

# ARCHITECTURAL CONSTRAINTS ON THE MORPHOGENESIS OF PRISMATIC STRUCTURE IN BIVALVIA

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**ABSTRACT.** Microscopic features of the regular simple, fibrous and non-denticular composite prismatic structures in twenty seven living and eight fossil bivalve species have been examined. Geometrical selection and reclination of prisms caused by competition for space were recognized in many species. The regular simple and non-denticular composite prisms are expressed as a product of aggregated spherulites, while the fibrous prisms as needle aggregates in druses. The main factor which causes geometrical selection of prisms is irregularity of the settling time among prisms. The density of prisms at the first stage appears to be a principal parameter controlling the degree of geometrical selection. The ratio of accretionary rate to growth rate of prisms at the shell edge mainly determines whether prisms become straight or reclined. Various architectural varieties of the prismatic structure can, therefore, be explained by the geometrical selection model originally developed for inorganic systems.

THE study of evolution of organisms in the Earth's history necessarily depends upon the morphology of fossilized hard tissue. In recent years, many palaeontologists have investigated the microstructure of such hard tissues and the process of their biomineralization, and has proved important for systematics, morphogenesis and palaeoecology. Especially in the Bivalvia, shell microstructure has been regarded as one of the important taxonomic characters (Bøggild 1930; Taylor *et al.* 1969, 1973; Carter 1980a, 1991; Uozumi and Suzuki 1981; Carter and Clark 1985). However, the variation in shell microstructure has not yet been satisfactorily explained. Until now, research on biomineralization has concentrated on physicochemical factors such as ion movement (Simkiss 1976; Enyikwola and Burton 1983), nucleation (Garside 1982; Greenfield *et al.* 1984), chemical composition of extrapallial fluid (Crenshaw 1972; Wada and Fujinuki 1976; Misogianes and Chasteen 1979), and function of organic matrix (Weiner and Traub 1984; Williams 1984).

The present paper focuses on the morphogenesis of bivalve biomineralization, which links the physical chemistry (mechanisms of formation of biominerals) and morphology (microstructure of hard tissues). Morphogenesis of the microstructure is discussed from the point of view that geometrical features of crystals are restricted by architectural constraints. It is generally thought that the microstructure of hard tissues is strongly controlled by phylogenetic factors (Kobayashi 1980, 1988), but it is also important to consider adaptational or architectural aspects of the constructional morphology (Seilacher 1970, 1973). Architectural convergence or divergence of shell microstructure may be controlled by geometrical or spatial rather than phylogenetic constraints. This is especially likely in the formation of molluscan shells, because they are made of closely packed aggregations of calcite or aragonite crystals. Prismatic structure is particularly suitable for morphogenetic analysis in relation to architectural constraints because (1) it is organizationally simple and consists of relatively large elements (prisms) which are easily observed under a microscope, (2) its mode of formation is assumed to be strongly influenced by spatial restriction, and (3) it is readily preserved in fossils, so that we can deal with both extant and extinct materials.

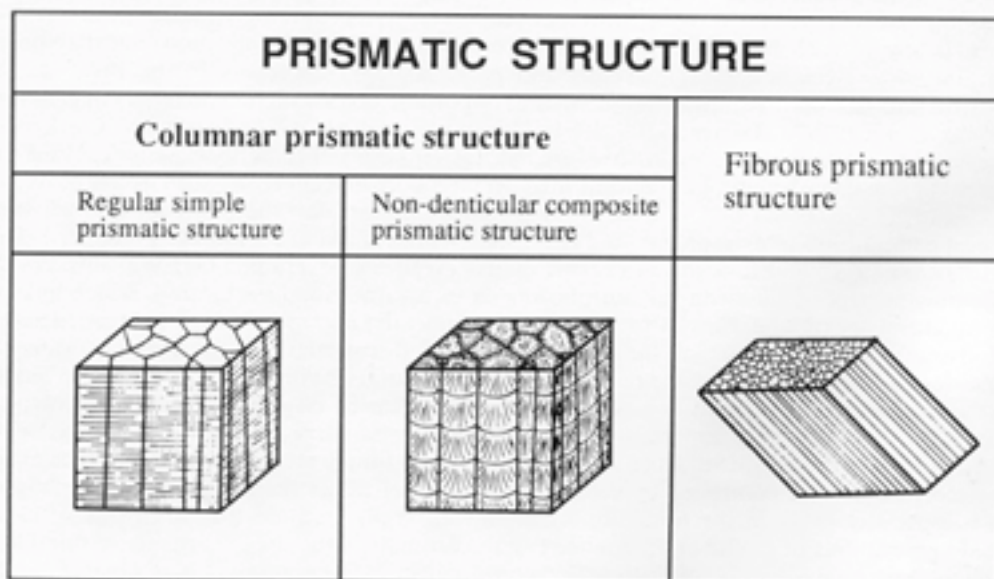
During growth of many mineral aggregates, a characteristic competition for space between neighbouring crystallites is common in nature (Grigor'ev 1965). Grigor'ev demonstrated that the group growth of spherulites on an uneven surface, and the growth of druses from the randomly

oriented incipient crystals, necessarily cause geometrical selection, i.e. termination of prisms by competition for space. Taylor *et al.* (1969) interpreted the morphology of prisms in bivalve shells using this geometrical selection model of spherulite growth, and it seems an excellent explanation for the morphogenesis of the prismatic structures from the viewpoint of spatial restriction. However, several questions arise. Does geometrical selection occur commonly in the formation of various prismatic layers of bivalves? What factors cause geometrical selection, and what parameters control the competition among prisms which is considered to determine the morphology of each prism and appearance of the microstructure?

The purpose of this paper is to evaluate the architectural constraints on the morphogenesis of the prismatic structure in the Bivalvia. For this purpose, the author has investigated the variation and the mode of crystal growth of the regular simple, fibrous and non-denticular composite prismatic structures in many living and fossil species, and considered the parameters which determine the geometrical features of prisms during successive stages of crystal growth.

#### NOTES ON PRISMATIC STRUCTURE IN BIVALVIA

According to Carter and Clark (1985) and Carter *et al.* (1991), prismatic structure consists of parallel, adjacent structural units (first order prisms) that do not strongly interdigitate along their mutual boundaries. Neighbouring prisms are surrounded and bounded by a sclerotized organic matrix. Prismatic structure has been subdivided into various groups (Bøggild 1930; Carter 1980a, 1980b; Uozumi and Suzuki 1981; Carter and Clark 1985; Kobayashi 1988; Carter *et al.* 1991), but in this paper only the regular simple prismatic, fibrous prismatic and non-denticular composite prismatic structures were investigated (Text-fig. 1).



TEXT-FIG. 1. Schematic block diagrams of the three types of prismatic structure used in this paper. The informal term 'Columnar prismatic structure' is used to unite the regular simple and the non-denticular composite prismatic structure.

In the nomenclature of Carter *et al.* (1991), regular simple prismatic structure consists of columnar calcite or aragonite prisms whose elongation axes are arranged nearly perpendicular to the outer shell surface. Each regular simple prism is not a single crystal (Wada 1956, 1958, 1961;

Watabe and Wada 1956) but lacks diverging arrangements of its second-order subunits. Non-denticular composite prismatic structure consists of columnar prisms as in the regular simple prismatic structure, but each prism consists of second-order diverging units toward the depositional surface. In this paper, the author uses the informal term 'columnar prismatic structure' which includes both the regular simple and the non-denticular composite prismatic structures. Fibrous prismatic structure consists of elongate calcite or aragonite prisms which are more slender than in regular simple prismatic structure. The elongation axes of fibrous prisms are commonly reclined or nearly parallel rather than perpendicular to the plane of the shell surface (Carter and Clark 1985). Suzuki and Uozumi (1981) mentioned that each fibrous prism consists of a single crystal without any particular intraprismatic microstructure.

Prisms are initially secreted on the inner surface of the periostracum at the growing shell edge, forming polygonal blocks on the outer shell surface. Growth of prisms is limited to one direction, namely inward, and as prisms elongate the prismatic layer becomes thicker. The periostracum and organic matrix are considered to play an important role in the calcification of prisms (Taylor and Kennedy 1969; Saleuddin and Petit 1983; Wilbur and Saleuddin 1983; Lowenstam and Weiner 1989; Simkiss and Wilbur 1989). There are irregularly spaced horizontal bands of organic material in the prisms (Watabe and Wada 1956; Wada 1957; Grégoire 1972), but it is uncertain whether or not these horizontal organic layers interrupt crystal growth.

#### MATERIALS AND METHODS

A total of thirty five species of extant and fossil bivalves were studied (Tables 1–2). Their surfaces and sections were observed by scanning electron microscopy (Hitachi S-2400) and optical microscopy (Olympus AHB7).

