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Bivalve shell structure and organic matrix

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Abstract

More than 10 morphological types of shell structure such as the simple prismatic, nacreous, foliated, composite prismatic, crossed lamellar structures and the others are discriminated in bivalve shells. The combination of these morphological types in each taxon is mainly divided into three groups: the nacreous, foliated and crossed lamellar groups [I. Kobayashi, Earth Science 73(1964) 1; I. Kobayashi, Sci. Rep. Niigata Univ., Ser. E 2(1971) 27.]. It should be emphasized that there is correlation between phylogenetic trends of bivalves and the groupings.

Organic matrices contained in bivalve shells showed great diversity in their molecular weights and amino acid compositions. Samata [T. Samata, The Veliger, 33(1990) 191.] demonstrated that the amino acid composition of organic matrix differed markedly in relation to the shell structures. The difference was most remarkable among three types of shell structures in particular, (1) the nacreous and prismatic, (2) the foliated and (3) the crossed lamellar groups, in which the total amount and degree of heterogeneity of organic matrix components, as well as the composition depended on the shell structure. The secretion of organic matrix is fundamentally controlled by genes involved in shell formation and it can be pointed out that shell structures might reflect the gene structures. Therefore, recognition of relationship between the morphological types seen in shell structures and primary structures of organic matrices (genes) can open a speculation for the further study of molluscan evolution.

Keywords: Shell structure; Bivalve; Morphological type; Organic matrix; Amino acid; Phylogeny

1. Introduction

Molluscan shell structures are one of the good recorders reflecting the long evolutional history of mollusks since Cambrian. This paper is focused to elucidate the relationship between diversity of shell morphology and structure of organic matrix. After 40 years study of molluscan biomineralization, data have been accumulated about shell structure and organic matrices in an independent manner. Shell structure of bivalve mollusks has been studied mainly by electron microscopic observations. Following to Bøggild [4], who carried out the first systematic study, several investigators found evolutional trends of shell structure in bivalve mollusks [5–7]. In these works, we emphasize the result of Kobayashi [8], who classified shell microstructures of bivalves into three groups in the viewpoint of evolutionary trend. On the other hand, the analysis of organic matrix lead to an interesting result that the amino acid composition of organic matrix differed markedly in relation to the shell structures [3]. The difference was most remarkable among the three types of shell layers in particular: (1) the nacreous and prismatic, (2) the foliated and (3) the crossed lamellar layers.

According to Shimamoto [9], the amino acid compositions of organic matrices of Venerid contained in the homogeneous and crossed-lamellar layers were similar to each other, but those in the composite prismatic layer were different from the former.

2. Biovariability of shell structure of bivalve mollusks

The shell structure of bivalve mollusks is divided into more than 10 morphological types [1,4,10,11]. Major shell structures are briefly explained as followings.

2.1. Simple prismatic structure

This structure (Fig. 1) is composed of the aggregation of polygonal prisms. The longer axes of them arrange nearly vertical to an inner shell surface [2]. The prisms show

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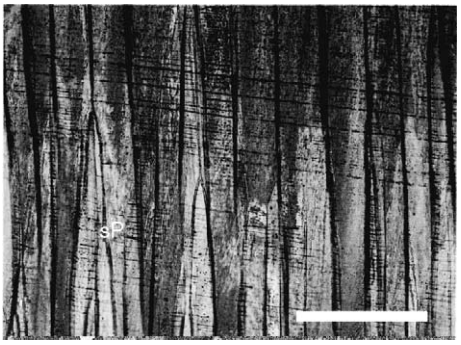

Fig. 1. *Pinctada maxima* (Jameson). Optic microscopic (OM) photograph under cross nicols with gypsum plate, of the vertical thin section of a simple prismatic layer. SP shows a prism of this structure. White scale bar is 250 μm.

polygonal honeycomb pattern in a cross section. They are composed of small elongate tablets of calcite (crystallites) (Fig. 2). The diameter of each prism is 20–100 μm. The breadth of interprismatic region is 1–3 μm. Tight organic sheaths (interprismatic organic matrix) are surrounded prisms.

2.2. Aragonite prismatic structure

This structure (Fig. 3) is similar to the simple prismatic structure [13]. It is composed of polygonal prisms arranged laterally. There are several differences between them. This structure is made of aragonite crystal. The shape and arrangement of crystals are different from the simple prismatic structure. Organic sheaths are thinner than those in the simple prismatic structure.

