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ORGANIC COMPONENTS OF PRISMATIC LAYERS IN MOLLUSCAN SHELLS

by

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(with 1 table and 5 plates)

Abstract

Organic components of typical prismatic layers in several molluscan shells were reexamined by applying scanning electron microscopy to preparations treated with the freeze-dry or the critical-point-dry method, with the result showing the following:

The interior of prisms is almost filled up with a spongy intraprismatic matrix. Also three principal types of prisms are distinguishable according to the state of development and the histochemical nature of a vertical (interprismatic) wall. Namely, prisms of type 1 are separated from their neighbor by a rigid vertical wall, and are represented by calcite simple prisms of *Pinctada* and aragonite simple prisms of *Anodonta;* prisms of type 2 are separated by a compound (partly rigid and partly spongy) vertical wall, and are represented by aragonite simple prisms of *Unio;* prisms of type 3 are separated by a spongy vertical wall, and are represented by composite prisms of *Tapes* and *Peronidia.* These findings suggest that type 2 is intermediate between types 1 and 3, and that transformation of an interprismatic matrix from a "primitive" rigid matrix to a more "advanced" spongy one has probably taken place in the course of evolution of prisms. In addition, the histochemical nature of the rigid matrix is acidophilic like the shell epidermis. Meanwhile, the spongy matrix, regardless of being inter- or intraprismatic, is basophilic, and will have some connections with mineralization of prisms.

Introduction

Prismatic structures are found clearly in molluscan shell layers, as have been described by a large number of authors since Carpenter's description (1844). It has been stated generally, that they are comparatively "primitive" among shell structures in molluscs. They have a characteristic built up to polygonal columnar prisms, aligned parallel to each longitudinal axis. And in a horizontal view, typical prisms show the so-called "honeycomb" pattern regardless of the chamber size, each prism being distinctly separated from its neighbor by a thick vertical organic wall.

The following portray seven types of prisms described until the present: calcite simple, aragonite simple, composite, fibrous, radiated, irregular, and myostracal (Kobayashi, 1964, 1968, 1971; Taylor *et al.*, 1969, 1973, Suzuki, 1979). The so-called "simple prismatic structure", built up of calcite or aragonite crystals, is the structure of the best known type and is found only in the outer layers of shells. Calcite simple prisms are found in the Pinnacea, Pteriacea and Ostreacea. Meanwhile, aragonite simple prisms are in the Unionacea and Trigonacea. Optically observed, the surfaces of prisms, whether calcite or aragonite, are rather smooth and structureless. But an electron microscopic observation reveals that they are built up of very small calcium carbonate crystals, as was previously pointed out by Watabe and Wada (1956), Tsujii *et al.* (1958), Taylor *et al.* (1969), and Nakahara and

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Bevelander (1971). The composite prismatic structure is found in the outer shell layers of the Veneroida; each prism is built up of many small acicular aragonite crystals, aligning radially within a prism. The other prisms, excepting the above-mentioned three prisms, are found in the following special shell layers: Fibrous prisms, which are found in the outer shell layers of the Mytilacea, are seemingly thin needles inclining towards the shell margin; each prism appears to consist of a calcite single crystal regardless of ultrastructures. Radiated prisms, which are found in the outer shell layers of the Myoida and in the regenerated shell layer of some molluscs, are fairly minute and arranged in a spherulite-like pattern; each prism appears to be an aragonite single crystal from the same standpoint as in fibrous prisms. Irregular prisms, which are found in the innermost shell layers of some marine snails and in the regenerated shell layers of some bivalves, vary greatly in size and in morphological orientation; each prism appearing to be an aragonite single crystal. Myostracal prisms, which are found in the extremely limited layer of a muscle attachment of bivalve shells, are considerably short in length, and irregular in shape and diameter, and arranged almost vertically to the surface of shells, each prism appearing to be an aragonite single crystal.

Though stated briefly above, these prismatic structures have been illustrated and discussed in detail by many authors (Beedham, 1958; Travis, 1968; Uozumi and Iwata, 1969a, b; Nakahara, 1978), and at present we have not any supplemental data on their architectures themselves. However, the relationship of mineral and organic components within a prism has not, hitherto, been demonstrated adequately. A description is given and a discussion is made especially in this paper of relationships between mineral and organic components within a prism in the simple and the composite prismatic structure, applying scanning electron microscopy to preparations treated with the freeze-dry or the critical-dry method which enables to preserve organic components satisfactorily.

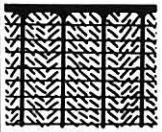
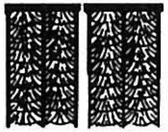
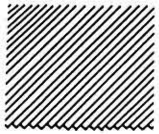
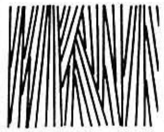
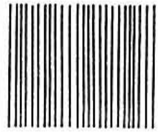
Before going further, the present writers express their deepest gratitude to Professor Seiji Hashimoto for his continued encouragement and valuable advice on necessary techniques for this study. To him they dedicate this paper in commemoration of his retirement from Hokkaido University. Acknowledgements are also due to Dr. Keiji Iwata for his kind discussion of problematic points, to Mr. Shigeshi Ohta for electron micrographs and technical assistance and to Miss Chiaki Sato for her help in laboratory work.