##### *Preparation for SEM*

For observation of fractured surfaces, the shell in all species was broken by hand normal to the outer shell surface and dried in air. Specimens of seven species were embedded in gypsum or epoxy resin and polished with carborundum and diamond paste. For observation of the intraprismatic microstructure, the polished surface was etched with 0.5 M EDTA solution buffered at pH 7–8 for several hours, and then critical-point-dried using a Hitachi HCP-2 machine. In order to remove the periostracum perfectly, the shells of *Anodonta woodiana* and *Pinctada fucata* were etched by a 3N aqueous solution of sodium hydroxide or sodium hypochlorite for several days, and the outer shell surface was observed. For observation of the initial stage of prism growth on the inner surface of the periostracum, the shell edge adjacent to the periostracum in *Atrina pectinata*, *Pinctada margaritifera*, *Isognomon ephippium*, *I. legumen*, *Ostrea denselamellosa*, *A. woodiana*, *Mytilus californianus* and *M. galloprovincialis* was carefully removed from the shell under a binocular microscope. In *M. californianus* and *M. galloprovincialis* the periostracum was etched with a solution of sodium hypochlorite. For SEM observations, all specimens were coated with platinum vanadium by an ion coater (Eiko IB-5).

##### *Preparation for optical microscopy*

Shells of most species were cut normal to the outer shell surface. These specimens were embedded in gypsum or epoxy resin and polished with carborundum. The polished plane of each specimen was etched with 5 per cent acetic acid for one minute, washed, and air dried. Subsequently an acetate peel was prepared for each specimen (Kennish *et al.* 1980), which were observed under ordinary light microscopy. Those of the prismatic shell were photographed and the number of prisms in the scale equivalent to a 1 mm length was counted on the photograph, to measure their size and density.

TABLE 1. List of extant specimens examined.

Family	Species	Sampling locality
Pteriidae	<i>Pinctada fucata</i> (Gould, 1850)	Aburatsubo Cove, Miura Peninsula, Kanto, Japan
	<i>P. margaritifera</i> (Linnaeus, 1758)	Ishigaki Island, Okinawa, Japan
	<i>P. maxima</i> (Jameson, 1901)	Indian Sea
	<i>Pteria breviajata</i> (Dunker, 1872)	Shikanoshima near Fukuoka, Kyushu, Japan
Isognomonidae	<i>Isognomon nucleus</i> (Lamarck, 1819)	Iriomote Island, Okinawa, Japan
	<i>I. ephippium</i> (Linnaeus, 1758)	Iriomote Island, Okinawa, Japan
	<i>I. legmen</i> (Gmelin, 1791)	Iriomote Island, Okinawa, Japan
	<i>I. perna</i> (Linnaeus, 1758)	Iriomote Island, Okinawa, Japan
Malleidae	<i>Malleus regula</i> (Forskål, 1775)	Iriomote Island, Okinawa, Japan
Pinnidae	<i>Atrina pectinata</i> (Linnaeus, 1758)	Osaka Bay, Kinki, Japan
	<i>A. teramachii</i> Habe, 1953	Amakusa Islands, Kyushu, Japan
	<i>A. vexillum</i> (Born, 1780)	Singapore
	<i>Pinna muricata</i> Linnaeus, 1758	Iriomote Island, Okinawa, Japan
Ostreidae	<i>P. nobilis</i> Linnaeus, 1758	Amakusa Islands, Kyushu, Japan
	<i>Crassostrea gigas</i> (Thunberg, 1793)	Aburatsubo Cove, Miura Peninsula, Kanto, Japan
Gryphaeidae	<i>Ostrea denselamellosa</i> Lischke, 1869	Iriomote Island, Okinawa, Japan
	<i>Neopycnodonte musashiana</i> (Yokoyama, 1920)	Amakusa Islands, Kyushu, Japan
Mytilidae	<i>Mytilus californianus</i> Conrad, 1837	Neah Bay, California, USA
	<i>M. galloprovincialis</i> Lamarck, 1819	Shikanoshima near Fukuoka, Kyushu, Japan
	<i>M. grayanus</i> , Dunker, 1853	Soya near Wakkanai, Hokkaido, Japan
Propeamussiidae	<i>Propeamussium sibogai</i> (Dautzenberg and Bavay, 1904)	Port Darwin, Northern Territory, Australia
	<i>P. sp.</i>	Owase, Kinki, Japan
Unionidae	<i>Anodonta woodiana</i> Lea, 1834	Biwa Lake, Kinki, Japan
	<i>Cristaria plicata</i> (Leach, 1815)	Biwa Lake, Kinki, Japan
	<i>Lanceolaria oxyrhyncha</i> (Martens, 1861)	Biwa Lake, Kinki, Japan
	<i>Unio daglasiae</i> (Griffith and Pidgeon, 1834)	Biwa Lake, Kinki, Japan
Trigoniidae	<i>Neotrigonia margaritacea</i> (Lamarck, 1804)	French Island, Victoria, Australia

## RESULTS

*Columnar prismatic structure*

SEM observations were made on the fractured surface of the columnar prismatic layer in all species listed in Tables 1 and 2. Various patterns were recognized in the geometry of the prisms. For example, the prismatic shells of *Pteria breviajata*, *Atrina pectinata*, *A. teramachii* and *Neopycnodonte musashiana* are constructed of prisms approximately uniform in width (simple type; Pl. 1, fig. 1). In *Isognomon perna*, *Malleus regula*, *Atrina sp.* and inoceramids, however, the prisms tend to grow continuously, showing a remarkable change in width (branched type; Pl. 1, figs 2-3) (Tsuji *et al.* 1958; Reddy *et al.* 1971). In the latter case, some prisms become larger and continue to grow, but others become smaller with growth and finally disappear within the prismatic layers, where a peculiar feature termed 'prism branching' (Bøggild 1930) or 'geometrical selection' (Taylor *et al.* 1969) is observed.



TABLE 2. List of fossil specimens examined.

Family	Species	Horizon	Locality
Inoceramidae	<i>Inoceramus amakusensis</i> Nagao and Matsumoto, 1940	Uf Member, Upper Yezo Group; Santonian, Cretaceous	Tappu area, Rumoi Province, Hokkaido, Japan
	<i>I. cordiformis</i> Sowerby, 1823	Haborogawa Formation, Upper Yezo Group; Coniacian, Cretaceous	Haboro area, Rumoi Province, Hokkaido, Japan
	<i>I. hobetsensis</i> Nagao and Matsumoto, 1939	Saku Formation, Middle Yezo Group; Turonian, Cretaceous	Tappu area, Rumoi Province, Hokkaido, Japan
	<i>I. undulatoplicatus</i> Roemer, 1849	Uij Member, Upper Yezo Group; Santonian, Cretaceous	Tappu area, Rumoi Province, Hokkaido, Japan
	<i>I. uwajimensis</i> Yehara, 1924	Ubc Member, Upper Yezo Group; Coniacian, Cretaceous	Tappu area, Rumoi Province, Hokkaido, Japan
	<i>Sphenoceramus naumanni</i> (Yokoyama, 1890)	Uf Member, Upper Yezo Group; Santonian, Cretaceous	Tappu area, Rumoi Province, Hokkaido, Japan
	<i>S. schmidti</i> (Michael, 1899)	Osoushunai Formation, Upper Yezo Group; Campanian, Cretaceous	Saku area, Teshio Province, Hokkaido, Japan
Pinnidae	<i>Atrina</i> sp.	Hiraiga Formation, Miyako Group; Aptian, Cretaceous	Hiraiga area, Miyako Province, Tohoku, Japan

The elongation axes of prisms are not always arranged strictly perpendicular to the outer shell surface; for instance, in species such as *Atrina pectinata*, *Pinctada fucata* and *Isognomon ephippium* they are, in *Unio daglasiae*, *Crassostrea gigas*, *Ostrea denselamellosa* and *Malleus regula* they are markedly curved and inclined toward the ventral margin (Pl. 1, fig. 8). The elongation axes of prisms and the growth line of the shell always intersect at 90°.

