論文の内容の要旨

論文題目：Evolution of parasitic strategies and morphological diversification in eulimid and pyramidellid gastropods

（ハナゴウナ科およびトウガタガイ科腹足類における寄生戦略の進化と形態多様化）

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Parasitism is one of the commonest and most successful modes of life on Earth.　Parasites have played a significant role in the evolution of other, non-parasitic organisms and hence contributed to the overall biodiversity.　Furthermore, they can alter the physiology and behavior of the hosts that have a significant role in systems, which in turn modifies community structure.　Illuminating current status and evolutionary transitions of host-parasite interaction is therefore crucial to understand the origin and maintenance mechanisms of biodiversity.　Diversification processes of parasites have indeed been investigated using molecular methods for various lineages in several phyla including Arthropoda, Nematoda, Platyhelminthes and Acanthocephala.　However, quite little is known about the timing of their ecological transitions, morphological evolution and species diversification, making it difficult to reveal a more complete picture of parasite evolution.　This scarcity of knowledge is attributable to the extremely rare fossil record for small and soft-bodied parasites.

The class Gastropoda offers an unmatched advantage for studying the evolution of parasites with its abundant fossil record.　Among parasitic gastropods, the Eulimidae and Pyramidellidae have achieved significant diversification during their Cenozoic radiation that resulted in thousands of extant species in each family.　Interestingly, ecological and morphological traits are quite different between the two groups.　Eulimids are exclusive parasites of echinoderms and exhibit rich varieties of parasitic strategies (temporary, ecto- and endoparasitism) and shell shapes

(slender, globose and capuliform). Pyramidellids in contrast parasitize on annelids and other mollusks, mostly as temporary parasites with rather uniformly high-spired shells. Despite being such fascinating targets for studies on parasite evolution, their ingroup relationships have been poorly understood due to the lack of comprehensive molecular phylogenies. Here in this dissertation, the evolutionary histories and diversification patterns are first illuminated and compared between these two largest families of parasites in Gastropoda.

The relationships of the Eulimidae among non-parasitic taxa are not well understood, while such knowledge is essential for the inference of the ancestral states and evolutionary transition in a parasitic lineage. In the Chapter 1 of this thesis, Bayesian and maximum likelihood phylograms are reconstructed to explore the phylogenetic position of Eulimidae within its parent taxon Hypsogastropoda, based on the nucleotide sequences of five genes (nuclear 18S/28S rRNA and Histone H3 and mitochondrial 16S rRNA and COI) from 58 species in 38 hypsogastropod families and from five cerithioideans as the outgroup. The phylogenetic trees suggest Vanikoridae as the sister group of Eulimidae; the two families are collectively placed in the newly redefined superfamily Vanikoroidea, with Truncatelloidea and Rissooidea as its closest relatives. Vanikorids are protandrous hermaphrodites as are many eulimids and are essentially carnivorous, differing from the mostly gonochoristic and herbivorous or detritivorous Truncatelloidea and Rissooidea. The parasitic lifestyle in the Eulimidae was probably derived from carnivorous mode of feeding as in the case of many other parasitic organisms.

The internal phylogeny of the Eulimidae and their evolutionary consequences are examined in the Chapter 2 by molecular phylogenetic reconstruction and morphometric analysis of shells. Phylogenetic trees are inferred from six-gene sequences (a total of 4.7 kb) from 101 eulimid species belonging to over 50 genera as well as three vanikorids for outgroup comparison. Reconstruction of ancestral character states and divergence time estimates based on the tree topology reveal that (1) eulimids exploiting each of the five echinoderm classes belong to two or three phyletic groups, (2) each of the teleoconch and radula has been lost more than once in the evolution of eulimids, and (3) globose to capuliform shells as well as endoparasitism have evolved independently and rapidly in several of the lineages. In addition, the principal component analysis based on seven measurements of eulimid shells reveals a strong correlation between shell morphology and parasitic strategy. These results indicate that the evolution of the Eulimidae involves the process of repeated adaptive radiation. Respective radiations have started from temporary parasitic ancestors bearing a slender shell and ended in permanent ectoparasites and endoparasites with globose to patelliform shells or without a shell. These radiations involving the adhesion and infiltration to the host of a particular echinoderm class thus have a strong deterministic component, as has shown in the replicated adaptive radiation by other organismal lineages on islands and in lakes. Fossil records suggest that the repeated radiation has occurred throughout the evolutionary history of Eulimidae, since well before and more frequently than it can be traced by the ancestral state reconstruction based on phylogenetic relationships among extant species and distribution of their ecological traits.

The Chapter 3 is devoted to illuminate evolutionary relationships and diversification process in the Pyramidellidae. A molecular phylogeny of the family is reconstructed based on six-gene sequences (5.1 kbp); also estimated are the ancestral conditions of the shell shapes and habitats. This phylogenetic analysis includes 59 pyramidellid species in more than 40 genera as well as 14 related taxa for comparison. The resulting trees reject the monophyly of the Pyramidellidae and all of its four subfamilies as currently defined based almost solely on shell morphology. Although many species of the family apparently exhibit low host specificity, which may decrease the diversity of accessible niches for colonization, they probably have achieved the great diversification through frequent shifts among different environments while often retaining dependence to a particular lineage of hosts, ranging from a single species to various taxa in a phylum. The reasons why pyramidelloids have not specialized to give rise endoparasites or why they have achieved a permanent ectoparasitic lifestyle only once are discussed in comparison with the repeated adaptive radiation of the Eulimidae.

Summing up, the diversification processes greatly differ in the two most speciose groups of parasitic gastropods, Eulimidae and Pyramidellidae: Recurrent specialization to the permanent parasitic lifestyle has enhanced the diversification in the former, while frequent habitat shifts among disjunct marine environments have contributed to the species richness of the latter. The present study on eulimid diversification provides perhaps the most complete and dynamic picture of parasite evolution in terms of the large number of parallel specialization events. This study also indicates that the fossil records of the Gastropoda can provide unmatched knowledge on the evolution of host-parasite interaction, particularly if a number of conchological characters are properly evaluated and only truly unique conditions are used to diagnose monophyletic groups. Further investigations on the evolutionary history of parasitic gastropod lineages, each of which exhibits different ecological and morphological conditions but unanimously benefits from the rich fossil record, would elucidate diversification of parasitic organisms in time and space.