An Observation on the Perforation Plates in Japanese Dicotyledonous Woods Using Scanning Electron Microscopy*

By

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走査型電子顕微鏡による本邦産双子葉木本植物のせん孔板の観察

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Introduction

A perforation plate is defined as the area of the common end walls of two adjacent vessel members, which is involved in their coalescence. As the perforation plate is a characteristic structure of the vessel, information about the structure of the perforation plate is very important to provide a better understanding of the structure and the physical properties not only of the vessel itself, but also of the dicotyledonous woods.

Since the perforation plates can be observed relatively easily with light microscopy, the investigations of the perforation plates in different species have been made for a long time from various standpoints. Perforation plate development in differentiating vessels has been investigated by PRIESTLY et al. (1935) and ESAU and HEWITT (1940) using light microscopy, by SASSEN (1965), YATA et al. (1970) and THOMAS and BONNER (1974) by using transmission electron microscopy, and by BUTTERFIELD and MEYLAN (1972), MEYLAN and BUTTERFIELD (1972 a) and OHTANI and ISHIDA (1976) using scanning electron microscopy. According to these works, the secondary wall is deposited on the primary wall, except for the areas to become the perforations, as well as the pit membranes, during the differentiation process of the vessel. The perforation partition, the primary walls and the intervening intercellular layer in the region of the perforation, remains intact, until the deposition of the secondary wall of the vessel members is almost complete, and then the partition is degraded by enzymatic action prior to the beginning of the transpiration stream, although different opinions exist as to the degradation process.

Occurrence and structure of various types of perforation plates in different dicotyledonous woods have been investigated by JEFFREY (1917), THOMPSON (1918), BLISS (1921), MACDUFFIE (1921), THOMPSON (1923), CHALK (1933), BAILEY and HOWARD (1941), and GOTTWALD and PARAMESWARAN (1964) using light microscopy, by MEYER and MUHAMMAD (1971) using transmission electron microscopy, and by BUTTERFIELD and MEYLAN (1971), MEYLAN and BUTTERFIELD (1972 b), MEYLAN and BUTTERFIELD (1973), PARAMESWARAN and LIESE (1973), PARHAM (1973), BUTTERFIELD and MEYLAN (1974), ISHIDA and OHTANI (1974), BUTTERFIELD and MEYLAN (1975) and MEYLAN and BUTTERFIELD (1975) using scanning electron microscopy. In recent years, microfibrillar webs located within scalariform perforation plate openings have attracted attention of a number of investigators. Electron micrographs of the substructures, i. e. the microfibrillar webs, in the scalariform perforation plates of the fossil plants have already been reported by WESLEY and KUYPER (1951) and FREY (1954). SEM micrographs of them in modern angiosperm were first represented as seen in *Cercidiphyllum japonicum* SIEB. et ZUCC. by ISHIDA (1969, 1970) and OHTANI (1970). MEYER and MUHAMMAD (1971) have also found them in tree species from six different plant families. They have found various textures of the microfibrillar webs, which were named orthogonal and reticulate microfibrillar webs, and have indicated the structural similarity between scalariform openings containing reticulate webs with closely spaced microfibrils and intervascular pit membranes at the ends of the scalariform perforation plates. MEYLAN and BUTTERFIELD (1972 b, 1975) have described that the microfibrillar webs are most common in vessels close to the cambium, where they appear to be a stage in the breakdown of the perforation partitions, and also that they are generally confined to the last few openings at each end of the perforation plate in mature wood. PARHAM (1973) has confirmed the existence of microfibrillar connections between bars of the scalariform perforation plates in mature wood of some species, and has described that the microfibrillar webs are probably primary wall substance that is not removed by enzymatic action. ISHIDA and OHTANI (1974) have found that the microfibrillar webs are sometimes present between bars in any openings, not only in the margin, but also in the central region of the scalariform perforation plates in mature wood of *Cercidiphyllum japonicum* SIEB. et ZUCC. and *Cornus controversa* HEMSLEY and have pointed out that the plates with the microfibrillar webs consist of many prominent bordered bars. In recent years, combination perforation plates have also been investigated by a number of workers, especially using scanning electron microscopy. The openings in each half perforation plate in adjacent vessel members normally coincide exactly in the species with only one perforation plate type, while the openings between adjacent vessel members may not be coincident and a perforation plate may consist of two different types of half perforation plates in the species with more than one perforation plate type. Such perforation plates have been referred to as combination perforation plates (MEYLAN and BUTTERFIELD, 1973). Various types of such combination perforation plates in different species have been illustrated clearly by MEYLAN and BUTTERFIELD (1973), OHTANI and ISHIDA (1973), PARAMESWARAN and LIESE (1973), BUTTERFIELD and MEYLAN (1975) and MEYLAN and BUTTERFIELD (1975).

Much attention to the perforation plates has been paid for a long time by many workers studying the origin and phylogenetic development of the vessel members in angiosperms (CHEADLE, 1953). The specialization of the perforation plates of vessel members of dicotyledonous woods has been studied by JEFFREY (1917), THOMPSON (1918), BLISS (1921), MACDUFFIE (1921), THOMPSON (1923), FROST (1930 a, 1930 b, 1931), CHALK (1933), BAILEY and HOWARD (1941) and BAILEY (1944). The studies on the evolutionary development of the vessel until 1952 have been reviewed by CHEADLE (1953). The scalariform perforation plate that is long, oblique, and with numerous perforations is considered to be the most primitive and the simple, horizontal one is the most advanced. It has been generally assumed that the simple perforation plates evolved from the scalariform perforation plates by the loss of dividing bars, and that the vessel members with scalariform perforation plates were derived from the tracheids with scalariform pitting. In recent years, PARAMESWARAN and LIESE (1973) have proposed a new hypothesis for the derivation of simple perforation plates along the following line: tracheids with scalariform pitting—vessel with net-like pitting—vessels with multiperforate perforations—vessels with simple perforations.

The term "perforation plate" which has been used in some standard reference books on wood anatomy is not always strictly consistent. According to the International Glossary of Terms published by the International Association of Wood Anatomists, the perforation plate is a term of convenience for the area of the wall (originally imperforated) involved in the coalescence of two members of a vessel. Although this definition has been used in some textbooks (ESAU, 1965; TSOUMIS, 1968; PANSHIN and DE ZEEUW, 1970), some botanists have described that the perforation plate is the more or less definitely delimited or outlined area of the wall in which perforation occurs (EAMES and MACDANIELS, 1947; CUTTER, 1969; FAHN, 1974). Moreover, the terms applied to the various forms of the multiple perforation plates are varied and confusing as pointed out by GRAY and DE ZEEUW (1974). Recently, GRAY and DE ZEEUW (1974) have proposed terminology for the multiple perforation plates in vessel members.

It has been considered that morphology of the perforation plates in the secondary xylem of dicotyledonous woods can be used as a diagnostic criterion for wood identification. For this reason, therefore, the morphology of the perforation plates in Japanese dicotyledonous woods has been investigated by light microscopy (KANEHIRA, 1926; KANESHI, 1931; YAMABAYASHI, 1938; SUDÔ, 1959). However, the description of the perforation plates themselves is relatively simple and is not necessarily sufficient.

The authors have already reported the substructures of the perforation plates in some dicotyledonous woods, such as the microfibrillar webs in *Cercidiphyllum* etc. and characteristic morphological variations in *Fagus*, on the basis of the SEM observations (OHTANI and ISHIDA, 1973; ISHIDA and OHTANI, 1974; OHTANI and ISHIDA, 1976). It is a very interesting problem whether these substructures and the other unknown ones are found in the other species of Japanese dicotyledonous woods or not. And also, it is expected that the SEM observations on the perforation plates in each of the different dicotyledonous woods provide valuable information, which has not yet been recorded by light microscopy, for the classification and identification of Japanese dicotyledonous woods. To obtain this evidence, the SEM observations on the perforation plates in Japanese dicotyledonous woods are necessary as much as possible. In order to obtain information on the structure of the perforation plates in the submicroscopic level, therefore, the authors observed the perforation plates in the 218 species belonging to 120 genera, 51 families, as one of the observations on the sculpturing of the cell wall in Japanese dicotyledonous woods, using scanning electron microscopy. In this paper, the structure of the perforation plates of many species which have not yet been recorded is illustrated with many SEM micrographs, and the species examined are classified into 6 groups on the basis of the morphological variation of the perforation plates in each species.

Materials and Methods

The species names (218 species, 120 genera, 51 families) examined in this study are listed in Tables 1-6.

Wood samples were collected from living trees and/or obtained from the wood collection of the Department of Forest Products, Hokkaido University. Small blocks were taken from the outer sapwood of them. The longitudinal radial surfaces to be observed were obtained by cutting with new razor blades. Specimens were finished in the form of ca. 7 mm × 7 mm × 1 mm and dried at room conditions. They were then stuck on the brass standard stubs with electrically conductive paste. Prepared stubs were coated with gold or carbon-gold by vacuum evaporation. Sputter coating was also used. Observations were made with a JSM-2 scanning electron microscope at 15 kV.

In order to confirm the morphological variation of the perforation plates in each species, observations were made across the annual rings in several specimens collected from each of the 218 species belonging to 120 genera, 51 families.

Results

Various forms of perforation plates were found in the present SEM observation. The terms for various forms of the multiple perforation plates except the scalariform in past works are not consistent (GRAY and DE ZEEUW, 1974). To avoid the confusion of the terms, therefore, the multiple perforation plates examined were distinguished into scalariform perforation plates and multiple perforation plates except the scalariform in this paper. On the basis of occurrence of various forms of perforation plates in each species, the examined species were divided into 6 main groups, as details are given as under (Tables 1-6). The species names used in Tables 1-6 mostly follow OHWI (1972).

1. Species with exclusively scalariform perforation plates

46 species belong to this group. The species names are listed in Table 1. The general structural feature of the scalariform perforation plate was essentially the same in all the species belonging to this group. That is, the corresponding bars in the half perforation plates in two adjacent vessel members were quite similar in form and formed a regular pair. Furthermore, such bars were situated at regular intervals and more or less at right angles to the vessel axis. The openings between bars at both ends of the plate were usually smaller than those in the other portion of the plate. When pits were present at the ends in the plate, the openings of the plate were often found to grade into the pits at the ends of it. This has already been reported in some species by the present authors (ISHIDA and OHTANI, 1974). The inclination of the plate, the width and number of the bars, and the form and size of the individual openings varied considerably between the examined species (Photos 1, 2 and 3), but not within a species, except for some species.

There was a strong correlation between the structure and the inclination of the scalariform perforation plates. The bars decrease in number and the scalariform openings become larger in width, as the inclination of the plate changes from the highly inclined position to the transverse position. As shown in Photos 1, 2 and 3, the scalariform openings become larger in width as the bars of the plates decrease in number. The bars within a scalariform perforation plate varied in num-

Table 1. Species with exclusively scalariform perforation plates

Family	Botanical name	Japanese name
Betulaceae	*Carpinus cordata* BLUME	Sawashiba
	Corylus sieboldiana BLUME	Tsunohashibami
	Betula maximowicziana REGEL	Udaikanba
	Betula platyphylla SUKATCHEV var. *japonica* (MIQ.) HARA	Shirakanba
	Betula ermanii CHAM.	Dakekanba
	Betula grossa SIEB. et ZUCC.	Yogusominebari
	Alnus firma SIEB. et ZUCC.	Yashabushi
	Alnus maximowiczii CALLIER	Miyamahannoki
	Alnus hirsuta TURCZ.	Keyamahannoki
	Alnus serrulatoides CALLIER	Kawarahannoki
	Alnus japonica (THUNB.) STEUD.	Hannoki
Cercidiphyllaceae	*Cercidiphyllum japonicum* SIEB. et ZUCC.	Katsura
Magnoliaceae	*Michelia compressa* (MAXIM.) SARG.	Ogatamanoki
	Liriodendron tulipifera L.	Yurinoki
Saxifragaceae	*Hydrangea petiolaris* SIEB. et ZUCC.	Gotôzuru
	Hydrangea paniculata SIEBOLD	Noriutsugi
	Deutzia crenata SIEB. et ZUCC.	Utsugi
Hamamelidaceae	*Hamamelis japonica* SIEB. et ZUCC.	Mansaku
	Distylium racemosum SIEB. et ZUCC.	Isunoki
Buxaceae	*Buxus microphylla* SIEB. et ZUCC. var. *japonica* (MUELL. ARG.) REHD. et WILS.	Tsuge
Aquifoliaceae	*Ilex macropoda* MIQ.	Aohada
	Ilex micrococca MAXIM.	Tamamizuki
	Ilex sugerokii MAXIM. var. *longipedunculata* (MAXIM.) MAKINO	Ushikaba
	Ilex crenata THUNB.	Inutsuge
	Ilex pedunculosa MIQ.	Soyogo
	Ilex rotunda THUNB.	Kuroganemochi
	Ilex integra THUNB.	Mochinoki
	Ilex latifolia THUNB.	Tarayô
Staphyleaceae	*Euscaphis japonica* (THUNB.) KANITZ	Gonzui
Sabiaceae	*Meliosma rigida* SIEB. et ZUCC.	Yamabiwa
Theaceae	*Stewartia monadelpha* SIEB. et ZUCC.	Himeshara
	Ternstroemia gymnanthera (WIGHT et ARN.) SPRAGUE	Mokkoku
	Cleyera japonica THUNB. (p.p., em. SIEB. et ZUCC.)	Sakaki
Cornaceae	*Cornus controversa* HEMSLEY	Mizuki
	Cornus brachypoda C. A. MEY.	Kumanomizuki
	Cornus kousa BUERGER, ex HANCE	Yamabôshi
Clethraceae	*Clethra barbinervis* SIEB. et ZUCC.	Ryôbu
Symplocaceae	*Symplocos coreana* (LÉVEILLÉ) OHWI	Tannasawafutagi
	Symplocos theophrastaefolia SIEB. et ZUCC.	Kanzaburônoki
	Symplocos glauca (THUNB.) KOIDZ.	Mimizubai
	Symplocos prunifolia SIEB. et ZUCC.	Kurobai
Styracaceae	*Styrax japonica* SIEB. et ZUCC.	Egonoki
	Styrax obassia SIEB. et ZUCC.	Hakuunboku
	Pterostyrax corymbosa SIEB. et ZUCC.	Asagara
Caprifoliaceae	*Viburnum dilatatum* THUNB.	Gamazumi
	Viburnum awabuki K. KOCH	Sangoju

ber from one (*Michelia compressa* (MAXIM.) SARG., *Liriodendron tulipifera L.*) to eighty or so (*Symplocos coreana* (LÉVEILLÉ) OHWI) in the present SEM observation. Typical examples of many-barred, intermediate-barred and few-barred scalariform perforation plates are shown in Photos 1, 2 and 3, respectively.

Microfibrillar webs were observed in the lateral margin of the scalariform openings of some plates in mature wood of 36 examined species (Photo 4). Moreover, complete microfibrillar webs, which were present in most or all regions of all the scalariform openings of a plate, were found in some plates in the limited species examined. Species with complete microfibrillar webs were as follows; *Cercidiphyllum japonicum* SIEB. et ZUCC., *Hydrangea petiolaris* SIEB. et ZUCC., *Hydrangea paniculate* SIEBOLD, *Ternstroemia gymnanthera* (WIGHT et ARN.) SPRAGUE, *Cleyera japonica* THUNB. (p. p., em. SIEB. et ZUCC.), *Cornus controversa* HEMSLEY, *Cornus brachypoda* C. A. MEY., *Cornus kousa* BUERGER, ex HANCE, *Clethra barbinervis* SIEB. et ZUCC., *Symplocos coreana* (LÉVEILLÉ) OHWI, *Symplocos theophrastaefolia* SIEB. et ZUCC., *Symplocos glauca* (THUNB.) KOIDZ., *Symplocos prunifolia* SIEB. et ZUCC., *Pterostyrax corymbosa* SIEB. et ZUCC., *Viburnum dilatatum* THUNB., *Viburnum awabuki* K. KOCH. Photos 5 and 6 show the complete microfibrillar webs in the plates in *Viburnum awabuki* K. KOCH and *Cercidiphyllum japonicum* SIEB. et ZUCC., respectively. These fibrillar strands were oriented more or less orthogonally between bars in the entire region of each scalariform opening. Photo 7 shows the complete microfibrillar webs in the plate in *Viburnum awabuki* K. KOCH. Most secondary walls of the bars on this side have been removed in this photo. It can be seen in the photo that each fibrillar strand across the opening branches near the bars. Photo 8 shows a part of the complete microfibrillar webs in the lateral margin of the scalariform openings in *Cornus controversa* HEMSLEY. These fibrillar strands are more dense in the lateral margin than in the central and are arranged at random. It should be noticed that the scalariform perforation plates with complete microfibrillar webs always had prominent bordered bars (Photos 7 and 8).

