

## The evolution of shell microstructure of protobranch bivalves

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Molluscs are the second largest taxa and most of them have the shell of calcium carbonate. Molluscan shells are composed of the complex structural units that are called shell microstructures. Molluscs demonstrate a great variety of microstructures which are similar in phylogenetically close taxa. Thus, investigations of shell microstructures can provide clues for systematic and phylogenetic analyses of molluscs, including fossil taxa. Additionally, these trends suggest the possibility that the shell microstructure had a crucial role in the evolution of Mollusca.

The Protobranchia is an ancestral group of the Bivalvia and comprise four superfamilies (Nuculoidea, Nuculanoidea, Manzanelloidea, and Solemyoidea). However, the systematics of protobranch bivalves has been also problematic, because their simple external shell morphology can provide an insufficient number of informative characters. Therefore, Comprehensive investigation of the shell microstructure and molecular phylogenetic study of protobranch bivalves are required for understanding molluscan evolutionary history. The purpose of this study is to reveal the relationship between the shell micro-structure of protobranch bivalves and molecular phylogeny, and to discuss the evolution of the shell microstructures and their significance as novel morphological characters.

As the result of molecular phylogenetic analysis, it is revealed that the species of protobranch bivalves formed a distinct clade with long branches expect for one exception. One species of Sareptidae were included in Nuculanoidean clade while Sareptidae is placed within Nuculoidea in earlier systematics. SEM observation revealed that each of four superfamilies has a distinct trend in the composition of shell microstructures. And the results of the molecular phylogenetic analysis and the observation of the shell microstructure were consistent with each other. This condition indicates the shell microstructures of the Resent protobranch bivalves show a phylogenetic constraint. Nevertheless, previous study shows this trend is imperfect in fossil taxa. Some fossil nuculoids have nacreous structures and some fossil nuculids possess homogeneous structures. The foliated aragonite that resembles nacreous structure is known as the most primitive shell microstructure. Ancestral nacreous structure was first originated in the Paleozoic protobranch bivalves prior to any other structures that are found in protobranchs of younger ages. Thus, the absence of the nacreous structure may represent the secondary condition in protobranchs. However, the loss of nacreous might be unreasonable, because nacreous structure is considered to be the strongest shell microstructure. In further studies, the evolution of the shell microstructure of protobranchs should be discussed in terms of the habitats and the production costs of the shells as well as protective functions of shells.

Keywords: shell microstructure, mollusca, bivalve, protobranch