Materials and methods

Prismatic layers were studied in many normal and regenerated shells of molluscs, whereby typical prisms of the following shells were examined thoroughly on mineral and organic components within a prism so that their relationships were clarified:

Atrina pectinata (Linnaeus), Kii peninsula, Wakayama Pref.
Malleus albus Lamarck, Kii Peninsula, Wakayama Pref.
Pinctada fucata martensii (Dunker), Kii Peninsula, Wakayama Pref.
Crassostrea gigas (Thunberg), Akkeshi Bay, Akkashi City, Hokkaido
Unio douglasiae (Griffith et Pidgeon), Teshio River, Wakkanai City, Hokkaido
Anodonta woodiana (Lea), Barato Park, Sapporo City, Hokkaido
Tapes philippinarum (A. Adams et Reeve), Usu Bay, Date City, Hokkaido
Peronidia venulosa (Schrenck), Hidaka Coast, Samani Cho, Hokkaido

Table 1 Main features of seven prismatic structures in bivalve shells

		MEGAPRISM			MICROPRISM			
		Calcite simple prism	Aragonite simple prism	Composite prism	Fibrous prism	Radiated prism	Irregular prism	Myostracal prism
Prism	Diagram							
	Mineral	Calcite	Aragonite	Aragonite	Calcite	Aragonite	Aragonite	Aragonite
	Diameter (in microns)	50 - 100	50±	20 - 50	0.5 - 5	0.5 - 2	0.5 - 2	0.5 - 2
	Orientation to shell surface	Vertical	Almost vertical	Parallel	Oblique	Radiated	Almost vertical	Vertical
Crystal	Form and Aggregation	Grannular - lathy Aggregation	Acicular Aggregation	Acicular Aggregation	Finely prismatic "Single crystal"	Finely prismatic "Single crystal"	Finely prismatic "Single crystal"	Finely prismatic "Single crystal"
	Arrangement pattern	Slightly oblique (Finely crossed)	Feathery	Feathery	--------	--------	--------	--------
Organic matrix	Interprismatic matrix	Acidophil	Acidophil / Acidophil and Basophil	Basophil	Basophil	Basophil	Basophil	Basophil
	Intraprismatic matrix	Basophil	Basophil	Basophil	--------	--------	--------	--------
Most relative structure		--------	Composite prismatic str.	Aragonite simple prismatic str.	Foliated str.	Difference of morphological orientation of prisms		
Main distribution		Outer layer of the Pinnacea and the Pteriacea.	Outer layer of the Unionoida.	Outer layer of some Veneroida.	Outer layer of the Mytilacea.	Outer layer of the Myoida. Regenerated shell.	Innermost layer of some snails. Regenerated shell.	Myostracum of molluscan shell.

Decalcified samples were prepared for SEM observations through the following process: Fractured or polished preparations were fixed in 2.5% glutaraldehyde solution for approximately three hours and treated with 0.5M EDTA for several hours to obtain the partially or entirely decalcified preparations. Subsequently, they were again soaked in the above-mentioned fixing solution for 1-3 hours and rinsed in distilled water. Some of them were frozen with dry ice and dried in a vacuum system. Others were dehydrated in a graded ethanol series; then, through isoamyl acetate, they were dried by a critical-point-CO_2 method.

Preparations were glued to brass stubs, coated with evaporated carbon-gold and observed with a JEOL JSM-U_3 scanning electron microscope, which were operated at 15 or 25 KV.

Observation

It follows from an overall examination of seven prismatic structures, stated above, that they can be grouped into two different types on the seeming basis of prism chamber size: megaprism group, 20-100 microns in chamber diameter, consisting of the calcite simple, aragonite simple and composite prisms; microprism group, 0.5-5 microns in chamber diameter, consisting of the rest of the prisms. Megaprisms are found only in the outer layers of bivalves, each prism appearing to be built up of many smaller calcium carbonate crystals, 0.1-2 microns in diameter, while microprisms are found in the special layers of shells, appearing to be composed a single crystal.

The main emphasis of this study was placed in reexamination of the interior (intraprismatic) appearance of several megaprisms, with careful observations of coexisting relationships between mineral and organic matrices within a prism as well as inter- and intraprismatic organic matrices. Such observations were very favorably carried out on the preparations which were treated with the critical-point-CO_2 method (see also Uozumi and Suzuki, 1979).

Calcite simple prisms of *Pinctada* show the irregular granular pattern, 0.1-0.3 microns in diameter, in horizontally fractured surfaces. The peeled surfaces of interprismatic organic walls are occasionally ornamented with a large number of linear bands and bead-like cords, as shown in Pl.1, Fig.6. However, the intraprismatic organic matrix is hardly observed on the fractured surfaces which were untreated with any decalcified solution, as shown in P1.3,

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Explanation of Plate 1

Figs. 1,4,5 Vertical sections of calcite simple prisms of *Pinctada fucata martensii.* The preparations were polished and then etched heavily with EDTA prior to drying with the critical-point-CO_2 method. Note that a prism abounds surprisingly in an intraprismatic spongy organic matrix.
Fig. 1: × 300; Fig. 4: × 3,000; Fig. 5: × 2,500.