Various forms of the plates which were different from the general form of the scalariform perforation plate stated above were found in a number of species belonging to this group. Photos 9 and 10 show a portion of the plates of *Stewartia monadelpha* SIEB. et ZUCC., giving examples of them. Although the scalariform perforation plates of this species generally had regular bars existing more or less at right angles to the vessel axis, some plates had branched bars (Photo 9) or markedly inclined bars (Photo 10). Such plates were also occasionally found in the species belonging to *Betula, Alnus, Cornus* etc. Photos 11 and 12 show examples of mismatching bars of the scalariform perforation plates. In Photo 11, showing a portion of a plate in *Viburnum awabuki* K. KOCH, the bars of the vessel member on the other side are situated at right angles to the vessel axis, while those on this side are inclined. In Photo 12, showing a plate in *Ternstroemia gymnanthera* (WIGHT et ARN.) SPRAGUE, mismatching bars of the adjacent vessel members are found as cross bars at the right. Such scalariform perforation plates

Table 2. Species with exclusively simple perforation plates

Family	Botanical name	Japanese name
Salicaceae	*Populus nigra* LINN. var. *italica* MUENCHH.	Seiyôhakayanagi
	Populus sieboldii MIQUEL	Yamanarashi
	Populus maximowiczii HENRY	Doroyanagi
	Salix bakko KIMURA	Bakkoyanagi
	Salix kinuyanagi KIMURA	Kinuyanagi
	Salix sachalinensis FR. SCHM.	Onoeyanagi
Juglandaceae	*Platycarya strobilacea* SIEB. et ZUCC.	Nogurumi
	Plerocarya rhoifolia SIEB. et ZUCC.	Sawagurumi
	Juglans ailanthifolia CARR.	Onigurumi
Betulaceae	*Ostrya japonica* SARG.	Asada
Fagaceae	*Quercus acuta* THUNB.	Akagashi
	Quercus sessilifolia BLUME	Tsukubanegashi
	Quercus gilva BLUME	Ichiigashi
	Quercus myrsinaefolia BLUME	Shirakashi
	Quercus glauca THUNB.	Arakashi
	Quercus salicina BLUME	Urajirogashi
	Quercus phillyraeoides A. GRAY.	Ubamegashi
	Quercus mongolica FISCHER	Mongorinara
	Quercus crispula BLUME	Mizunara
	Quercus serrata THUNB.	Konara
	Quercus dentata THUNB.	Kashiwa
	Quercus variabilis BLUME	Abemaki
	Quercus acutissima CARRUTH.	Kunugi
	Castanea crenata SIEB. et ZUCC.	Kuri
	Castanopsis cuspidata (THUNB.) SCHOTTKY	Tsuburajii
	Castanopsis cuspidata (THUNB.) SCHOTTKY var. *sieboldii* (MAKINO) NAKAI	Sudajii
	Pasania glabra (THUNB.) OERST.	Shiribukagashi
Ulmaceae	*Ulmus davidiana* PLANCH. var. *japonica* (REHD.) NAKAI	Harunire
	Ulmus laciniata (TRAUTV.) MAYR	Ohyô
	Zelkova serrata (THUNB.) MAKINO	Keyaki
	Celtis sinensis PERS. var. *japonica* (PLANCH.) NAKAI	Enoki
	Aphananthe aspera (THUNB.) PLANCH.	Mukunoki
Moraceae	*Morus bombycis* KOIDZ.	Yamaguwa
	Broussonetia papyrifera (LINN.) VENT.	Kajinoki
	Ficus pumila LINN.	Ôitabi
	Ficus erecta THUNBERG	Inubiwa
	Ficus erecta THUNBERG var. *yamadorii* MAKINO	Keinubiwa
Berberidaceae	*Berberis thunbergii* DC.	Megi
	Nandina domestica THUNB.	Nanten
Rosaceae	*Prunus mume* SIEB. et ZUCC.	Ume
	Prunus persica (LINN.) BATSCH.	Momo
	Prunus apetala (SIEB. et ZUCC.) FRANCH. et SAVAT.	Chôjizakura
	Prunus incisa THUNB.	Mamezakura
	Prunus pendula MAXIM. forma *ascendens* (MAKINO) OHWI	Edohigan

Family	Botanical name	Japanese name
Rosaceae (cont.)	*Prunus jamasakura* SIEB., ex KOIDZ.	Yamazakura
	Prunus sargentii REHDER	Ezoyamazakura
	Prunus maximowiczii RUPR.	Miyamazakura
	Prunus spinulosa SIEB. et ZUCC.	Rinboku
	Prunus ssiori FR. SCHM.	Shiurizakura
	Prunus grayana MAXIM.	Uwamizuzakura
	Prunus buergeriana MIQ.	Inuzakura
	Photinia glabra (THUNB.) MAXIM.	Kanamemochi
	Eriobotrya japonica (THUNB.) LINDL.	Biwa
	Malus sieboldii (REGEL) REHDER	Zumi
Leguminosae	*Albizia julibrissin* DURAZZ.	Nemunoki
	Acacia confusa MERR.	Sôshiju
	Gleditsia japonica MIQ.	Saikachi
	Caesalpinia japonica SIEB. et ZUCC.	Jaketsuibara
	Sophora japonica LINN.	Enju
	Maackia amurensis RUPR. et MAXIM. var. *buergeri* (MAXIM.) C. K. SCHN.	Inuenju
	Cladrastis platycarpa (MAXIM.) MAKINO	Fujiki
	Euchresta japonica HOOK. fil.	Miyamatobera
	Lespedeza bicolor TURCZ. forma *acutifolia* MATSUM.	Yamahagi
	Caragana chamlagu LAM.	Muresuzume
	Pueraria lobata (WILLD.) OHWI	Kuzu
	Wisteria floribunda (WILLD.) DC.	Fuji
	Millettia japonica (SIEB. et ZUCC.) A. GRAY	Natsufiji
	Robinia pseudo-acacia LINN.	Harienju
Rutaceae	*Zanthoxylum piperitum* (LINN.) DC.	Sanshô
	Zanthoxylum ailanthoides SIEB. et ZUCC.	Karasuzanshô
	Phellodendron amurense RUPR.	Kihada
Simaroubaceae	*Ailanthus altissima* SWINGLE	Niwaurushi
	Picrasma quassioides (D. DON) BENN.	Nigaki
Meliaceae	*Melia azedarach* LINN.	Sendan
	Cedrela sinensis JUSS.	Chanchin
Euphorbiaceae	*Mallotus japonicus* (THUNB.) MUELL. ARG.	Akamegashiwa
	Aleurites cordata R. BR.	Aburagiri
	Aleurites fordii HEMSL.	Shinaaburagiri
	Sapium japonicum (SIEB. et ZUCC.) PAX et HOFFM.	Shiraki
Anacardiaceae	*Rhus succedanea* LINN.	Haze
	Rhus verniciflua STOKES	Urushi
	Rhus sylvestris SIEB. et ZUCC.	Yamahaze
	Rhus trichocarpa MIQ.	Yamaurushi
	Rhus javanica LINN.	Nurude
Celastraceae	*Celastrus orbiculatus* THUNB.	Tsuruumemodoki
	Euonymus sieboldianus BLUME	Mayumi
	Euonymus oxyphyllus MIQ.	Tsuribana
Aceraceae	*Acer sieboldianum* MIQ.	Kohauchiwakaede

Family	Botanical name	Japanese name
Aceraceae (cont.)	*Acer japonicum* THUNB.	Hauchiwakaede
	Acer palmatum THUNB. var. *palmatum*	Irohamomiji
	Acer palmatum THUNB. var. *matsumurae* (KOIDZ.) MAKINO	Yamamomiji
	Acer mono MAXIM.	Itayakaede
	Acer miyabei MAXIM.	Kurobiitaya
	Acer distylum SIEB. et ZUCC.	Marubakaede
	Acer ukurunduense TRAUTV. et MEY.	Ogarabana
	Acer carpinifolium SIEB. et ZUCC.	Chidorinoki
	Acer crataegifolium SIEB. et ZUCC.	Urikaede
	Acer rufinerve SIEB. et ZUCC.	Urihadakaede
	Acer cissifolium (SIEB. et ZUCC.) K. KOCH	Mitsudekaede
Hippocastanaceae	*Aesculus turbinata* BLUME	Tochinoki
Sapindaceae	*Sapindus mukorossi* GAERTN.	Mukuroji
Rhamnaceae	*Zizyphus jujuba* MILL. var. *inermis* (BUNGE) REHD.	Natsume
	Hovenia dulcis THUNB.	Kenponashi
Elaeocarpaceae	*Elaeocarpus japonicus* SIEB. et ZUCC.	Kobanmochi
Tiliaceae	*Tilia japonica* (MIQ.) SIMONKAI	Shinanoki
Malvaceae	*Hibiscus syriacus* LINN.	Mukuge
Sterculiaceae	*Firmiana simplex* (LINN.) W. F. WIGHT	Aogiri
Thymelaeaceae	*Daphne kiusiana* MIQUEL	Koshônoki
	Daphne odora THUNB.	Jinchôge
	Daphne pseudo-mezereum A. GRAY	Onishibari
	Daphne kamtschatica MAXIM. var. *jezoensis* (MAXIM.) OHWI	Naniwazu
Lythraceae	*Lagerstroemia subcostata* KOEHNE	Shimasarusuberi
	Lagerstroemia indica LINN.	Sarusuberi
Araliaceae	*Aralia elata* (MIQ.) SEEMANN	Taranoki
	Dendropanax frifidus (THUNB.) MAKINO	Kakuremino
	Acanthopanax sciadophylloides FRANCH. et SAVAT.	Koshiabura
	Evodiopanax innovans (SIEB. et ZUCC.) NAKAI	Takanotsume
	Kalopanax pictus (THUNB.) NAKAI	Harigiri
Myrsinaceae	*Myrsine seguinii* LÉV.	Taimintachibana
Ebenaceae	*Diospyros morrisiana* HANCE	Tokiwagaki
	Diospyros lotus LINN.	Mamegaki
	Diospyros kaki THUNB.	Kakinoki
Oleaceae	*Ligustrum japonicum* THUNB.	Nezumimochi
	Ligustrum obtusifolium SIEB. et ZUCC.	Ibotanoki
	Osmanthus heterophyllus (G. DON) P. S. GREEN	Hiiragi
	Syringa reticulata (BLUME) HARA	Hashidoi
	Fraxinus spaethiana LINGELSH.	Shioji
	Fraxinus mandshurica RUPR. var. *japonica* MAXIM.	Yachidamo
	Fraxinus japonica BLUME	Toneriko
	Fraxinus lanuginosa KOIDZ.	Aodamo
Verbenaceae	*Clerodendrum trichotomum* THUNB.	Kusagi
Scrophulariaceae	*Paulownia tomentosa* (THUNB.) STEUD.	Kiri
Bignoniaceae	*Catalpa ovata* G. DON	Kisasage

with mismatching bars have already been reported in some species (MEYLAN and BUTTERFIELD, 1973, 1975; ISHIDA and OHTANI, 1974). Photos 13 and 14 show unusual scalariform perforation plates of *Cornus kousa* BUERGER, ex HANCE. In these plates, wall material forming no bars exists in the central region of the plate. Such plates correspond to the scalariform perforation plate with a projecting tongue of unperforated secondary wall described by MEYLAN and BUTTERFIELD (1975).

2. Species with exclusively simple perforation plates

133 species belong to this group. The species names are listed in Table 2. Some variation in the form and inclination of the plate was found both between the examined species and also between vessels occurring within an annual ring of the same species.

It was convenient here to classify the rims of the simple perforation plates into two major categories, i. e., bordered and non-bordered. From the cross view of the rims, moreover, the rims were classified into 4 types as shown in Fig. 1.

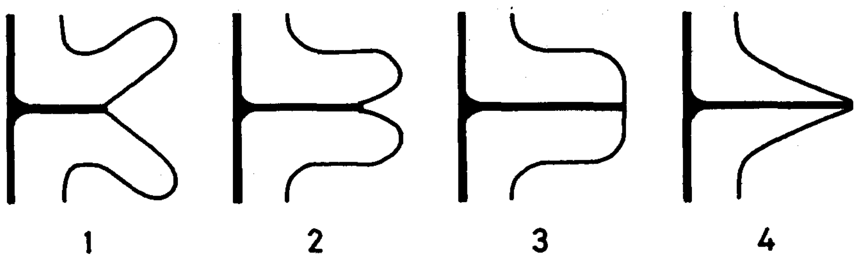

Fig. 1. Types of rims.

Photos 15 and 16 show the simple perforation plates with the prominent bordered rims (Type 1) in *Populus sieboldii* MIQUEL and *Zanthoxylum ailanthoides* SIEB. et ZUCC., respectively. This type of simple perforation plates was found only in 14 limited species among 133 species: *Populus sieboldii* MIQUEL, *Platycarya strobilacea* SIEB. et ZUCC., *Nandina domestica* THUNB., *Prunus spinulosa* SIEB. et ZUCC., *Photinia glabra* (THUNB.) MAXIM., *Eriobotrya japonica* (THUNB.) LINDL., *Euchresta japonica* HOOK. fil., *Caragana chamlagu* LAM., *Zanthoxylum piperitum* (LINN.) DC., *Zanthxylum ailanthoides* SIEB. et ZUCC., *Acanthopanax sciadophylloides* FRANCH. et SAVAT., *Diospyros kaki* THUNB., *Ligustrum japonicum* THUNB., *Ligustrum obtusifolium* SIEB. et ZUCC. The simple perforation plates with other types of rims were also always found in each of these species. Photos 17 and 18 show the simple perforation plates with the bordered rims (Type 2) in *Mallotus japonicus* (THUNB.) MUELL. ARG. and *Aesculus turbinata* BLUME, respectively. Photos 19 and 20 show the simple perforation plates with the non-bordered rims (Type 3) in *Populus maximowiczii* HENRY and *Prunus jamasakura* SIEB., ex KOIDZ., respectively. The edge of these rims is relatively flat. Photos 21, 22 and 23 show the simple perforation plates with the non-bordered rims (Type 4) in *Zelkova serrata* (THUNB.) MAKINO, *Sapindus mukorossi* GAERTN. and *Clerodendrum trichotomum* THUNB., respectively. The edge of these rims is very sharp, and when they are smaller in height, they are inconspicuous as shown in Photo 21 (arrows). Such examples were often found in the earlywood vessels of ring-porous woods examined. The simple perforation plates with the rims of Types 2, 3 and 4 were found together within an annual ring in most species examined. It was confirmed in most ring-porous woods that the simple perforation plates with the rims of Type 4 were found in the earlywood vessels and those with the rims of Types 2 and/or 3 were found in the latewood vessels.

As recognized in the simple perforation plates shown in Photos 15–23, regardless of the types of the rims stated above, the corresponding rims in the half plates of the two adjacent vessel members were generally quite similar in shape and formed a regular pair. However, it was occasionally found in some species that they did not form a regular pair. An example in *Zanthoxylum ailanthoides* SIEB. et ZUCC. is shown in Photo 24.

The edge of the rim, i. e., the margin of the perforation, was smooth in its outline in most simple perforations observed. However, it was occasionally found in some species that the edge of the rim was irregular in its outline as shown in Photo 25. The simple perforation plates with such irregular rims were generally found in the species with both simple and scalariform perforation plates.

Photo 26 shows a simple perforation plate with many small projections on the rim in *Caragana chamlagu* LAM. Resemblance between the projections and pit vestures in this species has been described elsewhere (OHTANI and ISHIDA, 1976).

Photo 27 shows an unusual interconnection between the adjacent vessel members in *Prunus jamasakura* SIEB., ex KOIDZ. An end of the vessel member at the bottom in this photo is connected to the members of the two different vessels at the top in this photo by the simple perforations. In other words, this photo shows the evidence of a forked vessel. Such examples were also found in *Prunus ssiori* FR. SCHM., but not in all the other species. Therefore it is reasonable to assume that the occurrence of such an interconnection between adjacent vessel members is very rare.

3. Species with both simple and scalariform perforation plates

21 species belong to this group. The species names are listed in Table 3. Two types of the plates occurred regularly in association with the position of the vessels within an annual ring in only 2 species, while they occurred irregularly in 19 species.

3–1. Species with simple and scalariform perforation plates occurring regularly within an annual ring

Pieris japonica (THUNB.) D. DON and *Myrica rubra* SIEB. et ZUCC. belong to this subgroup. Photos 28–36 show the morphological variation of the plates in *Pieris japonica* (THUNB.) D. DON. The simple perforation plates observed in the earlywood* vessels are shown in Photos 28–30. Photo 28 shows a simple perfora-

* For convenience, the terms "earlywood" and "latewood" used in this paper are defined as the parts which are formed in the early and late stages within an annual ring, respectively.

Table 3. Species with both simple and scalariform perforation plates

Family	Botanical name	Japanese name
Myricaceae	*Myrica rubra* SIEB. et ZUCC.	Yamamomo
Betulaceae	*Carpinus tschonoskii* MAXIM.	Inushide
	Carpinus laxiflora (SIEB. et ZUCC.) BLUME	Akashide
	Carpinus japonica BLUME	Kumashide
Magnoliaceae	*Magnolia obovata* THUNBERG	Hônoki
	Magnolia salicifolia (SIEB. et ZUCC.) MAXIM.	Tamushiba
	Magnolia kobus DC. var. *borealis* SARG.	Kitakobushi
Lauraceae	*Cinnamomum camphora* (LINN.) SIEBOLD	Kusunoki
	Cinnamomum japonicum SIEBOLD, ex NAKAI	Yabunikkei
	Machilus thunbergii SIEB. et ZUCC.	Tabunoki
	Lindera erythrocarpa MAKINO	Kanakuginoki
	Lindera umbellata THUNB.	Kuromoji
	Parabenzoin praecox (SIEB. et ZUCC.) NAKAI	Aburachan
	Neolitsea sericea (BLUME) KOIDZ.	Shirodamo
	Neolitsea aciculata (BLUME) KOIDZ.	Inugashi
	Actinodaphne lancifolia (SIEB. et ZUCC.) MEISN.	Kagonoki
	Actinodaphne longifolia (BLUME) NAKAI	Baribarinoki
Sabiaceae	*Meliosma myriantha* SIEB. et ZUCC.	Awabuki
Flacourtiaceae	*Idesia polycarpa* MAXIM.	Iigiri
Ericaceae	*Pieris japonica* (THUNB.) D. DON	Asebi
Caprifoliaceae	*Sambucus sieboldiana* BLUME, ex GRAEBN. var. *miquelii* (NAKAI) HARA	Ezoniwatoko

tion plate with smooth rim, while Photos 29 and 30 show simple perforation plates with irregular rims. Photos 31–34 show the perforation plates having an intermediate structure between typical simple and scalariform perforation plates in the middle portion of the annual ring. These intermediate types of plates have few complete bars and projections of wall material extending from the lateral margin of the perforation. Photo 35 shows a typical scalariform perforation plate in the latewood* vessel. Photo 36 shows a scalariform perforation plate in the terminal zone of the annual ring. This plate has remnants of the partition in the scalariform openings between bars.

Although the perforation plates in *Myrica rubra* SIEB. et ZUCC. were more or less similar in their morphological variation to those in *Pieris japonica* (THUNB.) D. DON described just above, the simple perforation plates were present in only few vessels at the beginning of the annual ring, and the scalariform perforation plates with several bars were present in those in the other part of the annual ring.

3-2. Species with simple and scalariform perforation plates occurring irregularly within an annual ring

The morphological variations of the plates in *Carpinus tschonoskii* MAXIM., *Carpinus laxiflora* (SIEB. et ZUCC.) BLUME and *Carpinus japonica* BLUME were similar. Photos 37–39 show various forms of the perforation plates in *Carpinus tschonoskii* MAXIM. Both types of the simple perforation plates with smooth (Photo

37) and irregular rims (Photo 38) were present in these species. The scalariform perforation plates had several thin bars and larger openings between them (Photo 39). The plates with an intermediate structure between the simple and the scalariform perforation plates as shown in *Pieris japonica* (THUNB.) D. DON (Photos 31–34) were also present in these species.

In *Idesia polycarpa* MAXIM. and *Sambucus sieboldiana* BLUME, ex GRAEBN. var. *miquelii* (NAKAI) HARA, the scalariform perforation plates were rarely found. They were more or less similar in form to those in the species belonging to *Carpinus.*

Photos 40–46 show the morphological variation of the plates in *Magnolia obovata* THUNBERG. Most perforation plates in this species were simple. The simple perforation plates with smooth (Photo 40) and irregular rims (Photo 41) were present. It was often found that they were long ovals along the vessel axis direction in smaller vessel members (Photo 42). Typical scalariform perforation plates were rarely found in smaller vessels (Photo 43). Photos 44–46 show the perforation plates showing an intermediate structure between typical simple and scalariform perforation plates. The morphological variation of the plates of *Magnolia salicifolia* (SIEB. et ZUCC.) MAXIM. and *Magnolia kobus* DC. var. *borealis* SARG. belonging to the same genus were quite similar to that of *Magnolia obovata* THUNBERG.

Photos 47–52 show the morphological variation of the perforation plates in *Cinnamomum japonicum* SIEBOLD, ex NAKAI. Although most perforation plates in this species were simple (Photo 47), some plates were scalariform with bars from one to several (Photos 48, 49 and 50). These plates often had inclined bars (Photos 49 and 50). It was occasionally found that the perforation plates had smaller irregular openings near the margin as shown in Photo 51 (arrows). It was occasionally found that two perforation plates at both ends of one vessel member were different in type. Such a typical example is shown in Photo 52. A vessel member at the right in this photo has a simple and a scalariform half perforation plate at the both lower and upper ends. Each of the two half plates is connected to the half plates of the adjacent vessel members forming a regular pair, resp. Such vessel members were occasionally found in all examined species belonging to Lauraceae.

The morphological variation in all the examined species belonging to Lauraceae was more or less similar to that in *Cinnamomum japonicum* SIEB., ex NAKAI which belongs to Lauraceae too, although occurrence of the simple and the scalariform perforation plates in each species was different between the species.

The scalariform perforation plates in *Meliosma myriantha* SIEB. et ZUCC. were similar in form to those in *Cinnamomum japonicum* SIEBOLD, ex NAKAI. However, occurrence of them in *Meliosma myriantha* SIEB. et ZUCC. was more or less similar in frequency to that of the simple perforation plates.

