論文の内容の要旨

論文題目　Thermal control on shell microstructural formation of Bivalvia (Mollusca)

（二枚貝類の貝殻微細構造形成に水温が与える影響）

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The cyclical changes in shell microstructures that occur within a single shell layer of the subfamily Anadarinae are the focus of this study, which endeavors to understand the environmental factors that control the cyclicity and the evolutionary significance of microstructural formation. This study consists of (1) a detailed description of the microstructures of *Scapharca broughtonii*, (2) a comparison between the fluctuation of the thickness changes in two microstructures and the observed environmental data in the field, (3) an experimental study of the shell microstructural formation of *Scapharca broughtonii*, (4) a comparison among the shell microstructures of the subfamily Anadarinae and its evolutionary context based on phylogenetic tree and geographic ranges, and (5) a detailed description of the microstructures of fossil Anadarinae to reveal the actual records of its evolutionary history.

Multiple cyclic changes arise in the shell microstructure of *Scapharca broughtonii* over the course of the organism’s lifetime. The characteristics of the microstructures of *S. broughtonii* are described using scanning electron microscopy (SEM) and the acetate peel method for observations of the shell in addition to transmission electron microscopy (TEM) and Mutvei's solution for observations of the organic membranes. The outer layer of the shells of this species is subdivided into a composite prismatic structure on the exterior side and a crossed lamellar structure on the interior side. The shape of the prisms (third-order lamellae) is common in both the composite prismatic and crossed lamellar structures. A transitional area exists between the two structures and exhibits non-uniform aggregations of first-order units of irregular and complex crossed lamellar structure. This transition occurs rather sharply, and the crystal formation is accordingly abrupt. The composite prismatic structure is more organic-rich than the crossed lamellar structure. The amount of organic matrix decreases gradually from the area of the composite prismatic structure to the outer part of the crossed lamellar structure. In the TEM micrographs, the organic membranes of the composite prismatic structure appear thick and low density, and reside between the first-order units. In the crossed lamellar structure, network-like thin organic membranes can be found.

A comparison with environmental data confirms that the cyclic changes in the shell microstructures serve as indicators of temperature seasonality in *S. broughtonii* in nine localities. The changes are traced by the thickness of the composite prismatic and crossed lamellar structures in the outer layer. At cooler temperatures, the outer layer exhibits multilayered structures and the relative thickness of the composite prismatic structure is increased. The crossed lamellar structure thickens at high water temperatures in summer. These results are verified by geochemical analysis for the first time in this study. Concentric bands observed in X-ray photographs of *S. broughtonii* reflect annual cycles of change in the relative thickness of the outer layer shell microstructure. The range of fluctuation in the relative thickness of the composite prismatic structure decreases with ontogeny in specimens from the northern area (Aomori, Miyagi, and Ishikawa Prefectures, Vladivostok). The shells of *S. broughtonii* contain records of temperatures above approximately 12 °C but lack records for winter temperatures. Water temperature is strongly correlated with the relative thickness of two microstructures. Poor correlations are found with the other factors, such as the shell growth rate and chlorophyll a.

A temperature experiment was performed to corroborate the thermal control of microstructural formation, and the cultured specimens were found to exhibit differences in shell formation by temperature. In this study, the investigated temperatures were 13 °C, 17 °C, 21 °C, 25 °C, and 29 °C, and the specimens were cultured for approximately 58 days. The shell sizes and increment of the shell deposition during the experiment show that the most rapid growth occurs at 17 °C. The thickness of the composite prismatic structure increases at higher water temperatures, and this trend is same as that of the field specimens. Accounting for the outer layer, the area of the composite prismatic structure increases at cooler temperatures, and the growth increment of the composite prismatic structure increases as the water temperature is reduced. This finding suggests that the optimum temperature for *S. broughtonii* growth as determined experimentally is consistent with the shell growth in the temperate area and that the formation of the composite prismatic structure increases the shell growth, especially the expansion of the growth increments in the outermost part of the outer layer.

A comparison of a phylogenetic hypothesis and the geographic distributions demonstrates a clear trend between habitat and microstructure in the family Arcidae. Twenty-nine species of Arcidae (14 species of Anadarinae), one species of Cucullaeidae, one species of Parallelodontidae, and two species of Glycymerididae are compared in the analysis. In Anadarinae, the species possessing only a crossed lamellar structure in the outer layer inhabit the subtropical and tropical areas. The species that possess two structures, the composite prismatic and crossed lamellar structures, in the outer layer tend to live in temperate to subarctic areas. The X-radiograph positives of genus *Scapharca* reveal distinct and concentric density band couplets (light and dark bands). The basal group, identified as the genus *Tegillarca*, only exhibits the crossed lamellar structure, and the acquisition of the composite prismatic structure occurred through speciation in other genera. This findings suggest that the genus *Scapharca* speciated in the northwestern region of the Pacific. In Arcidae, four groups are categorized based on the shell microstructures in the outer layer: (1) fibrous prismatic and crossed lamellar structures, (2) composite prismatic and crossed lamellar structures, (3) irregular complex crossed lamellar and crossed lamellar structures, and (4) only a crossed lamellar structure. The species that have a multi-layered outer layer (with composite prismatic and crossed lamellar structures or fibrous prismatic and crossed lamellar structures) are distributed in cooler regions than the species that have only a crossed lamellar structure.

Microstructural observations of the fossil specimens reveal an interesting evolutionary history, which is lacking in recent analyses of these species. Two clades are distinguishable based on their possession of one or two microstructures in the outer layer, even within the same genus, *Anadara*. The species possessing only a crossed lamellar structure have been distributed from the tropical to subtropical areas since the late Early Miocene. In contrast, the species with the composite prismatic and crossed lamellar structures have existed since the late Middle Miocene (approximately 12 Ma), and their habitat has ranged from temperate to subarctic areas. The acquisition of the composite prismatic structure in the outer layer might have been affected by global cooling, which has occurred since the Middle Miocene Climatic Optimum.