Relationships of Predaceous Beetles to Tropical Forest Wood Decay. Part II. The Natural History of Neotropical *Eurycoleus macularis* Chevrolat (Carabidae: Lebiini) and Its Implications in the Evolution of Ectoparasitoidism[1]

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ABSTRACT

The natural history and behavior of *Eurycoleus macularis* Chevrolat (Carabidae: Lebiini) are recorded for the first time. The role of this predaceous carabid beetle in tropical forest wood decay is discussed in detail. Predatory roles of other wood-associated carabid beetles are also discussed. A mimetic complex of beetles involving both larval and adult stages is shown to involve *Eurycoleus macularis*. A hypothesis is offered to explain how carabid beetles evolved ectoparasitoidism with the life cycle of *Eurycoleus macularis* representing an intermediate stage between free-living larvae and true ectoparasitoidism as found in *Brachinus* (bombardier beetles) and *Lebia* (colorful arboreal beetles). Immature stages of certain species of *Amphix* (Endomychidae) are shown to be the only food of *Eurycoleus macularis*. Erotylidae (*Priotelus* sp., ?*Homoeotelus* sp.) and Tenebrionidae (*Poecilesthus* sp.) are involved in the mimetic complex with *Eurycoleus*.

UNTIL RECENTLY, *Eurycoleus macularis* was known from only a few specimens from distantly separated localities from Mexico to Colombia. Reichardt (1972) in his review of the genus recorded only 54 specimens. Another 20 specimens were collected near Sontecomapan, Veracruz, by "Ball, Erwin, and Leech" in 1967. It was the discovery of these last specimens by George E. Ball which stimulated our interest in the natural history of the species. Ball first located the beetles on a standing tree which was covered on one side by polypore fungal bracts. The beetles were hiding in cracks in the bark, between fungal bracts, and under the bark, but there was no time during the expedition to engage in protracted rearing and behavior studies. *Eurycoleus macularis* is a lebiine carabid, a tribe in which both the mimicry and ectoparasitism relationships are known. So, after six years of speculation on the possible mimetic and ectoparasitism relationships, we have discovered the natural history of *Eurycoleus*.

Our continued interest in *Eurycoleus* was maintained because of the beetles' coloration and apparent connection with bracket fungi. Other lebiine species in the genera *Lebia* and *Lebistina* are known to be ectoparasitoid in their larval stages (Silvestri 1905; Chaboussou 1939; Lindroth 1954, 1971; Balsbaugh 1967); with the adult stage similar in appearance to their larval host's adult stage. With this in mind, we hypothesized that *Eurycoleus'* immature stages would be ectoparasitoids and the host would be a fungus beetle of the family Erotylidae; we also thought that the host, in its adult stage, would look like *Eurycoleus* members. Our hypothesis was wrong in predicting simplicity, although testing its merits did lead us in the right direction.

During our continuing study on the relationships of tropical forest wood decay and predaceous beetles, we[2] were able to concentrate on the *Eurycoleus* problem for two weeks in 1973 and a week in 1974 on Barro Colorado Island, Canal Zone, Panama. In all stages of its life cycle, *Eurycoleus macularis* is tied to the wood decay process of smooth barked trees (i.e., *Inga, Apeiba*). This relationship is described in detail below.

Eurycoleus Chaudoir

Since Bates (1883), only a few reports about *Eurycoleus* have been published. Reichardt (1972) provided a review, keyed the known six species, and indicated these species have a combined distributional

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[2] This paper resulted from a division of labor as follows: senior author responsible for field work, initial preparation of text, and final editing; junior author responsible for field observations, recording of data, field rearing, laboratory maintenance of *Amphix* spp. and *E. macularis* populations, and editing and reviewing initial text.

range extending from Durango, Mexico, to Bolivia and Rio de Janeiro, Brazil. Most species are poorly known because of their cryptic behavior in nature, resulting in a paucity of museum material. Reichardt noted that some Brazilian specimen labels indicated that *Eurycoleus* were found in or near *Polyporus* fungi; G. E. Ball's field note of 23 August 1967 indicates the same. Ball (1975) discussed generic relationships, and placed *Eurycoleus* among the pericaline lebiine carabids. Immature stage descriptions were provided by Erwin (1975).