Figs. 2,3 Oblique sections of calcite simple prisms of *Pinctada fucata martensii.* The preparations were etched heavily with EDTA prior to drying with the critical-point-CO_2 method. Fig. 2: × 500; Fig. 3: × 1,000.

Fig. 6 A fracture section of calcite simple prisms of *Pinctada fucata martensii.* The preparation was not treated with any solution. Note that an interprismatic wall (right) is ornamented with many linear bands and bead-like cords, and that it is difficult to discern an intraprismatic matrix on the vertical fracture surface of the prism (central). × 1,500.

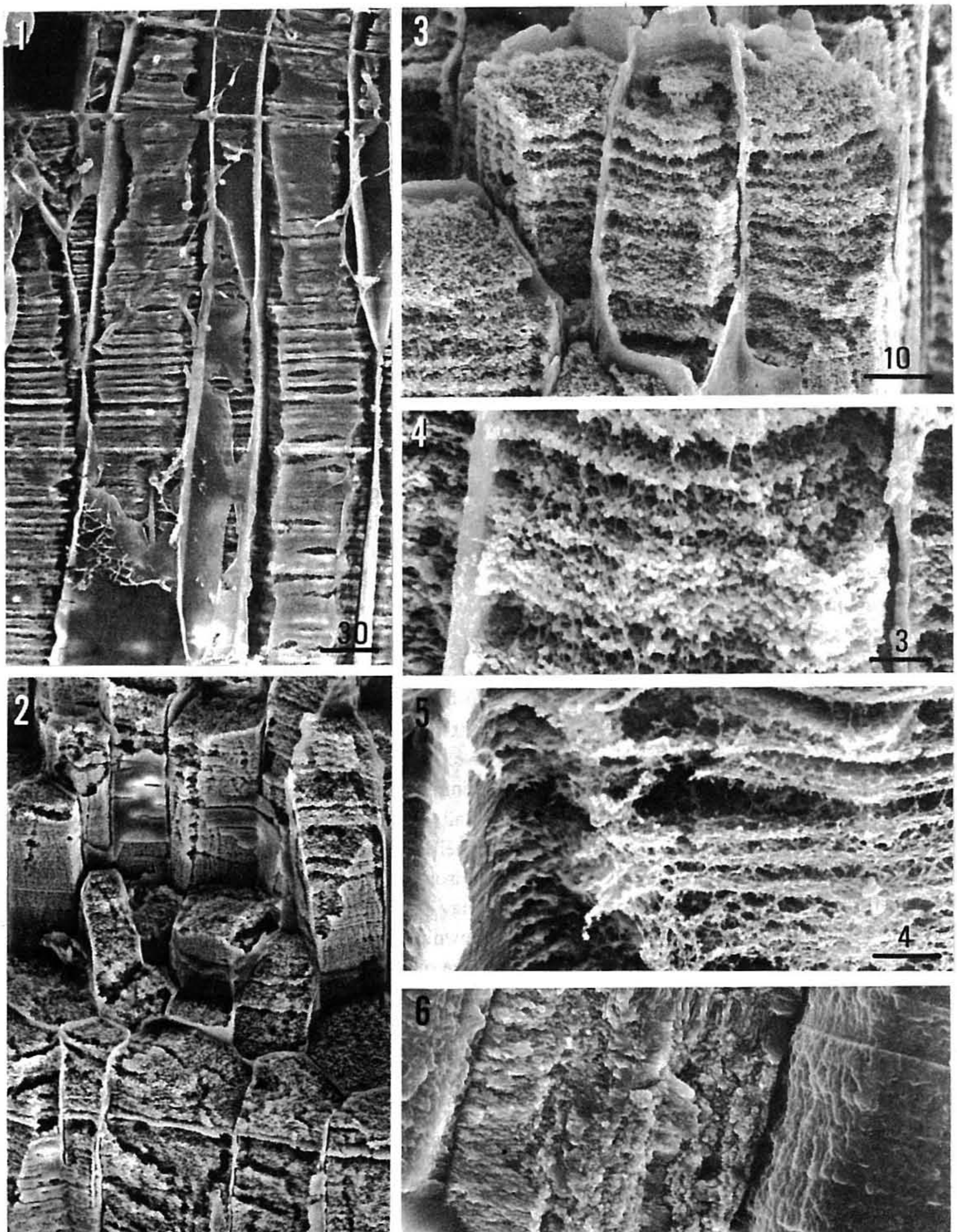
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Fig.3. In the almost fully decalcified preparations, it is noticed that the intraprismatic matrix is present rather abundantly within the prism. When observed at low magnification, the intraprismatic matrix appears to seemingly consist of sheet-like substances, which are transverse to the axis of the prism and parallel, aligned with each other, as shown in Pl.1, Figs.1,2. The apparent thickness of a sheet-like substance, mentioned above, which ranged up to 1 micron, is thicker than the vertical wall (interprismatic wall) of the prism. When observed at higher magnification, each sheet-like substance is not observed as a rigid sheet, but is rather a substance as spongy as shown in Pl.1, Figs.3-5. The sheet-like appearance at low magnification may result from the rhythmic alternation of compactness and looseness of the spongy substance. Such a change in density of the organic spongy substance may be accompanied with the growth pattern of the prism. When observed on partially decalcified preparations, fine acicular crystals, 0.1-0.2 microns in diameter, are found within the prism, inclining about 30 degrees to the axis of the prism, as shown in Pl.3, Fig.4. The morphological orientation of crystals appears not to be closely connected with the transverse organic spongy substances. In some cases, the arrangement of acicular crystals shows a finely crossed pattern, as shown in Pl.3, Fig.5. Such an arrangement resembles the crystal architecture of the homogeneous layer in an electron microscopic level (Taylor *et al.*, 1973, Pl.8, Fig.6). In calcite simple prisms of *Malleus* shells, minute crystals within the prism are more or less different in form and morphological orientation in comparison with that of *Pinctada.* They appear to be laths and aligned, obliquing steeply to the axis of the prism, as shown in Pl.3, Fig.2. But they appear to have no connection with the transverse spongy substances in the same manner as that of *Pinctada.*

