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Phylogeny and Host-parasite Relationships in Social Parasitism in *Lasius* Ants

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Abstract. Phylogenetic relationships and host-parasite relationships are compared among 4 subgenera of the ant genus *Lasius*. Estimated phylogeny based on mitochondorial DNA sequence indicated that the present host species belonging to phylogenetically ingroups. This result suggests that parasite species parasitize on the most closest species at past speciation and showed that Emery's rule was held in this genus.

Key words: Social parasitism, host-parasite relationship, phylogeny.

Introduction

Social parasitism is a way of life in which a queen of parasite exploits labor forces of other social insect colonies to rear her own brood. There are 3 distinct forms of social parasitism, *i.e.*, temporary social parasitism, dulosis and inquilinism (Wilson, 1971; Hölldobler & Wilson, 1991). A queen of temporary social parasites intrude into a colony of the host species and kills the host queen. The remained host workers rear broods of the parasite queen. Parasite workers work as in non-parasitic species, and after disappearance of host workers they engage in the all tasks in colonies such as foraging, brood care and nest maintenances. A queen of dulotic species found her colony in the same way with temporary social parasites, but eclosed parasite workers attack other nests of host species and bring back host-worker pupae to their nest in order to enslave them as labor forces. Thus, dulotic species depend permanentally on host workers. The dulotic species frequently show morphological or behavioural specialization to their specific life style (Hölldobler & Wilson, 1991). Inquilinism is an ultimate form of social parasitism. A parasite queen of this type intrude into a host colony, but does not kill the host queen. Almost all eggs laid by the parasite queen are developed into reproductives, and even when parasite workers exist they do not engage in social work (Hölldobler & Wilson, 1991). Thus, they have secondary lost sociality itself in responce to parasitic life.

Social parasitism is found in most subfamilies of the ants. The ant genus *Lasius* is a small genus and contains about 40 species belonging to 5 subgenera, *i.e.*, *Chthonolasius*, *Dendrolasius*, *Austrolasius*, *Lasius* s. str. and *Cautolasius* (Hölldobler & Wilson, 1991). The species belonging to the former 3 subgenera are known as temporaly social parasites and parasitize on other species in the genus *Lasius* (Hölldobler & Wilson, 1991). The parasitic species show specific behaviour to intrude into host nests (Hölldobler & Wilson, 1991), and interesting materials for comparative ethology. However, recent theories for comparative ethology does not allow analyses without phylogenetic relationship among the objective species (Harvey & Pagel, 1991). In this paper, I reported a molecular phylogenetic relationship among the subgenera within the genus *Lasius* in connection with the present host-parasite relationship in this genus as a step for understanding evolution of social parasitism in ants.

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Materials and Methods

Species of each subgenus of *Lasius* ants were collected during the summer of 1995. Table 1 shows species used in this study. For the subgenus *Austrolasius*, I could not obtain any sample, and this subgenus was excluded from the analysis. *Paratrechina flavipes* was selected as the outgroup for phylogenetic analyses. For each species, total DNA of an individual was extracted by following a common procedure (Werman *et al.*, 1990). A mitochondrial DNA region that encodes a part of cyochrome-oxidase subunit I (COI) gene was used to reconstruct phylogeny. Two primer pairs were designed to amplify two parts of COI region that overlapped partly to each other. The primer pairs could amplify 994 bp sequence in total. The target flagment was amplified by polymerase chain reaction and sequenced by an auto-sequencer. Detailed experimental procedures are described in elsewhere (E. Hasegawa, A. Tinaut & F. Ruano, in submitting).

Table 1. Species used for reconstruction of phylogenetic relationship among subgenera of the genus *Lasius*.

Species	Nation	Locality
Lasius (s. str.) *niger*	Spain	Sierra de Heuter, Granada
Lasius (*Cautolasius*) *flavus*	Japan	Gotemba, Shizuoka Pref.
Lasius (*Chthonolasius*) *meridionalis*	Japan	Kokubunji, Tokyo Met.
Lasius (*Dendrolasius*) *spathepus*	Japan	Hachioji, Tokyo Met.
Paratrechina flavipes	Japan	Manazuru, Kanagawa Pref.