Geometrical selection is also seen in acetate peels of the shell in several species. For example, in *Pinctada margaritifera* the density of prisms on the inner shell surface is much smaller than that on the outer surface of the prismatic layer (Pl. 1, fig. 6). Increase of average prism size inwards from the outer shell surface was reported in *Crassostrea virginica* by Tsujii *et al.* (1958). As shown in Text-figure 2, in all species examined the number of prisms per millimetre tends to decrease as the prisms grow. Termination of many prisms just below the outer shell surface is clearly seen in the honeycomb-like framework of the intercrystalline matrix in *P. margaritifera* (Pl. 1, fig. 7). Both simple type and branched type may represent end members of the wide variation of columnar prismatic structure, as confirmed in *Isognomon nucleus*, *Atrina vexillum*, *Pinna muricata*, *P. nobilis*, *Anodonta woodiana*, *Cristaria plicata*, *Unio daglasiae* and *Lanceolaria oxyrhyncha* (Pl. 1, fig. 4). Such a remarkable variation in the size, shape and density of prisms is also observed at different positions within a single shell. For instance, *Pinctada fucata*, *P. margaritifera*, *P. maxima*, *Isognomon ephippium* and *I. legumen* often abandon secretion of the shell at their venter, and newly secreted prisms cover the inner surface of the abandoned shell. The size of the newly secreted prisms is generally finer than that of the abandoned venter (Pl. 1, fig. 5). Geometrical selection seems to be prominent in such areas.

Taylor *et al.* (1969) pointed out that if spherulites start to grow on an uneven substratum, the growth of some prisms will be obstructed by the lack of space (Text-fig. 3A-C). This means that each prism may become broader if competition among prisms for occupancy of space is weak (free

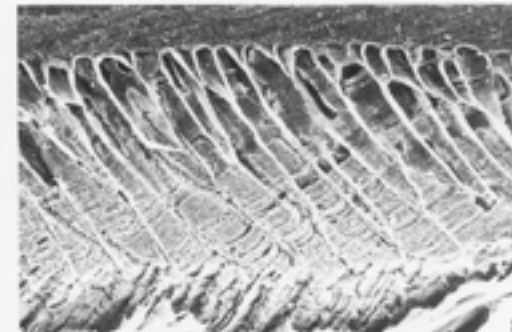
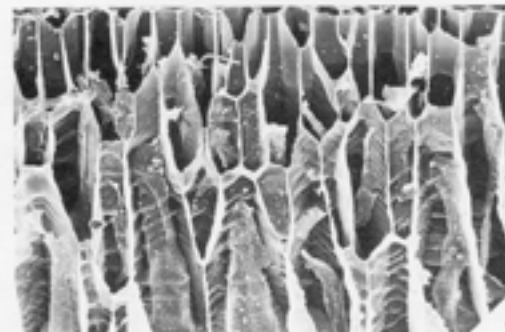
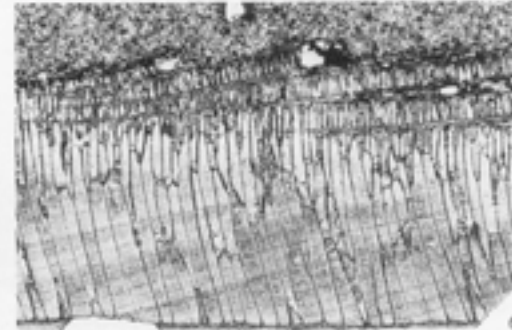
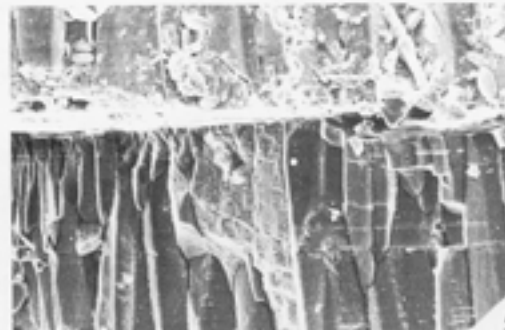
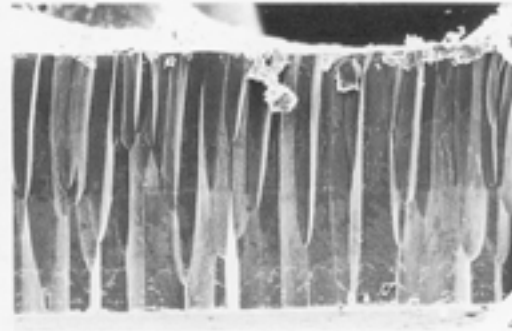
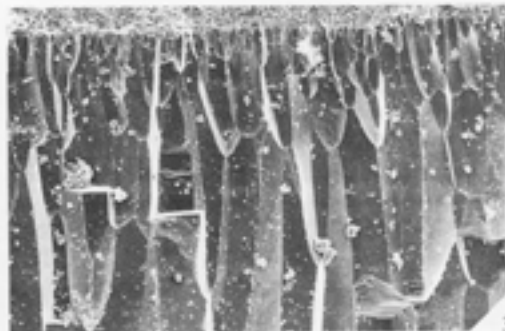
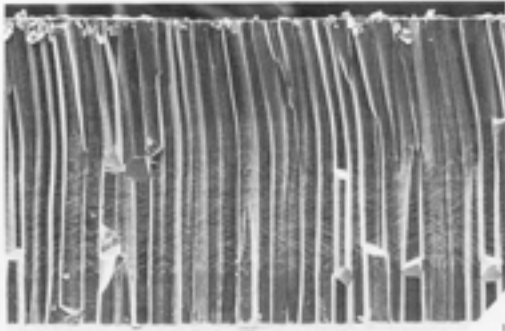
growth of prisms). Thus microscopic observations of the initial stages of crystal growth at the periostracal edge and of intraprismatic microstructures using living bivalves are necessary to understand the growth mode of prisms and its controlling factors. In *Pinctada margaritifera*, *Isognomon ephippium*, *I. legumen*, *Atrina pectinata*, *Ostrea denselamellosa* and *Anodonta woodiana*, many small, hemispherical prisms appear on the inner surface of periostracum at the shell edge, and they represent an initial stage of prism formation. Subsequently, they continued to grow until they came into contact with other prisms at their lateral sides (Pl. 2, figs 1-3; Wada 1961, fig. 8). On the outer shell surface of *A. woodiana*, the boundary of prisms appears to be similar to the contact of growing circles. The boundary between two contiguous prisms is gently curved and the smaller prism projects into the larger prism (Pl. 2, fig. 4). This means that the two prisms were at different stages of growth when they come into contact. In *P. margaritifera* and *A. woodiana*, hemispherical prisms at the shell edge show a marked variation in their size, suggesting a difference in the nucleation time of crystal growth among prisms (Pl. 2, figs 1-2). Sides of the larger hemispherical prisms generally curved inward, while in the smaller ones they are frequently projected toward the outer side. Preformed organic membranes, which may inhibit the crystal growth, do not occur in the initial stage of prism formation at the periostracal edge in any species examined.

Intraprismatic microstructure is observable in the slightly decalcified shells of *Pinctada margaritifera*, *Malleus regula*, *Atrina pectinata*, *Propeamussium sibogai*, *Anodonta woodiana*, *Unio daglasiae* and *Neotrigonia margaritacea*. From SEM observations, three types were recognized in the intraprismatic microstructure of these species. The first, called 'spongy type', is in the regular simple prisms of *P. margaritifera*, *M. regula* and *A. pectinata*. The intraprismatic matrix of this type appears to consist of many tablets which are nearly parallel to the shell surface (Pl. 2, fig. 5). At a higher magnification, intraprismatic organic sheets of this type exhibit a sponge-like structure (Pl. 2, fig. 6). Similar intraprismatic microstructures were reported in *Pinctada fucata* by Suzuki and Uozumi (1981). Within a prism of *A. pectinata*, organic substances arranged parallel to the elongation axis of the prism can be observed under the SEM (Pl. 2, fig. 5). The second type, observed in the non-denticular composite prisms of *A. woodiana*, *U. daglasiae* and *N. margaritacea*, appears to consist of radially diverging aciculate elements and horizontal bands, the latter being gently convex toward the inner direction (aciculate type; Pl. 2, fig. 7). This has been described by Suzuki and Uozumi (1981), and Carter and Lutz (1991). The third type is a foliate intraprismatic microstructure present in propeamussiids (microfoliate type) (Pl. 2, fig. 8; Pl. 3, fig. 1), which was described by Hayami (1988a, 1988b) in *Propeamussium watsoni* and *Cyclopecten bistriatus*. The foliation in this type seems to be nearly radial.