DESCRIPTION OF STUDY SITE

Holdridge and Budowski (1959) described the tropical lowland forest on Barro Colorado Island as "Tropical humid forest." Eisenberg and Thorington (1973) analyzed the mammal fauna. Rubinoff (1974) summarized detailed physical factors for the island and provided a list of tree species represented on the island. Numerous other papers dealing with elements of the flora and fauna are also available (Colby 1965).

In general, the island supports mature second-growth forest with few primary large trees. The canopy ranges from 17 to 27 meters above the ground and shades a varied understory of smaller trees and shrubs. There are numerous palms in parts of the forest. The undercanopy has plenty of downed wood, as trees and limbs fall during most of the year. Some of the downed wood is persistent, lasting for decades, but much of it disintegrates in a few months. There are many individuals of *Ficus* (two species predominating) and of *Inga*. Most of the observations recorded herein are from various *Inga* fallen trunks within 1500 meters of the research station clearing.

NATURAL HISTORY

BEHAVIOR OF ADULTS. After gaining full coloration (about three days), but before its cuticle is completely hardened, an adult *Eurycoleus* chews its way out of its pupal basket (described below) and moves under the bark until it finds an opening. It then moves to a large patch (sheet) of white polypore fungus *(Trametes scabrosa)*, which grows on the underside of logs, where the beetle remains while its exoskeleton hardens (figure 1).

We have seen as many as 50 individuals at one time on a fungal sheet about 150 square centimeters in size. Population samples indicate that females occur twice as often as males; males are rarely captured away from the logs with fungal sheets. Often we saw these beetles on sporulating bracts cleaning their legs, elytra, and antennae in the method described by Hlavac (1971) and Valentine (1973); this process probably allows ingestion of fungal spores and perhaps subsequent passage through the alimentary system. This site also serves as an aggregation point for both sexes. Mating occurs frequently, for females have no spermathecae for sperm storage and apparently must mate repeatedly to fertilize each egg clutch. The females disperse from the fungal sheets to oviposition sites which are smooth barked trees or logs that are infested with *Amphix* (Coleoptera: Endomychidae) colonies. A female *Eurycoleus* deposits a clutch of about 12 eggs within a few centimeters of a large assemblage of *Amphix* pupae (fig. 1). These eggs are wrapped with sticky silk and adherent debris. The eggs hatch within 3 to 5 days and the larvae begin feeding, as described below.

Adult *Eurycoleus* ingest fungal spores, feed on larvae, pupae, and teneral adults of *Amphix* (fig. 1); we also observed cuticular matter in their hind gut. As in other carabids, digestion begins preorally with regurgitation forming at the mouth during feeding. Adults stalk their prey by either a slow walk or a very rapid darting motion. The flat head is inserted beneath the tank-like shape of *Amphix* larvae and adults; the prey is flipped over with an upward jerk of the predator's head; then the mandibles chew their way into the soft underside. Adult *Eurycoleus* have no sclerotized proventriculus, thus soft cuticle and fluids are the major ingestants.

BEHAVIOR OF LARVAE AND PUPAE. A first instar larva emerges from the egg with the use of a bicarnate egg burster located on the middle of the frons. Several minutes before eclosion, small muscle contractions can be seen through the chorion. These contractions increase in frequency and the larval head makes one of two movements against the side of the egg wall with the egg burster. When the head breaks free of the chorion the larva gulps air. Bubbles, seen through the transparent cuticle, originate in the buccal cavity and pass caudally through the gut. After inflation, the larvae is about three times larger than when compacted into the egg. The larva rests for several hours until the cuticle is tanned and pigmented. Its proximity to the food source is a result of the oviposition site (see above), thus the new larva need not walk far for its first feeding. As the *Eurycoleus* larva approaches the group of *Amphix* pupae, its head swings slowly from side to side with the mandibles directed upward. The larva approaches an attached *Amphix* pupa (*Amphix* larvae attach themselves to the log or tree with an anal tube, then pupate) from the side and attempts to insert its