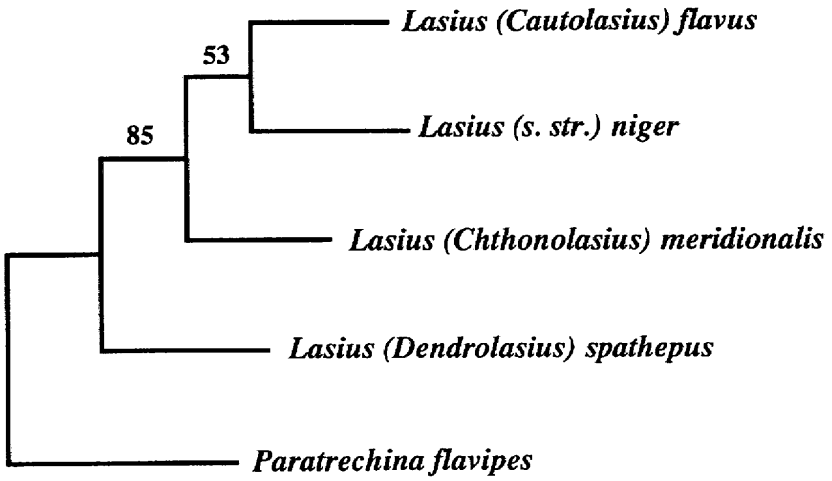

Fig. 1. Reconstructed phylogeny among 4 *Lasius* species using the most parsimonious algorithm. *Paratrechina flavipes* was used as the outgroup for phylogenetic analysis.

Results and Discussion

Because sequences near the primers could not determined unambiguously, I could obtain 974 bp sequence information of COI for all species. The obtained sequences are deposited in DDBJ data base (access No. AB007980–AB007984). Phylogenetic relationship among subgenera was reconstructed by two different algorithms, *i.e.*, the most parsimonious method (Swofford & Olsen, 1990) and the neighbor joining method (Saitou & Nei, 1987). Fig. 1 shows the obtained most parsimonious tree. The neighbor joining method resulted in the same topology and thus the obtained tree is not shown. The obtained phylogenetic relationship suggests that firstly *Dendrolasius*, secondary *Chthonolasius* speciated from the common ancestor, and lastly *Cautolasius* and *Lasius s. str.* were separated. This topology different from the result of Wilson (1955) that based on morphorogical characters. The present host-parasite relationships were gathered from references (Wilson, 1955; Yamauchi & Hayashida, 1968, 1979; Yamauchi 1979, 1980). As shown in Fig. 2, socially parasitic species (*Dendrolasius* and *Chthonolasius*) parasitize on the species belonging to phylogenetical ingroups.

E. O. Wilson argued that social parasitism is a dead-end of social evolution (Wilson, 1971; Hölldobler & Wilson, 1991). Because parasites depend colony founding and maintenance on host workers they cannot return to free-living life style when a robust host-parasite relationship has been constructed once. In fact, fat contents of an alate queen is significantly low in species that found nest by depending on other individuals (Keller & Passera, 1989). This suggests difficulties of independent colony founding in social parasites. Thus, when the host population was divided into two populations, a parasite population also separate into two independent groups, resulting in coevolution of the parasite with their host.

The observed host-parasite relationships seem to support the above hypothesis. The observed pattern well explained by asuming that *Dendrolasius* and *Chthonolasius* independently aquired social parasitism after speciation from the common ancestor with the rest subgenera (indicated by two arrows in Fig. 2). Thus, comparative studies on *Dendrolasius* and *Chthonolasius* should be meaningful.

Speciation pattern observed in the genus *Lasius* seems to support basically a hypothesis proposed by C. Emery, that a parasite species directly speciates from the common ancestor of their host species (Emery, 1909). However, there is no report for *Cautolasius* species as host of *Chthonolasius* species at present. Thus, it is important that whether *Chthonolasius* could escape from parasitism by *Chthonolasius* or *Chthonolasius* parasitise on *Lasius* s. str. after speciation between *Cautolasius* and *Lasius* s. str. More detailed behavioural study is required to answer these questions.

This study lacks molecular information of *Austrolasius* species that parasitize on *Lasius* s. str. species (Faber, 1967). In addition, only a single species in each subgenera was used to reconstruct the phylogeny. Thus, it is required to show the above relationship more clearly using molecular data of *Austrolasius* species and other species, especially *Dendrolasius* species that parasitize on species belonging to different subgenera. By comparing the phylogeny of *Dendrolasius* species and that of their host species, we can obtain more insight into evolution of social parasitism in social insects.

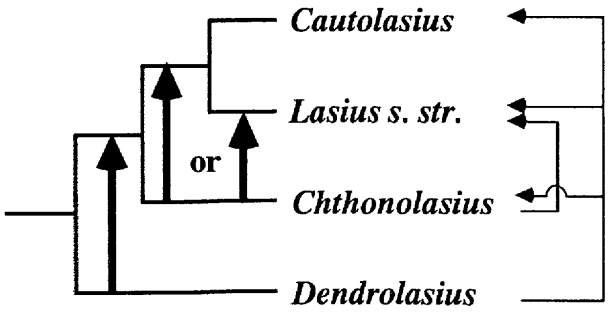

Fig. 2. Phylogenetic relationship and the present host-parasite relationships among 4 subgenera of the genus *Lasius*. Thin arrows shown at right side represent the present host-parasite relationships. Two thick arrows within phylogeny show ancestral host-parasite relationships estimated from the present relationships.

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