
By

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Introduction

Sculpturings in the vessel wall complicate the structure of it in dicotyledonous woods. From the light microscopic evidences, it is well known that the spiral thickenings, one of the sculptures, occur in the vessel members of certain dicotyledonous woods and thus the presence or absence of them may have diagnostic value.

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* Received 31 January 1978.
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Morphology of the spiral thickenings in the vessel wall can be not always sufficiently observed by the light microscopy, while the three-dimensional structure of them can be relatively easily and clearly observed by the SEM. The spiral thickenings in the vessel wall have not yet been investigated comprehensively at electron microscopic level (Kollmann and Côté, 1968; Parham and Kaustinen, 1973). Therefore, the information on the spiral thickenings in the various species, which is obtained by the SEM observation, is considered to contribute not only to elucidation on the structure of the vessel wall itself but also to a diagnostic criterion for the wood identification using the SEM.

From the standpoint described above, the authors observed, in more detail, occurrence and morphology of the spiral thickenings in the vessel wall in the 218 species belonging to 120 genera, 51 families, and this work was carried out as one of the observations on the sculpturing of the cell wall in Japanese dicotyledonous woods using the SEM which have been in progress by the authors. In this paper, the spiral thickenings of the species in which they occur are divided into 4 major categories on the basis of their helical direction and are illustrated with many SEM micrographs. And also, occurrence and morphology of the spiral thickenings in all the species examined are tabulated in Tables.

Materials and Methods

The species names (218 species, 120 genera, 51 families) examined in this study are listed in Tables 1-3.

Wood samples were collected from living trees and if possible/or obtained from the wood collection of the Department of Forest Products, Hokkaido University. Small blocks were taken from the outer sapwood of them. The longitudinal radial surfaces to be observed were obtained by cutting using new razor blades. Specimens were finished in the form of ca. 6 X 6 X 1 mm and were dried at room conditions. They were then stuck on the brass standard stubs with electrically conductive paste. Prepared stubs were coated with carbon-gold by vacuum evaporation. Sputter coating was also used. Observations were made with a JSM-2 scanning electron microscope at 15 kV.

In addition to the SEM observations, observations were also carried out with the transmitted light microscope in order to confirm the helical direction of the spiral thickenings. Material obtained from the small blocks of the species, in which the spiral thickenings were found by the SEM observations, was macerated in a solution of equal parts of 10% nitric acid and 10% chromic acid (Jeffrey’s solution). The helical direction of the spiral thickenings was examined by to trace the ridges of the spiral thickenings of the isolated vessel members moving slightly the focus up and down under the transmitted light microscope.

Results

The spiral thickenings were found in the vessel members in the 135 species. In each of the 62 species of them, the spiral thickenings were found in all the
vessel members. On the other hand, the vessel members with the spiral thickenings and without them were found in each of the remainder (73 species). The spiral thickenings were not found in any vessel members in the 83 species. These observations are given in Tables 1-3. The species names used in Tables 1-3 mostly follow Hwito (1972). In this study, the vessel members in which the spiral thickenings were restricted to only their ligulate tips were regarded as the ones without the spiral thickenings, because it was very difficult to confirm exhaustively their presence, if any in each of the species examined by the SEM observation.

The spiral thickenings found by the present SEM observation varied remarkably in their morphology. In order to describe the observations briefly and concisely, outer appearances of the spiral thickenings were divided into 4 major categories as follows, according to the helical direction of the spiral thickenings within a vessel member.

1. "S" spiral thickenings—All the spiral thickenings within a vessel member are "S" in their helical direction.
2. "Z" spiral thickenings—All the spiral thickenings within a vessel member are "Z" in their helical direction.
3. "S and Z" spiral thickenings—All the spiral thickenings within a vessel member are not constant in their helical direction.
4. Localized thickenings forming no spiral—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 about the vessel member axis.

Within these categories except 4, forms of the spiral thickenings were subdivided into 2 types: unbranched (including here rarely branched) and branched.

On the basis of this classification of the spiral thickenings, occurrence of the particular types of spiral thickenings in the species examined is tabulated in Tables 1 and 2. The number of the species with the vessel members in which the spiral thickenings of particular type occurred is summarized as follows.

1. "S" spiral thickenings ........................ 123 species
   Unbranched ................................ 34 species
   Branched .................................. 97 species
2. "Z" spiral thickenings ...................... 38 species
   Unbranched ................................ 13 species
   Branched .................................. 25 species
3. "S and Z" spiral thickenings ............. 37 species
   Unbranched ................................ 0
   Branched .................................. 37 species
4. Localized thickenings forming no spiral.. 27 species

All the photographs shown in this paper represent the surface view seen from the lumen side at an angle of ca. 45° to the direction of the vessel member axis, because specimen stage that was inclined 45° from horizontal was used in order to obtain the best secondary electron image. Therefore, the spiral thickenings
### Table 1. Species with spiral thickenings

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<th>Family</th>
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in all the vessel members

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<td><strong>Table 2.</strong> Species with spiral thickenings**</td>
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in some vessel members

<p>| &quot;S&quot; spiral thickenings | &quot;Z&quot; spiral thickenings | &quot;S and Z&quot; Localized | thickenings forming no |
|------------------------|------------------------|---------------------|-----------------------|-------|
| Unbranched | Branched | Unbranched | Branched | &quot;S and Z&quot; | spiral thickening forming no |
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### Spiral Thickenings Using Scanning Electron Microscopy (OHTANI • ISHIDA)

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Table 3. Species without spiral thickenings in all the vessel members

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<td><em>Picrasma quassioides</em> (D. DON) BENN.</td>
<td>Nigaki</td>
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<td>Euphorbiaceae</td>
<td><em>Daphniphyllum macropodum</em> MIQ.</td>
<td>Yuzurīha</td>
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<td><em>Daphniphyllum teijsmannii</em> ZOLL.</td>
<td>Himeyuzurīha</td>
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<td></td>
<td><em>Malolitus japonicus</em> (THUNB.) MUELL. ARG.</td>
<td>Akamegashiwa</td>
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<td></td>
<td><em>Aleurites cordata</em> R. BR.</td>
<td>Aburagiri</td>
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<td><em>Aleurites fordii</em> HEMSL.</td>
<td>Shinaaburagiri</td>
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<td><em>Sapium japonicum</em> (SIEB. et ZUCC.) PAX et HOFFM.</td>
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<td><em>Buxus microphylla</em> SIEB. et ZUCC. var. <em>japonica</em> (MUELL. ARG.) REHD. et WILS.</td>
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<td><em>Rhus succedanea</em> LINN.</td>
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<td><em>Rhus sylvestris</em> SIEB. et ZUCC.</td>
<td>Yamahaze</td>
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<td>Sabiaceae</td>
<td><em>Meliosma rigida</em> SIEB. et ZUCC.</td>
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<td><em>Meliosma myriantha</em> SIEB. et ZUCC.</td>
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<td><em>Zizyphus jujuba</em> MILL. var. <em>inermis</em> (BUNGE) REHD.</td>
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<td><em>Hovenia dulcis</em> THUNB.</td>
<td>Kenponashi</td>
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<td><em>Idesia polycarpa</em> MAXIM.</td>
<td>Iigiri</td>
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<td>Lythraceae</td>
<td><em>Lagerstroemia subcostata</em> KOEHNE</td>
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<td>Sarusuberi</td>
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<td><em>Aralia elata</em> (MIQ.) SEEMANN</td>
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<td>Kakuremino</td>
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<td>Koshiabura</td>
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<td><em>Evodia panax innovans</em> (SIEB. et ZUCC.) NAKAI</td>
<td>Takanotsume</td>
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<td><em>Kalopanax pictus</em> (THUNB.) NAKAI</td>
<td>Harigiri</td>
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<td><em>Cornus controversa</em> HEMSLY</td>
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<td><em>Cornus kousa</em> BUERGER. ex HANCE</td>
<td>Yamabōshi</td>
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<td>Benidōdan</td>
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<td><em>Diospyros morrisiana</em> HANCE</td>
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<td><em>Fraxinus mandshurica</em> RUFR. var. <em>japonica</em> MAXIM.</td>
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<td><em>Fraxinus japonica</em> BLUME</td>
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<td><em>Fraxinus lanuginosa</em> KOIDZ.</td>
<td>Aodamo</td>
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<tr>
<td>Verbenaceae</td>
<td><em>Clerodendrum trichotomum</em> THUNB.</td>
<td>Kusagi</td>
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in all the photographs are shown as those of flatter helical inclination compared with the actual spiral thickenings.