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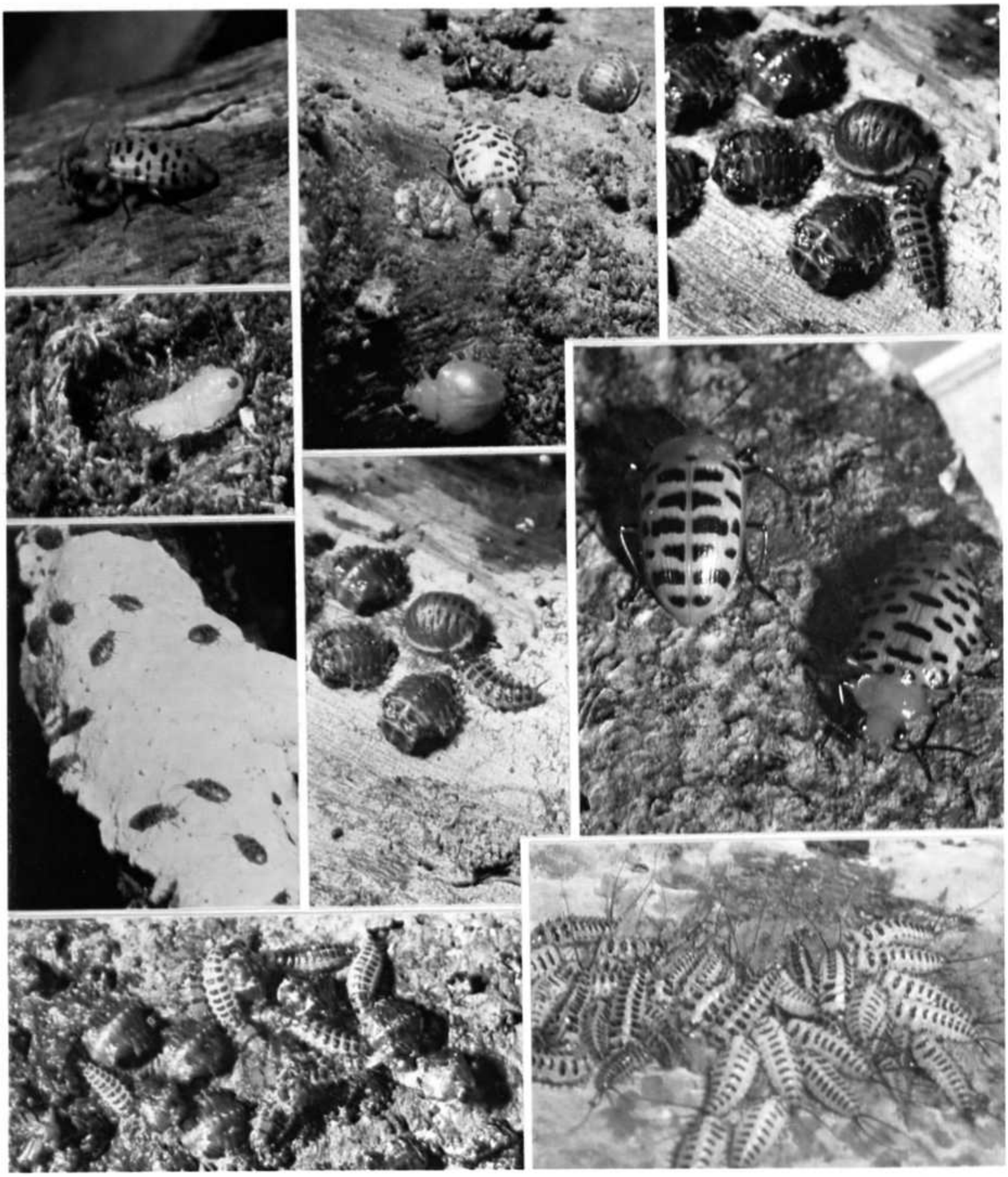

FIGURE 1. Top row from left to right: Adult *Eurycoleus macularis* feeding on *Amphix* larva; adult *E. macularis* ♀ near its egg clutch, *Amphix* adult below, larva above; larval *E. macularis* in *Amphix* pupal field, note attached *Amphix* larva not yet pupated. Second row: Pupal *E. macularis* in pupal basket. Third row: Congregation of *E. macularis* adults on polypore fungus, *Trametes scabrosa;* larval *E. macularis* in feeding position under *Amphix* attached larva; mimetic color patterns and stance of (left) *Priotelus* sp. and *E. macularis.* Bottom row: Mimetic color patterns and clumping of (left) *E. macularis* larvae and (right) *?Homoeotelus* sp. larvae.