4. Species with both scalariform and multiple perforation plates except scalariform

9 species belong to this group. The species names are listed in Table 4. Both

Table 4. Species with both scalariform and multiple perforation plates except scalariform

Family	Botanical name	Japanese name
Magnoliaceae	*Illicium religiosum* SIEB. et ZUCC.	Shikimi
Euphorbiaceae	*Daphniphyllum macropodum* MIQ.	Yuzuriha
	Daphniphyllum teijsmannii ZOLL.	Himeyuzuriha
Theaceae	*Camellia japonica* LINN.	Yabutsubaki
	Camellia japonica LINN. var. *hortensis* (MAKINO) MAKINO	Tsubaki
	Eurya japonica THUNB.	Hisakaki
Ericaceae	*Lyonia ovalifolia* (WALL.) DRUDE var. *elliptica* (SIEB. et ZUCC.) HAND.-MAZZ.	Nejiki
	Enkianthus cernuus (SIEB. et ZUCC.) MAKINO forma *rubens* (MAXIM.) OHWI	Benidôdan
Symplocaceae	*Symplocos lancifolia* SIEB. et ZUCC.	Shirobai

plates occurred regularly in association with the position of the vessels within an annual ring in 5 species, while they occurred irregularly in 4 species.

4-1. Species with both types of the plates occurring regularly within an annual ring

Photos 53, 54 and 55 show the morphological variation of the plates in *Camellia japonica* LINN. Typical scalariform perforation plates with several bars were present in the earlywood vessels (Photos 53 and 54), while the scalariform perforation plates with thick bars and the multiple perforation plates except scalariform were present in the latewood vessels (Photos 53 and 55). The morphological variation of the plates in *Camellia japonica* LINN. var. *hortensis* (MAKINO) MAKINO belonging to the same genus was quite similar to that in *Camellia japonica* LINN.

Although most perforation plates in *Eurya japonica* THUNB. were long scalariform with many bars, the multiple perforation plates except scalariform as shown in Photo 56 were present in the terminal zone of the annual ring.

Photos 57–59 show the morphological variation of the plates in *Enkianthus cernuus* (SIEB. et ZUCC.) MAKINO forma *rubens* (MAXIM.) OHWI. Photo 57 shows a portion of a long scalariform perforation plate with many bars in the earlywood vessel. Photo 58 shows a portion of a multiple perforation plate except scalariform with openings varying in size and form in the earlywood vessel. The microfibrillar webs are found in the openings at the lateral margin (at the left in this photo) and at the end of the plate. Photo 59 shows a portion of a multiple perforation plate except scalariform in the latewood vessel. Long multiple perforation plates except scalariform with many small slit-like openings as shown in Photo 59 were always present in the latewood vessels. Some openings (arrows) with the microfibrillar webs are present in the plate shown in Photo 59. The morphological variation in *Lyonia ovalifolia* (WALL.) DRUDE var. *elliptica* (SIEB. et ZUCC.) HAND.-MAZZ. was more or less similar to that in *Enkianthus cernuus* (SIEB. et ZUCC.) MAKINO forma *rubens* (MAXIM.) OHWI.

4-2. Species with both types of the plates occurring irregularly within an annual ring

Most perforation plates were long scalariform perforation plates with many bars in *Illicium religiosum* SIEB. et ZUCC. However, the plates as shown in Photo 60 were also observed. In Photo 60, the openings of scalariform and reticulate arrangement are found within the plate. Photo 61 shows a portion of the reticulate arrangement of the openings of the plate in Photo 60. The microfibrillar webs are present in the openings in the lateral margin of the plate.

In *Daphniphyllum macropodum* MIQ. and *Daphniphyllum teijsmannii* ZOLL., most perforation plates were typical scalariform (Photo 62). However, the multiple perforation plates except scalariform as shown in Photo 63 were also found. Photo 64 shows a plate with intermediate structure between the typical scalariform (Photo 62) and the multiple perforation plate except scalariform (Photo 63). Photo 65 shows a plate in *Daphniphyllum teijsmannii* ZOLL. Mismatching branched bars are found in the upper left in this plate.

Although typical scalariform perforation plates were generally found in *Symplocos lancifolia* SIEB. et ZUCC. (Photo 66), the multiple perforation plates except scalariform as shown in Photos 67 and 68 were also found. In Photo 67, various openings in size and form are present in the plate. In the plate shown in Photo 68, many round openings are arranged as alternate pitting and the microfibrillar webs are found in some smaller openings.

5. Species with both simple and multiple perforation plates except scalariform

5 species belong to this group. The species names are listed in Table 5. The perforation plates of both types were irregularly present within an annual ring in these species.

Table 5. Species with both simple and multiple perforation plates except scalariform

Family	Botanical name	Japanese name
Proteaceae	*Helicia cochinchinensis* LOUR.	Yamamogashi
Rosaceae	*Pourthiaea villosa* (THUNB.) DECNE. var. *laevis* (THUNB.) STAPF	Kamatsuka
	Sorbus commixta HEDL.	Nanakamado
	Sorbus alnifolia (SIEB. et ZUCC.) C. KOCH	Azukinashi
	Sorbus japonica (DECNE.) HEDL.	Urajironoki

Photos 69–73 show the morphological variation of the plates in *Helicia cochinchinensis* LOUR. Although most perforation plates were simple (Photos 69, 70 and 71), the multiple perforation plates except scalariform were found in some of the smaller vessels (Photos 70, 72 and 73). The perforation plates of two types, simple and multiple, were irregularly present within an annual ring as shown in Photo 70. The half perforation plate on this side of the vessel at the left in Photo 70 is simple, while the half perforation plate on the other side is multiple. Photo

71 shows a simple perforation showing an intermediate structure between typical simple (Photo 69) and multiple perforation plates except scalariform (Photos 72 and 73). The openings of two multiple half perforation plates, composing a multiple perforation except scalariform, between adjacent vessel members were always not coincident (Photos 72 and 73).

Photos 74–83 show the morphological variation of the plates in *Pourthiaea villosa* (THUNB.) DECNE var. *laevis* (THUNB.) STAPF. Most perforation plates in this species were simple. As shown in Photos 74 and 75, the simple perforation plates had always the prominent bordered rims. In Photo 76, the simple half perforation plate on this side has a smooth rim, while several projections of wall material with pointed end occur from the rim to the opening in the half plate on the other side. In such plates with these projections of wall material, the projections varied from one to several in number and the corresponding half plates were always normal simple perforations with smooth bordered rims. In Photo 77, a scalloped partition (single arrows), probably the primary wall, remains between the bordered rim in the region where the projections do not occur and is continuous to the outer surface of the projections (double arrows). In most cases, therefore, the projections consist of the primary and the secondary wall of the vessel member (Photos 76 and 77). However, it was rarely found that the projections consisted of the primary wall and a part of the secondary wall of the vessel member (Photo 78). Photos 79–83 show various forms of the multiple perforation plates except scalariform. In Photos 79, 80, 82 and 83, the half plates on this side are simple perforation plates with smooth rims, while those on the other side are multiple perforation plates with complicated irregular openings. It can be seen in Photo 81 that the inner surface of the wall material forming the outline of the irregular openings has a smooth continuity with that of the secondary wall of the vessel member. The half perforation plate on this side in Photo 83 is a simple perforation with smooth rim, while the half plate on the other side consists of many round openings. It should be noticed that the isolated wall material not connected to the rim is present in the half plates on this side in Photos 80, 82 and 83 (arrows in these photos). As shown in these photos, all the multiple perforation plates except scalariform observed always consisted of the simple and multiple half perforation plates. It was not confirmed that both of the two half perforation plates between adjacent vessel members were the multiple type.

Sorbus commixta HELD., *Sorbus alnifolia* (SIEB. et ZUCC.) C. KOCH and *Sorbus japonica* (DECNE.) HEDL. showed similar morphological variation of the plates. Photos 84–93 show the morphological variation of the plates in *Sorbus alnifolia* (SIEB. et ZUCC.) C. KOCH. All the perforation plates in larger vessels were simple perforations with non-bordered (Photo 84) and bordered rims (Photo 85). In Photo 86, projections of wall material with pointed end occur from the rim to the opening. Wall material extending from the rim in the half plate of the vessel member on the bottom in Photo 87 is complicated in form and consists of the primary wall and the secondary wall of the vessel member. Various forms of the multiple perforation plate except scalariform observed are shown in Photos 88–93. The inner surface of the wall material forming the outline of the complicated openings in these photos has a smooth continuity with that of the secondary wall of the vessel members. Fibrils (arrowed) in the openings in Photos 88, 89 and 90 appear to be the remnant of the partition. The multiple perforation plates as shown in Photos 91, 92 and 93 were observed in smaller vessels. The multiple perforation plates with many small openings are shown in Photos 92 and 93. One projection of wall material with pointed end extends from the rim in the half plate on this side in Photo 92, while many small openings are crowded in the half plate on the other side. It was not confirmed in the multiple perforation plates in *Sorbus alnifolia* (SIEB. et ZUCC.) C. KOCH that openings of two half plates between adjacent vessel members were exactly coincident.

6. Species with simple, scalariform and multiple perforation plates except scalariform

3 species belong to this group. The species names are listed in Table 6. *Fagus crenata* BLUME and *Fagus japonica* MAXIM. showed quite similar morphological variation of the plates. SEM observations on the morphological variation of the plates in *Fagus crenata* BLUME have been reported elsewhere (OHTANI and ISHIDA, 1973). Therefore, observations on the plates of the two species are not described here.

Table 6. Species with simple, scalariform and multiple perforation plates except scalariform

Family	Botanical name	Japanese name
Fagaceae	*Fagus crenata* BLUME	Buna
	Fagus japonica MAXIM.	Inubuna
Ericaceae	*Vaccinium bracteatum* THUNB.	Shashanbo

Photos 94–99 show the morphological variation of the plates in *Vaccinium bracteatum* THUNB. Simple (Photo 94) and scalariform perforation plates (Photo 95) were present in the earlywood vessels. Photos 96 and 97 show the scalariform perforation plates in the latewood vessels. Bars of the scalariform perforation plates were thicker and openings between bars of them were narrower in the latewood vessels than in the earlywood vessels (compared with Photo 95 and Photos 96 and 97). Photos 98 and 99 show the multiple perforation plates except scalariform in the terminal zone of the annual ring. The main axes of the slit-like openings in the multiple perforation plates except scalariform were oriented at right angles to the vessel axis.

Discussion and Conclusion

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

218 species belonging to 120 genera, 51 families were divided into 6 groups on the basis of the occurrence of various forms of the perforation plates in each species. Families that had species in more than one group were the following 10 families: Betulaceae, Fagaceae, Magnoliaceae, Rosaceae, Euphorbiaceae, Sabiaceae, Theaceae, Ericaceae, Symplocaceae and Caprifoliaceae. In the 7 families except Betulaceae, Sabiaceae and Symplocaceae, each of the genera of them had exclusively species belonging to the same group. Genera that had species in two groups were only the following 3 genera: *Carpinus* (Betulaceae), *Meliosma* (Sabiaceae) and *Symplocos* (Symplocaceae). This fact suggests that remarkable differences of morphological variation of the perforation plates are not found between species belonging to each of the genera except *Carpinus*, *Meliosma* and *Symplocos*. Prospects and limitations of the perforation plates as a diagnostic criterion for the classification and identification of dicotyledonous woods must be determined on the basis of the detailed and extensive observations of the perforation plates within species, genera, and families. In this connection, for more accurate classification of dicotyledonous woods by means of their anatomical features, accumulation of information on the anatomical features at the SEM level is necessary. Although the present SEM observations cannot produce sufficient evidence to determine taxonomic significance of the perforation plates, these observations suggest that the perforation plates can be utilized as a diagnostic criterion for the classification and identification, and also provide fundamental information on the perforation plates for the preparation of the key table at the SEM level.

Observations on occurrence of the perforation plates in a number of species obtained by the present SEM observation were different from the observations that have been reported by several investigators, on the basis of light microscope observation (KANEHIRA, 1926; YAMABAYASHI, 1938; SUDÔ, 1959). These disagreements were limited to the species with more than one perforation plate type determined by the present SEM observation.

Both simple and scalariform perforation plates were found in *Myrica rubra* SIEB. et ZUCC., *Magnolia obovata* THUNBERG (Photos 40–46), *Magnolia salicifolia* (SIEB. et ZUCC.) MAXIM., *Cinnamomum camphora* (LINN.) SIEBOLD and *Idesia polycarpa* MAXIM. in the present observation, though in *Myrica rubra* SIEB. et ZUCC. the simple perforation plates were few in their occurrence compared with the scalariform, and in the other species the latter is few compared with the former. According to KANEHIRA (1926), YAMABAYASHI (1938) and SUDÔ (1959), however, *Myrica rubra* SIEB. et ZUCC. and the other species have been described as possessing exclusively scalariform or multiple and exclusively simple perforation plates, respectively. Although both simple and scalariform perforation plates were found in *Pieris japonica* (THUNB.) D. DON (Photos 28–36) in the present observation, it has been reported by SUDÔ (1959) that this species has exclusively multiple perforation plates. Both simple and multiple perforation plates except scalariform were found in *Sorbus commixta* HEDL., *Sorbus alnifolia* (SIEB. et ZUCC.) C. KOCH (Photos 84-93) and *Sorbus japonica* (DECNE.) HEDL. in the present observation, while according to KANEHIRA (1926), YAMABAYASHI (1938) and SUDÔ (1959), these species have been described as possessing exclusively simple perforation plates. Simple, scalariform, and multiple perforation plates except scalariform were found in *Vaccinium bracteatum* THUNB. (Photos 94-99) in the present observation. According to the past works, however, this species has been recorded as possessing exclusively simple (YAMABAYASHI, 1938) or exclusively multiple perforation plates (SUDÔ, 1959).

It has been reported in some species that the morphology of the perforation plates varies associated with the position of the vessels within a tree even in the same species (THOMPSON, 1923; BAILEY, 1941; TABATA, 1964). TABATA (1964) has described that the morphology of the scalariform perforation plates of *Betula platyphylla* var. *japonica* varied in the number of bars due to the habitat on the basis of comparison of samples of this species collected from marshy sports with those from drained habitats. Therefore, it seems possible that the disagreement of the occurrence of the perforation plates in each species described above may mainly depend on the difference of the position within a tree or the growth condition of the tree from which the samples were obtained.

Additional reasons for the disagreement of the observations in *Sorbus commixta* HEDL., *Sorbus alnifolia* (SIEB. et ZUCC.) C. KOCH and *Sorbus japonica* (DECNE.) HEDL. are considered as follows. Firstly, simple perforation plates were present in most vessels. The multiple perforation plates except scalariform as shown in Photos 87-93 were few in their occurrence compared with the simple perforation plates. Secondary, the multiple perforation plates except scalariform as shown in Photos 92 and 93 may be difficult to be determined as the perforation plate by means of the light microscopy. It was confirmed in the present SEM observation that several pits which were quite similar in size and form to the openings shown in Photos 92 and 93 were crowded in a similar fashion to the openings in the multiple perforation plates except scalariform. Therefore, it is very difficult to strictly determine by light microscopy whether the region consists of the pits or the openings. Thirdly, some of the multiple perforation plates except scalariform described above as shown in Photos 87-90 had a delicate structure which is easily damaged during the specimen preparation and so were very difficult to be kept intact structures. Therefore, observation by means of the sections using light microscopy may lead to the misunderstanding that such plates were simple.

Occurrence of the microfibrillar webs in the openings near the ends of the scalariform perforation plates was found in the most examined species with the scalariform. In many cases, as the number of strands in the microfibrillar webs increases, reticulate webs of the scalariform openings in ends grade into typical intervascular pit membranes composed of randomly oriented microfibrils. Therefore, perforations and pits in the region can't be strictly distinguished. On the other hand, occurrence of the microfibrillar webs in the lateral margin of openings in the scalariform perforation plates was found in some scalariform perforation plates of many species. However, occurrence of them was not found in the species in which the scalariform perforation plates consisted of several thin bars and large openings between them in their width. On the other hand, the microfibrillar webs were often found in long scalariform perforation plates with many thick bars and narrow openings. In the plates with the microfibrillar webs, bars in the lateral margin were bordered even when those near the central region were non-bordered. On the other hand, the complete microfibrillar webs were found in some scalariform perforation plates in the limited species examined. Occurrence of them was restricted to the long scalariform perforation plates with many prominent bordered bars and narrow openings. This fact has already been pointed out in *Cercidiphyllum japonicum* SIEB. et ZUCC. and *Cornus controversa* HEMSL. by the present authors (ISHIDA and OHTANI, 1974). The microfibrillar webs, which well corresponded to those in the openings near the ends and the lateral margin of the scalariform perforation plates, were also found in some multiple perforation plates except scalariform. The openings in which they are present were surrounded by the prominent border. Therefore, the structure of both the perforations with the complete microfibrillar webs and the ones with the microfibrillar webs in the ends and the lateral margin of the plates is similar, especially in the positional relationship between the partition and the overarching border, to that of the intervascular bordered pits. The matrix substance of both the compound middle lamellae in the areas to become the perforations and the intervascular bordered pit membranes is removed by the enzymatic action as soon as the deposition of the secondary wall of the vessel members is almost complete (BONNER and THOMAS, 1972; THOMAS and BONNER, 1974). The microfibril component in the former is almost simultaneously removed by enzymatic action, probably cellulase (THOMAS and BONNER, 1974), while that in the latter is not removed. In this connection, THOMAS and BONNER (1974) have described that retention of pit membrane microfibrils may be the result of a secondary deposition of microfibrils with a molecular weight or crystallinity different from that of the primary wall microfibrils. Although it is not clear why the microfibrillar webs observed in the present SEM observation are not removed by the enzymatic action, it seems possible that the lignified overarching border might provide protection against enzymatic attack to remove the microfibril component. No way has yet been devised to clarify this possibility.

Mismatching perforation plates, in which the openings of the half perforation plates of the same type between adjacent vessel members do not coincide, were found in simple, scalariform, and multiple perforation plates except scalariform. They were occasionally found in some of the species with exclusively scalariform, exclusively simple, both simple and scalariform, and both scalariform and multiple perforation plates except scalariform. However, they were frequently found in the perforation plates except normal simple perforation plates with smooth rims of the species with simple and multiple perforation plates except scalariform. They were also frequently found in the multiple perforation plates except scalariform in

Fagus crenata BLUME and *Fagus japonica* MAXIM. which have simple, scalariform, and multiple perforation plates except scalariform.

BUTTFRFIELD and MEYLAN (1975) and MEYLAN and BUTTERFIELD (1975) 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 angiosperms families. They have suggested that it is possible that combination plates occur in most woods having more than one perforation plate type. In the present SEM observation, however, combination perforation plates were not found in the species having both simple and scalariform perforation plates, and both scalariform and multiple perforation plates except scalariform. In species with simple, scalariform, and multiple perforation plates except scalariform, combination perforation plates were occasionally found in *Fagus crenata* BLUME and *Fagus japonica* MAXIM. while they were not found in *Vaccinium bracteatum* THUNB. On the other hand, in all the species having simple and multiple perforation plates except scalariform, all the perforation plates except normal simple perforation plates with smooth rims were always mismatching or combination perforation plates. In other words, only the openings of the two normal simple half perforation plates with smooth rims between two adjacent vessel members in these species coincide exactly in form. Therefore, it is possible that such mismatching and combination perforation plates are one of the characteristic properties of the vessels in these species. In the species having more than one perforation plate type, why mismatching or combination perforation plates are frequently present in some species, but not in other is not clear. In this connection, MEYLAN and BUTTERFIELD (1973, 1975) have described that such mismatching or combination perforation plates presumably result from a lack of co-ordination in the deposition of the secondary wall of the end walls by the adjacent vessel members.