1. "S" spiral thickenings

1-1. Unbranched spiral thickenings

Photos 1–6 show representative examples of the spiral thickenings occurring in a regular pattern in certain species. Photos 1–3 show the spiral thickenings in the vessel wall in *Tilia japonica* (MIQ.) SIMONKAI. The ridges of the spiral thickenings were very prominent and were oriented at almost regular intervals. They exhibited a slight tendency for tapering into the wall (single arrow in Photo 2) and for branching (double arrow in Photo 2). Photo 3 shows the prominent ridges oriented at regular intervals and the intervacular pits between them. Although the ridges in Photos 1 and 3 are firmly attached to the wall, some of those were loosely attached to the wall. Photo 4 shows the spiral thickenings in the vessel wall in *Euonymus oxyphyllus* Miq. The ridges of the spiral thickenings varied slightly in their width and height and most of them were loosely attached to the wall (arrow in Photo 4). Similar spiral thickenings were also found in *Celastrus orbiculatus* Thunb. and *Euonymus sieboldianus* Blume. Photo 5 (*Prunus buergiana* Miq.) shows a representative example of the spiral thickenings occurring commonly in the 12 species examined belonging to *Prunus*. These spiral thickenings exhibited flat S helix and were smaller in width and height than those in *Tilia japonica* (MIQ.) SIMONKAI (Photos 1–3) and *Euonymus oxyphyllus* Miq. (Photo 4). They exhibited a slight tendency for branching. Photo 6 (*Ilex micrococca Maxim.*) shows a representative example of the unbranched spiral thickenings that were rarely found in each of the 7 species, except *Ilex integra* Thunb., belonging to *Ilex* and in *Aesculus turbinata* Blume, in which the branched spiral thickenings were dominantly found. As shown in this photo, the ridges of the spiral thickenings exhibited flat S helix at regular intervals.

Photos 7–11 show representative examples of the spiral thickenings occurring in an irregular pattern in some species. Photos 7 and 8 show the spiral thickenings in *Ostrya japonica* Sarg. and *Corylus sieboldiana* Blume, respectively. These spiral thickenings were oriented at irregular intervals and their ridges varied in width and height. They often tapered into the wall (arrow in Photo 8). Photos 9–11 show representative examples of the spiral thickenings occurring in association with the pits in the vessel wall. In *Ternstroemia gymnanthera* (Wight et Arn.) Sprague (Photo 9), *Viburnum awabuki* K. Koch (Photo 10) and *Viburnum dilatatum* Thunb. (Photo 11), the ridges of the spiral thickenings were always connected to the outer pit apertures. The helical direction of the ridges of the spiral thickenings was consistent with the direction of the main axis of the outer pit apertures in *Ternstroemia gymnanthera* (Wight et Arn.) Sprague (Photo 9), but not in *Viburnum awabuki* K. Koch (Photo 10) and *Viburnum dilatatum* Thunb. (Photo 11). The spiral thickenings in *Cleyera japonica* Thunb. (p. p., em. Sieb. et Zucc.) were quite similar to those shown in Photo 10. The spiral thickenings in some vessel members in *Camellia japonica* Linn., *Camellia japonica* Linn.
var. hortensis (MAKINO) MAKINO, Euscaphis japonica (THUNB.) KANITZ and Syringa reticulata (BLUME) HARA were similar to those shown in Photo 11.

1-2. Branched spiral thickenings

Photos 12-14 show the branched spiral thickenings in the vessel wall in Michelia compressa (MAXIM.) SARG. The spiral thickenings, which were similar in their appearances to those shown in these photos, were also commonly found in the 4 species belonging to Symplocos, in Pieris japonica (THUNB.) D. DON and in Vaccinium bracteatum THUNB. In Photo 12, the ridges of the spiral thickenings are forked and unbranched portions of them are oriented at regular intervals. In many cases, the direction of the microfibrillar orientation on the inner surface wall except the ridges of the spiral thickenings was not consistent with the helical direction of the ridges as shown in Photo 12. In the other cases, however, the former was consistent with the latter. Branching of the spiral thickenings in Photos 13 and 14 is more complicated than that in Photo 12. In Photos 13 and 14, the ridges themselves vary considerably in their width and height, and are irregularly branched. Crossed ridges that are different in helical inclination each other are shown in the left in Photo 14. That the ridges existing on the inner surface wall deposit separately on the underlying ones is clearly shown in Photo 14 (arrows). Photos 15-17 (Illex micrococca MAXIM.) show the variation of the branched spiral thickenings in each of the 7 species, except Illex integra THUNB., belonging to Illex and in Aesculus turbinata BLUME. Forked ridges of the spiral thickenings are found in the inner surface wall in Photo 15. In Photo 16, branching of the ridges of the spiral thickenings is complicated. The ridges of them exhibited a slight tendency for waving in the region where branching occurs conspicuously. Photo 17 is a higher magnification view of the area outlined in Photo 16. It can be seen in this photo that the direction of the microfibrillar orientation on the inner surface wall is very disturbed by branching and crossing of the ridges consisting of microfibrillar aggregates of parallel orientation. Photo 18 shows a representative example of the spiral thickenings in Illex integra THUNB. The spiral thickenings of this species were generally more prominent compared with those of the other 7 species belonging to Illex. In this species, the ridges of the spiral thickenings varied in their form, width and height, and were irregularly oriented. The thicker ridges of them were loosely attached to the wall. Photo 19 shows a representative example of the spiral thickenings in Helicia cochinchinensis LOUR. The ridges of the spiral thickenings varied in their width and height. They were irregularly branched. Photo 20 shows a representative example of the spiral thickenings in Elaeocarpus japonicus SIEB. et ZUCC. Forking and tapering into the wall of the ridges were often observed. Photo 21 shows a representative of the spiral thickenings in Stewartia monadelpha SIEB. et ZUCC. Irregularly branched ridges were generally found only near the perforation plates in some vessel members, although they were rarely found over the entire length of the vessel members. Photos 22 (Acer sieboldianum MIQ.), 23 (Acer mono MAXIM.) and 24 (Acer palmatum THUNB. var. palmatum.) show some examples of various forms of the
spiral thickenings found in the 12 species examined belonging to *Acer*. When the spiral thickenings were not conspicuous in their occurrence within a vessel member (Photo 22), the ridges of them were sporadically distributed on the vessel wall. Forking and tapering into the wall of the ridges occur irregularly in Photo 22. When the spiral thickenings became conspicuous in their occurrence, the ridges of them did not show a tendency for tapering into the wall and occurred compactly over the entire length of the vessel members. Photos 23 and 24 show appearances of the spiral thickenings in the vessel members in which they are conspicuous in their occurrence. In Photo 23, the ridges of the spiral thickenings vary in their width and height, and occur at irregular narrow intervals. In Photo 24, the ridges of them are irregularly branched and are considerably disturbed in the helical inclination.

Photos 25 and 26 show the spiral thickenings of the latewood vessel members in *Ulmus davidiana* Planch. var. *japonica* (Rehd.) Nakai and in *Celtis sinensis* Pers. var. *japonica* (Planch.) Nakai, respectively. Similar spiral thickenings were commonly found in the latewood vessel members of ring-porous woods, such as *Platycarya strobilacea* Sieb. et Zucc., *Ulmus laciniata* (Trautv.) Mayr, *Zelkova serrata* (Thunb.) Makino, *Aphananthe aspera* (Thunb.) Planch., *Broussonetia papyrifera* (Lin.) Vent., *Phellodendron amurense* Rupr., *Rhus verniciflua* Stokes, *Rhus trichocarpa* Miq., *Hibiscus syriacus* Linn. and *Catalpa ovata* G. Don, and in all the vessel members of *Euchresta japonica* Hook. fil. and *Caragana chamlaqu* Lam., and in many vessel members of the 4 species belonging to *Daphne*. In Photos 25 and 26, the ridges of the spiral thickenings are more prominent at the corners of the vessel members than in the other. This fact was generally found in the species having angular vessels in transverse section in which the spiral thickenings occur. In these species, the ridges of the spiral thickenings were more prominent especially in their height, in the smaller vessel members as shown in Photo 27 (*Hibiscus syriacus* Linn.).

