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# THE ANT LARVAE OF THE SUBFAMILY DORYLINAE: SUPPLEMENT

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This article has been prepared as a supplement to "The Larvae of the Army Ants" by G. C. Wheeler (1943). It includes (1) earlier references in the literature which has been overlooked, (2) subsequent references in the literature, (3) additional information on species described by G. C. Wheeler (1943), and (4) the description of one species not previously described.

In the twenty years elapsed since the previous article on this subfamily most of the literature has come from the pen of Dr. T. C. Schneirla and has dealt with the relation of larvae to the colony cycle. Two of his students (Lappano and Tafuri) have treated development and polymorphism. Other citations are mostly based on G. C. Wheeler (1943). The larvae of three additional species have been described by other authors.

## SUBFAMILY DORYLINAE

Fig. 1*b* shows a generalized (or synthetic) profile of a doryline larva. In our study of the body shapes of ant larvae we have used only profiles (i.e., outlines in side view), since dorsal and ventral views rarely show anything distinctive. To facilitate comparison of profiles we decided that all drawings would need to be of the same size. This, however, presented a problem with flexible larvae, because such larvae are preserved with various amounts of curving and contraction. Hence it was necessary to establish a standard measurement to be the same for the profiles of all genera. We chose the distance (on the drawing) from the anus to the first abdominal spiracle, for two reasons: (1) the abdomen is relatively inflexible and scarcely extensible; (2) these are two easily located points (in contrast, for example, to the posterior end, which would have to be designated arbitrarily on a curve). For our actual procedure see Wheeler and Wheeler, 1960. The generalized profile (Fig. 1*b*) for the subfamily was obtained by a sort of averaging of the three generic profiles.

Fig. 1*a* shows a generalized (or synthetic) doryline mandible derived by the same technique (see above), using the apex and the anterior condyle as the points of reference.

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## REFERENCES TO THE SUBFAMILY

Bernard, 1951:—"Larves eucéphales, carnivores; nourries par les ouvrières" (p. 1041). Brief description of larvae (after G. C. Wheeler, 1943) on p. 1048. Brief reference (p. 1049) to G. C. Wheeler's article on leg vestiges (1938).

Emery, 1899, p. 8—"Quello delle *Dorylinae* con la sua forma cilindrica allungata, la struttura speciale delle mascelle e la mancanza di peli d'attacco o di altre appendici del tegumento che non siano peli semplici."

Emery, 1910, p. 4—"Larves plus ou moins cylindriques, à poils courts, sans poils d'accrochage."

Gantes, 1949, p. 76:—"Les larves de dorylidés se rapprochent également beaucoup de *Formica* leur corps est couvert de poils simples et courts. La tête est grande, mais les pièces buccales sont plus courtes que chez les *Poneridae*. Ceci est donné d'après la description que G. C. Wheeler a faite d'un *Eciton*."

Wheeler (1920, p. 48) stated that the Dorylinae were exceptional in not having a beautifully developed trophorhinium.

### Genus **CHELIOMYRMEX** Mayr

Borgmeier, 1955, p. 59:—Description after G. C. Wheeler (1943).

#### **Cheliomyrmex megalonyx** Wheeler

Borgmeier, 1955, p. 68:—"Die Larve wurde von G. C. Wheeler (1943) beschrieben und abgebildet. Ich habe dei wichtigsten Charaktere bie der Gattungsdiagnose angefuehrt."

### Genus **DORYLUS** Fabricius
### Subgenus **ANOMMA** Shuckard

Bernard, 1951, p. 1051:—"Elles ne laissent pas les larves au soleil."

Emery, 1901, p. 430:—"È particolarmente interressante la presenza di un rudimento di antenna nelle larve di *Dorylus* . . . . Nella larva di *Dorylus* il capo è più piccolo e le mandibole più piccole e più deboli che nelle altre Doriline; le mascelle non hanno punte, e in generale l'armatura boccale è molto ridotta, condizione che indica un grado più inoltrato di perfezionamento delle cure materne, per parte della popolazione operaia . . . .Le larve . . . hanno la . . . forma cilindroide."

Schneirla, 1957, p. 124:— "No larval-excitatory factor seems indicated in Dorylus as far as influencing the arousal of an emigration is concerned."

Trabert (1957, p. 299) makes brief reference to G. C. Wheeler, 1943.

#### **Dorylus (Anomma) nigricans** Illiger

Cohic (1948, p. 237) translated into French G. C. Wheeler's description (1943, p. 322 and 324) of the male larva. He described (p. 233-237) and illustrated (Fig. 5-16) the soldier (*"macrocephale"* larva, which seems to be generally similar to the larva of *D. wilwerthi* Emery described by G. C. Wheeler (1943, p. 321); however, close comparison is not possible, because his drawing of the head is not in full-face view and because our material is damaged.

## Genus **AENICTUS** Shuckard

REVISED DEFINITION—Body hairs simple. Integument with few or no spinules; no papillae. Head hairs moderately numerous. Maxillary palp a short stout projection bearing three to six sensilla.