In the species with more than one perforation plate type, the perforation plates with intermediate structure which links the two different (typical) types of the plates into closer relations with each other were always found. In other words, the morphological sequence of the perforation plates between different types of the plates was always found in the same species. The morphological sequence of the different types of the perforation plates within the same species found in the present SEM observation is as follows. For convenience, the terms applied for the multiple perforation plates here follow those for the multiple perforation plates proposed by GRAY and DE ZEEUW (1974).

(1) Simple—Scalariform (Photos 28-36, Photos 40-46, Photos 47-52).
(2) Scalariform—Branched scalariform—Irregular reticulate (Photos 61 and 62, Photos 62-64).
(3) Scalariform—Branched scalariform—Irregular reticulate—Reticulate (or Foraminate) (Photos 57-59, Photos 66-68).
(4) Simple—Irregular reticulate (Photos 69-73).
(5) Simple—Irregular reticulate—Reticulate (or Foraminate) (Photos 84-93).
(6) Simple—Irregular reticulate—Foraminate (Photos 74-83).

(7) Simple—Scalariform—Branched scalariform—Irregular reticulate (Photos 94-99).

(8) Simple—Scalariform—Branched scalariform—Irregular reticulate—Reticulate (or Foraminate).

It is very interesting that the sequence of morphological changes of the perforation plates in each of (1)-(8) was found even in the limited area, especially in the outer secondary xylem, within the same species.

Some of the morphological sequences of the plates in (1)-(8) described above have already been found under the light microscope by a number of investigators. The sequence of the morphological changes between simple and scalariform perforation plates within the same species has been found in some species (THOMPSON, 1923; FROST, 1930; BAILEY and HOWARD, 1941). A sequence of the morphological changes which corresponds well to that of (2), (3) and (4), has been found in several species by THOMPSON (1923) and CHALK (1933). The sequence of the morphological changes of the plates in (8) has already been reported in *Fagus crenata* BLUME by OHTANI and ISHIDA (1973). Recently, a sequence of morphological changes which corresponds well to that of (8) has also been found in *Melieytus ramiflorus* (Violaceae) by MEYLAN and BUTTERFIELD (1974).

It has generally been supported that the simple perforation plate evolved from the scalariform perforation plate by the loss of dividing bars (FROST, 1930 a, 1930 b; BAILEY, 1944; CHEADLE, 1953). The sequence of the morphological changes from scalariform to simple perforation plates in the phylogenetic development corresponds well to that of (1) shown in the present SEM observation.

In recent years, PARAMESWARAN and LIESE (1973) have proposed a new line of phylogenetic derivation of multiple perforation plates (excluding scalariform) leading to simple perforation plates. The sequence of the morphological changes between simple and multiple perforation plates except scalariform of (4), (5) and (6) shown in the present SEM observation may support the possibility of the new evolutionary line suggested by PARAMESWARAN and LIESE (1973). Although the relationship between the morphological sequences of the different types of the perforation plates in each of (2)-(8) described above and evolutionary lines must be determined by other evidence, interesting results on the morphological sequence between various forms of the perforation plates within the same species revealed in the present SEM observation provide fundamental information for the discussion of evolutionary development of the vessel members.

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要　　約

本邦産双子葉木本植物 (51科, 120属, 218種) の二次木部のせん孔板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. 本研究で観察されたせん孔板の形態は, 極めて変化にとんでいた。せん孔板についての既往の研究報告によれば, 多孔せん孔板のうち階段せん孔板以外のものに適用されている用語は, 研究者によりまちまちであり混乱している。これらの用語の混乱をさけることも考慮して, 本研究で観察されたせん孔板は, 便宜上, 用語の内容がはっきりしている単せん孔と階段せん孔板, および事実上多様なものを含んでいる階段せん孔板以外の多孔せん孔板の3つのタイプに区別した。

2. 供試樹種のせん孔板の形態をもとにして, 供試樹種は次に示す6グループにわけられた。

1. 階段せん孔板のみを有する樹種 (Photo 1–14)。
2. 単せん孔のみを有する樹種 (Photo 15–27)。
3. 単せん孔と階段せん孔板を有する樹種 (Photo 28–52)。
4. 階段せん孔板とそれ以外の多孔せん孔板を有する樹種 (Photo 53–68)。
5. 単せん孔と階段せん孔板以外の多孔せん孔板を有する樹種 (Photo 69–93)。
6. 単せん孔・階段せん孔板および階段せん孔板以外の多孔せん孔板を有する樹種 (Photo 94–99)。

それぞれのグループに属する樹種名は Table 1–6 に記入されている。

3. 階段せん孔板のみを有する樹種は46樹種であった。これらの樹種について観察された階段せん孔板の形態 (せん孔板の道管軸に対する傾き, バーの数・太さ, せん孔の形・大きさなど) は, さまざまであったが, ほとんど大部分のせん孔板は, IAWA の定義どおりの構造を有しており, 上下に隣接する2つの道管要素のそれぞれのバーの間隔, 形, 大きさなどは等しく, それらは整然とした対をなしていた (Photo 1–3)。

階段せん孔板にみられる個々の横に長いせん孔の両端部付近に存在する Microfibrillar webs (ミクロフィブリルよりなる微細な網状構造) は36樹種のそれぞれのいくつかのせん孔板に認められた。それらのせん孔の両端部付近ではバーは必ず有縁であった (Photo 4)。一せん孔板のすべてのせん孔のほとんど全面に Microfibrillar webs が存在するせん孔板は, 15樹種においていくつかずつ観察された。この種のせん孔板では, バーの数が多く, バーはすべて有縁であり, バー間の開孔部すなわちせん孔の幅は狭い (Photo 5–8)。

上述した Photo 1–3 のような普通のせん孔板と形態が著しく異なるせん孔板がまれに認

められた。それらの例を Photo 9–14 に示す。

4. 単せん孔のみを有する樹種は133樹種であった。観察された単せん孔の形態（せん孔およびせん孔縁の形）はかなり変化にとむが，上下に隣接する2つの道管要素のそれぞれのせん孔（開孔部），せん孔縁の大きさ・形などは等しく，それらは整然とした対をなしているのが普通であった。せん孔縁には，有縁のものと有縁でないものがあり，さらにそれらは断面形によって Fig. 1 に示されるような4つのタイプに分けられた（Photo 15–23）。133樹種中14樹種にタイプ1のせん孔縁を有する単せん孔が認められた。大部分の樹種は，タイプ2・3・4のせん孔縁を有する単せん孔をもっていた。上述した Photo 15–23 のような普通の単せん孔とは異なる形態を有する単せん孔が Photo 24–26 に示されている。

1つの道管要素の一端に2個の単せん孔が存在し，それぞれの単せん孔が別個の2つの道管の要素細胞の単せん孔と対をなして連結している例がヤマザクラ，シウリザクラに極めてまれに認められた（Photo 27）。これは1つの道管が2つに分岐していることを意味している。

5. 単せん孔と階段せん孔板の両者を有する樹種は21樹種であった。このうち，単せん孔が早材部に，階段せん孔が晩材部に存在する樹種は2樹種（アセビ・ヤマモモ）のみであった。アセビのせん孔板の形態変動は Photo 28–36 に示されている。

単せん孔と階段せん孔板が年輪内で不規則に出現する樹種は19樹種であった。アカシデ・イヌシデ・クマシデ・イイギリ・エゾニワトコの5樹種のせん孔板の形態変動は，ほぼ同じ傾向を示した（Photo 37–39）。これらの樹種とは異なるが，ホオノキ・キタコブシ・タムシバのせん孔板は同じ形態変動の傾向を示した。ホオノキのせん孔板の形態変動は，Photo 40–46 に示されている。クスノキ科に属する10樹種およびアワブキのせん孔板の形態変動は，ほぼ同じ傾向を示した。ヤブニッケイのせん孔板の形態変動は Photo 47–52 に示されている。

6. 階段せん孔板とそれ以外の多孔せん孔板を有する樹種は9樹種であった。両タイプのせん孔板が年輪内で規則的に出現する樹種は5樹種であった。ヤブツバキ・ツバキのせん孔板の形態変動は同じ傾向を示した。すなわち，早材部には階段せん孔板のみが存在し，晩材部には階段せん孔板とそれ以外の多孔せん孔板が存在した（Photo 53–55）。ヒサカキでは，大部分の道管は階段せん孔板を有していたが，年輪のターミナル部に階段せん孔板以外の多孔せん孔板が存在した（Photo 56）。ベニドウダンおよびネジキでは，早材部に階段せん孔板とそれ以外の多孔せん孔板が存在し，晩材部に階段せん孔板以外の多孔せん孔板が存在した（Photo 57–59）。

両タイプのせん孔板が年輪内で全く不規則に出現する樹種は4樹種であった。シキミのせん孔板は，大部分が階段せん孔板であったが，Photo 60・61 に示されているような多孔せん孔板も認められた。ユズリハ・ヒメユズリハでは，大部分のせん孔板は階段せん孔板であったが，階段せん孔板以外の多孔せん孔板も認められた（Photo 62–64）。シロバイでは，大部分のせん孔板は階段せん孔板であったが，階段せん孔板以外の多孔せん孔板も認められた（Photo 66–68）。

7. 単せん孔と階段せん孔板以外の多孔せん孔板を有する樹種は5樹種であった。これら

の樹種では両タイプのせん孔板が年輪内で不規則に出現した。ヤマモガシでは大部分のせん孔板は単せん孔であったが，階段せん孔板以外の多孔せん孔板も認められた。ヤマモガシのせん孔板の形態変動は Photo 69-73 に示されている。カマツカでは大部分のせん孔板は単せん孔であったが，いろいろな形態をした階段せん孔板以外の多孔せん孔板も認められた。カマツカのせん孔板の形態変動は Photo 74-83 に示されている。ナナカマド・アズキナシ・ウラジロノキのせん孔板の形態変動は同じ傾向を示した。すなわち，大部分のせん孔板は単せん孔であったが，比較的直径の小さな道管には階段せん孔板以外の多孔せん孔板が認められた。アズキナシのせん孔板の複雑な形態変動は Photo 84-93 に示されている。

8. 単せん孔・階段せん孔板および階段せん孔板以外の多孔せん孔板を有する樹種は3樹種であった。ブナ・イヌブナでは，早材部では単せん孔が存在し，年輪のほぼ中央部では階段せん孔板が，また晩材部では階段せん孔板以外の多孔せん孔板が存在した。シャシャンボでは，単せん孔と階段せん孔板が早材部に存在し，階段せん孔板とそれ以外の多孔せん孔板が早材以外の部分に存在した。シャシャンボのせん孔板の形態変動は Photo 94-99 に示されている。

9. いくつかの樹種（ヤマモモ・ホオノキ・タムシバ・クスノキ・イイギリ・アセビ・ナナカマド・アズキナシ・ウラジロノキ・シャシャンボ）のせん孔板の形態についての本研究の観察結果は，光学顕微鏡観察による既往の記載と一致しなかった。その理由は，供試木の生育条件のちがいや一樹幹内での観察部位のちがいなどが考えられるが，樹種により光学顕微鏡観察では見落されがちな多孔せん孔板が存在することなども考えられる。すなわち，ナナカマド・アズキナシ・ウラジロノキでは光学顕微鏡観察では必ずしも明確に判断しにくいと考えられる階段せん孔板以外の多孔せん孔板が存在することや，ホオノキ・タムシバ・クスノキ・イイギリでは単せん孔にくらべ階段せん孔板の出現頻度が非常に少ないことなどが考えられる。

10. 単せん孔と階段せん孔板以外の多孔せん孔板を有する樹種（ヤマモガシ・カマツカ・ナナカマド・アズキナシ・ウラジロノキ）では，平滑なせん孔縁を有する単せん孔を除くすべてのせん孔板は，Mismatching perforation plate か Combination perforation plate であった。単せん孔・階段せん孔板および階段せん孔板以外の多孔せん孔板を有するブナ・イヌブナでは，階段せん孔板やそれ以外の多孔せん孔板にしばしば Mismatching perforation plate や Combination perforation plate が認められた。しかし，上記樹種以外の樹種には，Mismatching perforation plate や Combination perforation plate は，まれにしか認められなかった。したがって，Mismatching perforation plate や Combination perforation plate は，上記樹種の道管の特徴的な構造の一つと考えられる。

11. いくつかの異ったタイプのせん孔板を有する樹種では，一樹種内で異ったタイプのせん孔板を関連づける中間的な形態を示すせん孔板が必らず認められた。すなわち，これらの樹種のせん孔板の形態変動にはある連続性が認められた。本研究で示されたこれらの形態変動の連続性は，道管の進化の過程を考える上での一つ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 photographs (↕). The term "multiple perforation plate" used here is defined as the multiple perforation plate (IAWA) except scalariform.

Photo 1. *Symplocos coreana* (LÉVEILLÉ) OHWI Portion of a long scalariform perforation plate many bars closely spaced.

Photo 2. *Ilex pedunculosa* MIQ. A scalariform perforation plate showing intermediate form between those scalariform perforation plates shown in photos 1 and 3.

Photo 3. *Michelia compressa* (MAXIM.) SARG. A short scalariform perforation plate with only two bars.

Photo 4. *Cornus kousa* BUERGER, ex HANCE Portion of a scalariform perforation plate with microfibrillar webs in the lateral margin of scalariform openings.

Photo 5. *Viburnum awabuki* K. KOCH Portion of a scalariform perforation plate with complete microfibrillar webs. Fibrillar strands are oriented more or less orthogonally between bars in the all region of each scalariform opening.

Photo 6. *Cercidiphyllum japonicum* SIEB. et ZUCC. Portion of a scalariform perforation plate with complete microfibrillar webs. Microfibrillar webs in this photo are denser than those in photo 5.

Photo 7. *Viburnum awabuki* K. KOCH Portion of a scalariform perforation plate with complete microfibrillar webs. Most secondary walls of the bars on this side are removed.

Photo 8. *Cornus controversa* HEMSLEY Portion of a scalariform perforation plate with complete microfibrillar webs. Most secondary walls of the bars on this side are removed. Fibrillar strands are more densely present in the lateral margin than in the central region of the scalariform openings and they are arranged at random.

Photo 9. *Stewartia monadelpa* SIEB. et ZUCC. Portion of a scalariform perforation plate with branched bars.

Photo 10. *Stewartia monadelpa* SIEB. et ZUCC. Portion of a scalariform perforation plate with inclined bars.

Photo 11. *Viburnum awabuki* K. KOCH Portion of a scalariform perforation plate with mismatching bars.

Photo 12. *Ternstroemia gymnanthera* (WIGHT et ARN.) SPRAGUE A scalariform perforation plate with mismatching bars. Mismatching bars of the adjacent vessel members are found as cross bars at the right in this photo.

Photo 13. *Cornus kousa* BUERGER, ex HANCE Portion of an unusual scalariform perforation plate with the wall material forming no bars in its central region.

Photo 14. *Cornus kousa* BUERGER, ex HANCE Portion of an unusual scalariform perforation plate with the wall material forming no bars in its central region. Microfibrillar webs are oriented orthogonally between bars.

Photo 15. *Populus sieboldii* MIQUEL Portion of a simple perforation with the prominent bordered rim.

Photo 16. *Zanthoxylum ailanthoides* SIEB. et ZUCC. Portion of a simple perforation with the prominent bordered rim exposed by a radial cut.

Photo 17. *Mallotus japonicus* (THUNB.) MUELL. ARG. Portion of a simple perforation with the bordered rim.

Photo 18. *Aesculus turbinata* BLUME Portion of a simple perforation with the bordered rim exposed by a radial cut.

Photo 19. *Populus maximowiczii* HENRY Portion of a simple perforation with the non-bordered rim.

Photo 20. *Prunus jamasakura* SIEB., ex KOIDZ. Portion of a simple perforation with the non-bordered rim by a radial cut.

Photo 21. *Zolkova serrata* (THUNB.) MAKINO Portion of simple perforations (arrows) with the non-bordered rims in the earlywood vessel.

Photo 22. *Sapindus mukorossi* GAERTN. Portion of a simple perforation with the non-bordered rim.

Photo 23. *Clerodendrum trichotomum* THUNB. Portion of a simple perforation with the non-bordered rim exposed by a radial cut.

Photo 24. *Zanthoxylum ailanthoides* SIEB. et ZUCC. A simple perforation with the corresponding half rims forming no regular pair.

Photo 25. *Ostrya japonica* SARG. Portion of a simple perforation with irregular rim.

Photo 26. *Caragana chamlagu* LAM. Portion of a simple perforation with many small projections on the rim.

Photo 27. *Prunus jamasakura* SIEB., ex KOIDZ. An unusual interconnection between the adjacent vessel members. An end of the lower vessel member of this photo is connected to the members of the two different vessels at the upper through two simple perforations.

Photo 28. *Pieris japonica* (THUNB.) D. DON Portion of a simple perforation with smooth top surface of rim.

Photo 29. *Pieris japonica* (THUNB.) D. DON Portion of a simple perforation with irregular rim.

Photo 30. *Pieris japonica* (THUNB.) D. DON Portion of a simple perforation with irregular rim. Irregularity of the rim in this photo is more remarkable than that in photo 29.

Photo 31. *Pieris japonica* (THUNB.) D. DON A perforation plate with one bar.

Photo 32. *Pieris japonica* (THUNB.) D. DON A scalariform perforation plate with two complete bars.

Photo 33. *Pieris japonica* (THUNB.) D. DON Portion of a scalariform perforation plate with few bars.

Photo 34. *Pieris japonica* (THUNB.) D. DON Portion of a scalariform perforation plate showing bars and projections of wall material extending from the lateral margin.

Photo 35. *Pieris japonica* (THUNB.) D. DON Portion of a typical scalariform perforation plate in the latewood vessel.

Photo 36. *Pieris japonica* (THUNB.) D. DON Portion of a scalariform perforation plate in the vessel in the terminal zone of the annual ring. Remnants of the partition are found in the scalariform openings between bars.

Photo 37. *Carpinus tschonoskii* MAXIM. Portion of a simple perforation with smooth rim.

Photo 38. *Carpinus tschonoskii* MAXIM. A simple perforation with irregular rim.

Photo 39. *Carpinus tschonoskii* MAXIM. Portion of a scalariform perforation plate.

Photo 40. *Magnolia obovata* THUNBERG Radial surface showing two vessels having simple perforations with smooth rims.

Photo 41. *Magnolia obovata* THUNBERG Radial surface showing two vessels having simple perforations with irregular rims.

Photo 42. *Magnolia obovata* THUNBERG Radial surface showing three vessels with simple perforations. The simple perforation of the vessel in the middle in this photo is long oval in form along the vessel axis direction.

Photo 43. *Magnolia obovata* THUNBERG Portion of a typical scalariform perforation plate.

Photo 44. *Magnolia obovata* THUNBERG A perforation plate showing intermediate form between simple and scalariform.

Photo 45. *Magnolia obovata* THUNBERG Portion of a long perforation plate showing intermediate form between simple and scalariform.

Photo 46. *Magnolia obovata* THUNBERG Portion of a long scalariform perforation plate with several incomplete bars.

Photo 47. *Cinnamomum japonicum* SIEBOLD, ex NAKAI A simple perforation with smooth bordered rim.

Photo 48. *Cinnamomum japonicum* SIEBOLD, ex NAKAI Radial surface showing two vessels with scalariform perforation plates.

Photo 49. *Cinnamomum japonicum* SIEBOLD, ex NAKAI Portion of a perforation plate with one inclined bar.

Photo 50. *Cinnamomum japonicum* SIEBOLD, ex NAKAI A scalariform perforation plate with several inclined bars.

Photo 51. *Cinnamomum japonicum* SIEBOLD, ex NAKAI A perforation plate with small irregular openings (arrows) near the margin.