Photo 28 shows the spiral thickenings of a latewood vessel member in *Robinia pseudo-acacia* Linn. Morphology of the spiral thickenings of this species has been reported by the authors (Ishida and Ohtani, 1970). Similar spiral thickenings were also found in the latewood vessel members in ring-porous woods, such as *Morus bombycis* Koidz., *Gleditsia japonica* Miq., *Sophora japonica* Linn., *Maackia amurensis* Rupr. et Maxim. var. *buergeri* (Maxim.) C. K. Schn., *Cladrastis platycarpa* (Maxim.) Makino, *Wisteria floribunda* (Willd.) DC., *Millettia japonica* (Sieb. et Zucc.) A. Gray, *Atlanthus altissima* Swingle, *Rhus javanica* Linn. and *Firmiana simplex* (Linn.) W. F. Wight, and in the larger vessel members in *Nandina domestica* Thunb. In these species except *Nandina domestica* Thunb., the spiral thickenings were more prominent, especially in their width, in the smaller vessel members as shown in Photo 29 (*Rhus javanica* Linn.) (compare with Photo 27). In several species belonging to Leguminosae, when the spiral thickenings met the pit apertures, some ends of them entered into the pit chamber from the pit aperture and branched like ventures in their appearance as shown in Photo 30 (*Sophora*
japonica LINN.). And also, vestures-like projections occurred occasionally from the ridges of spiral thickenings. These facts have been reported elsewhere (OHTANI and ISHIDA, 1976).

Photos 31–33 show representative examples of the spiral thickenings found commonly in the latewood vessel members in Melia azedarach LINN., Cedrela sinensis JUSS. and Sapindus mukorossi GAERTN. Photo 31 (Melia azedarach LINN.) shows a representative of the spiral thickenings in the larger vessel members in the latewood in Melia azedarach LINN. Photo 32 is a higher magnification view of the area outlined in Photo 31. Photo 33 shows a representative of the spiral thickenings in the smaller vessel members in Sapindus mukorossi GAERTN. As shown in photos 31–33, the spiral thickenings were more prominent, as the vessel members in which they occurred became smaller in their diameter. They exhibited a wavy appearance in the larger vessel members (Photos 31 and 32), and the ridges of the spiral thickenings themselves were twisted in the smaller ones (Photo 33). Photos 34–37 show representative examples of the branched spiral thickenings occurring in association with the pits in the vessel wall. Photos 34 and 35 show the spiral thickenings in a larger and a smaller vessel member in Photinia glabra (THUNB.) MAXIM., respectively. In this species, the ridges of the spiral thickenings were very prominent and compactly occurred in the smaller vessel members. Photo 36 shows a representative of the spiral thickenings in Pourthiaea villosa (THUNB.) DECNE. var. laevis (THUNB.) STAPF. Similar spiral thickenings were also commonly found in Eriobotrya japonica (THUNB.) LINDL. and Malus sieboldii (REGEL) REHDER. Photo 37 shows a representative of the spiral thickenings in Illicium religiosum SIEB. et ZUCC. As shown in Photos 34–37, the ridges of the spiral thickenings positioned above and below the pit apertures were oriented at irregular intervals, and branching and tapering into the wall of the ridges of them occurred frequently. Photo 38 (Sorbus japonica (DECNE.) HEDL.) shows a representative of the spiral thickenings that were found in some vessel members in the early zone of the annual rings in the 3 species belonging to Sorbus. Fine ridges of the spiral thickenings were distributed at irregular intervals in the inner surface wall. As will describe later on, the spiral thickenings of Z helix occurred dominantly in these species.

Photos 39–41 (Magnolia salicifolia (SIEB. et ZUCC.) MAXIM.) show representative examples of the spiral thickenings found in some vessel members in the 3 species belonging to Magnolia. Although the ridges of the spiral thickenings were very wide, they were not prominent in their height (Photos 39 and 40). When the ridges were conspicuous in their occurrence, the regions except the ridges (arrows in Photo 41) were restricted to the smaller areas. Parallel orientation of the microfibrils was found on the surface of the ridges along their helical direction as shown in Photos 40 and 41. The direction of the microfibrillar orientation on the inner surface wall except the ridges was different from that on the ridges.

Photos 42 and 43 show representative examples of the spiral thickenings in Carpinus tschonoskii MAXIM. and Carpinus laxiflora (SIEB. et ZUCC.) BLUME, respectively. Fine ridges of the spiral thickenings were densely distributed on the
inner surface wall and, in some cases, exhibited a slight tendency for waving. These fine ridges were more prominent as the vessel members became smaller in their diameter (Photo 43). Fine spiral thickenings, similar to those in Photos 42 and 43, were also observed in *Carpinus japonica* BLUME and *Carpinus cordata* BLUME, and in the 3 species belonging to *Ficus*. Photos 44 and 45 show the fine spiral thickenings in *Machilus thunbergii* SIEB. et ZUCC. These fine spiral thickenings were also commonly found in some vessel members in each of *Populus sieboldii* MIQUEL, *Myrsine seguinii* LEV. and the 10 species examined belonging to Lauraceae. Photo 46 shows a representative of the fine ridges of the spiral thickenings in the latewood vessel members in *Paulownia tomentosa* (THUNB.) STEUD. Branching and tapering into the wall of the ridges occurred irregularly. Photo 47 shows an example of the spiral thickenings in *Caesalpinia japonica* SIEB. et ZUCC. Fine ridges of the spiral thickenings and vestures-like projections were irregularly distributed on the inner surface wall of many vessel members. Their occurrences varied conspicuously between the vessel members in this species (OHTANI and ISHIDA, 1976).

2. "Z" spiral thickenings

2-1. Unbranched spiral thickenings

Unbranched spiral thickenings of Z helix were found in some vessel members in the 12 species examined belonging to *Prunus*. A representative example of them is shown in Photo 48 (*Prunus jamasakura* SIEB., ex KOIDZ.). They exhibited generally flat Z helix. They were quite similar in their appearance except for the direction of the helix to those of S helix shown in Photo 5. Unbranched spiral thickenings of flat Z helix were also found in some vessel members in *Ternstroemia gymnanthera* (WIGHT et ARN.) SPRAGUE. They were quite similar in their appearance except for the direction of the helix to those of S helix shown in Photo 9.

2-2. Branched spiral thickenings

Photos 49 and 50 show the spiral thickenings in *Berberis thunbergii* DC. The ridges of the spiral thickenings were more prominent and exhibited steeper Z helix, as the vessel members became smaller in their diameter (Photo 49). Prominent ridges of the spiral thickenings were loosely attached to the wall (Photo 50). Similar spiral thickenings of flat Z helix were also found in the smaller vessel members in *Nandina domestica* THUNB. Photos 51–54 show the spiral thickenings of Z helix in *Sorbus japonica* (DECNE.) HEDL. Photo 51 shows a radial surface of the early zone of the annual ring in this species. Although the spiral thickenings of the flat S helix occur in the one vessel member at the left in this photo, those of the Z helix occur in the others. Several prominent ridges of the spiral thickenings were aggregated and exhibited steep Z helix in many vessel members as shown in Photo 52. The ridges of the spiral thickenings were irregularly branched and often tapered into the wall. Photos 53 and 54 show the aggregation of the several prominent ridges of the spiral thickenings. The aggregation of them is more conspicuous in magnitude in the smaller vessel members (Photo 54) than in the larger
ones (Photo 53). Helical inclination of the ridges was steeper in the former than in the latter. The spiral thickenings, quite similar to those shown in Photos 51-54, were also found in *Sorbus alnifolia* (Sieb. et Zucc.) C. Koch, but not in *Sorbus commixta* Hedl. belonging to the same genus. A representative of the spiral thickenings of Z helix in *Sorbus commixta* Hedl. is shown in Photo 55. The aggregation of several ridges of the spiral thickenings as found in *Sorbus japonica* (Decne.) Hedl. and *Sorbus alnifolia* (Sieb. et Zucc.) C. Koch was not found in this species. The ridges of them were not conspicuous and exhibited flatter Z helix compared with those in *Sorbus japonica* (Decne.) Hedl. and *Sorbus alnifolia* (Sieb. et Zucc.) C. Koch.