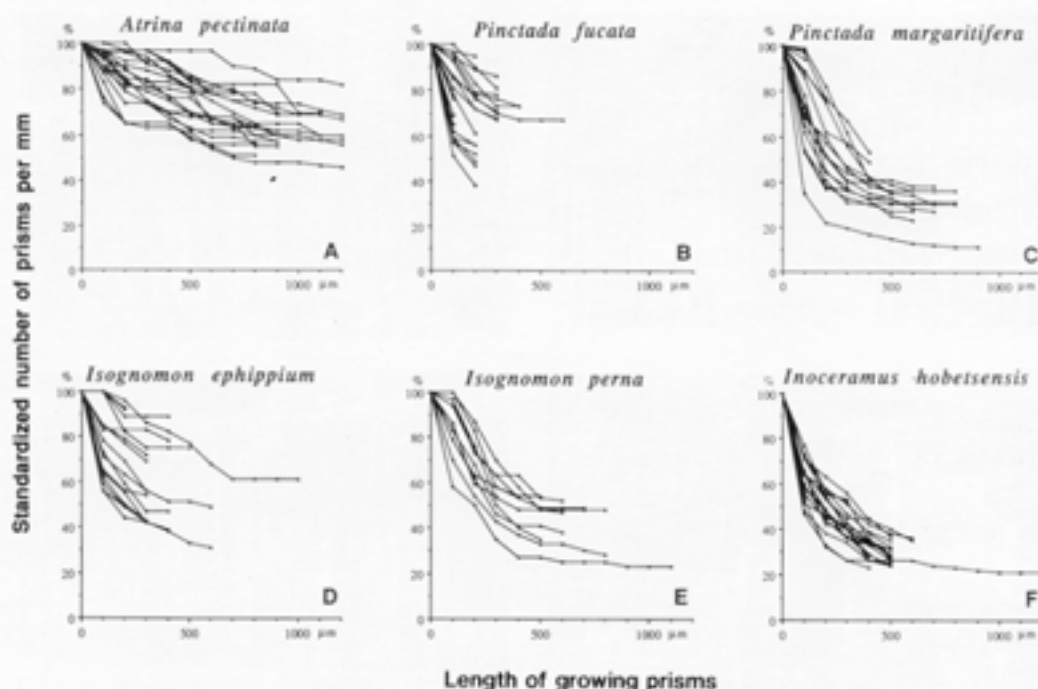
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#### EXPLANATION OF PLATE I

- Figs 1-5. SEM photographs of vertical section of the columnar prismatic shell. 1, *Atrina pectinata* (Linné). UMUT RM 19612; Recent; Osaka Bay, Kinki, Japan; simple type of the regular simple prisms;  $\times 70$ . 2, *Malleus regula* (Forsk.). UMUT RM 19613; Recent; Iriomote Island, Okinawa, Japan; branched type of the regular simple prisms;  $\times 35$ . 3, *Inoceramus hobetsensis* Nagao and Matsumoto. UMUT MM 19614; Saku Formation, Middle Yezo Group, Cretaceous (Turonian); Tappu area, Rumoi Province, Hokkaido, Japan; branched type of simple prisms;  $\times 40$ . 4, *Pinna nobilis* Linné. UMUT RM 19615; Recent; Amakusa Islands, Kyushu, Japan; intermediate type between simple and branched type;  $\times 45$ . 5, *Pinctada margaritifera* (Linné). UMUT RM 19616; Recent; Ishigaki Island, Okinawa, Japan; newly secreted prisms under an abandoned venter;  $\times 120$ .
- Fig. 6. *Pinctada margaritifera* (Linné). UMUT RM 19617; Recent; Ishigaki Island, Okinawa, Japan; optical micrograph of acetate peel of vertical section of the regular simple prismatic shell;  $\times 40$ .
- Figs 7-8. SEM photographs of decalcified columnar prisms. 7, *Pinctada margaritifera* (Linné). UMUT RM 19618; Recent; Ishigaki Island, Okinawa, Japan; conchiolin framework of the simple prisms;  $\times 130$ . 8, *Unio daglasiae* (Griffith and Pidgeon). UMUT RM 19619; Recent; Biwa Lake, Kinki, Japan; reclined type of composite prisms;  $\times 130$ . In each figure, the outer surface of the shell is at the top and the ventral side to the right.



UBUKATA, bivalve prismatic structure



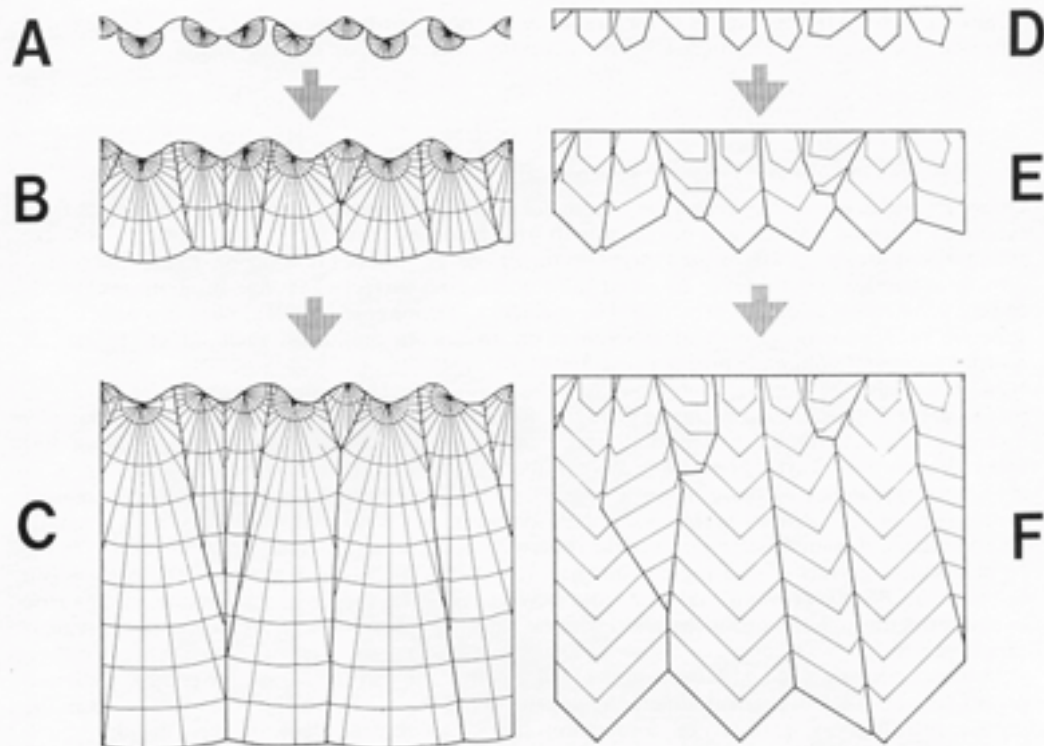
TEXT-FIG. 2. Survival rate of prisms through prism growth in six selected bivalve species. Length of growing prisms represents the distance from the outer shell surface of the prismatic layer. Standardized number of prisms is expressed by the ratio of the number of prisms per millimetre at different stages to the number of prisms on the outer shell surface. Number of prisms per millimetre was counted at various positions on a single shell in vertical section.

In *Propeamussium* sp., the radially elongate simple prisms and the regular simple prisms seem to alternate throughout the growth of the prismatic layer (Pl. 3, fig. 2). Among the radially elongate simple prisms in *P.* sp. geometrical selection occurs in the radial direction. The regular simple prisms in *Propeamussium sibogai* and *P.* sp. do not show geometrical selection because of their growth mode or smaller dimensions. The growth mode of prisms in *Propeamussium* is still unknown, because incipient prisms could not be found in any specimen examined.

#### *Fibrous prismatic structure*

Fractured surfaces of the fibrous prismatic layers were examined in *Mytilus californianus*, *M. galloprovincialis* and *M. grayanus*. Long and narrow prisms are regularly arranged with their elongation axes reclined or nearly parallel to the outer shell surface. However, in the early stage the prisms are rather fine (about 0.5 μm in diameter) and exhibit an irregular spherulitic structure (Pl. 3, figs 3-4). The prisms become coarser as crystals grow and finally attain a uniform diameter (2-5 μm) and are inclined to the shell surface. Similar changes of the size and orientation of prisms during their growth were described by Uozumi and Suzuki (1981) in *M. galloprovincialis* and by Uozumi and Iwata (1969a, 1969b) in *Mytilus coruscus*. The remarkable lateral expansion observed in the regular simple prisms of inoceramids does not occur in the fibrous prisms of the three *Mytilus* species.





TEXT-FIG. 3. Schematic lateral views showing geometrical selection during crystal growth (after Grigor'ev 1965). First settlement and growth rate are regular among prisms. A-C, stages of group growth of spherulites on an uneven substratum; A, stage of secretion of discrete spherulites; B, stage during which neighbouring spherulites come in contact with one another and, as a result, geometrical selection occurs; C, stage of mature spherulites showing the columnar prismatic structure. D-F, stages of group growth of single crystals; D, stage of secretion of minute separate crystals; E, stage of druse growth showing geometrical selection; F, stage of parallel-arranged growth.