Photo 52. *Cinnamomum japonicum* SIEBOLD, ex NAKAI Radial surface showing three vessels with different perforation plates in form, respectively. A vessel member at the right in this photo has a simple and a scalariform half perforation plate at the ends. Each of the half plates is connected to the half plates of the adjacent vessel members forming a regular pair.

Photo 53. *Camellia japonica* LINN. Radial surface showing the morphological variation of the perforation plates. Arrow shows the boundary of annual rings.

Photo 54. *Camellia japonica* LINN. Portion of a scalariform perforation plate with thin bars in the earlywood vessel.

Photo 55. *Camellia japonica* LINN. Portion of a multiple perforation plate in the latewood vessel.

Photo 56. *Eurya japonica* THUNB. Portion of a long multiple perforation plate in the terminal zone of the annual ring.

Photo 57. *Enkianthus cernuus* (SIEB. et ZUCC.) MAKINO forma *rubens* (MAXIM.) OHWI Portion of a long scalariform perforation plate with many bars in the earlywood vessel.

Photo 58. *Enkianthus cernuus* (SIEB. et ZUCC.) MAKINO forma *rubens* (MAXIM.) OHWI Portion of a multiple perforation plate with various openings in size and form in the earlywood vessel. Microfibrillar webs are found in the openings in the lateral margin (at the left) and at the end of the plate.

Photo 59. *Enkianthus cernuus* (SIEB. et ZUCC.) MAKINO forma *rubens* (MAXIM.) OHWI Portion of a long multiple perforation plate with many small slit-like openings in the latewood vessel. Arrows show the openings with microfibrillar webs.

Photo 60. *Illicium religiosum* SIEB. et ZUCC. Portion of a long multiple perforation plate. The openings of reticulate and scalariform arrangement are found within the perforation plate.

Photo 61. *Illicium religiosum* SIEB. et ZUCC. A higher magnification view of the area outlined in photo 60. Microfibrillar webs are found in the openings in the lateral margin of the plate.

Photo 62. *Daphniphyllum macropodum* MIQ. Portion of a scalariform perforation plate.

Photo 63. *Daphniphyllum macropodum* MIQ. A multiple perforation plate with various openings in size and form.

Photo 64. *Daphniphyllum macropodum* MIQ. A perforation plate showing intermediate form between typical scalariform (photo 62) and multiple perforation plate (photo 63).

Photo 65. *Daphniphyllum teijsmannii* ZOLL. A perforation plate with mismatching branched bars in the upper left in this photo.

Pohto 66. *Symplocos lancifolia* SIEB. et ZUCC. Portion of a scalariform perforation plate.

Photo 67. *Symplocos lancifolia* SIEB. et ZUCC. Portion of a multiple perforation plate with various openings in size and form.

Photo 68. *Symplocos lancifolia* SIEB. et ZUCC. Portion of a multiple perforation plate with many round openings. Microfibrillar webs are found in some of the smaller openings.

Photo 69. *Helicia cochinchinensis* LOUR. A simple perforation with smooth rim.

Photo 70. *Helicia cochinchinensis* LOUR. Radial surface showing two vessels with simple (at the right) and multiple perforation plate (at the left). The half perforation plate on this side of the vessel at the left is simple, while the half perforation plate on the other side is multiple.

Photo 71. *Helicia cochinchinensis* LOUR. A simple perforation showing intermediate form between simple (photo 69) and multiple perforation plates (photos 72 and 73).

Photo 72. *Helicia cochinchinensis* LOUR. A multiple perforation plate. Openings of the two multiple half perforation plates, composing a multiple perforation plate, between adjacent vessel members are not coincident.

Photo 73. *Helicia cochinchinensis* LOUR. A multiple perforation plate. Openings of the two multiple half perforation plates, composing a multiple perforation plate, between adjacent vessel members are not coincident.

Photo 74. *Pourthiaea villosa* (THUNB.) DECNE. var. *laevis* (THUNB.) STAPF A simple perforation with the prominent bordered rim exposed by a radial cut.

Photo 75. *Pourthiaea villosa* (THUNB.) DECNE. var. *laevis* (THUNB.) STAPF A simple perforation with the prominent bordered rim.

Photo 76. *Pourthiaea villosa* (THUNB.) DECNE. var. *laevis* (THUNB.) STAPF Portion of a simple perforation with several projections of wall material arising from rim to opening. The half rim on this side is smooth, while several projections of wall material extend from the half rim on the other side.

Photo 77. *Pourthiaea villosa* (THUNB.) DECNE. var. *laevis* (THUNB.) STAPF Portion of a simple perforation with two projection of wall material arising from the half rim (of the vessel member in the upper). Scalloped partition (single arrows) remains between bordered rim and is continuous to the portion of the projections (double arrows).

Photo 78. *Pourthiaea villosa* (THUNB.) DECNE. var. *laevis* (THUNB.) STAPF Portion of a simple perforation with a projection of wall material arising from the half rim (of the vessel member in the upper in this photo).

Photo 79. *Pourthiaea villosa* (THUNB.) DECNE. var. *laevis* (THUNB.) STAPF The half perforation plate on this side is simple with smooth bordered rim, while the half plate on the other side is multiple with irregular openings.

Photo 80. *Pourthiaea villosa* (THUNB.) DECNE. var. *laevis* (THUNB.) STAPF Portion of a multiple perforation plate consisting of a simple half perforation plate (on this side) and a multiple half perforation plate (on the other side). Arrows show the isolated wall material not connected to the rim of the vessel member on this side.

Photo 81. *Pourthiaea villosa* (THUNB.) DECNE. var. *laevis* (THUNB.) STAPF Portion of a multiple perforation plate with irregular openings.

Photo 82. *Pourthiaea villosa* (THUNB.) DECNE. var. *laevis* (THUNB.) STAPF Portion of a multiple perforation plate consisting of a simple half perforation plate (on this side) and a multiple half perforation plate (on the other side). Arrows show the isolated wall material not connected to the rim of the vessel member on this side.

Photo 83. *Pourthiaea villosa* (THUNB.) DECNE. var. *laevis* (THUNB.) STAPF A multiple perforation plate consisting of a simple half perforation with smooth rim (on this side) and a multiple half perforation plate with many round openings (on the other side). Arrows show the isolated wall material not connected to the rim of the vessel member on this side.

Photo 84. *Sorbus alnifolia* (SIEB. et ZUCC.) C. KOCH A simple perforation with the non-bordered rim.

Photo 85. *Sorbus alnifolia* (SIEB. et ZUCC.) C. KOCH A simple perforation with the bordered rim.

Photo 86. *Sorbus alnifolia* (SIEB. et ZUCC.) C. KOCH Portion of a simple perforation. Arrows show the projections of the wall material arising from the rim.

Photo 87. *Sorbus alnifolia* (SIEB. et ZUCC.) C. KOCH A multiple perforation plate exposed by a radial cut. Irregularly branched wall material extending from the rim of the vessel member in the under fell over inner surface of the lateral wall during the specimen preparation.

Photo 88. *Sorbus alnifolia* (SIEB. et ZUCC.) C. KOCH Portion of a multiple perforation plate with irregular openings in form. Arrows show the remnants (fibrils) of the partition.

Photo 89. *Sorbus alnifolia* (SIEB. et ZUCC.) C. KOCH Portion of an unusual multiple perforation plate. Wall material extending from the rim of the vessel member on this side is very complicated in form. Arrows show the remnants (fibrils) of the partition.

Photo 90. *Sorbus alnifolia* (SIEB. et ZUCC.) C. KOCH A multiple perforation plate with irregular openings. Arrows show the remnants (fibrils) of the partition.

Photo 91. *Sorbus alnifolia* (SIEB. et ZUCC.) C. KOCH A multiple perforation plate with irregular openings.

Photo 92. *Sorbus alnifolia* (SIEB. et ZUCC.) C. KOCH A multiple perforation plate consisting of a simple half perforation plate (on this side) and a multiple half perforation plate with many small openings (on the other side) in a smaller vessel.

Photo 93. *Sorbus alnifolia* (SIEB. et ZUCC.) C. KOCH A multiple perforation plate with many small openings in a smaller vessel.

Photo 94. *Vaccinium bracteatum* THUNB. A simple perforation in the earlywood vessel.

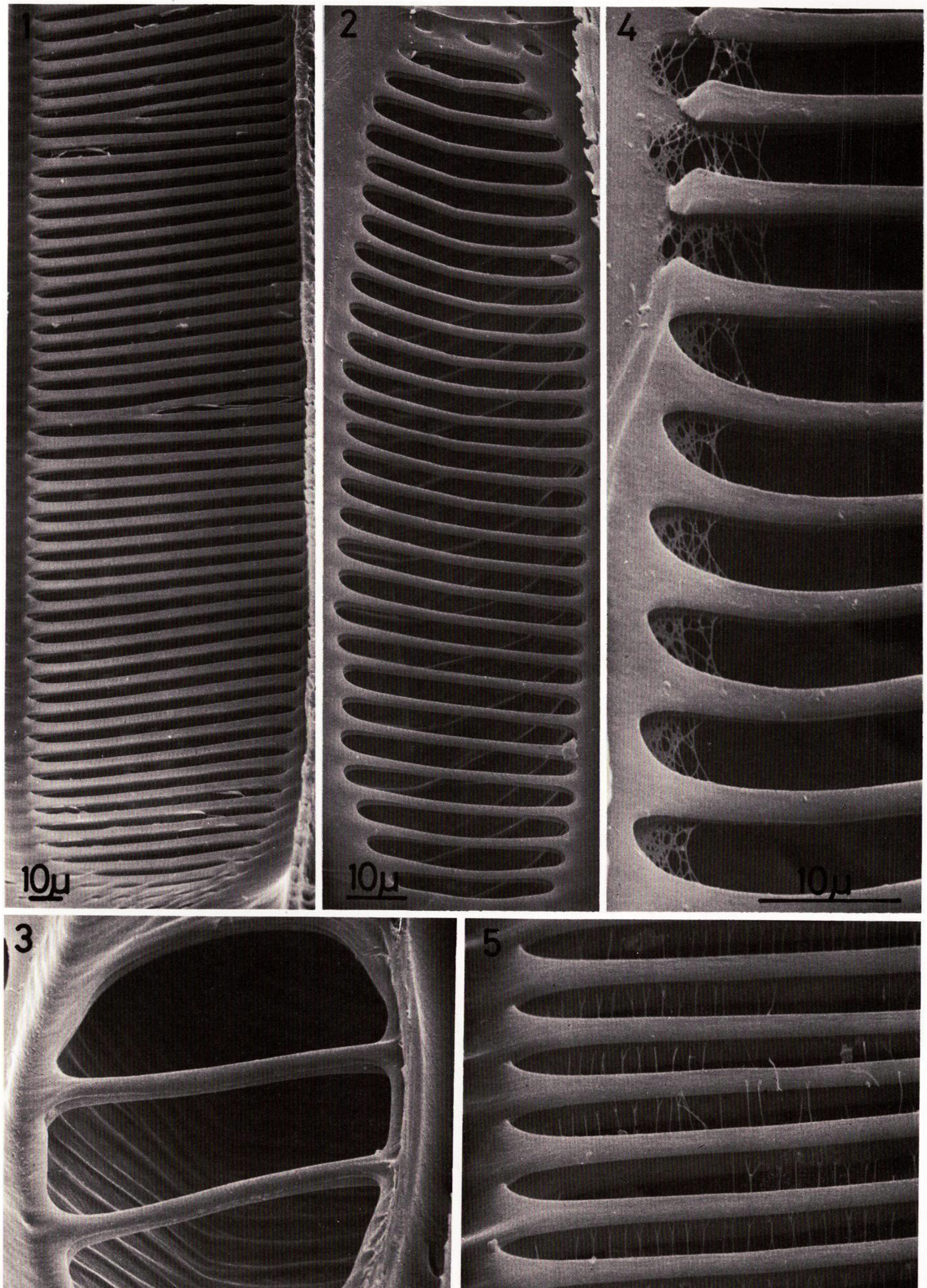
Photo 95. *Vaccinium bracteatum* THUNB. Portion of a scalariform perforation plate in the earlywood vessel.

Photo 96. *Vaccinium bracteatum* THUNB. Portion of a scalariform perforation plate with narrow openings between thick bars in the latewood vessel viewed from the lumen side.

Photo 97. *Vaccinium bracteatum* THUNB. A scalariform perforation plate in the latewood vessel exposed by a radial cut.

Photo 98. *Vaccinium bracteatum* THUNB. Portion of a multiple perforation plate in the latewood vessel.