Photo 56 (*Daphne kamtschatica* Maxim. var. jezoensis (Maxim.) Ohwi) shows a representative of the branched spiral thickenings found commonly in the 4 species belonging to *Daphne*. Similar spiral thickenings were also found in the smaller vessel members in *Platycarya strobilacea* Sieb. et Zucc. The branched spiral thickenings of flat Z helix were also found in some vessel members of *Pieris japonica* (Thunb.) D. Don and *Aesculus turbinata* Blume. They were similar in their appearance except for the direction of the helix to those of S helix (cf. Photos 12 and 15). Photos 57 and 58 show representative examples of the spiral thickenings in *Osmanthus heterophyllus* (G. Don) P. S. Green. Inclination of Z helix is steeper in the larger vessel members in this species (Photo 57). Prominent ridges of steeper Z helix were irregularly crooked in the larger vessel members (Photos 57 and 58). Similar spiral thickenings were also found in *Osmanthus fragrans* var. auranticus Makino belonging to the same genus. Photo 59 shows a representative of the spiral thickenings in *Ligustrum japonicum* Thunb. The ridges of them were oriented at irregular intervals. Similar spiral thickenings were also found in *Ligustrum obtusifolium* Sieb. et Zucc. belonging to the same genus.

Photos 60 (*Photinia glabra* (Thunb.) Maxim.) and 61 (*Poutrhiaea villosa* (Thunb.) Decne. var. laevis (Thunb.) Stapf) show the branched spiral thickenings occurring in association with the pits in the vessel wall. Some of the ridges passed above and below the pit apertures are irregularly branched and exhibit flat Z helix in these photos. The spiral thickenings, similar to those shown in Photo 61, were also found in some vessel members in *Eriobotrya japonica* (Thunb.) Lindl. and *Malus sieboldii* (Regel) Rehder.

Photos 62 and 63 show the very fine ridges in the inner surface wall of the latewood vessel members in *Albizia julibrissin* Durazz. Photo 63 is a higher magnification view of the area outlined in Photo 62. It can be seen in Photo 63 that some warts (vestures-like projections) occur on the fine ridges. Similar fine ridges of S helix were rarely found in this species. Photo 64 (*Ficus erecta* Thunberg var. yamadorii Makino) shows a representative example of the fine ridges of the spiral thickenings found commonly in the 3 species examined belonging to *Ficus*. The fine ridges of Z helix were rarely found in *Caesalpinia japonica* Sieb. et Zucc. Appearances of them were similar to those of S helix (cf. Photo 47).
3. "S and Z" spiral thickenings

3-1. Unbranched spiral thickenings

Unbranched spiral thickenings were not found in the species examined.

3-2. Branched spiral thickenings

Although the branched spiral thickenings were found in the 37 species, they varied in their occurrence between the species. In each of all the species in which this type of the spiral thickenings occurred, the spiral thickenings of the other type were dominantly found. The branched spiral thickenings of the species in which they were rather relatively frequently observed among these species are shown in Photos 65-78.

Although the unbranched spiral thickenings of S helix were dominantly found in Corylus sieboldiana Blume (Photo 8) and Ostrya japonica Sarg. (Photo 7), the branched spiral thickenings that were not constant in their helical direction within a vessel member were occasionally found. Representatives of them are shown in Photos 65 (Corylus sieboldiana Blume) and 66 (Ostrya japonica Sarg.). These thickenings were irregularly distributed in the inner surface wall. Photo 67 shows an example of the spiral thickenings disturbed in the helical direction in Prunus buergeriana Miq. Although the unbranched spiral thickenings of S helix were dominantly found in each of the 12 species examined belonging to Prunus, the spiral thickenings disturbed in the helical direction were also occasionally found in the 10 species of them. They were often branched and tapered into the wall. The spiral thickenings that were not constant in helical direction within a vessel member were relatively often found in the 5 species belonging to Acer compared with the other species in which they occurred. Photos 68-71 show examples of them. In Photo 68 (Acer mono Maxim.), the ridges are irregularly branched and the helical direction of them is very disturbed. In Photo 69 (Acer mono Maxim.), the ridges exhibit a tendency for swirling. In Photo 70 (Acer sieboldianum Miq.), the ridges show the reticulate thickenings and the helical direction of them is disturbed. Photo 71 (Acer mono Maxim.) shows the irregularity in occurrence of the spiral thickenings within a vessel. The spiral thickenings of flat S helix occur in the vessel member at the upper in this photo, while those disturbed in the helical direction do in the vessel member at the bottom. Irregularity in occurrence of the "S and Z" spiral thickenings within a vessel as shown in Photo 71 was commonly found in the all species in which they occurred. Photos 72 and 73 show examples in Robinia pseudo-acacia Linn. Occurrence of the spiral thickenings that were not constant in helical direction within a vessel member was the most conspicuous in this species among the species examined. The ridges of the spiral thickenings in the vessel members shown in Photo 72 and at the left in Photo 73 exhibit a tendency for swirling. Similar ridges were also often observed in Morus bombycis Koidz. Several ridges in the vessel member shown at the right in Photo 73 are oriented almost straight forming no spiral from one end to the another. Photo 74 (Sorbus japonica (Decne.) Hedl.) shows an example of the spiral thickenings found in Sorbus alnifolia (Sieb. et Zucc.) C. Koch and Sorbus japonica
In this photo, fine ridges exhibit flat S helix, while several aggregated prominent ridges at the right do Z helix. Photo 75 shows an example of the ridges, exhibiting a slight tendency for swirling, in *Sapindus mukorossi* Gaertn. Photo 76 shows an example of the fine branched ridges, exhibiting disorder of their helical direction, in *Carpinus cordata* Blume. Similar ridges were occasionally found in *Carpinus laxiflora* (Sieb. et Zucc.) Blume. Photo 77 shows an example of the ridges, exhibiting disorder of helical direction, in *Ilex integra* Thunb. Photo 78 shows irregularly branched spiral thickenings in *Cleyera japonica* Thunb. (p. p., em. Sieb. et Zucc.). The ridges around the projected part of the prominent ridges in the center in this photo are disturbed in their helical direction.

4. **Localized thickenings forming no spiral**

Photo 79 (*Acer sieboldianum* Miq.) shows a representative of the localized thickenings forming no spiral found commonly in all the species examined belonging to *Acer*. In these species, ridges of short range forming a pair occurred sporadically on the vessel wall, as shown in this photo. Photos 80 (*Pourthiaea villosa* (Thunb.) Decne. var. *laevis* (Thunb.) Staff), 81 (*Syringa reticulata* (Blume) Hara) and 82 (*Viburnum awabuki* K. Koch) show the short localized thickenings positioned above and below the pit apertures forming no spiral. Similar thickenings were also found in *Euscaphis japonica* (Thunb.) Kanitz, *Camellia japonica* Linn., *Camellia japonica* Linn. var. *hortensis* (Makino) Makino and *Viburnum dilatatum* Thunb. These thickenings resemble in their appearances to Callitroid thickenings (Davies and Ingle, 1966; Panshin and de Zeeuw, 1970).