On the shell surface of the periostracal edge, nucleation sites of prisms are localized rather than distributed randomly or uniformly (Pl. 3, fig. 6). In *Mytilus californianus* and *M. galloprovincialis* incipient prisms on the inner surface at the periostracal edge consist of euhedral calcite crystals (Pl. 3, fig. 7), which are randomly oriented and clustered (Pl. 3, figs 6-7). Until a cluster comes in contact with surrounding clusters, crystals continue to grow spherically, but they are not typical spherulites such as observed in turtle eggshell (Silyn-Roberts and Sharp 1986). Immediately after the formation of clusters of prisms, the elongation axes of the prisms become irregularly oriented (Pl. 3, figs 3-4). Afterwards, each prism assumes a preferred orientation as crystal growth proceeds, and finally the perfectly regular pattern of typical fibrous prismatic structure is established (Pl. 3, fig. 5). Uozumi and Suzuki (1981) described this as an example of geometrical selection.

In *Mytilus grayanus*, prisms are more or less reclined to the shell surface in the juvenile stage of the shell, as in the case of *Mytilus galloprovincialis*. In the adult stage of the *M. grayanus* shell, however, prisms become more strongly reclined and finally become nearly parallel to the shell surface. At any point of the shell in the three species of *Mytilus* examined, the elongation axes of

prisms are inclined to the plane of the shell surface; in other words, prisms are extended in the radial direction. Fibrous prisms and growth lines generally intersect at an oblique angle.

## DISCUSSION

### *Morphogenesis of columnar prismatic structure*

Grigor'ev (1965) discussed the genesis of mineral aggregates, especially the growth of druses from randomly oriented crystals and group growth of spherulites (Text-fig. 3). According to him, the simultaneous group growth of the spherulites on an uneven surface (Text-fig. 3A-C) and the similar growth of various spherulites at irregular rates on an even surface (Text-fig. 4B), both necessarily cause a geometrical selection, exemplified by malachite. Taylor *et al.* (1969) applied this geometrical selection model to the growth of spherulites on an uneven molluscan shell surface to explain morphogenesis of columnar prisms (Text-fig. 3A-C).

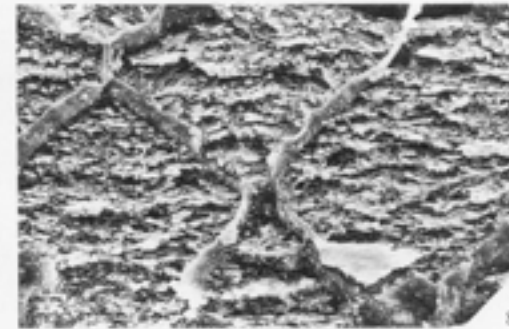
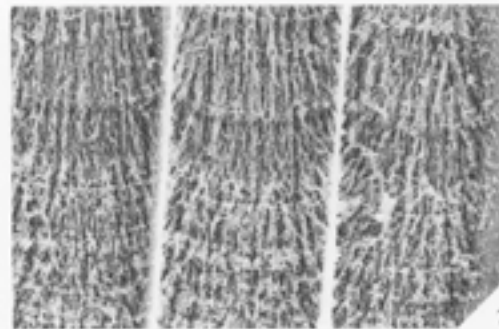
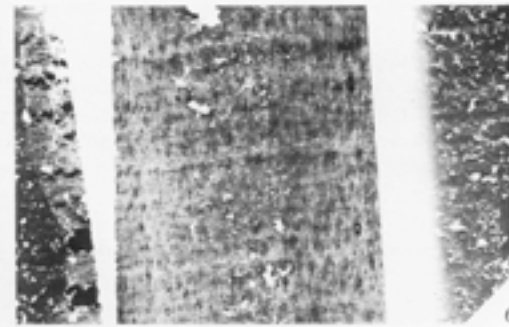
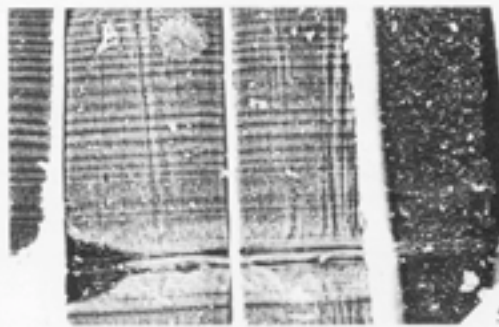
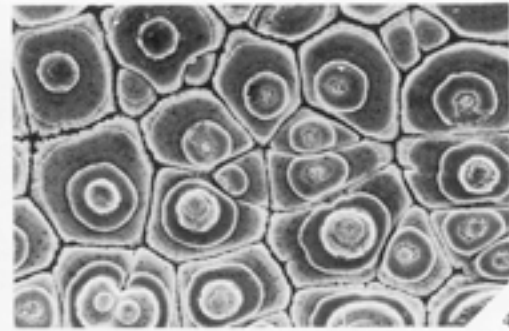
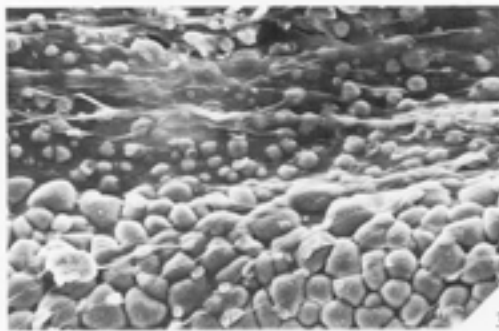
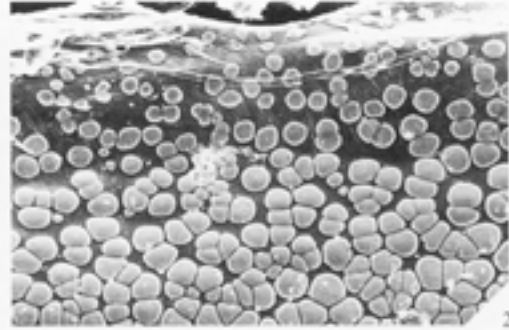
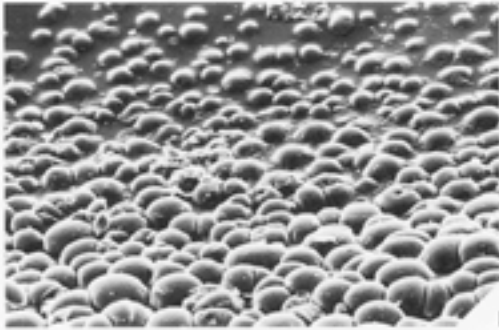
In this study the author confirmed that the non-denticular composite prisms of *Anodonta woodiana* (Pl. 2, fig. 7), *Unio daglasiae* (Pl. 1, fig. 8) and *Neotrigonia margaritacea* consist of radially diverging aciculate subunits. This indicates that the prisms in these species are made of fine spherulitic crystals (Taylor *et al.* 1969; Wilbur and Saleuddin 1983), whose morphological features are somewhat similar to those in turtle eggshell (Silyn-Roberts and Sharp 1986). In the regular simple prisms of *Atrina pectinata*, radial elements are observed, but the intraprismatic microstructure remains uncertain, since the spherulitic microstructure is not preserved clearly in the regular simple prisms of the present material (Pl. 2, fig. 5). In their study of the early prism formation in *Pinctada radiata*, Nakahara and Bevelander (1971) suggested that minute crystals arise in envelopes through the prism chamber, without showing spherulitic crystal growth in the regular simple prisms.

In the species examined with the non-denticular composite and regular simple prisms, the initial prisms consist of hemispherical mineral aggregates (Pl. 2, figs 1-3), which become modified in the subsequent stage as a result of competition for space independent of their intraprismatic microstructures. As for *Propeamussium* with microfoliated regular simple prisms, incipient prisms and growth process of prisms were not observed. Bevelander and Nakahara (1969) proposed a hypothetical model in which an extracellular framework of organic material is formed in the nacreous layer before crystal formation, and that the growth of crystals is inhibited by these organic walls (compartment model; Bevelander and Nakahara 1969, 1980; Nakahara 1979; Lowenstam and Weiner 1989). However, the present author could not observe such a preformed organic framework in the early stage of prism mineralization of any of the specimens examined (Pl. 2, figs 1-3). This indicates that the observed morphologies are well explained by geometrical selection. Although each prism may not always develop hemispherically throughout its growth, it should be

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## EXPLANATION OF PLATE 2

- Figs 1-3. Incipient columnar prisms at the periostracal edge; the upper is the ventral side. 1, *Anodonta woodiana* Lea. UMUT RM 19620; Recent; Biwa Lake, Kinki, Japan;  $\times 400$ . 2, *Pinctada margaritifera* (Linné). UMUT RM 19621; Recent; Ishigaki Island, Okinawa, Japan;  $\times 200$ . 3, *Atrina pectinata* (Linné). UMUT RM 19622; Recent; Osaka Bay, Kinki, Japan;  $\times 650$ .
- Fig. 4. *Anodonta woodiana* Lea. UMUT RM 19623; Recent; Biwa Lake, Kinki, Japan; the outer surface of the non-denticular composite prismatic shell etched with NaOH solution;  $\times 500$ .
- Figs 5-8. Intraprismatic microstructure of slightly decalcified columnar prisms; the upper is the outer side. 5, *Atrina pectinata* (Linné). UMUT RM 19624; Recent; Osaka Bay, Kinki, Japan; spongy type;  $\times 500$ . 6, as Fig. 5;  $\times 1300$ . 7, *Anodonta woodiana* Lea. UMUT RM 19625; Recent; Biwa Lake, Kinki, Japan; aciculate type;  $\times 650$ . 8, *Propeamussium sibogai* (Dantzenberg and Bavay). UMUT RM 19626; Recent; Port Darwin, Northern Territory, Australia; microfoliate type;  $\times 1000$ .



