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3.13. A Review of the Natural History and Evolution of Ectoparasitoid Relationships in Carabid Beetles

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Introduction

This paper is a review of the exotic life histories known to occur in carabid beetles, with comments on how some carabids possibly became ectoparasitoids in the larval stages. Most carabid life histories are rather mundane, with singly deposited eggs; three larval stages, each with active, usually predaceous or herbivorous feeding habits; a pupal stage sequestered in a log or earthen cell; and finally emergence to a free-living adult. However, a few carabid groups have evolved a more elaborate life cycle involving parasitoidism or symbiosis with ants or termites. Parasitoidism is convergent in a number of disparate lineages.

Specialized Relationships

Several students of carabid natural history have described how various, normal carabids undergo development from egg to adult; notable are Shelford (1908), Burgess & Collins (1917), Willis (1967), Kirk (1973, 1974, 1975), and Goulet (1974). Some, such as Goulet, Kavanaugh, and Thompson in North America, have recently done much rearing and have a wealth of unpublished data on the more normal developing carabids. The more exotic life styles have been less commonly described, by such workers as Dimmock & Knab (1904), Silvestri (1905), Moore (1964, 1974), Balsbaugh (1967), and myself (1967, 1976). Studying these more exotic life styles is more difficult, as they are ectoparasitoids or symbionts and one must deal with the host's natural history as well as with that of the carabid.

Symbiotic relationships, all with ants or termites, are now known to occur in the paussines, ozaenines, pseudomorphines, orthogoniines, some morionines, some oodines, some tachyines, and believed to occur in helluonines, helluodines, and some siagonines (see Table I for details and references).

Only a bit more is known of ectoparasitoid relationships—ectoparasitoid defined here as a one to one relationship where the one host always is killed and eaten by the one parasitoid. This kind of life history is now known to occur in the brachinines, lebiines, and peleciines with details known only in a few species of *Brachinus* and *Lebia* (Table I). Other possible symbiotic or ectoparasitic carabid groups are Agonicini, Promecognathini, Disphaericini, certain Panagaeini (e.g., *Brachygnathus*), *Nototylus*, and Crepidogastrini. The first four mentioned are similar to Peleciini, some members of which specialize in eating millipeds

(Erwin, MS). The larvae of *Pelecium* were discovered by Salt (1928) to be ectoparasitoid on young millipeds and chrysomelid pupae. *Nototylus*, a unique carabid without antennal combs on the front tibiae, has the general aspect of an ozaenine derived independent of the paussids. I predict this ground beetle will be found living in ant nests. The Crepidogastrini are bombardier beetles closely related to the Brachinini. They live in dry upland biotopes and are probably parasitoids with the same nature as *Brachinus crepitans* rather than *Brachinus pallidus* (Erwin, 1972). All of these groups need study in order that ectoparasitoidism be more fully understood in the Carabidae.

Recent work on the natural history of *Brachinus* (Erwin, 1967) and *Eurycoleus* (Erwin & Erwin, 1976) allowed speculation on the evolution of ectoparasitoidism, that is, the sequential steps from a free-living larval stage to a host-dependent, structurally reduced larval stage (Table II). Life histories of other pericaline carabids such as *Stenoglossa* and *Lelis* should be investigated. Based on adult structural evidence, Ball (1975) proposed that these two groups are "Eurycoleoids" and generally more primitive than *Eurycoleus*. If so, their life histories may reflect additional evidential steps along the transformation series leading from free-life to apotypic stage I ectoparasitoidism. Investigations of the life histories of primitive bombardier beetles such as *Crepidogaster*, *Pheropsophus*, and *Mastax* may shed light on evolutionary steps between apotypic stages I and II.

Summary

For the most part, ground beetles have free-living larval stages, with larvae of many species being active foragers on live, dead, or dying invertebrates (including eggs) and those of many other species eating plant material such as seeds. Of the 76 ± tribes of carabids, seven are known to have members with specialized larval histories: three are ant symbionts, one is a termite symbiont, and three are ectoparasitoid on other invertebrates. Of the three tribes in the last category, two also have subgroups which are specialized predators rather then ectoparasitoids. Five additional tribes have suspected symbiotic relationships with ants or termites. Six more tribes are here predicted to be symbionts or ectoparasitic. This is a total of 18 tribes or about 24%. However, not all members of many of these tribes are symbionts or ectoparasitic, and it is unlikely that these specialized life styles are of great importance in the family as a whole.

The important thing is that several tribes have independently evolved similar life styles of symbiosis or ectoparasitism and the present stage of development of these is very similar. Both symbionts and ectoparasitoids have similar structural reduction, yet no single tribe evolved both life styles.

What driving forces or selection pressures caused the dual convergence described above, that is, life style convergence between tribes and convergence of structural form between symbionts and ectoparasitoids? How many other carabids have specialized feeding behaviour? What is its nature? How has it affected the structure of the feeding form? How has the