Two types of aragonite megaprisms are known *i.e.* aragonite simple prisms and composite prisms. The former have seemed, heretofore, to have a close relationship with calcite simple prisms. Such an assumption may be probably traceable to the morphological similarity of prisms and their vertical arrangements to the shell surface. Namely, both simple prisms are usually of the pentagonal or the hexagonal column and are separated entirely or partially from their neighbor by a thick interprismatic wall, as shown in Pl.2, Figs.1-4. And they are arranged almost vertically to the surface of shells. Meanwhile composite prisms are not delineated by a thick and rigid wall in comparison with that of two simple prisms. This interprismatic wall appears to be a rather spongy substance, which is fairly similar to the intraprismatic matrix within the prism, as shown in Pl.5, Figs.1-4. Moreover, composite prisms are arranged almost in parallel to the surface of shells.

Nevertheless, from the viewpoints of architecture of a prism, composite prisms appear to rather resemble aragonite simple prisms, as shown in Pl.3, Fig.1 and Pl.4, Fig.4. Firstly, both prisms, now a question in point, are built up of smaller aragonite crystals; secondly, they show seemingly a feathery internal appearance. Of course, minor differences between

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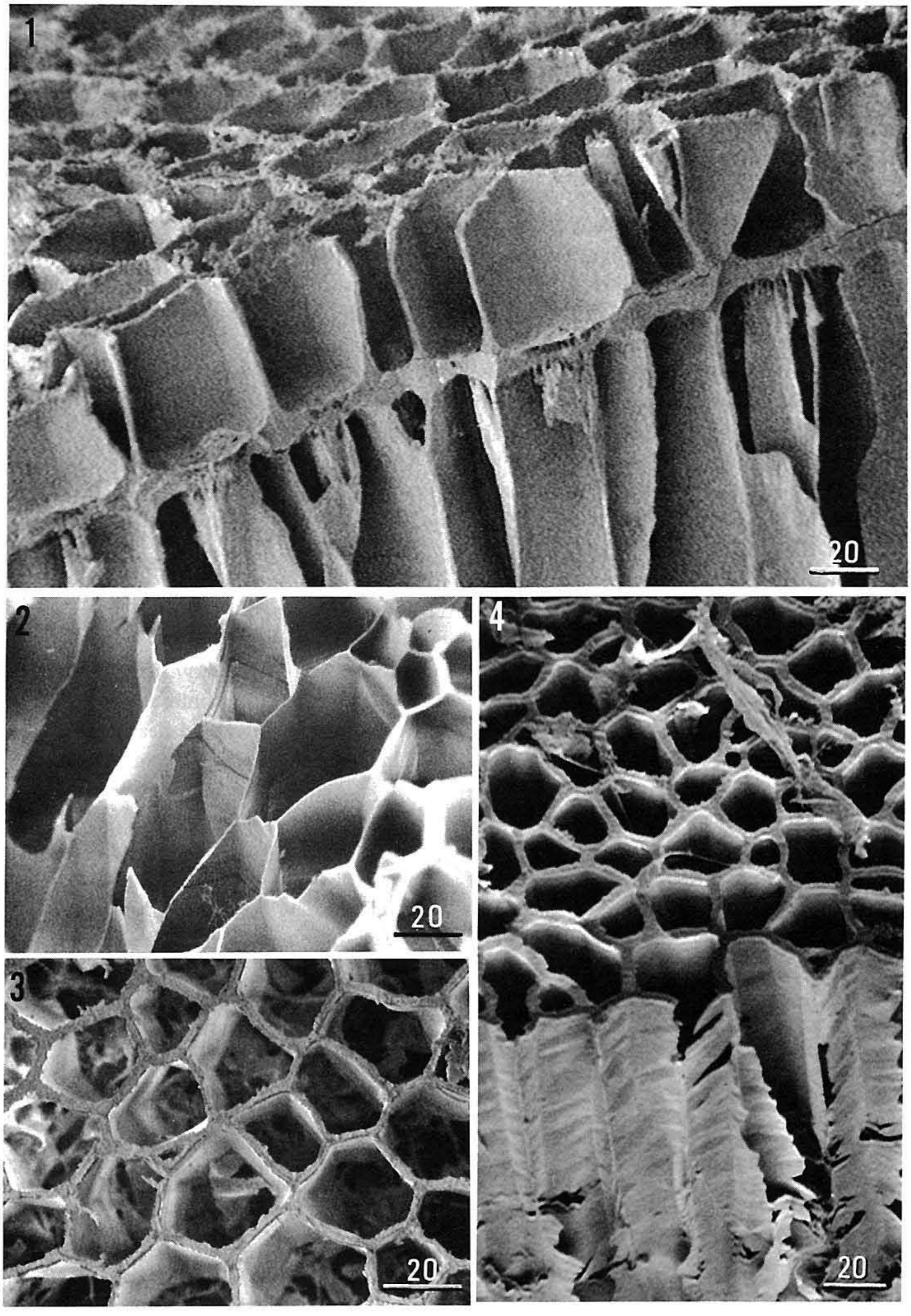
Explanation of Plate 2