UBUKATA, bivalve prismatic structure

emphasized that geometrical selection occurs *a priori* when prisms possibly grow laterally, and that the appearance of a given structural type (e.g. branched type) can not be explained without lateral growth of prisms, regardless of intraprismatic microstructure.

From the architectural viewpoint, two hierarchies can be considered in the morphogenesis of the non-denticular composite prisms; the prism level and the intraprismatic crystal level. The growth mode of prisms (aggregation of minute crystals) may possibly control geometrical selection, independent of the growth mode of the intraprismatic minute crystals. Therefore, the columnar prisms in many bivalves, excluding propeamussiids, are regarded as a product of group growth of spherulites.

Geometrical selection of prisms caused by unevenness of the periostracum is known in *Margaritifera margaritifera* (Taylor and Kennedy 1969, fig. 2). Such phenomena are, however, not common in most species, and the outer surface of the prismatic layer and the inner surface of the periostracal edge both appear rather smooth in most species examined (Pl. 1, figs 1–2). Consequently, unevenness of the inner surface of a periostracum may not be the main cause of geometrical selection.

The following two factors may affect geometrically selected crystal growth in the columnar prismatic structure of bivalves: (1) different settling time among prisms (Text-fig. 4A), and (2) irregular growth rate within individual prisms (Text-fig. 4B). As already described, in *Anodonta woodiana* and *Pinctada margaritifera*, hemispherical mounds of initial prisms scattered on the inner surface of the periostracal edge exhibit a marked variation in their dimensions (Pl. 2, figs 1–2), suggesting the difference of timing in crystal initiation among them. If the growth rate of neighbouring prisms is not constant, geometrical selection would occur in any growth stage of the prisms (Text-fig. 4B). However, the density of prisms rapidly decreases after the initial stage of their formation and seems to be nearly constant in the later stage (Text-fig. 2). This evidence suggests that the growth rate is almost regular in each prism. Where growth rate is different among prisms, geometrical selection is expected to occur when aggregates of prisms grow more or less spherically. Such a spherical pattern of prisms is found in the hinge area of *Inoceramus* (Pl. 3, fig. 8). Geometrical selection commonly occurs in the prismatic shell of inoceramids (Pl. 1, fig. 3), but is absent in the prismatic hinge area of *Inoceramus*. This suggests an almost constant growth rate among the columnar prisms in this region.

In summary, geometrical selection in the columnar prismatic layer appears to be caused mainly by different nucleation times among prisms (Text-fig. 4A). According to this model, the degree of geometrical selection may be controlled by the two factors: (1) the degree of irregularity of start of

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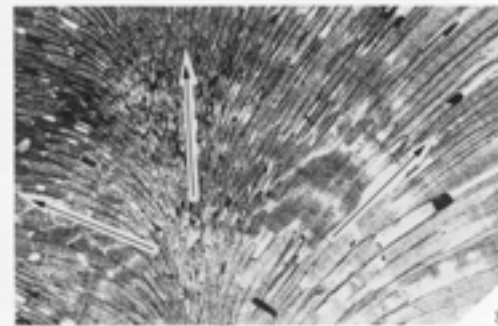
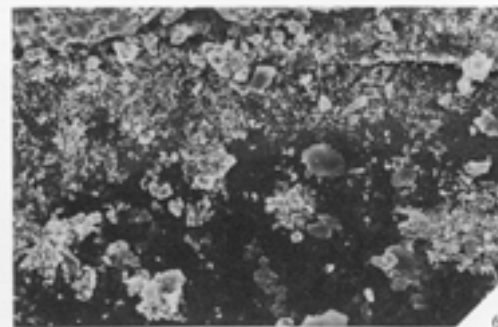
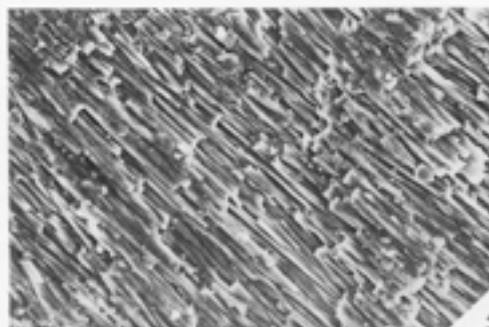
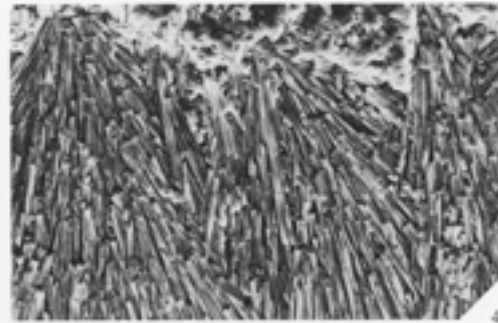
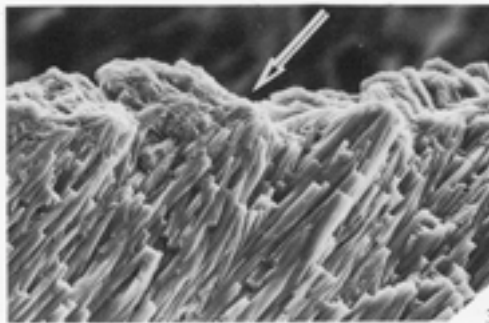
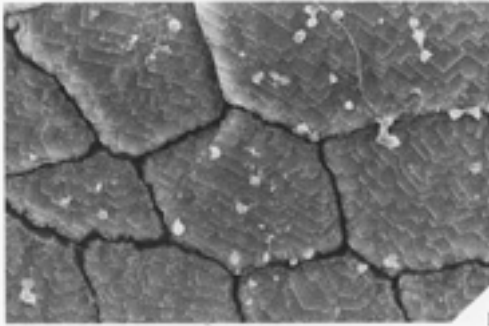
#### EXPLANATION OF PLATE 3

Figs 1–2. SEM photographs of the inner surface of the simple prismatic layer of propeamussiids; the lower is the ventral side. 1, *Propeamussium sibogai* (Dantzenberg and Bavay). UMUT RM 19627; Recent; Port Darwin, Northern Territory, Australia;  $\times 2000$ . 2, *Propeamussium* sp. UMUT RM 19628; Recent; Owase, Kinki, Japan;  $\times 200$ .

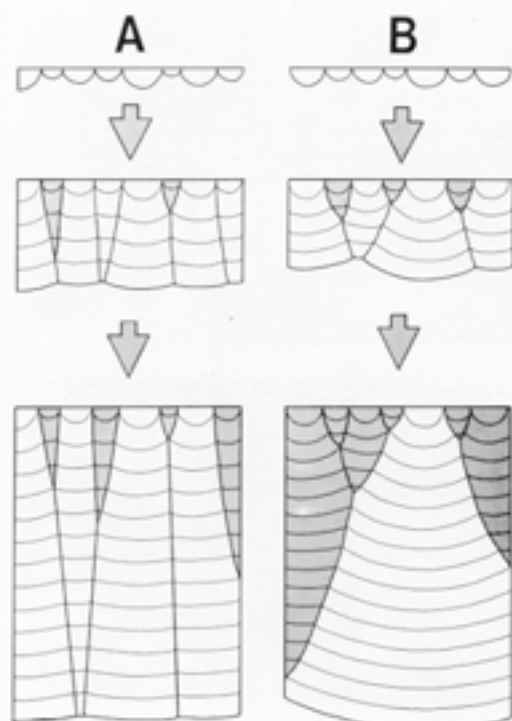
Figs 3–7. SEM photographs of the fibrous prisms. 3, *Mytilus galloprovincialis* Lamarck. UMUT RM 19629; Recent; Shikanoshima near Fukuoka, Kyushu, Japan; early stage of prisms showing irregular structure; the arrow shows the vertical side;  $\times 1300$ . 4, *M. californianus* Conrad. UMUT RM 19630; Recent; Neah Bay, California, USA; the outer surface of the shell showing spherulitic structure; the lower is the ventral side;  $\times 650$ . 5, *M. grayanus* Dunker. UMUT RM 19631; Recent; Soya near Wakkanai, Hokkaido, Japan; the upper is the outer and the right is the ventral side;  $\times 650$ . 6, *M. californianus* Conrad. UMUT RM 19632; Recent; Neah Bay, California, USA;  $\times 400$ . 7, as Fig. 6; incipient prisms on the inner surface of the periostracal edge; the lower is the ventral side;  $\times 2000$ .