Pohto 99. *Vaccinium bracteatum* THUNB. Portion of a multiple perforation plate in the latewood vessel viewed from the lumen side.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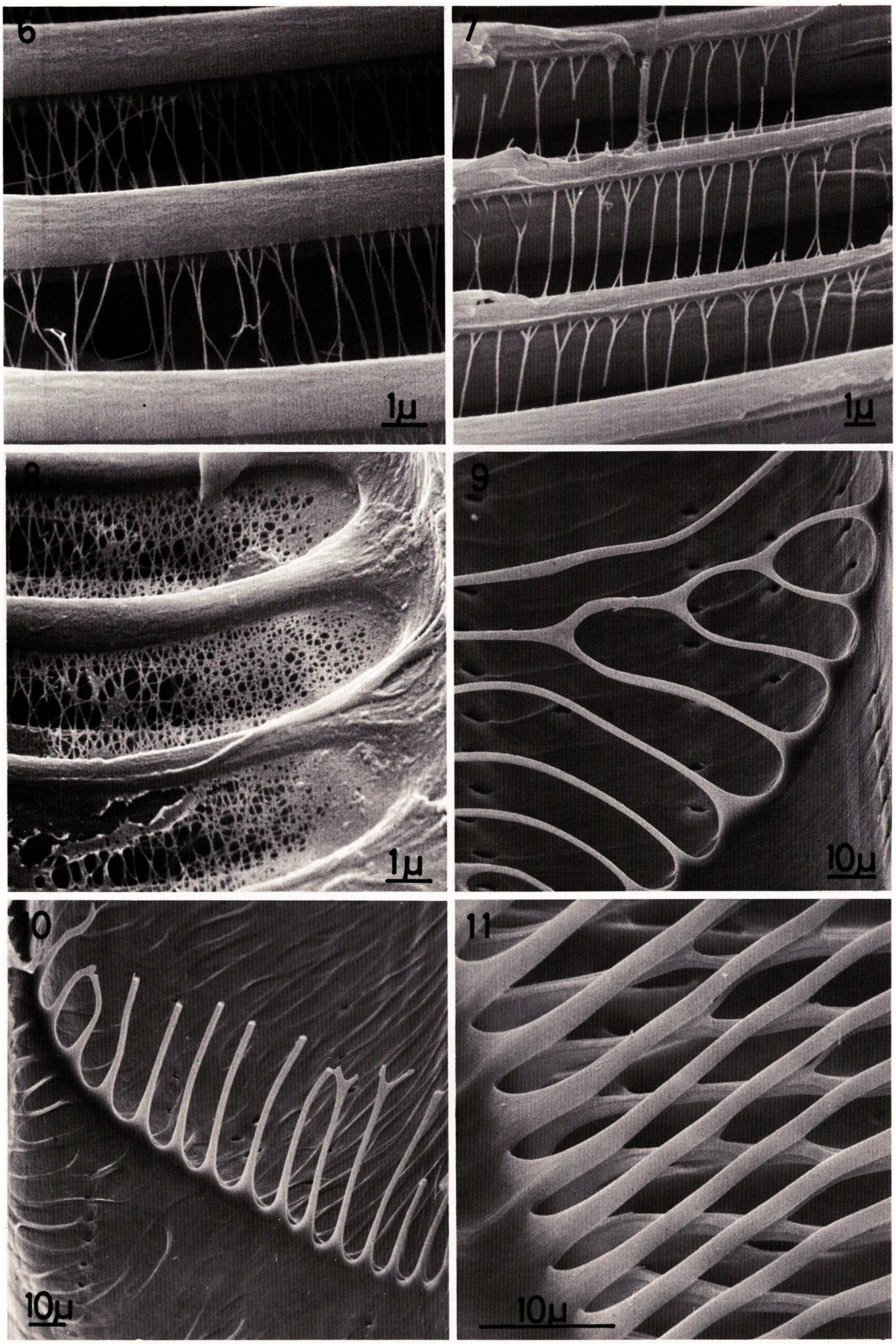
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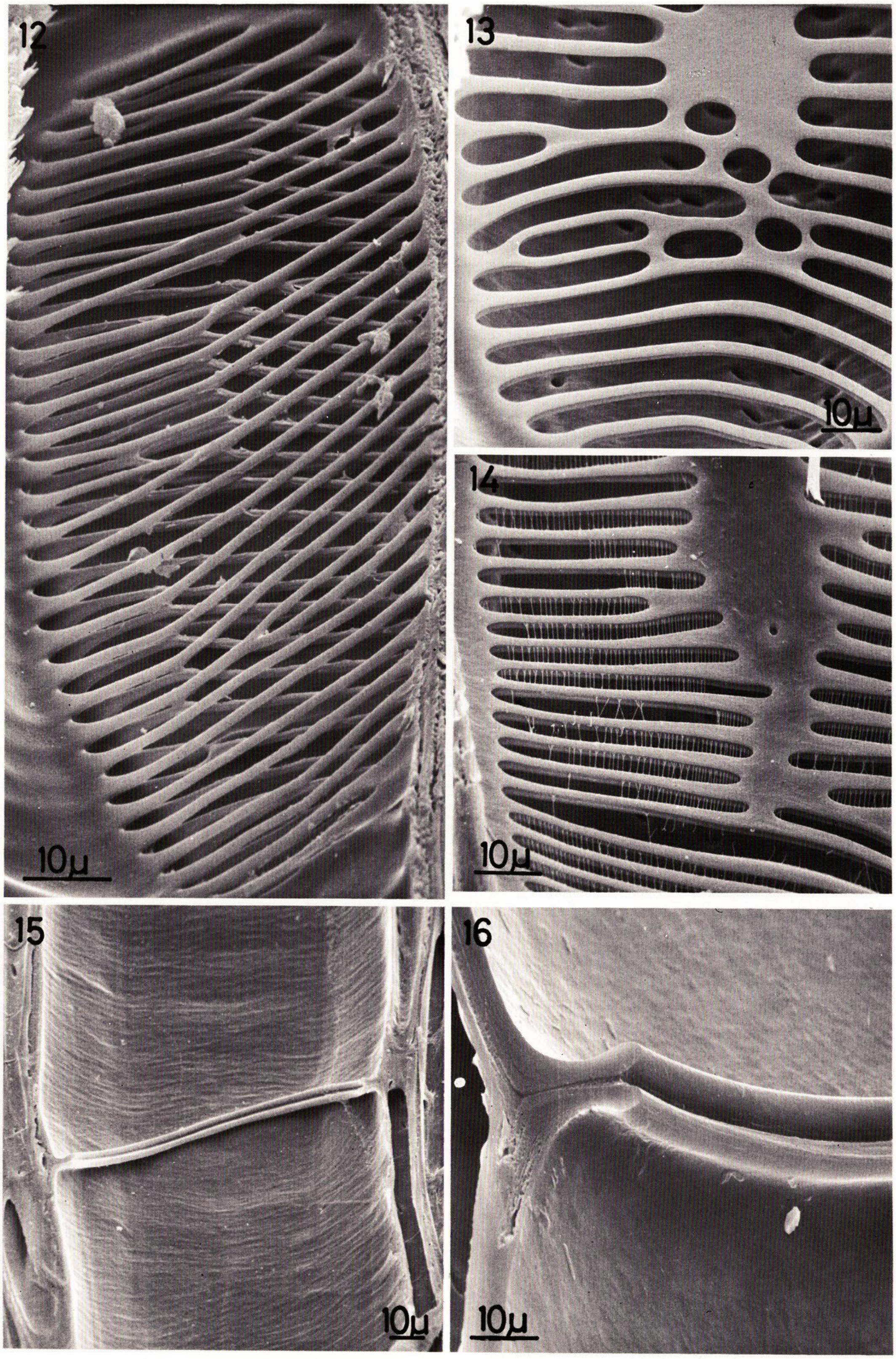
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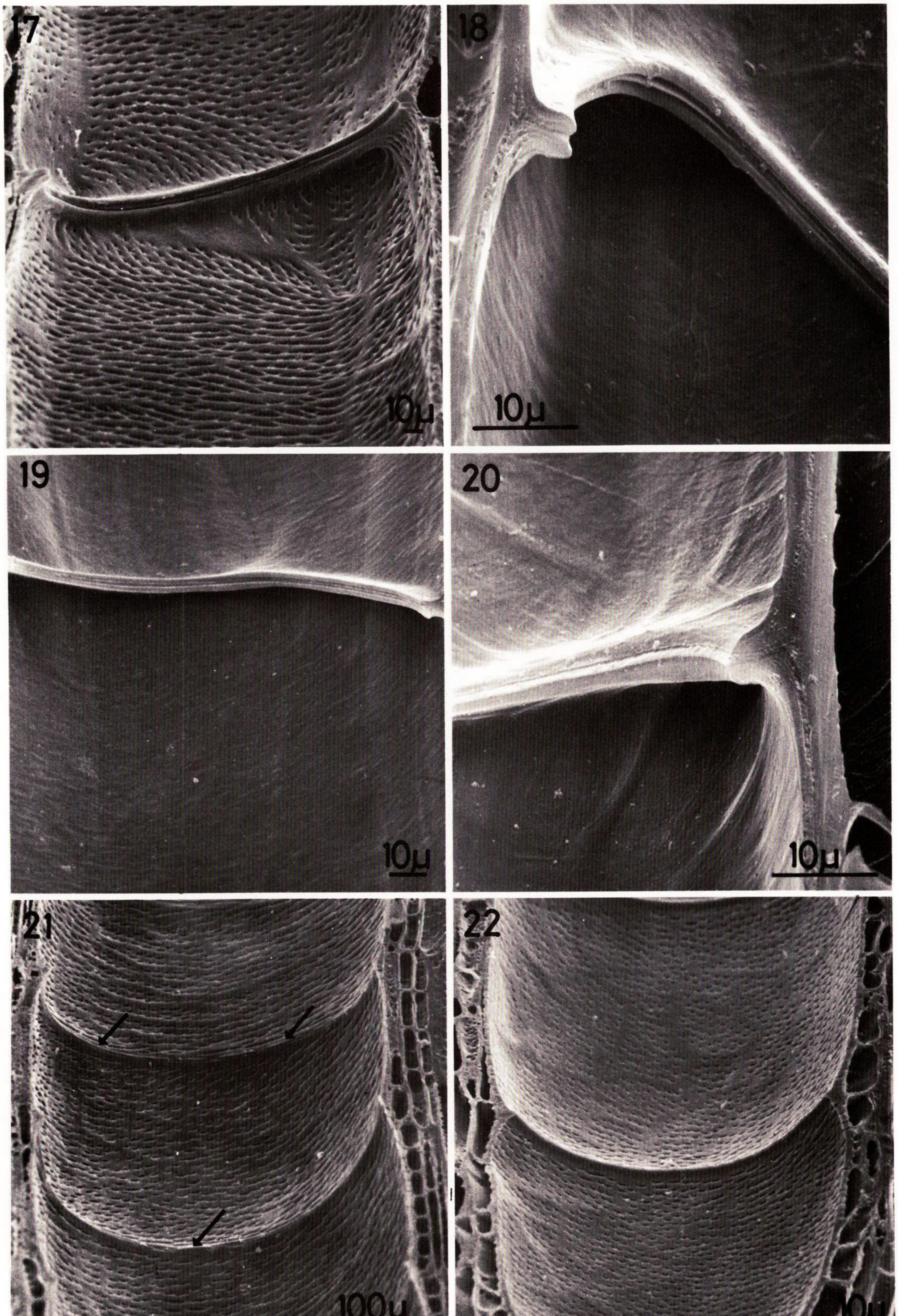
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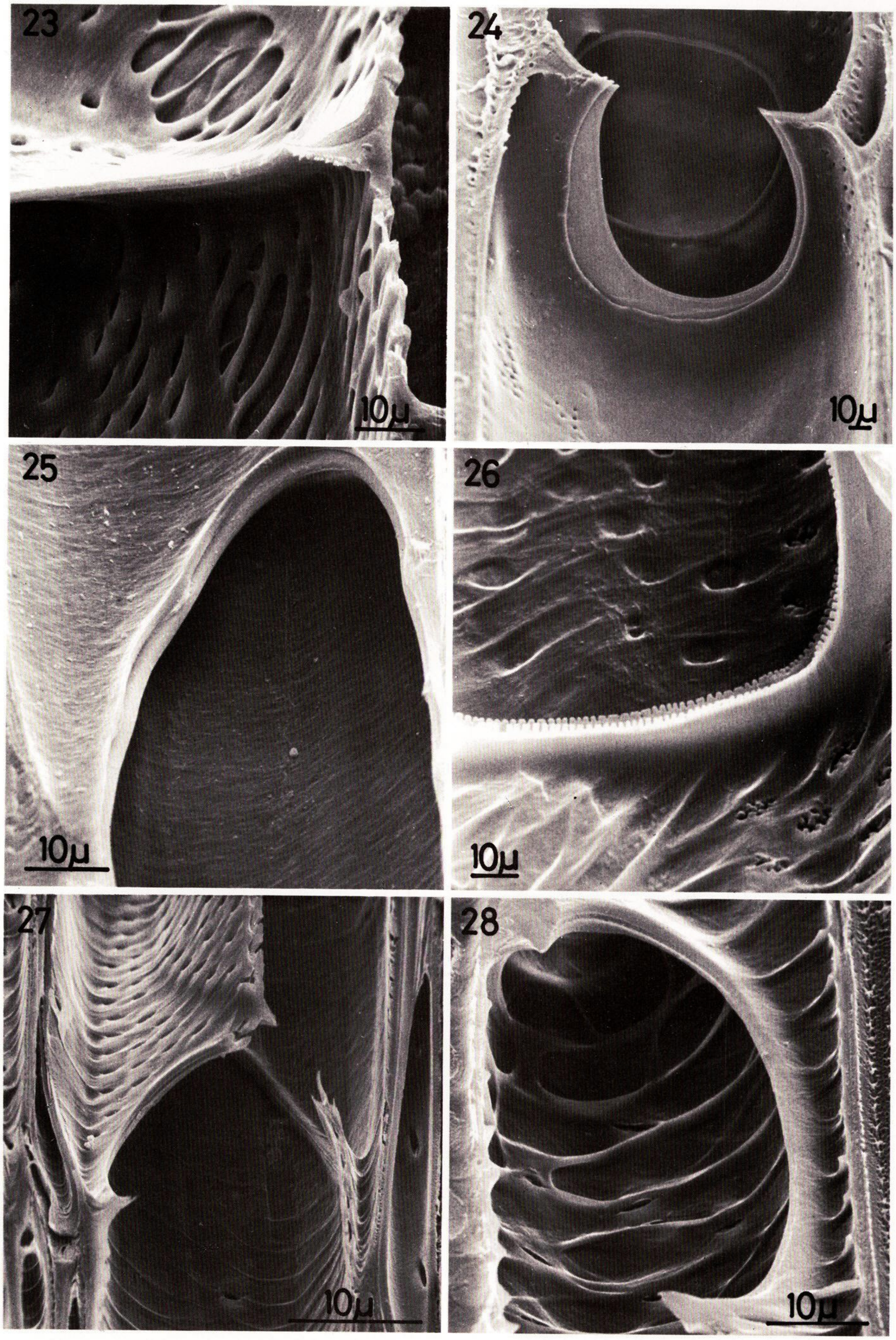
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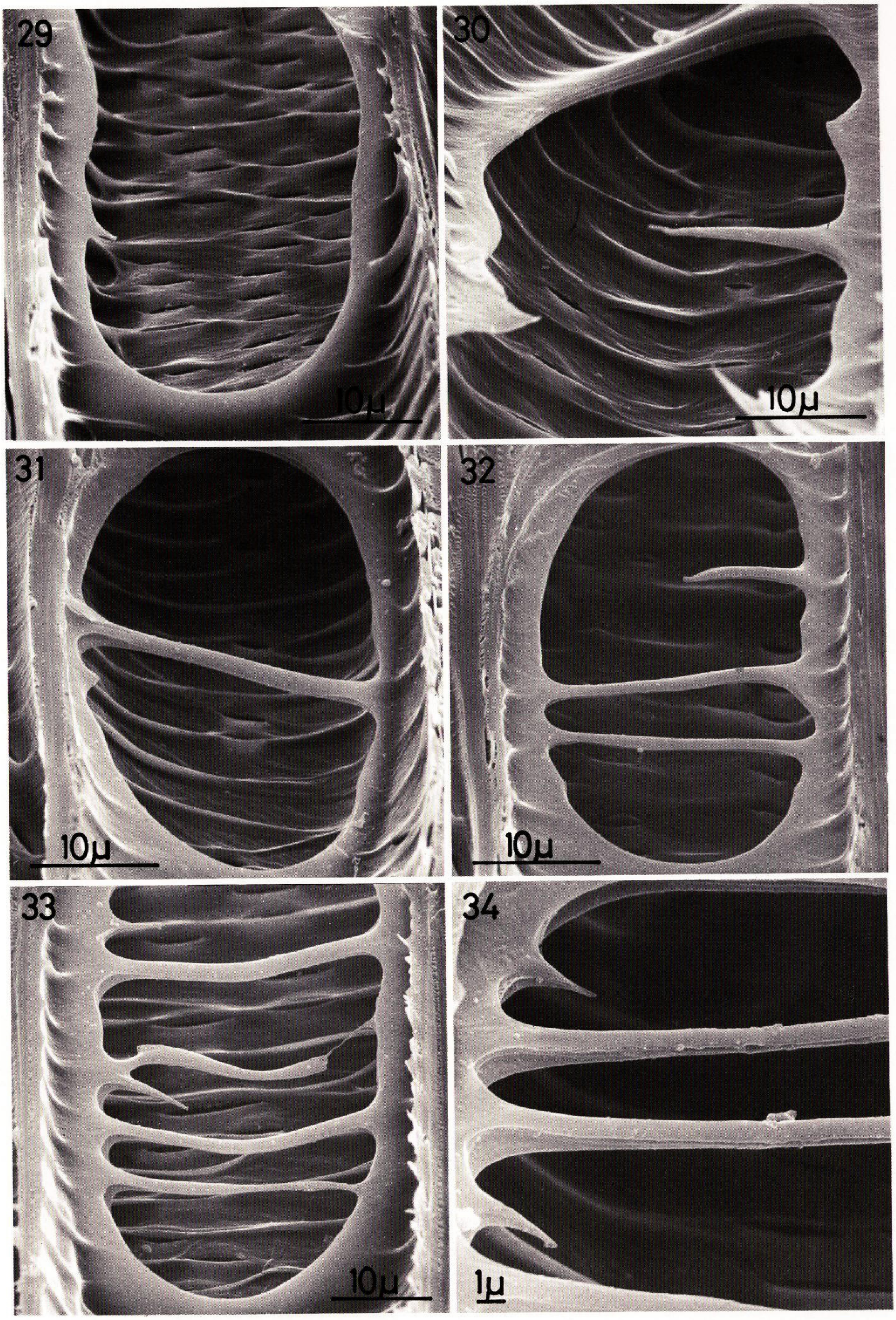
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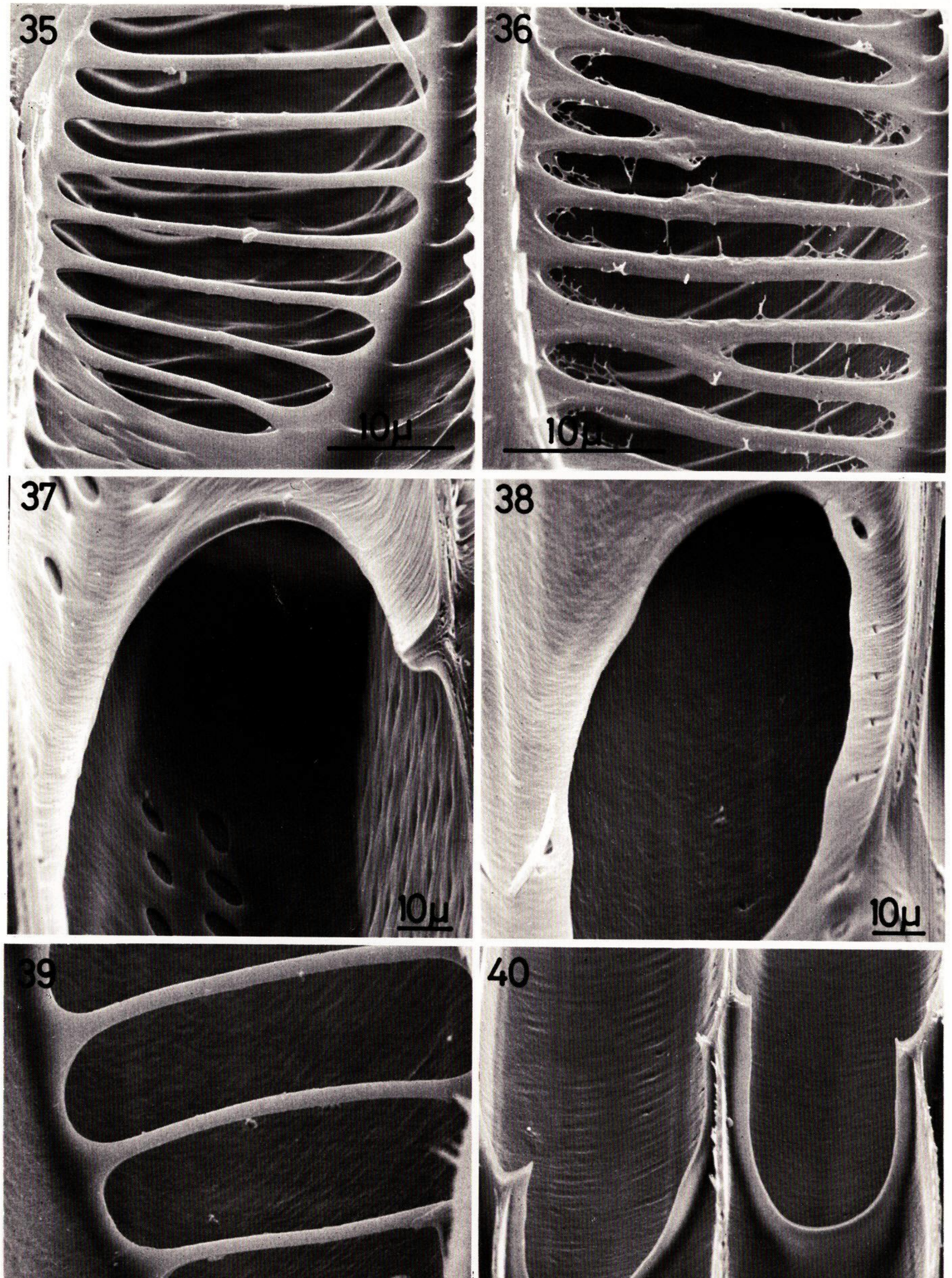
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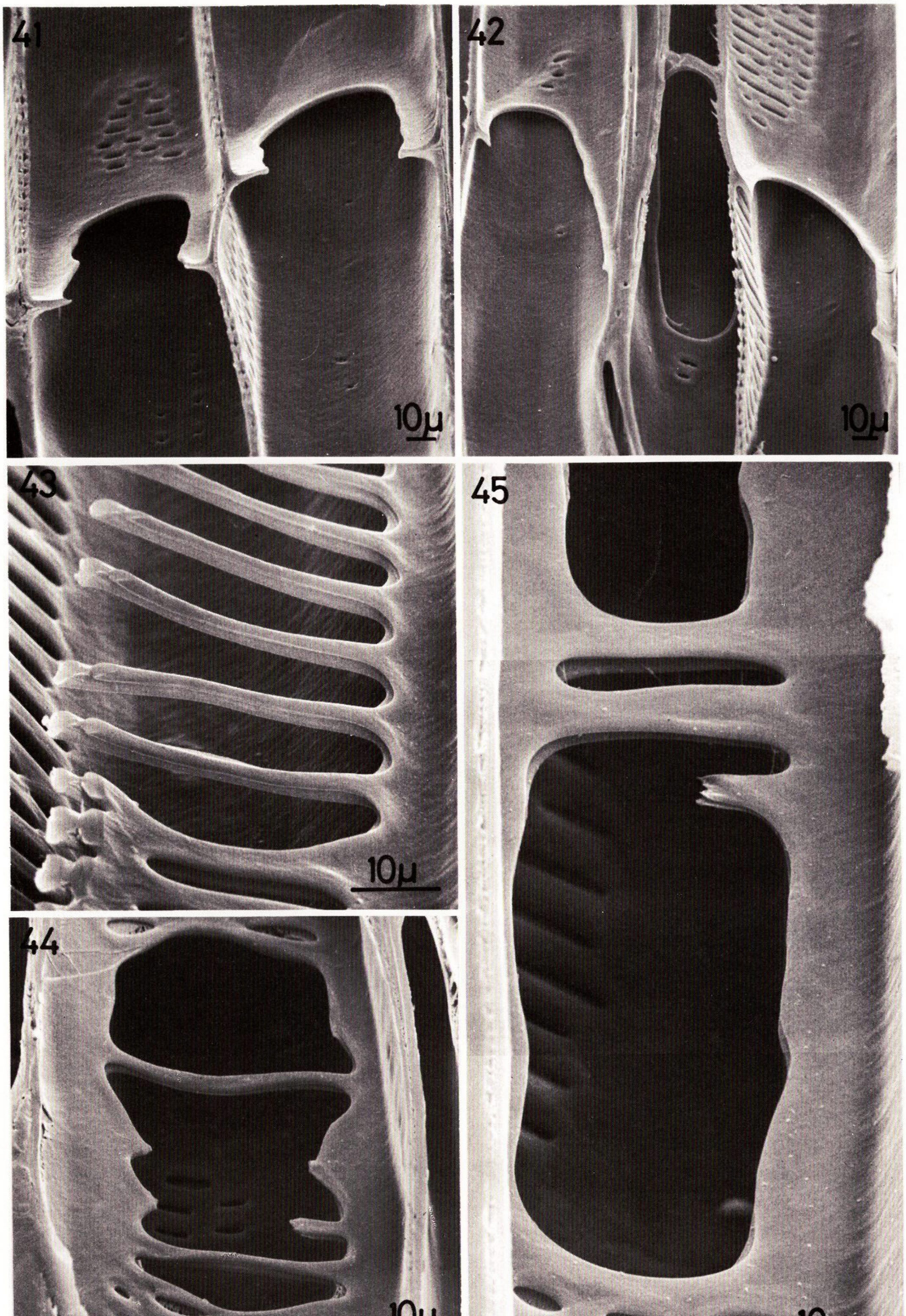