Photo 83 shows a representative of the localized thickenings in *Sambucus sieboldiana* Blume, ex Graebn. var. *miquelii* (Nakai) Hara. These thickenings occurred in short range more or less transversely and tapered into the wall at their ends. They exhibited a slight tendency for branching. They were sporadically distributed in a limited region in the inner surface wall in some vessel members. Photo 84 shows the fine ridges of the localized thickenings in *Lyonia ovalifolia* (Wall.) Drude var. *elliptica* (Sieb. et Zucc.) Hand.-Mazz. These ridges were oriented in parallel with the microfibrillar orientation on the inner surface wall. They did not extend so long as they formed spiral about the vessel member axis and tapered into the wall. They were distributed sporadically in the inner surface wall of some vessel members in the terminal zone of the annual ring. Photo 85 shows a representative of the fine branched ridges in *Clethra barbinervis* Sieb. et Zucc. They were occasionally found in the region near the scalariform perforation plates in some vessel members. As shown in this photo, warts were uniformly distributed on the inner surface wall of vessel members. They also occurred on the fine ridges. Photos 86 and 87 show the fine ridges in *Eurya japonica* Thunb. They were oriented at almost right angles to the vessel member axis in regular intervals. They did not extend so long as they formed spiral about the vessel member axis. They were often found in the region near the scalariform perforation plates in the vessel members in the terminal zone of the annual ring (Photo 86). They were also rarely found in the region except for near the per-
foration plates (Photo 87). Although warts were densely distributed on the inner surface wall, they were not found in the region between the ridges (Photos 86 and 87).

Photos 88 and 89 show the wall projections in the inner surface wall in *Quercus mongolica* Fischer. These projections were occasionally found in the latewood vessel members. Similar projections were also occasionally found in the latewood vessel members in *Quercus crispula* Blume and *Quercus serrata* Thunb.

**Discussion and Conclusions**

The present SEM observation on the spiral thickenings of the vessel members in Japanese dicotyledonous woods revealed morphology of the spiral thickenings of many species which have not yet been recorded and also confirmed the known occurrence of the spiral thickenings in the species already recorded from the light microscope observation. Moreover, three-dimensional structure of the spiral thickenings could be revealed in more detail with the SEM observation.

Various forms of the spiral thickenings found in the 135 species in the present SEM observation were first divided into 4 major categories on the basis of their helical direction within a vessel member. In each of the categories, branched spiral thickenings were found in very numerous species compared with unbranched ones. That all the spiral thickenings within a vessel member were strictly unbranched was very rare. Many of the spiral thickenings, which were recorded as the unbranched spiral thickenings in this study, were rarely branched. Therefore, it should be rather described that the subdivisions within the categories were made according to the magnitude of branching.

The spiral thickenings of S helix were found in the 123 species (Photos 1-47). 52 of these species had exclusively the spiral thickenings of S helix. Although the spiral thickenings of the other type(s) in the helical direction were also found in the remainder (71 species), the spiral thickenings of S helix were dominantly found in 44 of these species. These results suggest that spiral thickenings of S helix existed in most species examined. This corresponds to the general description that the spiral thickenings are usually oriented in an S helix (Panshin and de Zeeuw, 1970).

The spiral thickenings of Z helix were found in the 38 species (Photos 48-64). Occurrence of them was restricted within the species belonging to certain genera. Regardless of the frequency of their occurrence, they occurred in all the species examined belonging to *Ficus* (Photo 64), *Prunus* (Photo 48), *Sorbus* (Photos 51-55), *Daphne* (Photo 56), *Ligustrum* (Photo 59) and *Osmanthus* (Photos 57 and 58). Especially, they occurred in the all of 19 species examined belonging to Rosaceae, though the spiral thickenings of the other type(s) also occurred in each of them. Only the following 5 species had exclusively the spiral thickenings of Z helix: *Berberis thunbergii* DC. (Photos 49 and 50), *Ligustrum japonicum* Thunb. (Photo 59), *Ligustrum obtusifolium*Sieb. et Zucc., *Osmanthus fragrans* var. *aurantiacus* Makino and *Osmanthus heterophyllus* (G. Don) P. S. Green (Photos 57 and 58).
Although the spiral thickenings of the other type(s) were also found in the 33 species except these 5 species, the spiral thickenings of Z helix were dominantly found in the 3 species belonging to *Sorbus*. Therefore, it is assumed that the species belonging to *Sorbus* (Photos 51–55), *Berberis* (Photos 49 and 50), *Ligustrum* (Photo 59) and *Osmanthus* (Photos 57 and 58) are characterised by the presence of exclusively or mostly the spiral thickenings of Z helix.

The spiral thickenings that were not constant in their helical direction within a vessel member were found in the 37 species (Photos 65–78). Even in the species in which their occurrence is the highest in frequency, the spiral thickenings of the other type were dominantly found. They varied considerably in occurrence between the species. Occurrence of them was relatively high in frequency in *Carpinus cordata* Blume (Photo 76), *Ostrya japonica* Sarg. (Photo 66), *Acer mono* Maxim. (Photos 68, 69 and 71), *Morus bombycis* Koidz. and *Robinia pseudo-acacia* Linn. (Photos 72 and 73). Occurrence of them was rare in the other species. Regardless of the frequency of their occurrence, they were found in 10 (Photo 67) of 12 species examined belonging to *Prunus*, in 2 (Photo 76) of 4 in *Carpinus* and in 5 (Photos 68–71) of 12 in *Acer*. In this connection, PARHAM and KAUSTINEN (1970) have already reported that swirled spiral thickenings are distinct in all vessel in *Acer saccharum* Marsh. and in some vessels of *Carpinus caroliniana* Walt. near the cell tips. They have also reported that *Prunus serotina* Ehrh. and *Acer rubrum* L. exhibit a slight tendency for swirling. Although it is not clear why the spiral thickenings disturbed in the helical direction occur in the limited species, these facts suggest that morphology of them may be a characteristic feature of the vessel member in the species belonging to *Carpinus, Ostrya, Prunus, Acer, Robinia* and *Morus*.

Although localized thickenings forming no spiral were found in the 27 species (Photos 79–89), they occurred rarely in these species. Moreover, occurrence of them was restricted within the species belonging to certain genera. They were found in all the species examined belonging to *Acer* (Photo 79), *Camellia* and *Viburnum* (Photo 82). They were almost similar in form in the species belonging to the same genus. The spiral thickenings of the other type(s) were dominantly found in 20 of the 27 species. Remainder (7 species) had exclusively localized thickenings forming no spiral.

Morphological variation of the spiral thickenings was evident both between the various species examined and also between the vessel members of the same species. Occurrence and morphology of the spiral thickenings within a species varied according to the diameter and the position in the annual ring of the vessel members in which they occurred. Generally, the spiral thickenings were more conspicuous in their development in the smaller vessel members than in the larger ones, when the vessel members existed in about same position within an annual ring. The spiral thickenings were larger in width and height of their ridges in the vessel members formed in the late stage than in those formed in the early stage, when the vessel members were about the same in their diameter. The typical
examples suggesting this fact were usually found in the ring-porous woods with the spiral thickenings. The spiral thickenings were confined to the latewood vessel members in them. Moreover, the spiral thickenings were the most conspicuous in their development in the smaller vessel members in the terminal zone in the latewoods compared with in the other (Photos 25–33).

It has been reported by Wardrop and Dadswell (1951) that the angle of inclination of the spiral thickenings to the longitudinal cell axis was less in longer than in shorter cells in Pseudotsuga. It has also been reported that the angle of inclination of the spiral thickenings to the longitudinal cell axis varies with the lumen diameter (Panshin and de Zeeuw, 1970). This fact was found in many of the species in which all the spiral thickenings were oriented in the same helical direction. However, this was not always clearly found in some of these species. The exception of this was found in the two species belonging to Osmanthus as shown in Photos 57 and 58. In these species, helical inclination of the spiral thickenings is steeper as the vessel members become larger in their diameter.