Fig. 8. *Inoceramus hobetsensis* Nagao and Matsumoto. UMUT MM 19633; Saku Formation, Middle Yezo Group, Cretaceous (Turonian); Tappu area, Rumoi Province, Hokkaido, Japan; optical micrograph of an acetate peel of vertical section in the hinge plate; the arrows show growing directions of prisms;  $\times 30$ .





UBUKATA, bivalve prismatic structure

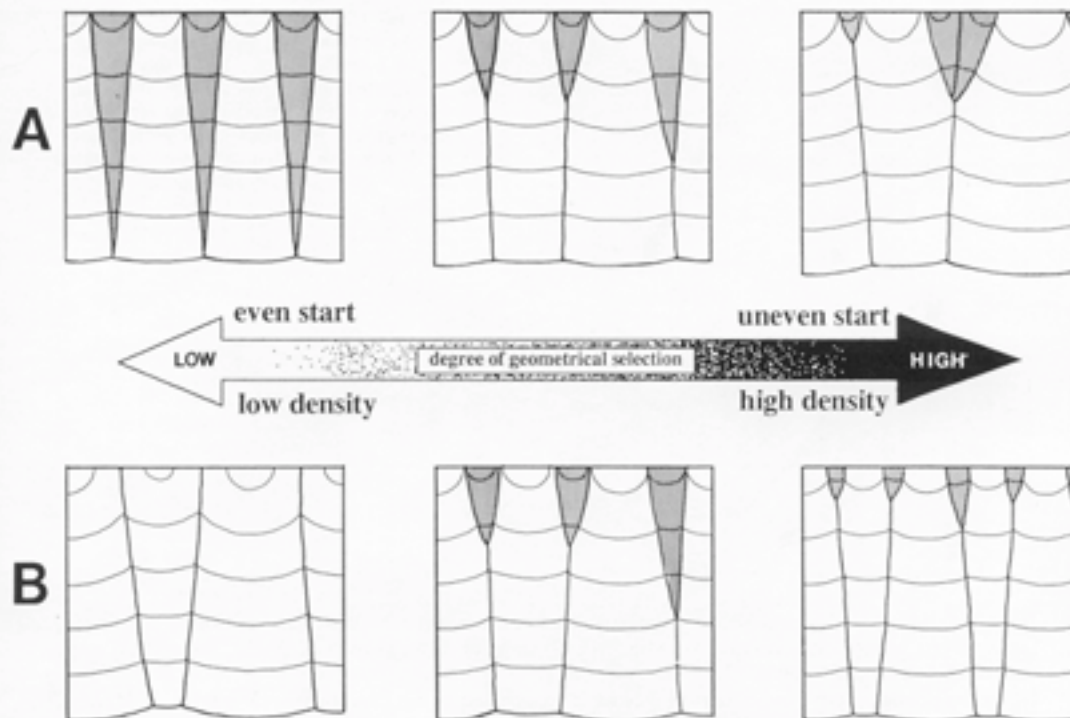


TEXT-FIG. 4. Schematic lateral views showing the successive stages of prism growth starting from spherulites on a flat substratum. A, process of geometrical selection caused by unevenness of starting time among prisms; at the mature stage, prisms exhibit parallel-arranged structure. B, process of geometrical selection caused by irregular growth rate within individual prisms; termination or expansion of prisms occurs at any growth stage. Stippled areas show terminated prisms.

growth (Text-fig. 5A) and (2) the density of primary prismatic crystals if the prisms are not uniformly distributed on the shell surface (Text-fig. 5B).

In the next step, local variation in the density of prisms was examined in each species. For this purpose, the number of prisms on the outer shell surface was successively counted at intervals of one millimetre in longitudinal thin section cut along the dorso-ventral axis. The density of prisms on the outer shell surface is markedly variable in different parts of a shell. This suggests that the density of prisms at the initial stage may be one of the controlling factors determining the variation of the columnar prismatic structure, namely simple type or branched type (Text-fig. 5B). *Atrina pectinata*, with typical simple type prisms, retains a large size and a relatively uniform density in the prisms on the outer shell throughout ontogeny (Pl. 1, fig. 1). On the other hand, in *Inoceramus hobetsensis*, which has a higher density of prisms, geometrical selection is common in any part of its shell (Pl. 1, fig. 3). As already stated, the newly secreted prismatic layer on the inner surface of the abandoned venter consists of relatively fine prisms as a product of marked geometrical selection (Pl. 1, fig. 5). In *Pinctada fucata* and *P. margaritifera* the density of prisms per unit interval is markedly variable throughout their growth. At the point of the newly secreted prismatic layer on the inner surface of the abandoned venter, the density of prisms is always small (Pl. 1, fig. 5). As a result, a close relationship exists between the density of prisms on the outer shell surface and the termination rate of prisms of all species examined. The initial density of prisms is thus regarded as the main factor which controls the degree of geometrical selection.

The timing of the initial deposition of prisms also has an important role in determining the straightness of prisms. Irrespective of the existence of geometrical selection, prisms would be oriented with their elongation axes perpendicular to the shell surface, if the starting time of prism formation in a limited area was uniform or random (Text-fig. 4A). However, in all cases, prisms on



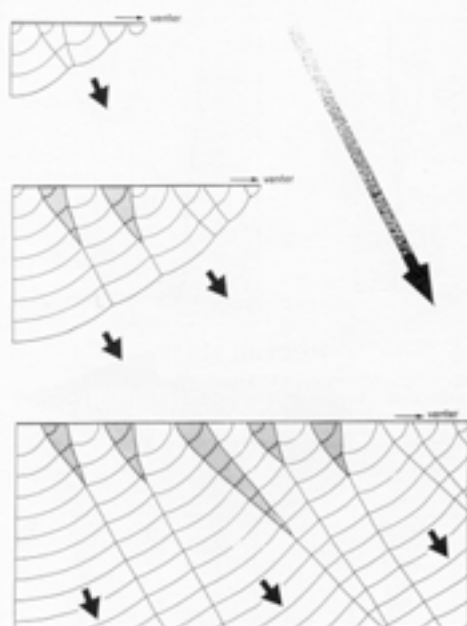
TEXT-FIG. 5. Two possible controls on the degree of geometrical selection, resulting in variation of the prismatic structure. *a*, unevenness of starting time within individual prisms. *b*, density of primary prisms just below the periostracum. As the start of growth among prisms is uneven, or as the density of initiation of prisms is high, geometrical selection becomes significant. Regular and constant growth rate of prisms on the flat substratum is assumed in both cases. Stippled areas show terminated prisms.

the dorsal side were made earlier than those on the ventral side. Therefore, in a limited area prisms on the dorsal side generally tend to be extended to the venter, to obstruct the growth of the prisms on the ventral side (Text-fig. 6). It is therefore concluded that the gradual retardation of settling time of prisms in the longitudinal direction appears to provoke a remarkable reclination of those prisms. In other words, the ratio of the accretionary rate of prisms to growth rate of prisms is considered to determine the degree of reclination of prisms.

#### *Morphogenesis of fibrous prismatic structure*

According to Grigor'ev (1965), in the formation of druse of ore-bearing rocks, euhedral minerals commonly grow with their elongation axes randomly oriented, and geometrical selection occurs because of anisotropy of growth rate (Text-fig. 3D-F). It should be noted that in such a system the mode of geometrical selection differs from the competition for space that occurs with expanding spheres (Text-fig. 3A-C). The author considers that the former represents a process of competition among minerals, while the latter is the process of competition among clusters of mineral aggregates, e.g. spherulites. According to Grigor'ev (1965), crystals in the druse with a given preferred orientation are selected by competition for space because of anisotropy of growth rate. Grigor'ev





TEXT-FIG. 6. Schematic diagrams showing the growth of reclined columnar prisms. In a limited area, the prisms that are secreted earlier grow laterally and occupy space, so that the prisms that are secreted later are prevented from growing vertically. Stippled areas show terminated prisms.