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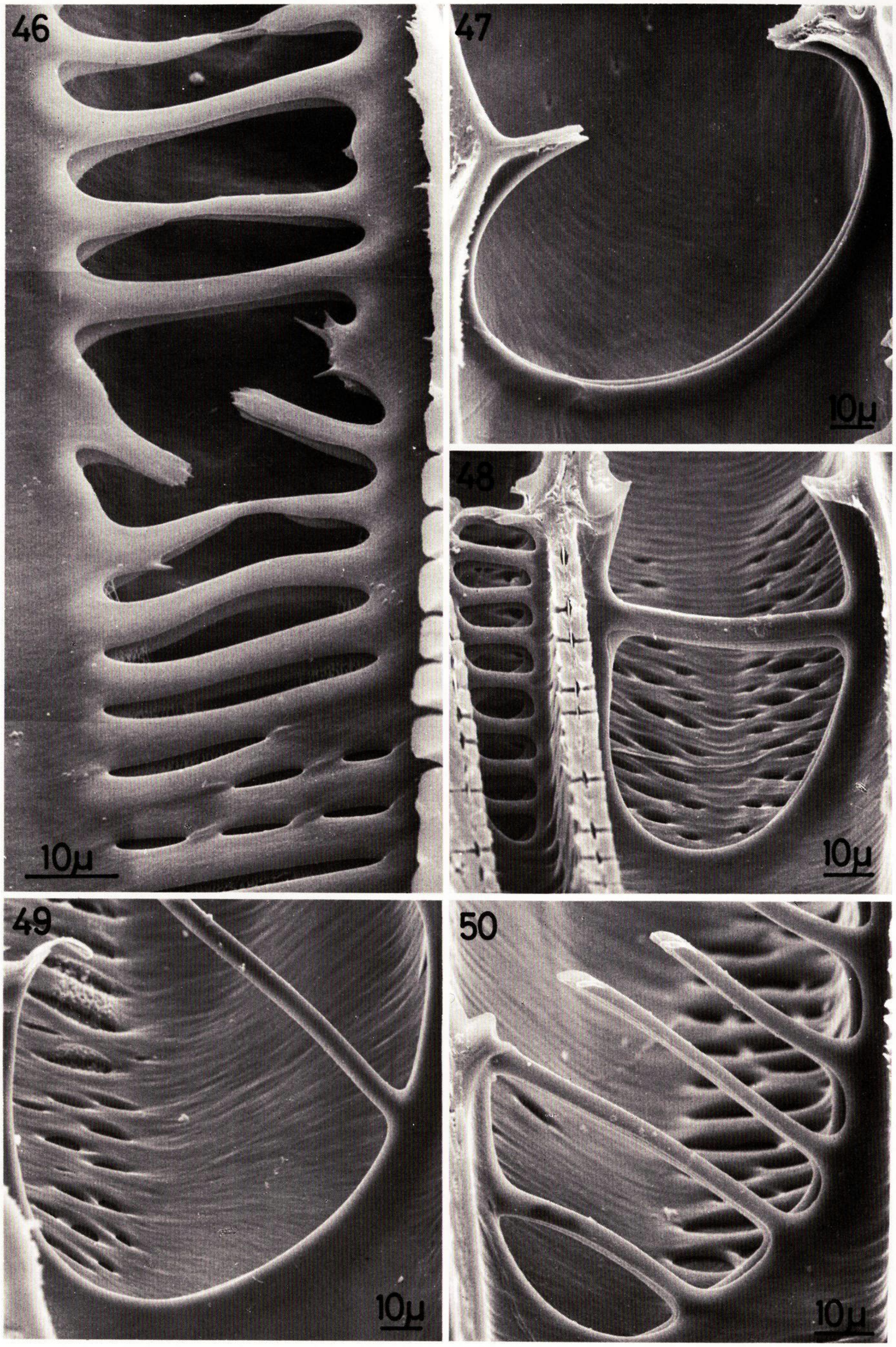
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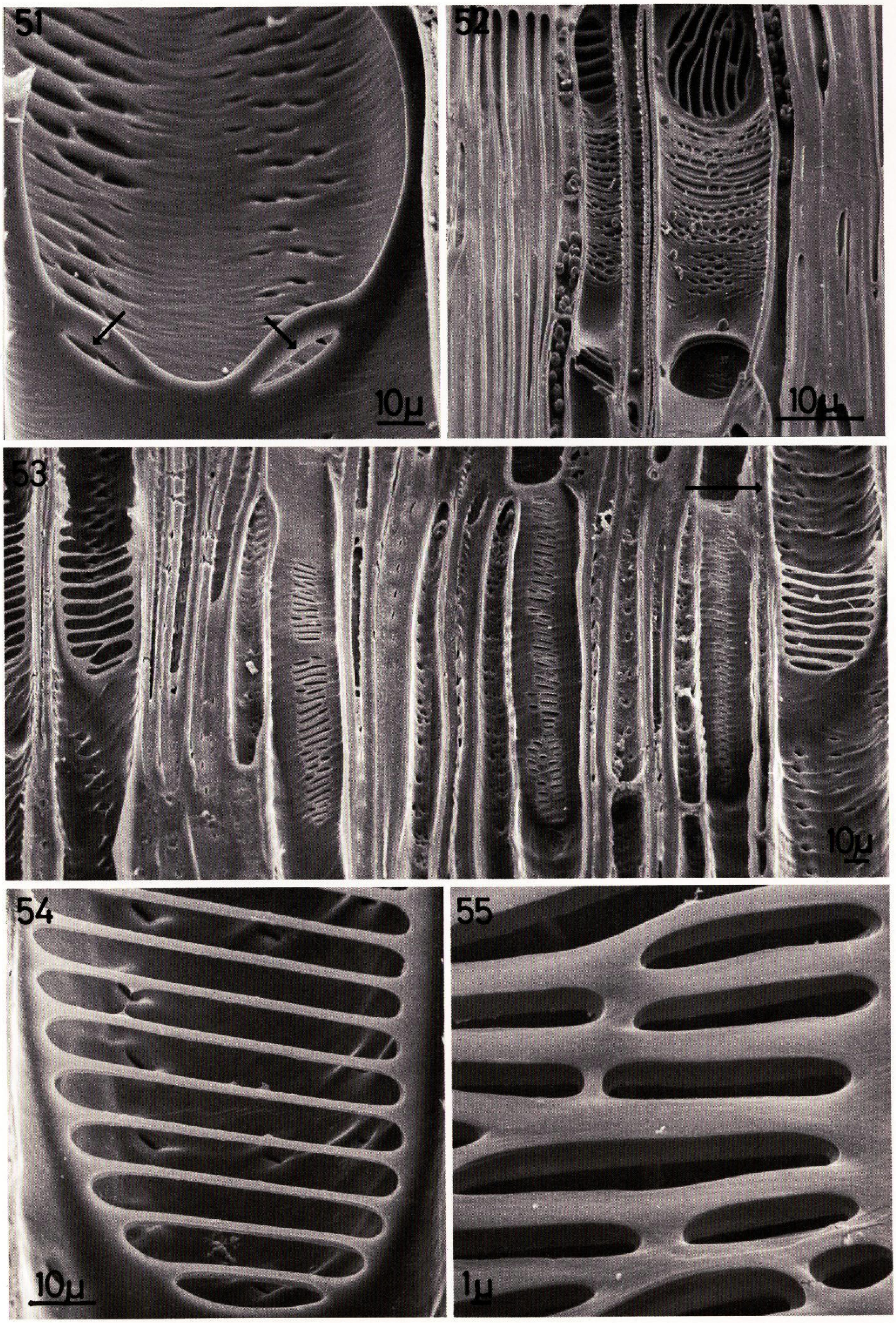
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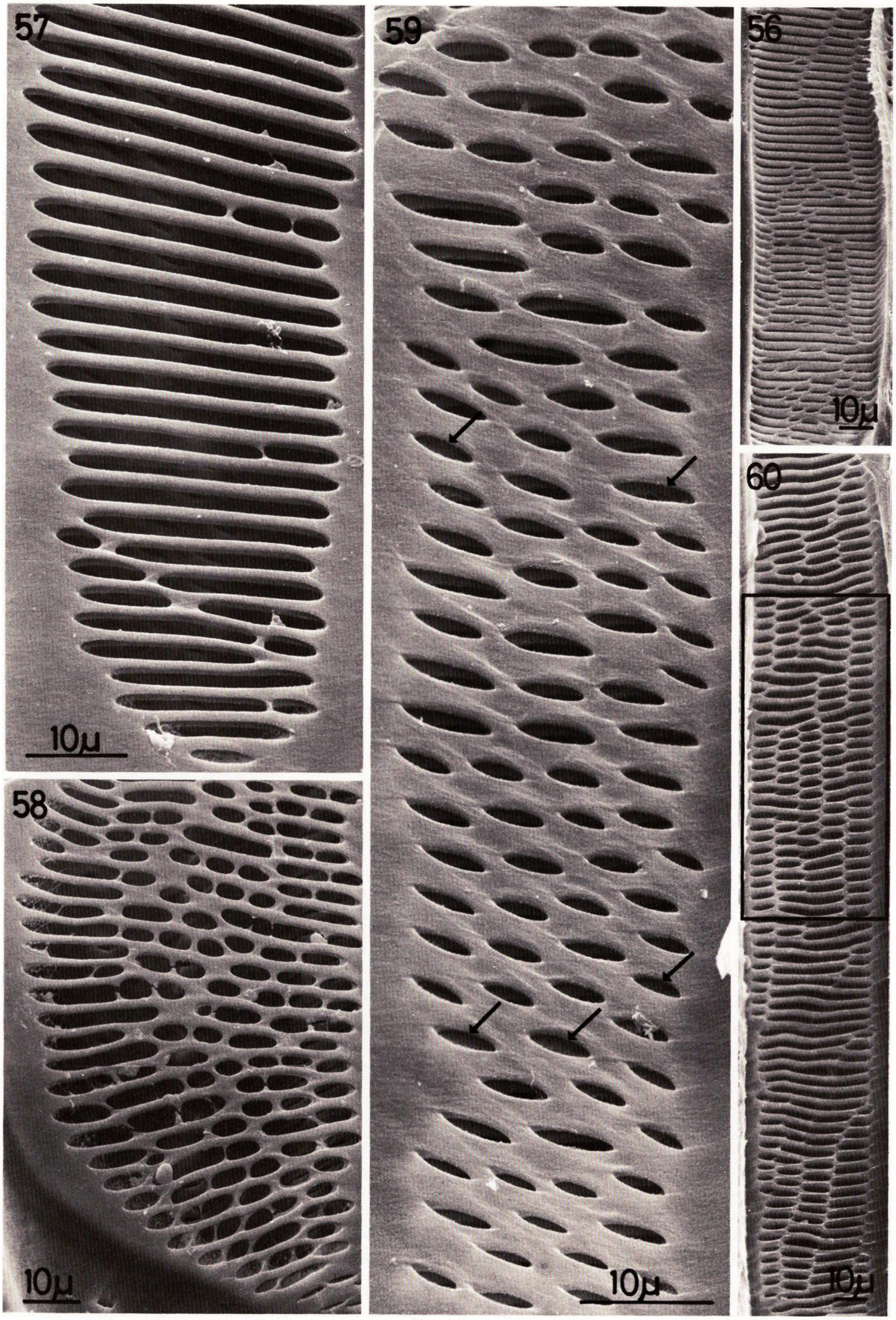
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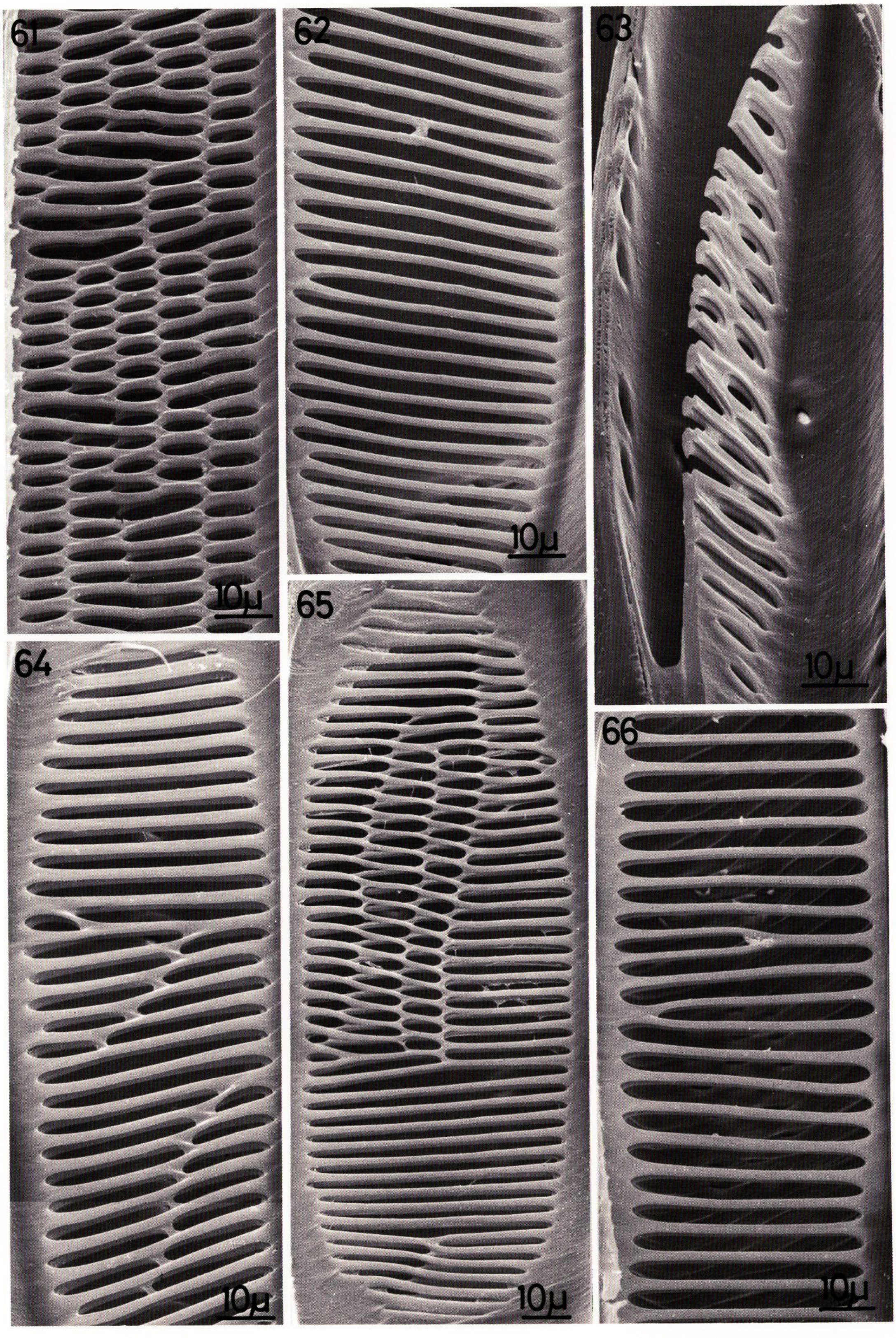
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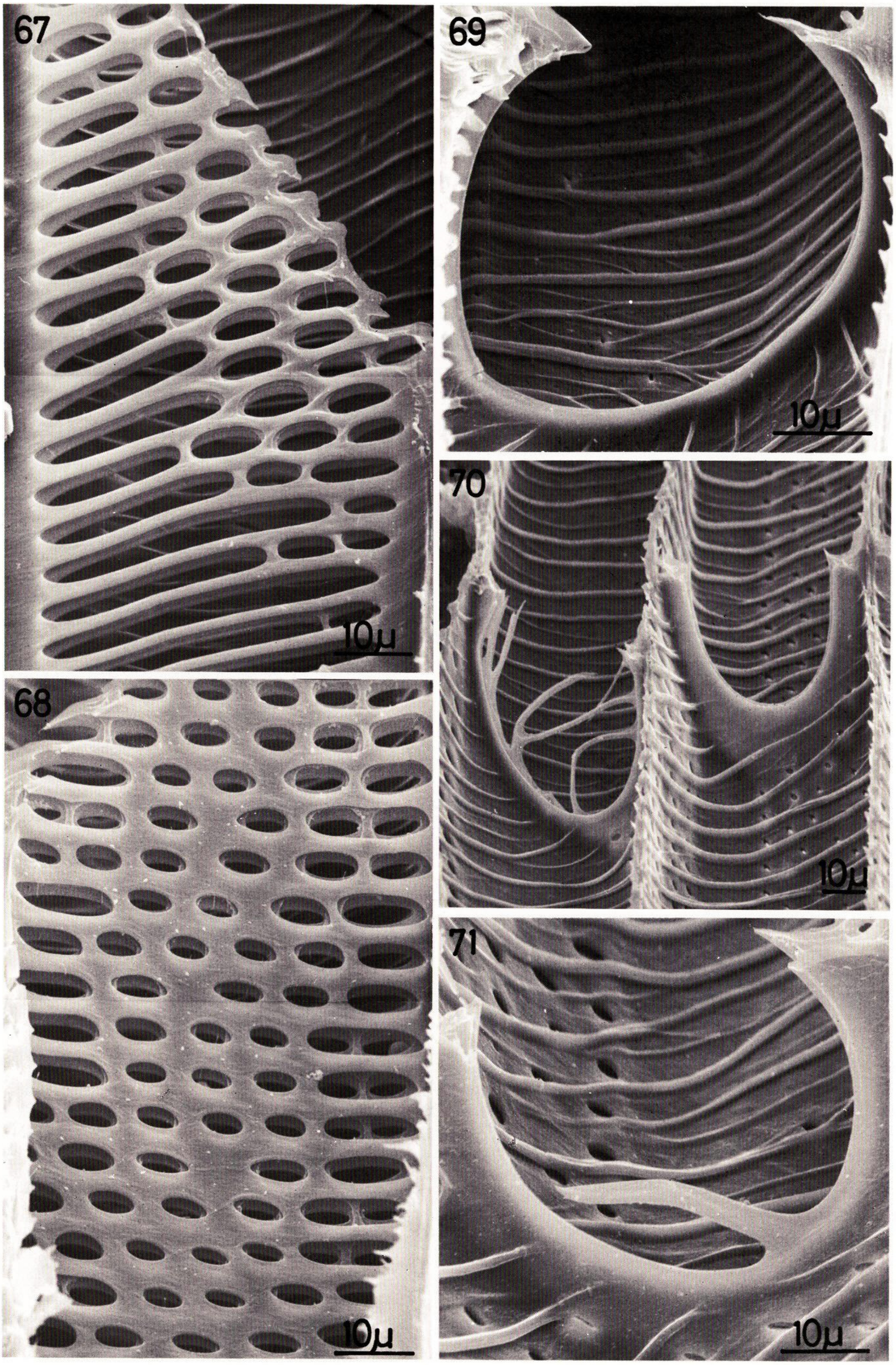
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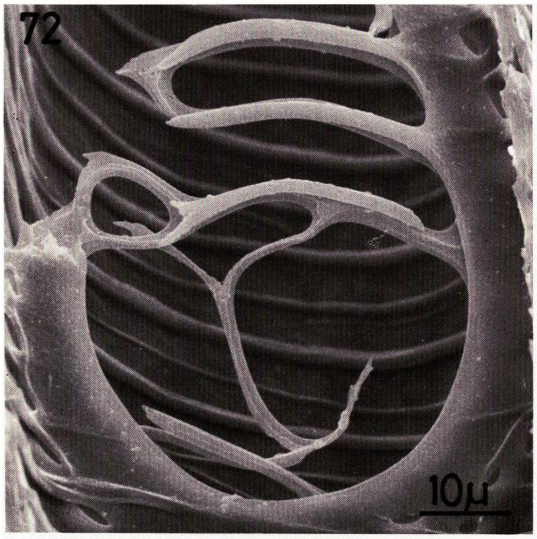
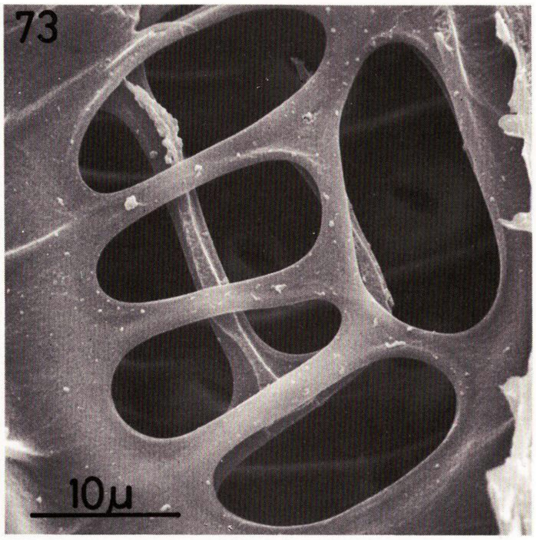
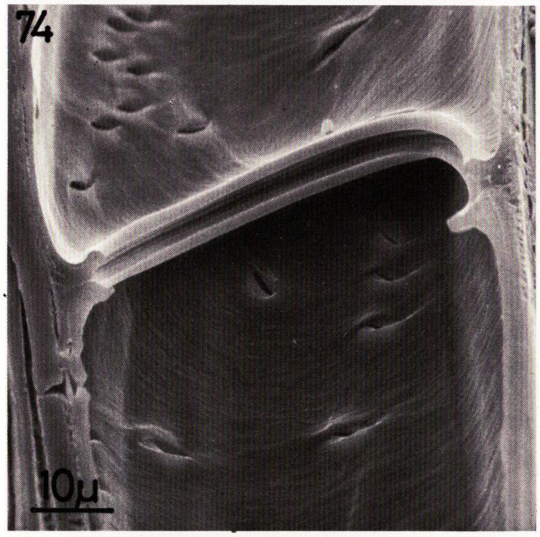
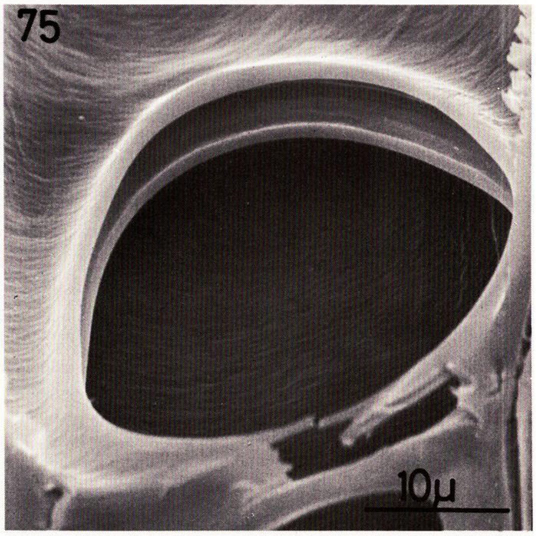
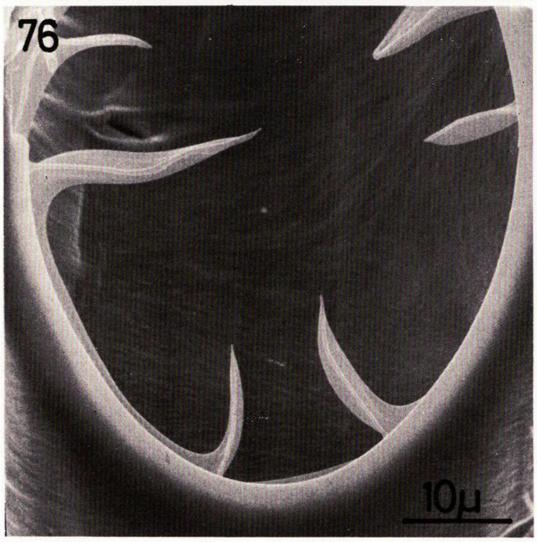
10μ
69
10μ
70
10μ
71
10μ