Fine ridges of the spiral thickenings were found in some or all of the vessel members in the 23 species in the present SEM observation (Photos 42–47, 62–64 and 76). They occurred in all the species examined belonging to Carpinus (Photos 42, 43 and 76), Ficus (Photo 64), Cinnamomum, Lindera, Neolitsea and Actinodaphne. Especially, they occurred in all of 10 species (Photos 44 and 45) examined belonging to Lauraceae. The fine ridges were also observed as the minute striations in the macerated vessel members under the transmitted light microscope. It is considered that they correspond to the striations that have already been described by Kanehira (1926), Kaneshi (1931) and Yamabayashi (1938, 1964) from the light microscopic observations. In this connection, Kaneshi (1931) has described that the striations exist as indistinct fine ridges of horizontal orientation on the inner surface wall. Yamabayashi (1938, 1964) has also described that the striations which resemble the spiral thickenings occur in the vessel wall in some species and it is very difficult to detect them clearly under the light microscopy because they are very minute compared with the spiral thickenings. Although occurrence of them in Populus sieboldii Miquel and Carpinus laxiflora (Sieb. et Zucc.) Blume has already been reported by Kanehira (1926) and Yamabayashi (1938), occurrence of them in the other species revealed by the present SEM observation has not yet been recorded from the light microscope observations.

Some different opinions as to the exact nature of the spiral thickenings have been reported. On the basis of an electron microscope study in Pseudotsuga taxifolia (Lamb.) Britt. (Hodge and Wardrop, 1950; Wardrop, 1964), Wardrop (1964) has reported that the thickenings consist of microfibril aggregates, formed in addition to the layer S3 and differing in their direction of orientation from that of the microfibrils present in this layer. On the other hand, Wergin and Casperson (1961) have described that the thickenings are definitely an integral part of the S3 in Taxus baccata L. From the examination on spiral thickening in normal and compression wood of Taxus baccata L. and Torreya california Torr., Patel
(1963) has reported that the orientation of the spiral thickenings, both in normal and compression tracheids, may indicate the microfibrillar angle in the secondary wall layers on which such thickenings are laid down. Côte (1967, 1968) has described that thickenings appear to be part of the S3 in electron micrographs of the sections of a *Tilia americana* L. and a *Pseudotsuga menziesii* (Mirb.) Franco. He has also described that in many cases, for instance *Pseudotsuga menziesii* (Mirb.) Franco, the helical thickenings blend into the last-formed layer of the wall, and that this is true even though the thickenings have an orientation somewhat different from the microfibrils of the underlying layer (Kollmann and Côte, 1968).

In the present SEM observation, although it was confirmed that the microfibrillar orientation in the inner surface wall except the ridges of the spiral thickenings exhibited flat S helix in many species, the microfibrillar orientation on the ridges of the spiral thickenings was not always confirmed in all the species. According to Hodge and Wardrop (1950), Panshin and de Zeeuw (1979) and Wardrop (1964), the ridges of the spiral thickenings are formed by the deposition of parallel bundle of microfibrils. If the ridges of all the spiral thickenings examined consist of the deposition of parallel bundle of microfibrils along the helical direction of them, the microfibrillar orientation in the ridges of flat S helix is consistent with that in the inner surface wall except the ridges in many cases. In the other cases, the former is not consistent with latter. In this connection, the ridges in some vessel members in the 3 species belonging to *Magnolia* must be noticed. As shown in Photos 40 and 41, the ridges showing flat S helix consisted of the parallel bundle of microfibrils along their helical direction and microfibrillar orientation of steep Z helix was found in the inner surface wall except the ridges. Kishi et al (1977) have reported that the secondary wall of vessel in *Magnolia obovata* Thunberg is distinguished into the typical three layers. And also, microfibrillar orientation of flat S helix was observed in the inner surface wall in the vessel members without the spiral thickenings in these species. Therefore, it is assumed that the ridges correspond to the S3 layer and the microfibrillar orientation except the ridges shows that in the S2 layer or in the outer part of the S3 layer. In other words, the ridges in these species occur due to localized absence of the deposition of all or the inner part of the S3 layer. Microfibrillar orientation of Z helix in the last-formed layer except the ridges was observed in some species, for instance *Michelia compressa* (Maxim.) Sarg. (Photo 12). Therefore, the microfibrillar orientation in the ridges is not consistent with that in the inner surface wall except the ridges in such cases, even though the ridges of the spiral thickenings exhibit flat S helix.

These facts suggest that the relationship in the microfibrillar orientation between the ridges of the spiral thickenings and the inner surface wall except the ridges varies considerably not only between the species but also between the vessel members in certain species. In certain species, moreover, the relationship varies even within the vessel member. In order to determine whether the spiral thickenings are a part of the S3 layer (or last-formed layer) or not, therefore, further observations in each of the species with the spiral thickenings are necessary. This problem
should be resolved on the basis of the formation process of the spiral thickenings in addition to the microfibrillar orientation of the spiral thickenings and the last-formed layer in each of the species with the spiral thickenings.

It is well known that the spiral thickening is an important diagnostic feature (Panshin and de Zeeuw, 1970). For the wood identification by means of the light microscopy, the presence or absence of the spiral thickenings have generally been used as a diagnostic criterion because morphology of them cannot be clearly observed by the light microscopy. On the other hand, morphology of them can be easily and clearly observed using the SEM, as shown by the present SEM observation. Therefore, the results of occurrence and morphological variation of the spiral thickenings in each of the 218 species shown in the present SEM observation provide a useful fundamental information as a diagnostic criterion for the wood identification of Japanese dicotyledonous woods using the SEM.

References

本邦産双子葉木本植物（51科，120属，218種）の道管要素のらせん肥厚の有無およびそれらの形態が走査型電子顕微鏡により観察された。得られた結果を要約すれば次の通りである。

1. 18科，30属，62種のすべての道管要素に，らせん肥厚が存在した。それらの樹種名は，Table 1に示されている。28科，50属，73種に，らせん肥厚が存在する道管要素と存在しない道管要素がみとめられた。それらの樹種名は，Table 2に示されている。27科，47属，83種のすべての道管要素に，らせん肥厚が存在しなかった。それらの樹種名は，Table 3に示されていている。

2. 観察されたらせん肥厚の形態は，極めて変化にとんでいた。らせん肥厚の形態は，一道管要素内でどのらせん肥厚の存在状態をもとにしていくつかのタイプに分けられた。まず，一道管要素内ですべてのらせん肥厚のらせん方向をもとにして，4つのタイプに分けられた。すなわち，1）一道管要素内ですべてのらせん肥厚がSらせんを示すもの，2）一道管要素内ですべてのらせん肥厚がZらせんを示すもの，3）一道管要素内でらせん肥厚のらせん方向が一定していないもの，4）一道管要素内でらせん状を示さない部分的な隆起線状の壁肥厚。1）～3）のタイプに属するらせん肥厚は，さらに分岐していないもの（ごくまれに分岐しているものをも含む）と分岐しているものの２つのタイプに分けられた。

3. それぞれのタイプのらせん肥厚が存在する道管要素を有する樹種名は Table 1およびTable 2に示されている。また，それぞれのタイプのらせん肥厚が存在する道管要素を有する樹種の数は次に示すとおりであり，それぞれのタイプのらせん肥厚は，いくつかの代表例を示すSEM写真により説明されている。

らせん肥厚のタイプ                   樹種数            SEM写真
1）一道管要素内ですべてのらせん肥厚
   がSらせんを示すもの  ……………… 123       Photo 1-47
   1-1）分岐していないもの  ……………… 34       Photo 1-11
   1-2）分岐しているもの  ……………… 97       Photo 12-47

2）一道管要素内ですべてのらせん肥厚
   がZらせんを示すもの  ……………… 38       Photo 48-64
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2-1) 分岐していないもの 13  Photo 48
2-2) 分岐しているもの 25  Photo 49-64

3) 一樹種に内ろらせん厚厚のらせん
   方向が一定していないもの 37  Photo 65-78
3-1) 分岐していないもの 0
3-2) 分岐しているもの 37  Photo 65-78

4) 一樹種に内ろらせん状を示さない
   局部的な隆起線状の壁厚 27  Photo 79-89

4. 一樹種内でのらせん厚厚の出現およびそれらの発達の程度は、道管要素の直径および年輪内の位置に密接な関係がある場合が多く、年輪内におけるほぼ同じ位置の道管要素では、直径の小さいもの程らせん厚厚の発達が顕著であった。また、ほぼ同じ直径の道管要素では、年輪内の早期に形成された道管要素におけるよりも終期に形成された道管要素におけるがららせん厚厚の発達が顕著であった。このことは、らせん肥厚を有する環孔材に典型的に示されている。すなわち、らせん肥厚は早材部の道管要素に存在しないが、晩材部のそれらには存在する。晩材部ではターミナル部の直径の小さい道管要素において、らせん肥厚の発達が最も顕著である場合が多かった。