(1965) subdivided the process of geometrical selection in genesis of druses into three stages: (1) growth rate of separate crystals (Text-fig. 3D), (2) stage of druse growth (Text-fig. 3E), and (3) stage of parallel-arranged growth (Text-fig. 3F).

In the present study, these three stages were recognized in the fibrous prismatic layer of *Mytilus*. On the inner surface of the periostracal edge of *M. californianus* and *M. galloprovincialis*, randomly oriented incipient prisms occur locally on the substratum (Pl. 3, figs 6-7), and this corresponds to the growth stage of separate crystals.

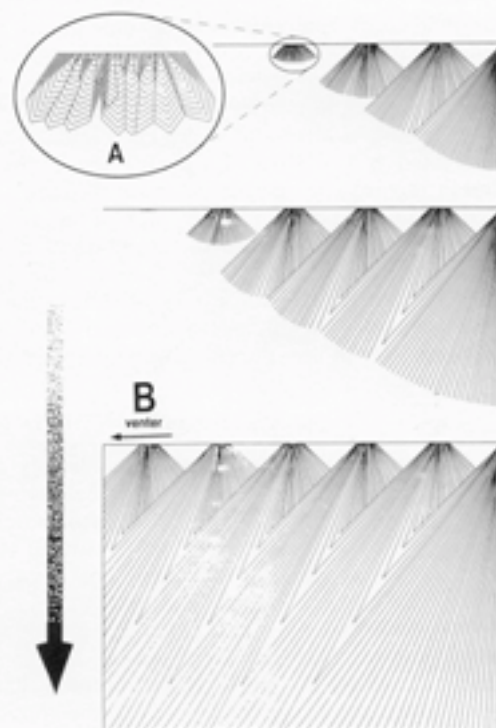
In the next stage, the prisms continue to grow spherically, which is similar to the stage of druse growth. However, the stage of spherical growth of fibrous prisms may not show significant geometrical selection because of the localization of nucleation sites (Pl. 3, figs 3-4). This is quite in contrast with the druse growth, during which competition for space is predominant. The process of competition for space among fibrous prisms is somewhat different from quartz growth in the druse, because initial prisms are aciculate at the stage of separate crystals, and because the rate of lateral growth of prisms is much smaller than that of vertical growth (Pl. 3, fig. 7; Text-fig. 7A). The initial aggregate of the fibrous prisms, for example, is similar to that of goethite needles initiated on quartz in a pegmatite vein.

When clusters come in contact with one another, competition 'among clusters' occurs. This stage is different from any stage in the genesis of druse, but corresponds to competition among hemispheres of the simple prisms. Such appearance of spherulites is also observed in the intraprismatic microstructure of the non-denticular composite prisms (Pl. 2, fig. 7), but organic sheets which envelope clusters of spherulites are not observed in the fibrous prismatic structure. Initial sites of clusters of incipient fibrous prisms are distributed at intervals of about 20-50  $\mu\text{m}$  (Pl. 3, figs 3-4, 6), and are closely correlated in order of magnitude with the intervals among initial sites of the columnar prisms. The final stage represented by the regular arrangement of prisms may thus correspond to the stage of parallel-arranged growth in druse (Pl. 3, fig. 5; Text-fig. 7B).

As is common in druse growth, crystals perpendicular to the substratum are most likely to survive (Text-fig. 3D-F). In the case of fibrous prisms, however, those on the dorsal side are formed earlier than those on the ventral side. Consequently, newly secreted prisms are limited in their growth



TEXT-FIG. 7. Schematic diagrams showing the formation of the fibrous prismatic structure. The distribution of crystal initiation points restricted distribution on the inner surface of periostracal edge, and crystals form clusters. Incipient crystals are randomly but almost spherically oriented (A) and subsequent growth of crystals forms an aciculate structure. As in reclined columnar prisms, previously secreted clusters inhibit the growth of later secreted prisms, and consequently elongation axes of the fibrous prisms are reclined to the outer shell surface (B).



direction by already formed larger crystals (Uozumi and Suzuki 1981). Under such structural constraint, prisms tend to recline toward the venter (Text-fig. 7B). In conclusion, the ratio of accretionary rate of prisms to the growth rate of prisms at the shell margin appears to determine the direction of prisms.

#### *Phylogenetic and palaeontological implications*

Prismatic structure is one of the most important shell microstructures for the taxonomy and phylogeny of fossil Mollusca because of its frequent occurrence in fossilized hard tissue. It is widely distributed not only in the Bivalvia (e.g. Pterioidea, Ostreoida, Pectinoidea, Solemyoida, Myoidea, Pholadomyoidea, Nuculoida, Arcoidea, Mytiloidea, Veneroidea, Unionoidea, and Trigonoidea), but also in other members of almost all classes of the Mollusca. Moreover, prismatic structure is often described as the primitive structure (Taylor 1973) because of its distribution in the Monoplacophora, Archaeogastropoda and Nautiloidea.

However, fabrication divergence or convergence may be derived from geometrical or spatial constraints in architectural fabrics. As stated above, architectural varieties in each prismatic structure can be regarded as fabrication divergence by different conditions of spatial restriction in the morphogenesis of prisms. Such architectural varieties do not necessarily reflect phylogenetic constraints, because they are observed at different positions within a single shell in *Pinctada* and *Isognomon* (Pl. 1, fig. 5). Such fabrication divergence may be derived in other shell microstructures, e.g. nacreous, foliated and crossed lamellar structures.

Carter and Clark (1985) suggested that the most shell microstructures are characterized by convergence at various taxonomic levels. Particularly prismatic structure is organizationally simple and may be easily fabricated in nature. 'Prismatic'-like structures are found in honey-comb,

colonial coral, epidermal cells of some plants, and even in inorganic minerals, which are clearly not 'monophyletic'. The regular simple prisms in propeamussiid species indicate the fabricational convergence, i.e. polyphyly of regular simple prismatic structure, because intraprismatic microstructure in propeamussiids is quite different from that in other bivalve species which have a regular simple prismatic shell. The regular simple and non-denticular composite prisms are both expressed as a product of a hemisphere at the first order structural level (except propeamussiids), but intraprismatic microstructure of the regular simple prisms is distinguished from that of the non-denticular composite prism by lack of radially diverging aciculate elements. This fact may indicate fabricational convergence of the mode of growth of the first order structural units in columnar prismatic structure.

In this paper, the author only introduces the potential of the morphogenetic aspect of the skeletal microstructure for phylogeny and taxonomy and emphasizes that palaeontologists should take it into account in any consideration of the phylogenetic significance of skeletal microstructures in fossil organisms.

### CONCLUSIONS

1. Marked variation in the size and density of crystals was observed in the columnar prismatic structure of thirty two bivalve species belonging to ten families. For example, the simple type of this structure is constructed by prisms approximately uniform in width, while the branched type consists of prisms with variable width, as a result of competition for space among prisms and consequent geometrical selection. Prisms are not always perpendicular to the outer shell surface, being occasionally oblique to it.
2. Hemispherical incipient columnar prisms were observed at the periostracal edge in *Pinctada margaritifera*, *Isognomon ephippium*, *I. legumen*, *Atrina pectinata*, *Ostrea denselamellosa*, and *Anodonta woodiana*. Both regular simple calcite, and non-denticular composite aragonite, prisms generally grow almost spherically in the species examined, except in propeamussiids.
3. It is considered that geometrical selection in the columnar prismatic structure of bivalves is caused by irregularity in the initial time of deposition among prisms. The degree of geometrical selection appears to be controlled mainly by the initial density of prisms on the inner surface of the periostracum at the ventral shell edge.
4. Incipient fibrous prisms in *Mytilus californianus* and *M. galloprovincialis* seem to consist of euhedral and needle-like calcite crystals without a preferred orientation. Nucleation sites of the fibrous prisms in the two species appear to aggregate. Consequently prisms grow almost spherically, forming a cluster.
5. When clusters of fibrous calcite prisms come in contact with one another, aggregations of prisms appear to become irregular because of the dominance of geometrical selection. The mode of geometrical selection in the process of competition for space in fibrous prisms differs from that in columnar prisms, because the latter shows typical spherulitic growth. The mode of geometrical selection of fibrous prisms corresponds to that of needle-like crystal aggregates in druses.
6. Reclination of the columnar and fibrous prisms is caused by the retardation of nucleation time of prisms in the longitudinal direction and the ratio of accretionary rate versus growth rate of prisms.
7. Architectural varieties in each prismatic structure are regarded as fabricational divergence. Various intraprismatic microstructures of the columnar prisms indicate fabricational convergence of columnar prismatic structure.

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