### **Aenictus leviceps** (F. Smith)

CORRECTION—The maxillary palp has two apical sensilla.

### **Aenictus turneri** Forel

Length (through spiracles) 2.6 mm. Generally similar to *Aenictus* (*T.*) *leviceps* (F. Smith) except as follows: Integument with short rows of minute spinules on the dorsal surface of abdominal somites IX and X. Maxillary palp an irregular projection with four sensilla; galea a short frustum with two apical sensilla. Opening of sericteries a short transverse slit on the anterior surface near the base of the labium. (Material studied: ten larvae and semi-pupae from Queensland, courtesy of Dr. W. L. Brown.)

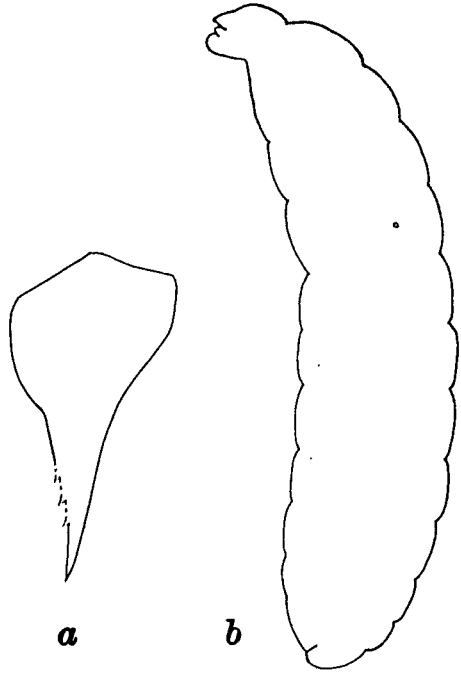


Fig. 1: *a*, generalized mandible (anterior view) for the subfamily Dorylinae; *b*, generalized body profile for the subfamily Dorylinae.

## Genus **ECITON** Latreille

## Subgenus **ECITON** Latreille

Borgeier, 1955, p. 163—Brief description of larva (after G. C. Wheeler, 1943 and Weber, 1943).

Emery (1901, p. 430) reported that the larvae have a cylindroid shape; he did not find antennal rudiments.

Emery (1911, p. 5) characterized the larvae as "à peu près cylindrique."

Marcus, 1954:—"Mi idea es, que las larvas nutridas con trozos de Termitas producen sexuales y que las larvas que no reciben esta substancia T resultan trabajadoras" (p. 6). Outline drawing of larva of *Eciton* sp. in side view (Fig. 6a on p. 11).

Wheeler, 1903, p. 207:—Larvae are carried by the neck, with the long slender body extending back between the legs of the worker. On p. 209 he compared the larvae with those of *Cerapachys*.

### **Eciton burchelli** and **E. hamatum**

Dr. T. C. Schneirla has published 30 articles on the behavior of these two species. The following account is based on two of these articles (1954, 1957).

The worker brood is always a unitary population of great size (approximately 30,000 individuals in *E. hamatum* and 50,000 in *E. burchelli*) and all of its members are at essentially the same stage of development. There are, however, individual differences in size.

Eggs are laid only in the middle of the statary phase. By the beginning of the following nomadic phase (induced by the ecolsion of the previous brood) the newly hatched larvae are concentrated in a single small mass near the center of the bivouac, where they are tended by minims; consequently their stimulative effect on the colony is negligible. By the fourth or fifth day of the nomadic phase the larvae have grown considerably and their stimulative effect has begun to accelerate. They occupy an expanding central portion of the bivouac, the larger larvae near the periphery, the smaller near the center. After the middle of the nomadic phase, an ever increasing number of intermediate and large workers take part in the care of the larvae—stroking, licking, holding, feeding and carrying them on migration. As the larvae mature there is a progressive increase in the intensity of nomadism, as evidenced by the enhanced vigor of raiding and by the greater distance of emigration.

With the approach of maturity the largest larvae (the potential major workers) are the first to cease feeding. The workers carry them out of the bivouac and lay them in near-by wood dust or other detritus, which soon covers them and in which they are able to spin cocoons. Smaller individuals spin later.

With the completion of spinning the stimulation of the workers by the larvae ceases abruptly and the colony enters upon the statary phase, which persists while this brood is in the pupal stage and terminates when the callows emerge; then the next nomadic phase begins. As mentioned above, the next brood has already been started by eggs laid in the middle of the statary phase.

After discussing (1957, p. 110-111) trophallaxis between larva and worker Schneirla extended the definition of that term "from the effects of exchange of nutrient as such to the many and varied ways in which specific stimulation independent of nutrient gains arouses or increases action or serves to facilitate physiological processes in the colony . . . . The brood-energizing factor is therefore held to be the

*necessary* factor for nomadic behavior and for propagation of the cyclic pattern itself."

Bernard, 1951, p. 1049-1051—A resumé of Schneirla's work on the influence of larvae on the behavior of the colony.