Figs. 1-4 Interprismatic rigid walls of calcite simple prisms of *Crassostrea gigas* (Figs. 1,2) and *Atrina pectinata* (Figs. 3,4). The preparations were decalcified entirely with EDTA prior to a treatment with the freeze-dry method. Note that intraprismatic organic matrices have been almost completely fallen off in the freeze-drying method. Fig. 1: × 500; Fig. 2: × 500; Fig. 3: × 600; Fig. 4: × 500.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them will be recognized in the arrangement of crystals, although their feathery appearance closely resemble each other. In aragonite simple prisms, minute aragonite crystals are scale-like in form, variable in size, and not so orderly in arrangement. In composite prisms, minute aragonite crystals are acicular in form and arranged in an appearance of orderly radiation, which is produced by acicular crystals diversing from the axis of the prism. Moreover, in the decalcified preparations, aragonite simple prisms are remarkable to be crossed rhythmically by numerous transverse organic layers, as seen in calcite simple prisms, as shown in Pl.4, Figs.2,3. Meanwhile, composite prisms are not so remarkably crossed by transverse organic layers as shown in Pl.5, Figs.1,4. Also, the morphological orientation of scale-like crystals within a prism appears to have no connection with such rhythmic transverse organic layers. Organic sheaths, which envelop each crystal, excepting such transverse organic layers, may be present within the simple prism, although a satisfactory photograph to discern them clearly has not been obtained yet.

In comparison with aragonite simple prisms, the intraprismatic matrix of composite prisms seems to be the striking "cast-off skin" of crystals. Prisms are surrounded by spongy walls and the interior of a prism is almost filled up with the intraprismatic organic substances which are made up of many organic sheaths. They appear to enclose each acicular crystal and be arranged as a whole in a radiated appearance within the interprismatic wall, as shown in Pl.5, Fig.4.

Apart from the architecture of prisms, it is necessary to look into the state of development and the histochemical natures of the interprismatic wall. As for the former, the walls of megaprisms are divisible into three types: rigid wall, compound wall (rigid in the upper half and spongy in the lower half) and spongy wall. The first is commonly found in the most typical prisms such as calcite simple prisms of *Pinctada* and aragonite simple prisms of *Anodonta* as shown in Pl.4, Figs.2,3; in this case every prism is delineated clearly from its neighbor by a thick rigid wall. The second is found in the aragonite simple prism of *Unio* as shown in Pl.4, Fig.1, and the upper half of the prism is enveloped by a rigid wall, which is closely similar to that of the first, and the lower half of it is enveloped by a spongy wall. The third is commonly found in composite prisms of *Tapes* and *Peronidia*, and the morphological appearance of the wall is very similar to the spongy wall of the lower half of the second type. In other words, the second type seems to be intermediate between the first and the third. Moreover, the rigid wall of the first type appears to be smoothly continuous to the