72
10μ

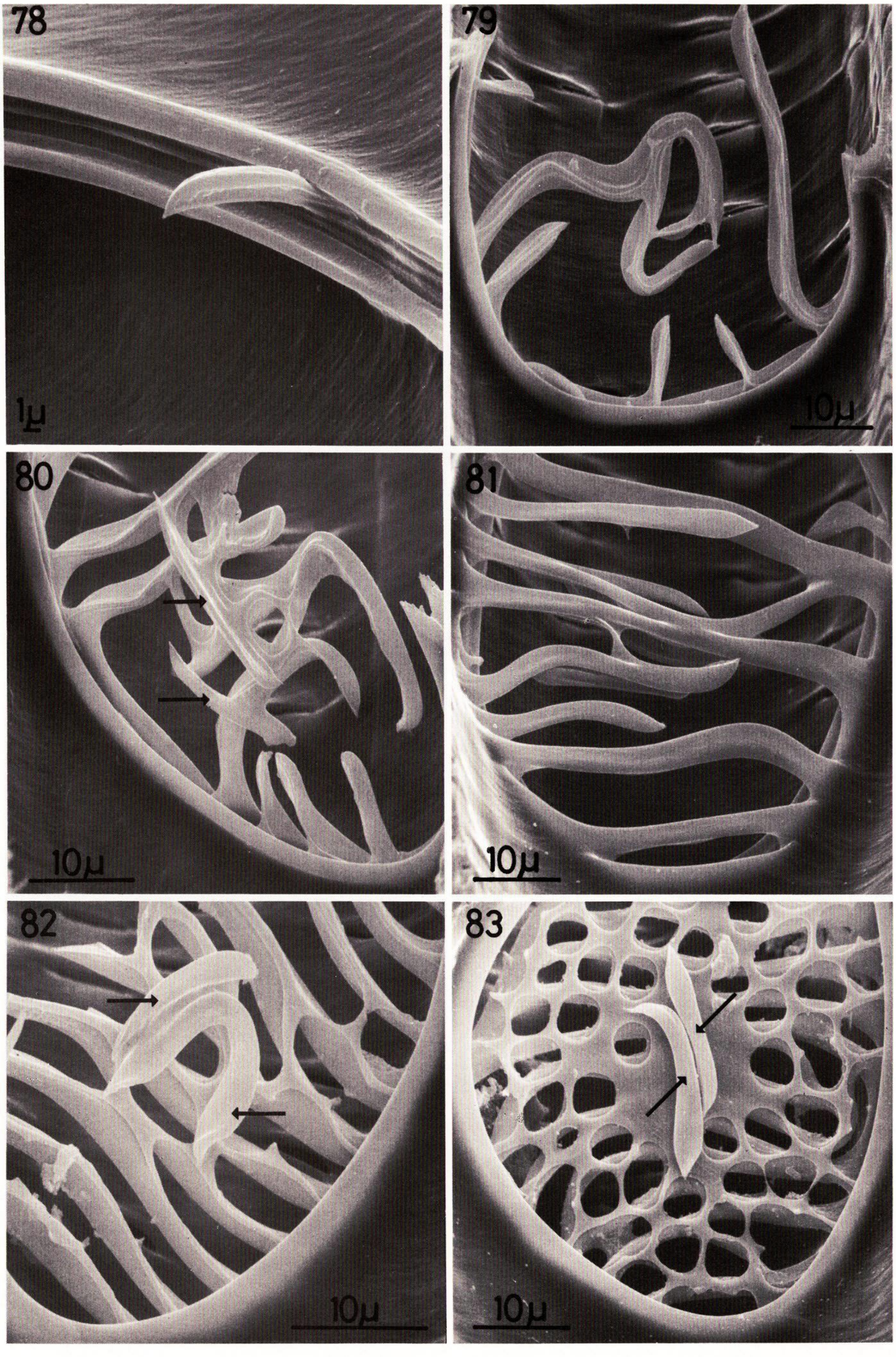

73
10μ

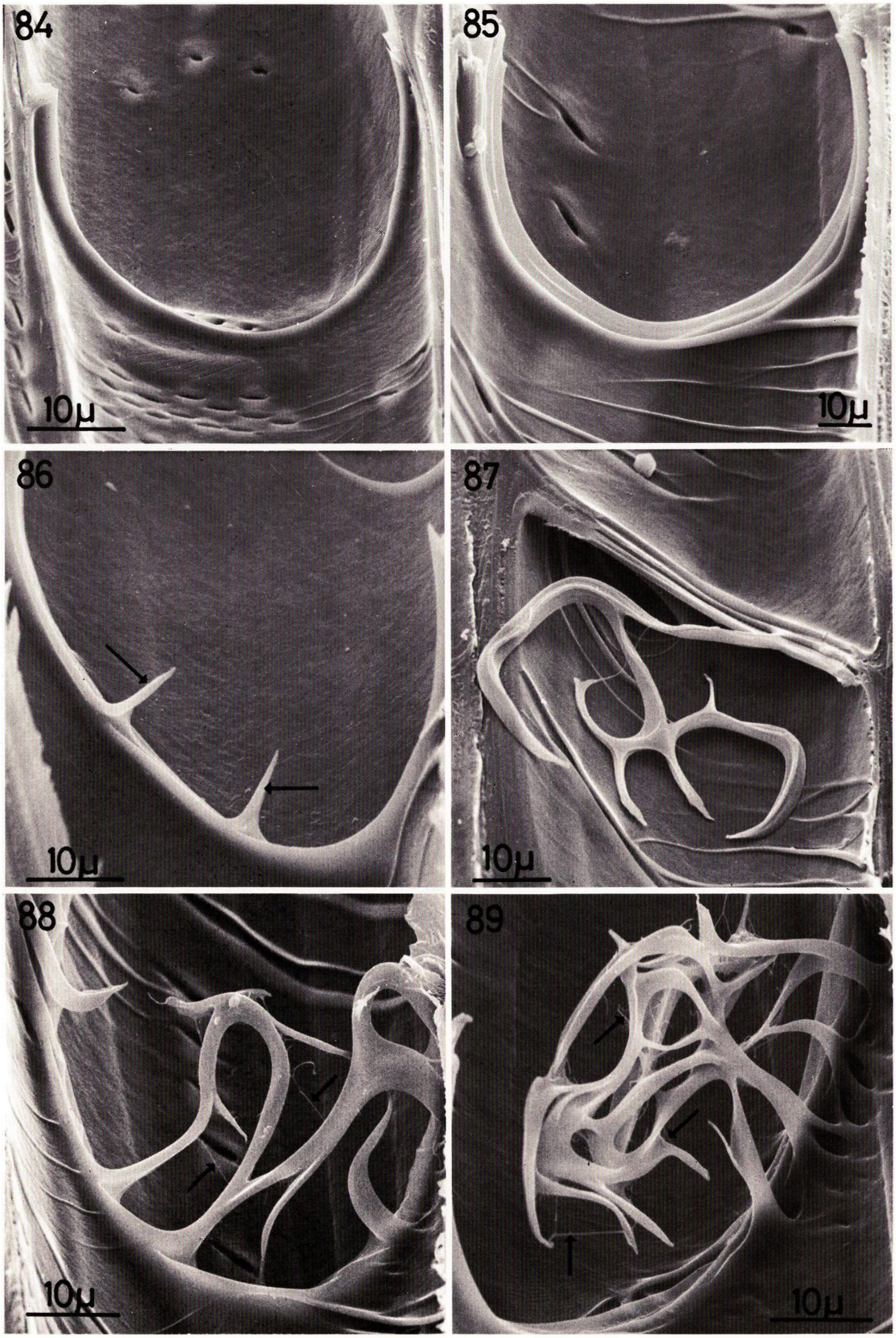

74
10μ

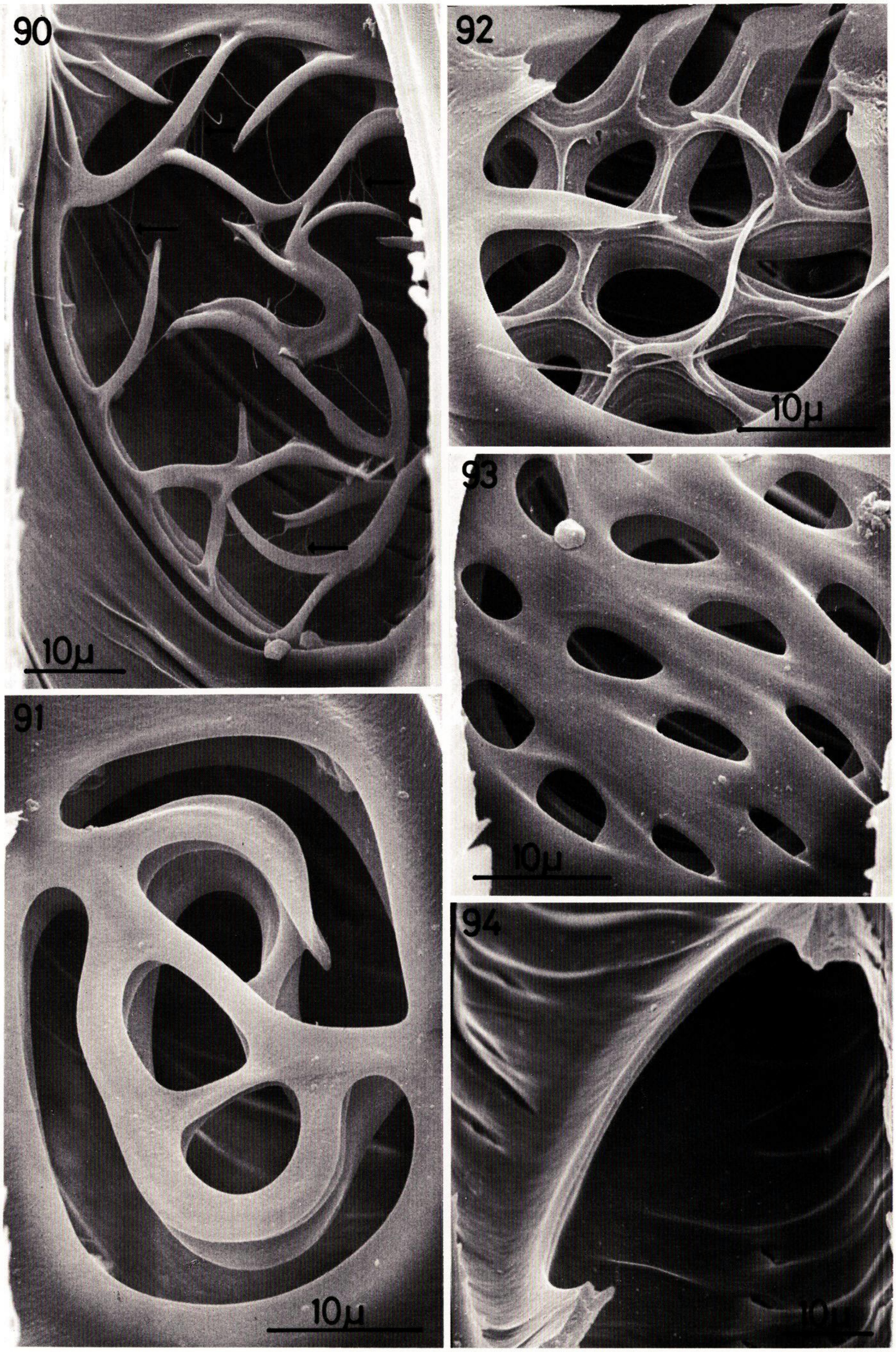

75
10μ

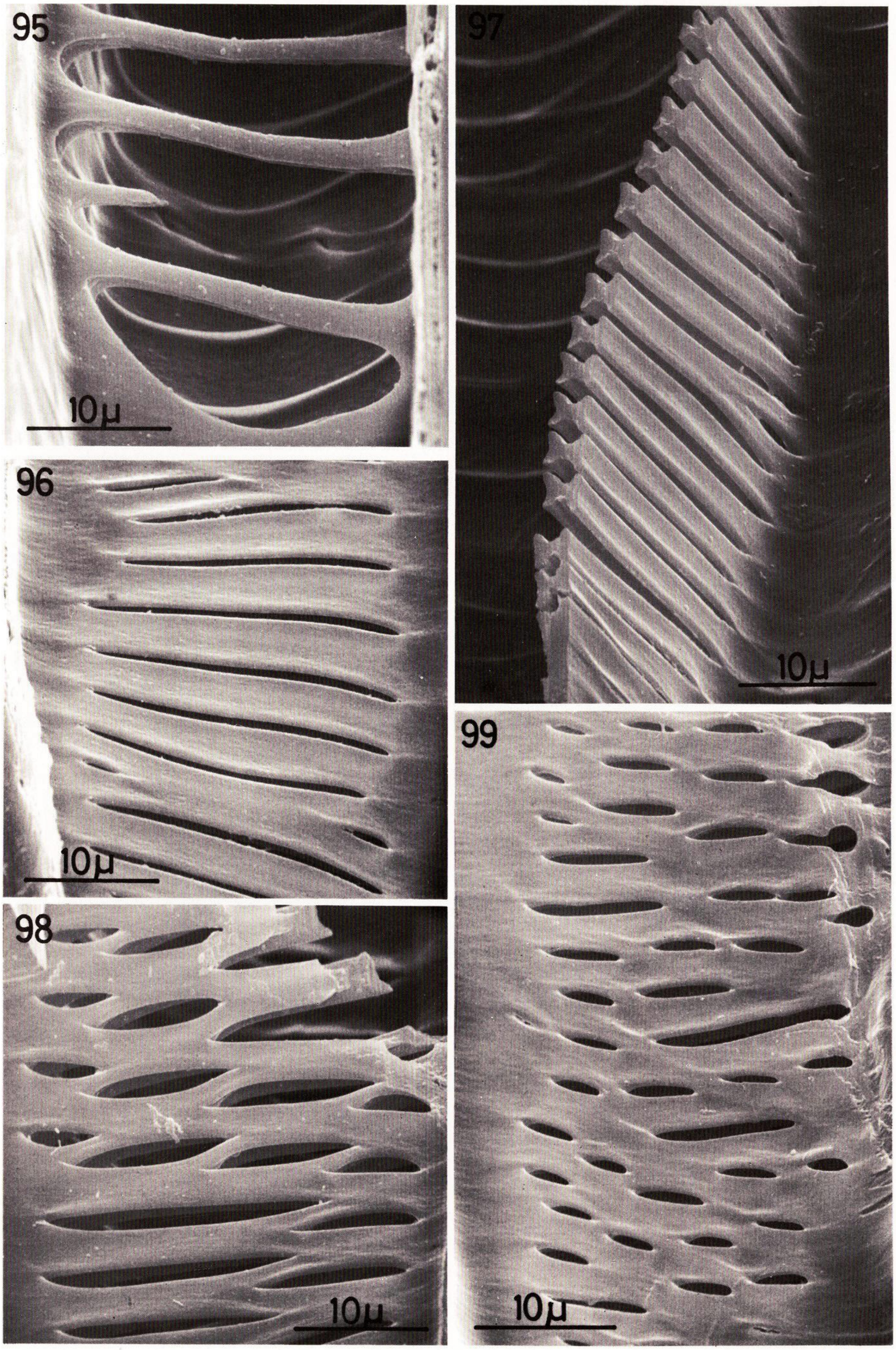

76
10μ


77
10μ


78
1μ
79
10μ
80
10μ
81
10μ
82
10μ
83
10μ


84
10μ
85
10μ
86
10μ
87
10μ
88
10μ
89
10μ


90
10μ
92
10μ
93
10μ
91
10μ
94
10μ


95
10μ
97
10μ
96
10μ
99
10μ
98
10μ