2.3. Nacreous structure

This structure is made of the accumulation of polygonal tablets [2,13]. Polygonal tablets are made of aragonite crystals. The vertical section shows finely accumulating lamellae parallel to an inner shell surface. The thickness of a tablet is about 0.5–1.0 μm. Organic matrices are located around and in the tablets.

Two types of the nacreous structure are discriminated by Taylor et al. [12] and Wise [14]. The first one (Fig. 4) is called as the lenticular or pillar nacreous structure. This structure is

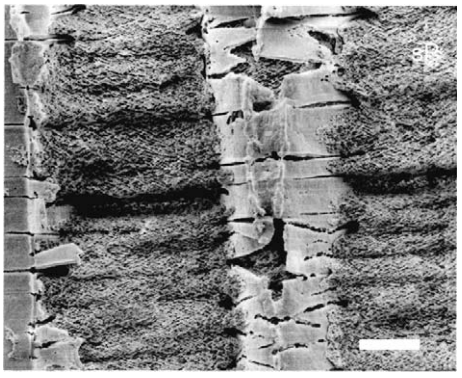

Fig. 2. *Pinctada maxima* (Jameson). Scanning electron microscopic (SEM) photograph of the thin vertical polished section of a simple prismatic structure. It shows a prism (SP) of this structure, calcite crystallites, lateral lines and insoluble organic sheaths. White scale bar is 10 μm.

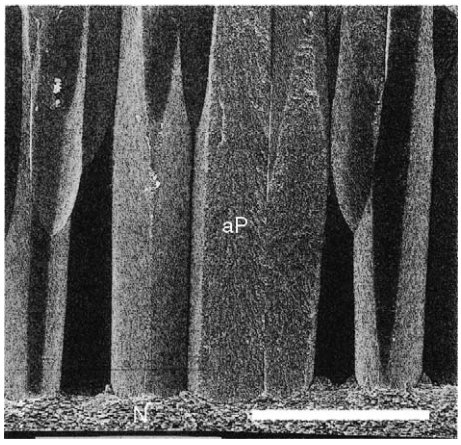

Fig. 3. *Cristalia plicata* (Leach). SEM photograph of the vertical fractured section of an aragonite prismatic layer (AP). It shows arranged prisms vertical to the middle layer of the nacreous structure (N). A prism is made of aragonite crystallites. White scale bar is 100 μm.

composed of vertically piled tablets like prism, arranged side by side. The other one (Fig. 5) is called as the sheet nacreous structure. This is composed of aggregation of roughly polygonal tablets. In a radial section, horizontally arranged tablets can be observed giving a brick-wall appearance.

2.4. Foliated structure

This structure (Fig. 6) is composed of elongate tablets of calcite (crystallites), which accumulate like the nacreous structure [2]. The view of a vertical section looks like cross bedding. The terminal free edges on a growing shell surface show rhombohedral appearance. The breadth of a tablet is approximately 2–4 μm.

2.5. Composite prismatic structure

This structure (Fig. 7) is composed of aggregation of prisms, which are made of elongate rectangular rods. It is similar to the

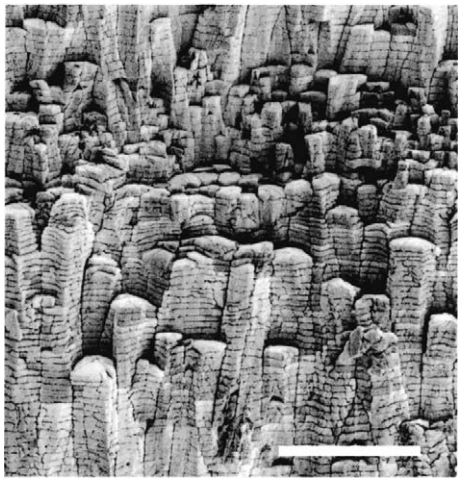

Fig. 4. *Lamprotula* aff. *Paihoensis* collected from the Quaternary, China. SEM photograph of the vertical fractured section of a pillar nacreous structure. It shows vertically piled polygonal tablets forming like a prism. A tablet is made of aragonite crystal. White scale bar is 50 μm.