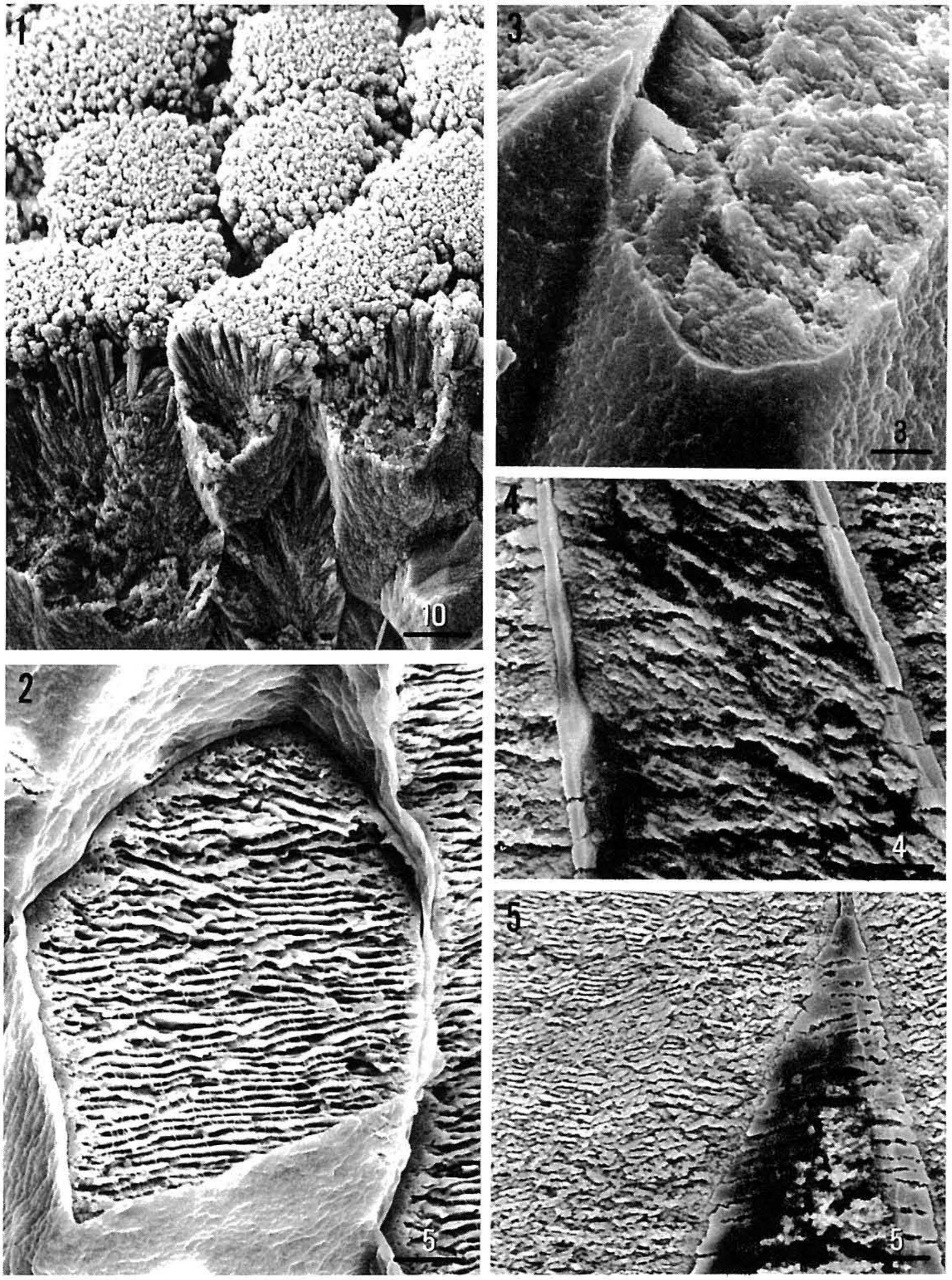
Explanation of Plate 3

Fig. 1 An oblique section of composite prisms of *Tapes philippinarum.* The preparation was treated briefly with sodium hypochlorite solution to remove organic materials. × 1,000.

Fig. 2 An oblique section of calcite simple prisms of *Malleus albus.* The preparation was partially decalcified with EDTA prior to drying with the critical-point-CO_2 method. Note that lathy crystals and fibrous intraprismatic matrix can be clearly discerned. × 2,000.

Fig. 3 An oblique fracture surface of calcite simple prisms of *Pinctada fucata martensii.* The preparation was not treated with any solution. × 3,000.

Figs. 4,5 Vertical sections of calcite simple prisms of *Pinctada fucata martensii.* The preparations were treated briefly with EDTA after polishing. Note that the arrangement of acicular crystals shows a finely crossed pattern which is fairly similar to that of a homogeneous structure in an electron microscopic level. Fig. 4: × 2,500; Fig. 5: × 2,000.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periostracum of a shell in its uppermost edge. Probably the rigid wall and periostracum may be made up of the similar organic matrix. Meanwhile, spongy wall appears to be continuous to the intraprismatic matrix within a prism. The intraprismatic matrices of megaprisms, irrespective of the wall types, are similar to each other in morphological appearance.

From the histochemical features of interprismatic walls, the rigid wall, stated above, is acidophilic like the periostracum of a shell, while the spongy wall is as basophilic as the intraprismatic matrix (Wada, 1964; Suzuki and Uozumi, 1979). On the contrary, it is remarkably noticed that inter- and intraprismatic matrices of microprisms are all basophilic without exception.

The main characteristic of three megaprisms, together with that of four microprisms, are summarized in Table 1.

Summary

1) Seven types of the so-called prismatic structures have been hitherto known. From the size of a prism and the aggregated pattern of constituting crystals within it, prisms are classified into two groups: megaprism and microprism groups. The former is represented by the calcite simple prismatic structure; its prism is comparative as large in size as several ten microns in diameter, and built up of many smaller crystals. The latter is represented by the fibrous prismatic structure; its prism is so small as several microns in diameter, and built up of a "single crystal".

2) The megaprisms are divided further into three types from the nature of the interprismatic organic wall. That is, their organic walls are rigid, or compound (partly rigid and partly spongy) or spongy. As for the wall the second type is intermediate between the first and the third, and is found among some aragonite simple prisms. Calcite simple prisms are all enclosed by the wall of the first type, and composite prisms are the wall of the third type.

