ベスチャー”と“いぼ状突起”の関係について検討された。両構造物の発達が顕著である樹種の壁孔内および壁内表面に存在する突起物の形・大きさ・分布および化学的性質についての詳細な観察・検討から，両構造物は本来同じ性質のものであると結論された。したが

って，本報告ではこれらすべての突起物をベスチャーと呼び，壁孔縁から壁孔こうへベスチャーが生じている壁孔はベスチャード壁孔と定義された。

観察された壁孔内のベスチャーの形・大きさは，極めて変化にとんでいた。枝分れしていないベスチャーは，観察されたベスチャーのなかで小さなものに限られた。枝分れしているベスチャーは，それらが大きくなるにしたがい形状が複雑になる傾向が認められた。観察されたベスチャーの基部の径および高さは，それぞれほぼ1μおよび3μ以下であった。

壁孔内のベスチャーの微細形態はそれらの発達程度と密接な関係があることから，一壁孔内のベスチャーの発達程度をもとにして，観察されたベスチャード壁孔は次の3タイプに分けられた。1) ベスチャーの発達が少ない壁孔，2) ベスチャーの発達が中庸の壁孔，3) ベスチャーの発達が顕著な壁孔。

樹種内のベスチャード壁孔の有無をもとにして，供試樹種は次の3グループに分けられた(Table 9)。1) ベスチャード壁孔のみを有する17樹種 (17属6科), 2) ベスチャード壁孔とベスチャーが存在しない壁孔を有する21樹種 (10属6科), 3) ベスチャーが存在しない壁孔のみを有する185樹種 (96属48科)。さらに，樹種内に認められるベスチャード壁孔のタイプをもとにして，上記1), 2)のグループに属する樹種は，それぞれ4サブグループ (Table 10) および5サブグループ (Table 11) に分けられ，ベスチャード壁孔の微細形態の樹種的特徴が述べられた。

2.2. 壁孔壁

道管相互壁孔の壁孔壁，とくにトールスの有無について調べられた。従来，広葉樹材の壁孔壁にはトールスは存在しないと言われてきたが，ジンチョウゲ科ジンチョウゲ属ジンチョウゲ節ジンチョウゲ亜節に属する3樹種とモクセイ科モクセイ属に属する7樹種の2科2属10樹種の道管相互壁孔の壁孔壁にはトールスが常に存在することが認められた (Table 12)。なお，供試樹種中197樹種 (110属50科) には道管相互壁孔が認められ，187樹種 (109属50科) のそれらの壁孔壁にはトールスは存在しなかった。

次に，トールスを有する壁孔壁の微細構造がフィールドエミッションSEMおよび透過電子顕微鏡 (レプリカ法) により観察され，これらの微細構造はジンチョウゲ亜節内およびモクセイ属内では同じであるが両者間では異なることが示された (Fig. 1)。

3. らせん肥厚

観察されたらせん肥厚は，一道管要素内でのらせん肥厚のらせん方向をもとにして次の4タイプに分けられた。1) Sらせんのもの，2) Zらせんのもの，3) らせん方向が一定していないもの，4) らせん状を示さないもの。

次に，樹種内のらせん肥厚の有無をもとにして，供試樹種は次の3グループに分けられた (Table 13)。1) らせん肥厚が存在する道管要素のみを有する71樹種 (32属19科), 2) らせん肥厚が存在する道管要素と存在しない道管要素を有する70樹種 (47属27科), 3) らせん肥厚が存在しない道管要素のみを有する82樹種 (46属27科)。それぞれのグループに属する樹種名は

Table 14～16 に示されている。さらに，樹種内に認められるらせん肥厚のタイプをもとにして，上記 1)，2) のグループに属する樹種は，それぞれ 8 サブグループ (Table 14) および 5 サブグループ (Table 15) に分けられ，らせん肥厚の微細形態の樹種的特徴が述べられた。

4. ベスチャー

壁孔以外の道管壁内表面のベスチャーの観察結果が述べられた。

観察されたベスチャーは，それらの形から枝分れしていないものと枝分れしているものに大別された。前者は従来いぼ状突起と呼ばれていたものと一致し，ベスチャーを有する樹種のすべてに認められた。それらの形は，半球状・円錐状・棒状・塊状などであった。後者は供試樹種中 12 樹種に認められたが，それらの形は変化にとんでいた。観察されたベスチャーの基部の径は 50～700 nm であったが，大部分のベスチャーを有する樹種ではそれらは 50～500 nm であった。

一道管要素内でのベスチャーの分布状態をもとにして，観察されたベスチャーは次の 2 タイプに分けられた。1) 散在するか局部的に存在するもの，2) 密に存在するもの。

次に，樹種内のベスチャーが存在する道管要素の有無をもとにして，供試樹種は次の 3 グループに分けられた (Table 17)。1) ベスチャーが存在する道管要素のみを有する 20 樹種 (15 属 10 科)，2) ベスチャーが存在する道管要素と存在しない道管要素を有する 25 樹種 (9 属 4 科)，3) ベスチャーが存在しない道管要素のみを有する 178 樹種 (101 属 47 科)。さらに，樹種内に認められるベスチャーのタイプをもとにして，上記 1)，2) のグループに属する樹種は，それぞれ 2 サブグループ (Table 18) および 2 サブグループ (Table 19) に分けられ，ベスチャーの微細形態の樹種的特徴が述べられた。

5. トラベキュレー

供試樹種中 11 樹種 (11 属 8 科) にトラベキュレーの存在が認められた (Table 20)。トラベキュレーは同一樹種でも個体により存在する場合と存在しない場合があること，さらにそれらは材中で不規則に存在することなどから，トラベキュレーの存在は樹種固有の特徴ではないと考えられた。

6. 道管壁変異の微細形態の樹種的特徴

本研究で明らかにされた道管壁変異の微細形態の樹種的特徴が要約された。すなわち，トラベキュレーを除き，せん孔板・壁孔 (ベスチャード壁孔・壁孔壁)・らせん肥厚・ベスチャーの微細形態の樹種的特徴が樹種別に整理され，一覧表にして示された (Table 21)。本研究で得られた道管壁変異の多様な微細形態から樹種間の共通性をひきだす観点から，供試樹種の道管壁変異の微細形態が整理・記述された。

本研究では，従来光学顕微鏡により明らかにされていた事項のさらに微細な形態を立体的に把握するとともにいくつかの新たな知見を得，道管壁変異ひいては道管壁構造に関する知見

を拡大発展させることができた。

本報告に示された知見は，今後道管壁の微細構造の研究を体系的に行う場合の基礎的資料として役立つであろう。また，これらの知見は，木材利用上本邦産主要広葉樹材の諸性質を組織構造の面から解明するための一助となると考えられるが，とくに SEM による広葉樹材の樹種識別の可能性を示していることが注目される。本研究で得られた知見に加えて，道管要素以外の構成要素についての SEM レベルでの知見を蓄積し, SEM による樹種識別の検索表を作成することが今後に残された重要な課題の一つであろう。