head under the pupa in the area of pupal sterna II to V (fig. 1). The larva's head is now flexed upward at nearly 90° to the body. Attempts are made to penetrate the soft abdominal cuticle of the *Amphix* pupa. During this process the *Amphix* pupa responds by "slapping" the *Eurycoleus* larva on the head and body by contracting muscles in the post abdomen, elevating the pupal head away from the substrate with the body of the pupa vertical to the log. The results of this action greatly retard single first instar larvae; none of the observed attacks by the first instar larva were successful. It is likely that several first instars attack together, as do later instars, but we had only one animal to observe. Later instars work at least in pairs and usually in groups of 3 to 6; they insert their heads beneath the pupa with the mandibles directed upwards. The pupa's slapping motion is of benefit to the pupa in preventing the predator larva from biting, but when the larva does finally insert its head beneath the prey pupa the leverage of the slap is of benefit to the larva by aiding mandibular penetration.

As several larvae move slowly under the pupa, the pupa's arc of slapping motion diminishes until finally the pupa is immobilized in a vertical position. By this time, the larvae have penetrated the soft underside of the pupa and have begun eating. This process continues as larvae move from pupa to pupa throughout the assemblages. *Amphix* pupate in assemblages of 10 to 150 pupae, so a large group will be nearly eliminated by a dozen *Eurycoleus* larvae in three days of feeding activity.

When resting or moulting, the *Eurycoleus* larvae hide under or among the prey pupae. Since endomychid larvae release drops of fluid and the adults are aposematically colored, it seems likely that they are chemically protected. The presence of the chemical in the larvae and adults indicates its probable presence in the pupae. Therefore, the *Eurycoleus* larva gains protection by staying among the *Amphix* pupae. In addition, the *Eurycoleus* larvae are very colorful and may themselves be chemically protected by the eating of *Amphix* pupae and the ingestion of *Amphix* protective secretions. We saw no other predators of *Amphix,* no predator of *Eurycoleus,* and reared no parasites from *Amphix* or *Eurycoleus.*

After feeding and moulting three times, the large, swollen 4th instar *Eurycoleus* larva leaves the pupal assemblage (fig. 1) and seeks an opening under the bark of the host tree or log. This habit seems to be possible because *Amphix* invades a tree only at a state of decay in which the bark is loose yet intact. It is probable that this particular stage of wood decay is suitable for *Amphix* because of the fungal and lichen development which provides food for *Amphix* larvae. When a *Eurycoleus* larva gains entrance beneath the bark, it seeks an area with abundant shreds of bark fiber which it forms into a small basket. The larva orients itself so that its dorsum is next to the hard wood of the tree or log and its venter toward the bark. It then pupates in the basket. The transformation to adult requires 7 to 10 days.

The pupa's abdominal appendages (Erwin 1975) are thus oriented in a radial fashion (fig. 1), so that any predator working its way under the bark and through the basket wall first finds the end of the appendage pointing in that particular direction. It is our hypothesis that these appendages, composed of about 9 to 11 "beads," contain repellent chemicals and that any under-bark predators will be repelled before biting the pupa itself. Since the appendage is composed of several "beads," the pupa can sustain several attacks by different predators coming from the same direction. We have tested the chemical from the beads on two under-bark predators, *Pachyteles* sp. and *Morion cordatus* (both carabid beetles), by rubbing their mandibles and palpi with it. Both insects reacted violently and continued digging their mouthparts into the substrate (bark shreds, frass, and under-bark soil) for several minutes. The *Morion* was tested twice and reacted the same both times. This reaction was not elicited by touching the beetles' mouthparts with dry probes.

The known defense methods of all stages of *Eurycoleus macularis* are summarized in table 1.

IMPACT OF *Eurycoleus macularis* ON WOOD DECAY. Members of *E. macularis* have an acceleration effect on the process of wood decay in tropical lowland forests in at least two groups of smooth barked trees,

TABLE 1. Eurycoleus macularis *defense.*

eggs	clutch fastened with sticky silk clutch partially covered with woody debris
larvae	aposematic coloration mimic of erotylid larvae (*?Homoeotelus*) distasteful from eating endomychids association with endomychid pupal fields release of regurgitant from mouth
pupae	abdominal appendages basket pupal chamber under bark
adults	pygidial glands resemblance to erotylids (*Priotelus* sp.) resemblance to tenebrionids (*Poecilesthus* sp.) association with fungus as resting site