It may be said that the simple prisms, associated with the wall of the first type, are comparatively primitive among megaprisms and that such an interprismatic wall has tended to decline in the course of evolution of the megaprism series.

3) The intraprismatic organic matrix exists surprisingly abundantly within all megaprisms, although it has not been observed adequately until the present time. The morphological appearance of its matrix is spongy, resembling that of the spongy interprismatic wall, stated above. Such a matrix is also similar to the those of the inter- and

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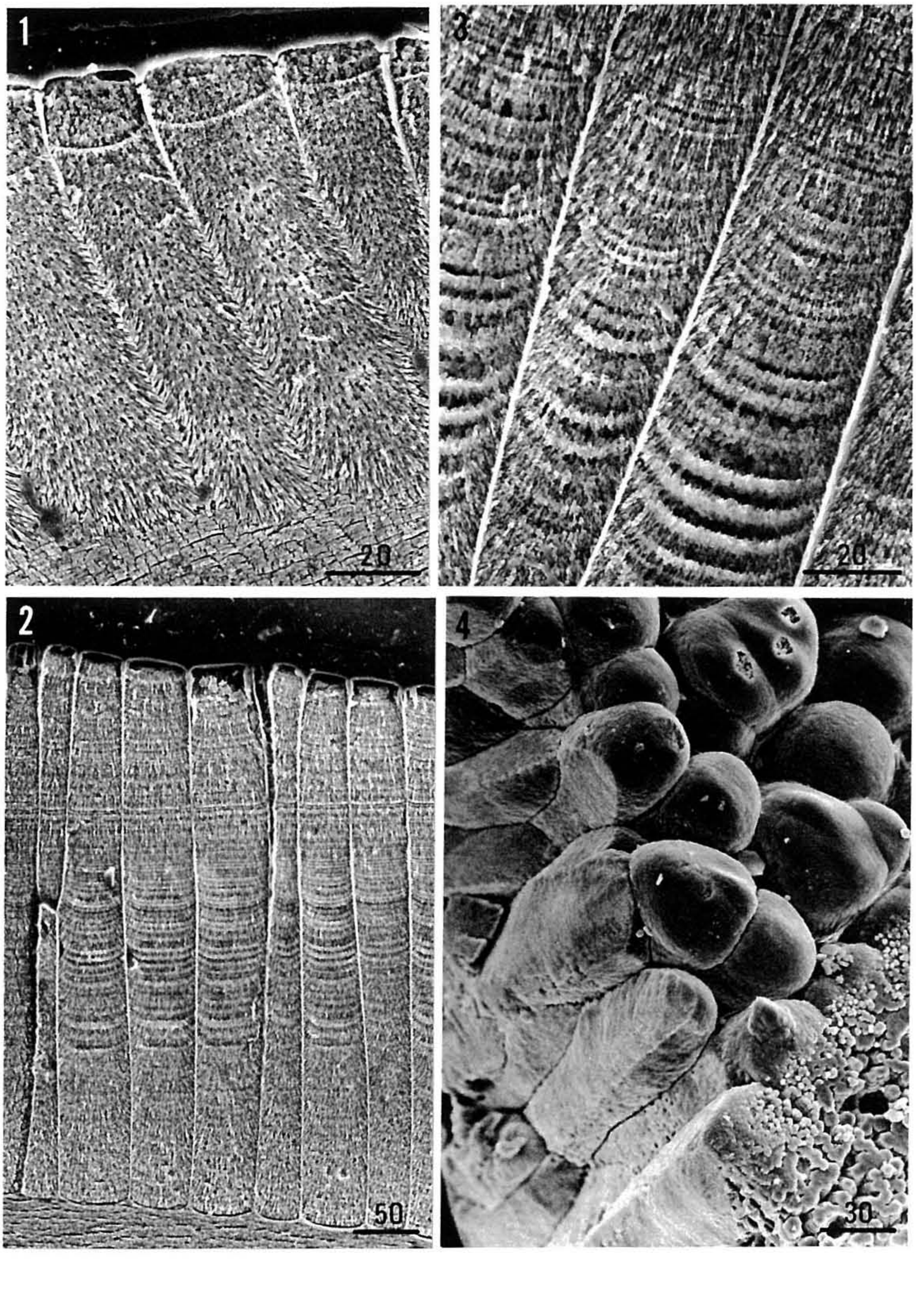
Explanation of Plate 4

Fig. 1 A vertical section of aragonite simple prisms of *Unio douglasiae*. The preparation was etched briefly with EDTA after polishing. Note that an interprismatic rigid wall cannot be discerned in the lower half of prisms. × 750.

Fig. 2 A vertical section of aragonite simple prisms of *Anodonta woodiana*. The preparation was etched briefly with EDTA after polishing. Note that an interprismatic rigid wall envelops the prism fully from and to end. × 200.

Fig. 3 Higher magnification of prisms in Fig. 2 showing the feathery appearance of aragonite crystals within a prism. × 750

Fig. 4 Aragonite simple prisms of *Unio douglasiae* showing the inner (growth) surface (upper right) and the peeled surface of the side wall (lower left) of prisms. × 400.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intraprismatic matrices of microprisms.

