

Evolution of Unionoid Mussels in Japan

著者	Sano Isao
学位授与機関	Tohoku University
学位授与番号	11301甲第19948号
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Evolution of Unionoid Mussels in Japan （日本産イシガイ目貝類の進化）

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佐野 勲

Understanding the mechanisms that create biodiversity is a major challenge in ecology and evolutionary biology. Freshwater bodies have played a major role in biodiversity and provide an excellent model for understanding the mechanisms of diversification. To date, many extensive researches have been conducted to assess biodiversity, and the Japanese archipelago has been reported to be one of the world's predominant biodiversity hotspots. However, most previous studies which tried to clarify freshwater biodiversity in the Japanese archipelago have focused mainly on vertebrates such as fishes, and studies investigating invertebrate biodiversity in Japan have been rather limited. Therefore, large part of the mechanisms that maintain and create the remarkable diversity found in the regions surrounding the Japanese Archipelago remain unclear.

Traditionally, only taxa with high dispersal ability have been used to elucidate the maintenance and creation of biodiversity in freshwater areas of the Japanese archipelago. However, it may be difficult to accurately assess the impact of geological history on biodiversity when taxa with high dispersal ability were used as materials. In this study, I examined the effects of geological history and adaptations on species diversity using the mussels, which are thought to have lower dispersal ability than other taxa.

Freshwater mussels *Sinanodonta calipygos*, endemic to the ancient Lake Biwa, are characterized by ball-like strongly bulged shells compared with other freshwater mussels. On the other hand, closely related species with flat shell morphology inhabit the East Asia and the Japanese archipelago, and the ancient Lake, and these can be easily distinguished as the two contrasting types (Later, they are called round-type and flat-type mussels.). Sano et al. (2020) suggested that the round-type mussels may be a sibling group that occurred in parallel in multiple distinct lineages. Therefore, the mussels are an excellent model for understanding how adaptations to environments enhance diversities.

In chapter 2, I analyzed the mitochondrial 16S rDNA of all Japanese mussel species to verify the species framework of Japanese mussel species, which has traditionally been based solely on morphology. Japanese unionoid mussels were classified into 2 families (Margaritiferidae and Unionidae), 12 genera, and 18 species based on the morphological characteristics of both adults and larvae, but there are some debates regarding their systematics. In this study, I determined mitochondrial 16S ribosomal DNA sequences (347-bp) for 60 specimens belonging to 18 species and constructed trees to elucidate phylogenetic relationships and evaluate the current systematics of Japanese unionoid mussels. The results showed that, with the exception of *Inversiunio yanagawensis*, *Sinanodonta lauta*, *S. japonica*, and *Margaritifera laevis*, almost all species formed monophyletic clades, even though two or more specimens were collected from distant localities. All genera except *Sinanodonta* formed highly supported monophyletic clades. Phylogenetic relationships obtained in this study supported systematics based on morphological and larval traits. Therefore, the current phylogenetic relationships and systematics of Japanese unionoid mussels are more reliable than before with the support of genetic data.

In chapter 3, the evolutionary history and diversity of unionoid mussels in East Asia was clarified, shedding light on the formation process of the unique fauna of Japan. Because of their low dispersal ability, unionoid mussels are thought to have been strongly influenced by the formation of the archipelago. Therefore, the speciation and diversification processes of mussels before and after the archipelago's formation were investigated by analyzing the nuclear and mitochondrial DNA of a wide range of species, particularly those inhabiting East Asia. The evolutionary history and divergence time of these mussels were examined. Unionoid mussels were found to have higher endemism than other freshwater organisms. Although most of the endemic unionoid mussels of Japan are likely to have diverged before the formation of the Japanese archipelago, some other Japanese unionoid mussel species, including species endemic to Lake Biwa, an ancient lake in Japan, potentially diverged after the Japanese archipelago began to separate from the continent. This suggests that adaptation to the unique habitat of Lake Biwa has resulted in the diversification of the endemic species of Lake Biwa.

In chapter 4, I have elucidated the formation mechanism of sympatric parallel evolution between closely related species using genome-wide data by ddRAD-seq and mitochondrial data, habitat information, and shell morphology. The evolutionary history of unionoid mussels in the Japanese archipelago, which was not sufficiently understood until now, was clarified at high resolution. The results showed statistically significant differences between round and flat shell shapes. On the phylogenetic tree, I found a strong correlation between shell morphology and habitats. Both northern and southern lineages were found to give rise to the round shells adapted to the ancient lake environment. Until now, speciation with morphological differentiation has been much focused in previous studies. The present study suggests that several closely related populations with similar morphology utilize the same niche, but are reproductively isolated and multiple species coexist. Therefore, this study prompts a reconsideration of the current multispecies coexistence model, which mainly focuses on niche differentiation through interspecific competition. This is an original study that demonstrates the importance of the "hidden diversification processes" that has been overlooked.

This study focused on evolution of unionoid mussels in Japan. In this study, mitochondrial and genome-wide data, habitat information, and shell morphology were analyzed using a wide range of East Asian unionoid species. Based on the present results, I estimated the evolutionary history, the divergence time, the history of population dynamics, the genetic structure, the diversity of morphology, the effects of geologic history on biodiversity, and the effects of adaptation to environment on species diversification.