論文の内容の要旨

Evolution of shell microstructure in Protobranchia (Mollusca: Bivalvia)

（原鰓類（軟体動物：二枚貝綱）における貝殻微細構造の進化）

佐藤圭

Molluscan shells are composed of structural units of calcium carbonate called shell microstructure. Variation in molluscan shell microstructure is more noticeable relative to other animal phyla and subphyla. Generally shell microstructure is similar among phylogenetically close taxa. Shell microstructural variation also reflects differences in mechanical properties such as shell strength. Hence, shell microstructural architecture has significance in studies on adaptive radiation and macro-/microscopic morphological evolution. This study focusses on protobranchs to clarify evolution of shell microstructures through the origin and diversification of the basal groups of bivalves. Various shell microstructures were examined through scanning electron microscopy and characterized by crystallographic textures. Furthermore, they were evaluated phylogenetically through molecular phylogenetic analysis using DNA sequences.

An ML-based phylogenetic analysis was performed based on nine molecular loci (16S rRNA, 18S rRNA, 28S rRNA, cytochrome c oxidase subunit 1 [COI], histone H3, ATP synthase β, elongation factor-1α, myosin heavy chain type II and RNA polymerase II) in 107 protobranch species in total. The resulting ML tree supported the monophyly of four superfamilies of Protobranchia with a major change in the position of the family Sareptidae. Sareptidae has been considered as the Nuculoidea but was paraphyletic to the Nuculanoidea in the resulting ML tree. In addition, multiple polyphyletic conditions were revealed among genera and families validated in previous classifications.

Shell microstructures of 38 protobranch species were newly described using scanning electron microscopy. The topology of the obtained phylogenetic tree and shell microstructural composition are consistent at the superfamily level in protobranchs. The microstructural design is similar among Nuculidae in having outer prismatic and middle/inner nacreous structures in common. Outer prismatic structures of protobranchs were divided into five subtypes. In Solemyoidea, four groups were recognized in accordance with the genus-level phylogeny. On the other hand, fine prismatic, homogeneous and fine complex crossed lamellar structures are shared in Nuculoidea. Sareptids were previously classified in Nuculidae but here were transferred to Nuculanoidea based on the molecular phylogenetic tree. In agreement with the molecular phylogeny, similar shell microstructures are shared by sareptids and other nuculanoideans.

The crystallographic textures of shell microstructures in protobranch bivalves were analyzed for 14 specimens of 13 species. Six groups of crystallographic patterns were recognized among 12 microstructures in 13 species. By comparing the crystallographic textures within each type of shell microstructure, several cases of convergence were found among closely related taxa, for instance, the inner layer of solemyids and the outer layer of nuculids. These examples may imply that morphologically similar microstructures have different phylogenetic origins.

Shell microstructural grouping found in this study was consistent with the division of higher taxa suggested by molecular phylogenetic analysis. This indicates that shell microstructure of protobranchs reflect their phylogenetic origin. In addition, the descriptions of shell microstructures in previous studies suggest that all ancestral protobranchs had a nacreous structure, although the nacreous structure is never found in the Recent Solemyoidea and Nuculanoidea, suggesting that the shell microstructure of protobranchs evolved from a nacreous to non-nacreous structure, in general. These changes seem to have occurred during the Silurian to Carboniferous in "Malletidae-like" Nuculanoidea and Nuculoidea, and in the Cenozoic in Nuculanoidea. The homogeneous structure, which is dominant in non-nacreous species is advantageous to the energy cost of shell formation. In the latter event, the distribution of Nuculanoidea shifted to high-latitude and deep-water regions and increased their diversity, probably related to the appearance and divergence of infaunal heterodont bivalves, which occupy a similar habitat. A possible driving force for the shell microstructural evolution is insoluble in the former event. However, species appeared after those event is superior in having low-cost shell microstructure.