5. 一樹種内でのらせん厚厚のらせんの角度（道管要素軸とらせん厚厚のなす角度）は、道管要素の内腔径が小さくなるにつれ大きさくなる場合が多くの樹種に観察された。しかし、両者の関係が明確に認められない場合もあった。また、上記の逆の関係を示す樹種、たとえば、ヒイラギ（Photo 57）・キンモクセイ、も認められた。

6. 一樹種内でらせん方向が一定していないらせん厚厚は、37種類に認められた（Photo 65-78）。しかし、これらの樹種では、他のタイプのらせん厚厚の出現がはるかに多かった。それらのらせん厚厚の出現の頻度が高かった樹種は、サワシバ（Photo 76）・アサダ（Photo 66）・ヤマグワ・ハリエンシュウ（Photo 72・73）・イタヤカエデ（Photo 68・69・70）であった。サクラ属に属する12種類のうち10種類に、カエデ属に属する12樹種のうち5樹種に、クマシテ属に属する4種類のうち2種類に、それらのらせん厚厚が認められた。これらの事実は、一樹種内でらせん方向が一定していないらせん厚厚はクマシテ属・アサダ属・クサ属・サクラ属・ハリエンシュウ属・カエデ属に属する樹種の道管要素の構造的面を示唆していると考えられる。

7. 普通のらせん厚厚でなく、きわめて細いらせん厚厚が、23種類（Photo 42-47, 62-64, 76）に認められた。これらのらせん厚厚は、従来光学顕微鏡観察の結果と呼ばれていたものと考えられる。

8. らせん厚厚の隆起部のミクロフィブリルの配向をすべての樹種について確認することはできなかった。らせん厚厚の隆起部を除く道管壁の内表面のミクロフィブリルの配向は多く
の樹種ではゆるやかなSヘリックスであった。したがって、らせん肥厚の隆起部のミクロフィブリルがらせん肥厚のらせん方向にそって平行に配向しているとすれば、一般的にいえば、ゆるやかなSヘリックスのらせん肥厚の部分とその道管壁の内表面とのミクロフィブリルの配向は一致するが、ゆるやかなSヘリックス以外のらせん肥厚の部分とその道管壁の内表面とのミクロフィブリルの配向は一致しない。しかし、ホオノキ・タムシバ（Photo 39-41）・キタコブシに認められたS3層の欠如によりできたと考えられるらせん肥厚や、ゆるやかなSヘリックスのらせん肥厚を有するいくつかの樹種、たとえばオガタマノキ（Photo 12）、認められたように、道管壁のらせん肥厚の隆起部以外の内表面のミクロフィブリルがZヘリックスを示す場合があるように、らせん肥厚の隆起部とそれ以外の道管壁の内表面のミクロフィブリルの配向の関係はきわめて複雑である。両者のミクロフィブリルの配向の関係は、樹種間で異なることはもちろん同一樹種内の道管要素間のみならず道管要素内でも異なる場合がある。

9. 本研究で得られた木質双子葉木本植物の道管要素のらせん肥厚の有無およびそれらの形態についての観察結果は、これらの樹種の道管壁構造の解明ののみならずSEMによる樹種識別の基準としてのらせん肥厚の使用のための基礎的知見を提供するものと考えられる。
Explanation of photographs

Note: The vessel axis is vertical in all the photographs (-sizing). All the photographs show the inner surface of the vessel wall viewed from the lumen side at an angle of ca. 45° to the direction of the vessel axis. Therefore, the spiral thickenings in all the photographs are shown as those of flatter helical inclination compared with the actual spiral thickenings.

Photos 1–11 show the unbranched spiral thickenings of "S" helix.

Photo 1. *Tilia japonica* (MIQ.) SIMONKAI Prominent ridges of the spiral thickenings occurring at regular intervals.

Photo 2. *Tilia japonica* (MIQ.) SIMONKAI The spiral thickenings showing a slight tendency for tapering into the wall (single arrow) and for branching (double arrow).

Photo 3. *Tilia japonica* (MIQ.) SIMONKAI The prominent ridges oriented at regular intervals and the intervascular pits between them.

Photo 4. *Euonymus oxyphyllus* MIQ. The ridges are loosely attached to the wall (arrow).

Photo 5. *Prunus buergeriana* MIQ. The ridges of the spiral thickenings exhibit flat S helix and are smaller in width and height than those in Photos 1–4.

Photo 6. *Ilex micrococca* MAXIM. The ridges of the spiral thickenings occurring at regular intervals.

Photo 7. *Ostrya japonica* SARG. The ridges of the spiral thickenings occurring at irregular intervals.

Photo 8. *Corylus sieboldiana* BLUME The ridges of the spiral thickenings occurring at irregular intervals. Arrow shows a ridge tapering into the wall.

Photo 9. *Ternstroemia gymnanthera* (WIGHT et ARN.) SPRAGUE. The ridges of the spiral thickenings occurring in association with the pits.

Photo 10. *Viburnum awabuki* K. KOCH The ridges of the spiral thickenings occurring in association with the pits.

Photo 11. *Viburnum dilatatum* THUNB. The ridges of the spiral thickenings occurring in association with the pits.

Photos 12–47 show the branched spiral thickenings of "S" helix.

Photo 12. *Michelia compressa* (MAXIM.) SARG. Forked ridges of the spiral thickenings. The direction of the microfibrillar orientation on the inner surface wall except the ridges of the spiral thickenings is not consistent with the helical direction of the ridges.

Photo 13. *Michelia compressa* (MAXIM.) SARG. Irregularly branched ridges of the spiral thickenings.

Photo 14. *Michelia compressa* (MAXIM.) SARG. Crossed ridges of the spiral thickenings (arrows).

Photo 15. *Ilex micrococca* MAXIM. Forked ridges of the spiral thickenings.

Photo 16. *Ilex micrococca* MAXIM. Irregularly branched ridges of the spiral thickenings.
Ilex micrococca MAXIM. A higher magnification view of the area outlined in Photo 16.

Ilex integra THUNB. Various ridges of the spiral thickenings in width and height are irregularly oriented.

Helicia cochinchinensis LOUR. Irregularly branched ridges of the spiral thickenings.

Elaeocarpus japonicus SIEB. et ZUCC. The spiral thickenings showing a tendency for tapering into the wall and forking.

Stewartia monadelpha SIEB. et ZUCC. Irregularly branched ridges of the spiral thickenings.

Acer sieboldianum MIQ. The ridges of the spiral thickenings occurring in an irregular pattern.

Acer mono MAXIM. The ridges of the spiral thickenings occurring densely at irregular narrow intervals.

Acer palmatum THUNB. var. palmatum Irregularly branched ridges of the spiral thickenings.

Ulmus davidiana PLANCH. var. japonica (REHD.) NAKAI The spiral thickenings in a latewood vessel member.

Celtis sinensis PERS. var. japonica (PLANCH.) NAKAI The spiral thickenings in a latewood vessel member.

Hibiscus syriacus LINN. The spiral thickenings of a smaller vessel member in the latewood.

Robinia pseudo-acacia LINN. The spiral thickenings in a latewood vessel member.

Rhus javanica LINN. The spiral thickenings of a smaller vessel member in the terminal latewood. The ridges of the spiral thickenings are more prominent in width than in height (compare with Photo 27).

Sophora japonica LINN. Vestures-like branched ridges of the spiral thickenings in the pit chambers.

Melia azedarach LINN. The ridges of the spiral thickenings of a larger vessel member in the latewood.

Melia azedarach LINN. A higher magnification view of the area outlined in Photo 31.

Sapindus mukorossi GAERTN. The spiral thickenings of a smaller vessel member in the latewood.

Photinia glabra (THUNB.) MAXIM. The ridges of the spiral thickenings occurring in association with the pits in a larger vessel member.