4) From the histochemical viewpoints, the above-mentioned spongy matrix, regardless of being inter- or intraprismatic, is all basophilic. Meanwhile, the rigid wall is as acidophilic as the periostracum of a shell. Probably it seems that the spongy matrix will have some connections with mineralization of a prism. But the rigid wall will not be entirely associated with mineralization of a prism, nor the periostracum either.

5) Microprisms have been roughly observed for a comparison with megaprisms. They are found in a special limited shell layer; each prism is built up of a "single crystal". The organic matrices of them, inter- and intraprismatic, are all basophilic without exception. Assumably microprisms appear to be formed and mineralized in a somewhat different process in comparison with that of megaprisms.

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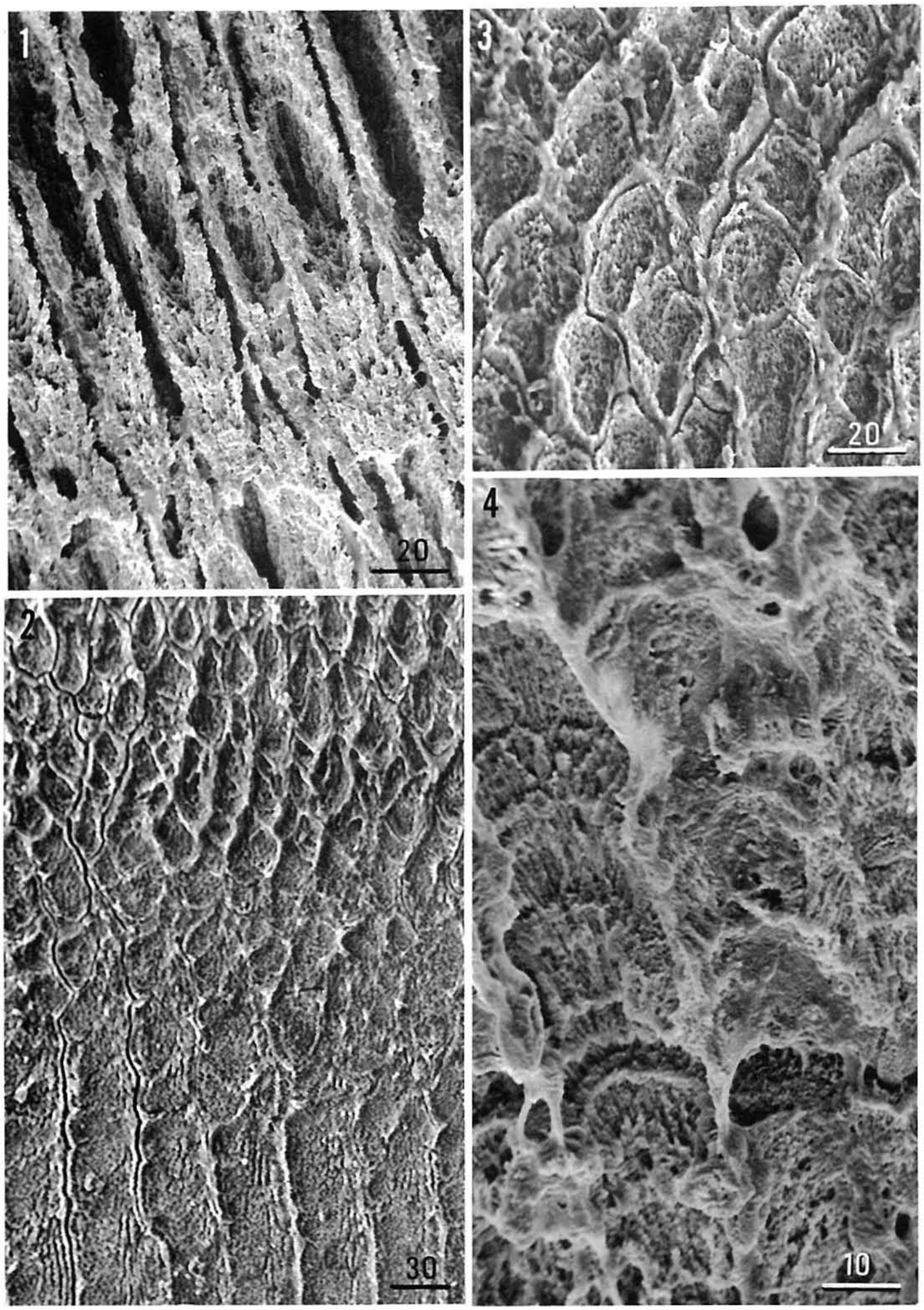
Explanation of Plate 5

Figs. 1-4 The decalcified composite prismatic organic matrix of *Tapes philippinarum.* Oblique sections of prisms were decalcified entirely or partially with EDTA after polishing, and subsequently treated with the freeze-dry method. Note that it is difficult to discern an interprismatic rigid wall, while an intraprismatic spongy matrix is surprisingly abundant and is like a striking "cast-off skin" of feathery arranged crystals within a prism.

Figs. 1 and 4: Entirely decalcified prisms. × 600; × 1,200. Figs. 2 and 3: Partially decalcified prisms. × 300; × 600.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