

論文の内容の要旨

森林科学専攻

平成 16 年度博士課程入学 (進学)

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論文題目 Diversity and evolution of reproductive traits in carabid beetles of the tribe Pterostichini
(Coleoptera: Carabidae)

ナガゴミムシ族 (コウチュウ目: オサムシ科) における繁殖形質の
多様性と進化

Differentiations of reproductive traits are one of the important processes of speciation, because they could facilitate reproductive isolation among different populations of an ancestral species. Theoretical and experimental studies have suggested that the sexual selection plays important roles for the diversification and evolution of these traits. Sexual selection comprises three different, but probably not mutually exclusives, mechanisms: sperm competition (male-male competition), cryptic female choice, and sexual conflict. Recent numerous studies have suggested that the main factor in the evolution of reproductive traits varies at species-level, and that our knowledge on this issue is yet insufficient. Therefore, for the better understanding of the mechanisms underlying the evolution of reproductive traits, the respective morphologies need to be described and compared among species.

The tribe Pterostichini is one of the most diverse groups of the Carabidae (Coleoptera), and is distributed throughout all zoogeographic regions. It includes about 2500 species, and members of the tribe are abundant in almost all major terrestrial habitats. Taxonomists have reported on the diversity in the genitalia of this group, but little is known about evolutionary process and the underlying mechanisms of the elaborated genitalia. This study aims to describe highly diversified reproductive traits of Pterostichini, investigate associations among the traits, and discuss the mechanisms underlying their evolution within the framework of sexual selection theory.

In Chapter 1, the morphologies of the ejaculates (spermatophore and sperm bundles) and genitalia (male endophallus and female spermatheca) are described, and morphological associations among traits are determined to exist. All the species examined formed a spermatophore and sperm bundles. Morphology of spermatophore could be classified into three types (Small, Large, and Plug) based on its relative volume in the female vaginal cavity and the presence or absence of a pluglike conformation. Sperm bundles are composed of a rod-shaped

structure (spermatodesm) and sperms on the spermatodesm surface, both of which vary among species. Spermatodesm includes three types (Left-helical, Right-helical, and without conspicuous spiral structure), and sperms on the spermatodesm surface have two conditions (with the tail free-moving, or forming a thin, sheetlike structure). Male endophallus could be divided into four types (Straight, *Bothriopterus*, Bent, and *Lyrothorax*) by the direction of the endophallus and gonopore. Female spermatheca could be divided into five types (Cylindrical, Balloon, Right-helical, Left-helical, and Long) based on their shape (e.g., spiral direction). A morphological association between spermatophores and male genitalia is recognized; species with a large, strongly bent endophallus formed a large, pluglike spermatophore, whereas species with slender, straight endophallus formed small spermatophore, suggesting the correlated evolution between endophallus and spermatophore. An association between sperm-bundle and spermatheca is also recognized; sperm-bundle length and spermatheca length are significantly positively correlated, suggesting the correlated evolution between spermatheca and sperm bundles.

In Chapter 2, the phylogeny of Pterostichini is studied using two nuclear gene sequences: wingless and 28SrDNA. Although separate analyses of each gene sequence result in unresolved trees, simultaneous analyses of combined data provide well resolved phylogeny of this group. Some novel aspects are recognized in the resultant tree, and their implication for the taxonomy of Pterostichini are discussed.

In Chapter 3, the evolutionary processes of reproductive traits are reconstructed on the molecular phylogenetic tree, and the correlations among traits are investigated using the method of phylogenetically independent contrasts. Because of the insufficient species-level data, the result uncovers most of the character states on deeper node. The results of comparative analyses suggest that positive correlation among three traits: endophallus volume and spermatheca length; sperm-bundle length and spermatheca length; and sperm-bundle length and endophallus volume. Because endophallus and spermatheca cannot physically contact each other in Pterostichini, the correlation between two traits may be the result of the correlated evolution between endophallus and spermatheca via ejaculates. Endophallus volume and sperm-bundle length exhibit positive allometry relative to spermatheca length, although most previous studies investigating the correlation between male and female reproductive traits (e.g., sperm and spermatheca) have reported positive allometry of female traits relative to male ones. Theoretical and empirical studies have suggested that the positive allometry of female traits is the result of inter-sexual selection (cryptic female choice or sexual conflict); thereby, the result of this study may suggest the relative importance of sperm-competition (male-male competition) in the evolution of reproductive traits in Pterostichini.

In General discussion, novel aspects of this study are discussed. Species diversity of derived clades of Pterostichini is also discussed in terms of differentiation of reproductive traits via sexual selection. Finally, suggestions for future study are provided.