Photinia glabra (THUNB.) MAXIM. The ridges of the spiral thickenings occurring in association with the pits in a smaller vessel member.

Pourthiaea villosa (THUNB.) DECNE. var. laevis (THUNB.) STAFF The ridges of the spiral thickenings occurring in association with the pits.

Illicium religiosum SIEB. et ZUCC. The ridges of the spiral thickenings occurring in association with the pits.
Photo 38. *Sorbus japonica* (DECN.) HEDL. The spiral thickenings of a vessel member in the early zone of the annual ring.

Photo 39. *Magnolia salicifolia* (SIEB. et ZUCC.) MAXIM. Irregularly branched ridges of the spiral thickenings.

Photo 40. *Magnolia salicifolia* (SIEB. et ZUCC.) MAXIM. Although the ridges are very wide, they are not prominent in height.

Photo 41. *Magnolia salicifolia* (SIEB. et ZUCC.) MAXIM. Inner surface wall showing microfibrillar orientation of the ridges and the regions except the ridges (arrows).

Photo 42. *Carpinus tschonoskii* MAXIM. Fine ridges of the spiral thickenings showing a slight tendency for waving.

Photo 43. *Carpinus laxijlora* (SIEB. et ZUCC.) BLUME The ridges of the spiral thickenings are more prominent in a smaller vessel member (in the right) than in a larger one (in the left).

Photo 44. *Machilus thunbergii* SIEB. et ZUCC. Fine ridges of the spiral thickenings.

Photo 45. *Machilus thunbergii* SIEB. et ZUCC. Fine ridges of the spiral thickenings showing a tendency for tapering into the wall and forking.

Photo 46. *Paulownia tomentosa* (THUNB.) STEUD. Fine ridges of the spiral thickenings in a latewood vessel member.

Photo 47. *Caesalpinia japonica* SIEB. et ZUCC. Inner surface wall showing fine ridges of the spiral thickenings and vestures-like projections.

Photo 48 shows the unbranched spiral thickenings of “Z” helix.

Photo 48. *Prunus jamasakura* SIEB., ex KOIDZ. The ridges of the spiral thickenings showing flat inclination of Z helix.

Photos 49-64 show the branched spiral thickenings of “Z” helix.

Photo 49. *Berberis thunbergii* DC. The ridges of the spiral thickenings showing steep Z helix (in the right).

Photo 50. *Berberis thunbergii* DC. Prominent ridges of the spiral thickenings are loosely attached to the wall.

Photo 51. *Sorbus japonica* (DECN.) HEDL. A radial surface of the early zone of the annual ring. Although the spiral thickenings of flat S helix occur in the one vessel member in the left, those of Z helix occur in the two vessel members in the right.

Photo 52. *Sorbus japonica* (DECN.) HEDL. Irregularly branched ridges of the spiral thickenings. Several prominent ridges are aggregated.

Photo 53. *Sorbus japonica* (DECN.) HEDL. The aggregation of the several prominent ridges of the spiral thickenings in a larger vessel member.

Photo 54. *Sorbus japonica* (DECN.) HEDL. The aggregation of the several prominent ridges of the spiral thickenings in a smaller vessel member. Helical inclination of the ridges is steeper in this photo than in Photo 53.

Photo 55. *Sorbus commixta* HEDL. Irregularly branched ridges of the spiral thick- enings.
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Photo 56. *Daphne kamtschatica* MAXIM. var. *jezoensis* (MAXIM.) OHWI The ridges of the spiral thickenings occurring at almost regular intervals.

Photo 57. *Osmanthus heterophyllus* (G. DON) P. S. GREEN A radial surface showing various forms of the spiral thickenings.

Photo 58. *Osmanthus heterophyllus* (G. DON) P. S. GREEN Prominent ridges of steep Z helix in a larger vessel member.

Photo 59. *Ligustrum japonicum* THUNB. The ridges of the spiral thickenings occurring at irregular intervals.

Photo 60. *Photinia glabra* (THUNB.) MAXIM. The ridges of the spiral thickenings occurring in association with the pits.

Photo 61. *Pourthiaea villosa* (THUNB.) DECNE. var. *laevis* (THUNB.) STAPF The ridges of the spiral thickenings occurring in association with the pits.

Photo 62. *Albizia julibrissin* DURAZZ. Inner surface wall of a latewood vessel member showing fine ridges and warts (vestures-like projections).

Photo 63. *Albizia julibrissin* DURAZZ. A higher magnification view of the area outlined in Photo 62.

Photo 64. *Ficus erecta* THUNBERG var. *yamadorii* MAKINO Fine ridges of the spiral thickenings.

Photos 65-78 show the branched spiral thickenings of “S and Z” helix.

Photo 65. *Corylus sieboldiana* BLUME The ridges of the spiral thickenings disturbed in the helical direction.

Photo 66. *Ostrya japonica* SARG. Irregular spiral thickenings in the helical direction.

Photo 67. *Prunus buergeriana* MIQ. The ridges of the spiral thickenings disturbed in the helical direction. They exhibit a tendency for tapering into the wall and branching.

Photo 68. *Acer mono* MAXIM. The ridges of the spiral thickenings disturbed in the helical direction. They are irregularly branched.

Photo 69. *Acer mono* MAXIM. Swirled ridges of the spiral thickenings.

Photo 70. *Acer sieboldianum* MIQ. The ridges showing reticulate thickenings.

Photo 71. *Acer mono* MAXIM. An example showing irregularity in occurrence of the spiral thickenings within a vessel. Although the spiral thickenings of flat S helix occur in the vessel member at the upper, those disturbed in the helical direction occur in that at the bottom.

Photo 72. *Robinia pseudo-acacia* LINN. The ridges of the spiral thickenings disturbed in the helical direction. Swirled ridges are found in the upper right.

Photo 73. *Robinia pseudo-acacia* LINN. The ridges of the spiral thickenings in the vessel member in the left exhibit a tendency for swirling. Several ridges in the vessel member in the right are oriented almost straight forming no spiral from one end to the other.

Photo 74. *Sorbus japonica* (DECNE.) HEDL. Although fine ridges exhibit flat S helix, several aggregated prominent ridges in the right do Z helix.
Photo 75. *Sapindus mukorossi* GAERTN. The ridges of the spiral thickenings showing a slight tendency for swirling.

Photo 76. *Carpinus cordata* BLUME Fine branched ridges disturbed in the helical direction.

Photo 77. *Ilex integra* THUNB. Prominent ridges disturbed in the helical direction.

Photo 78. *Cleyera japonica* THUNB. (p. p., em. SIEB. et ZUCC.) Irregularly branched ridges of the spiral thickenings.

Photos 79-89 show the localized thickenings forming no spiral.

Photo 79. *Acer sieboldianum* MiQ. The ridges of short range forming a pair.

Photo 80. *Fourthiaea villosa* (THUNB.) DECNE. var. *laevis* (THUNB.) STAPF Short localized thickenings positioned above and below the pit apertures.

Photo 81. *Syringa reticulata* (BLUME) HARA Short localized thickenings positioned above and below the pit apertures.

Photo 82. *Viburnum awabuki* K. KOCH Short localized thickenings positioned above and below the pit apertures.

Photo 83. *Sambucus sieboldiana* BLUME, ex GRAEBN. var. *miquelii* (NAKAI) HARA Localized thickenings occurring in short range more or less transversely.

Photo 84. *Lyonia ovalifolia* (WALL.) DRUDE var. *elliptica* (SIEB. et ZUCC.) HAND.-MAZZ. Localized thickenings in a vessel member in the terminal zone of the annual ring.

Photo 85. *Clethra barbinervis* SIEB. et ZUCC. Inner surface wall showing fine branched ridges and warts.

Photo 86. *Eurya japonica* THUNB. Fine ridges occurring at regular intervals in transverse direction near the scalariform perforation plate.

Photo 87. *Eurya japonica* THUNB. Fine ridges occurring at regular intervals in transverse direction.

Photo 88. *Quercus mongolica* FISCHER Wall projections occurring irregularly in the inner surface wall.

Photo 89. *Quercus mongolica* FISCHER Inner surface wall showing wall projections and microfibrillar orientation near them.