Schneirla, 1948, p. 109:—"Results show that a male brood has trophallactic stimulative relationships with workers comparable to those ordinarily exerted by a worker brood. Once larval development is well under way, the energizing effect of a male brood is comparable to that exerted by a worker brood roughly ten times its population size. Since male developmental phases are largely the same as those of worker broods, the appearance of the male broods occasions no substantial modification of the (nomad-statary) cycle of colony behavior changes."

### **Eciton burchelli** (Westwood)

Bernard, 1951, p. 1048:—Stomach and food of larva (after Wheeler and Bailey, 1920, p. 254-255).

Emery, 1899, p. 6:—"Nella larva di *Eciton* (fig. 6) il capo è più piccolo e meno staccato dal tronco; le mandibole strette e minute non oltrepassano il labbro superiore, anzi, non lo raggiungono neppure. I1 cono laterale delle mascelle è sostituito da un gruppo di piccoli tubercoli (fig. 6 *c*)."

Lappano (1958) described polymorphism, external anatomy, internal anatomy and histology. "The description of the external morphology . . . herein presented conforms to and extends the general descriptions given . . . by Emery (1899 and 1901) and G. C. Wheeler (1943)" (p. 49). Photographs (p. 51) of larvae of three sizes (Fig. 1) and of the head in anterior view (Fig. 2) and side view (Fig. 3).

Marcus, 1954, Fig. 6 b and c (p. 11):—Outline drawings of larvae in side view (after Schneirla).

Schneirla, 1945:—"During bivouac-change the larvae were carried individually, gripped anteriorly in the carrier's mandibles and slung underneath her body in the typical Eciton manner. In general, larvae were transported in the latter half of the movement" (p. 177).

Schneirla, 1948, p. 91:—A male brood numbers about 3000 larvae, which are subcylindrical and of approximately the same size. Mature larvae are 22-24.8 mm long. The production of males seems to be confined to the dry months. Photographs of male larvae of three sizes and of a male semipupa, Pl. I.

Schneirla and Brown, 1952, Pl. I:—Photographs of queen and male larvae.

Wheeler, 1921, p. 304:—"From what is now known of ant-larvae it can be positively asserted that Müller's description and Fig. 2 refer to larvae of the Ponerine genus *Pachycondyla*," not to *Eciton* larvae.

### **Eciton burchelli jeanae** Weber

Weber, 1943, p. 90:—"Larvae slender, curved, with numerous fine, flexuous hairs which are mostly simple and of variable size but are sometimes bifid, trifid or multifid; mandibles slender, falcate."

### **Eciton hamatum** (Fabricius)

IMMATURE MALE LARVA—Length (through spiracles) 5.6 mm. Generally similar to the worker larva except in the following details: Body hairs 0.036-0.132

mm, longest and most slender anteriorly, shorter ventrally and stouter posteriorly. Labrum feebly bilobed and with six sensilla on the ventral border near the middle. Maxillary palp with seven to nine sensilla. Hypopharynx with short rows of spinules.

MATURE MALE LARVA—Length (through spiracles) 24 mm. Generally similar to the worker larva. Body hairs longer (0.08-0.23 mm long), longest posteriorly and dorsally. Head hairs moderately numerous (about 60). Labrum with six sensilla on the ventral border near the middle.

Material studied: numerous larvae from the Panama Canal Zone, courtesy of Dr. T. S. Schneirla.

Allee et al., 1949, p. 432:—A photograph of workers transporting larvae slung under their bodies during change of bivouac. (Same as Buchsbaum, 1948, p. 292-26.)

Bernard, 1951, Fig. 949 on p. 1048:—Larva in side view, head in anterior view (after G. C. Wheeler, 1943).

Morley, 1953, Fig. 2a on p. 21:—Head in anterior view (after G. C. Wheeler, 1943); erroneously labelled *Acromyrmex*.

Schneirla, 1944:—Developmental period (p. 186); embryonic and early larval growth (colony statary), 10 days; completion of larval growth (colony nomadic), 17 days; pupal period (colony statary), 19 days; total, 46 days. Mature larvae ranged in length from 0.36 to 0.73 mm (p. 171).

Tafuri, 1955:—The largest larvae are fed to the limit; the smallest are deprived of food and forced to pupate while small. The following characteristics were correlated with days of the nomadic phase: size and development of leg discs; shape of head; appearance of imaginal discs; transparency; and pilosity. The leg discs have a growth rate independent of body length, which makes possible the separation of larvae of equal lengths into different developmental stages of the different worker castes; they also indicate larval age. Pl. I, photographs of larvae of assorted sizes in side view. Pl. II, drawing of head in anteroventral view and three drawings of thorax in ventral view. Pl. III-IV, photographs of larvae in ventral view.

Trabert, 1957, p. 299:—Brief reference to G. C. Wheeler, 1943.

### **Eciton conquistador** Weber

Weber, 1949, Fig. 5 on p. 4:—"Outline of 4.5 mm. larva from below. The uniformly simple hairs are not indicated."

### **Eciton rapax** F. Smith

Marcus, 1953, p. 63-66:—An account of glandular hairs of what is alleged to be *E. rapax*. But a correction slip pasted in the reprint reads: "De los valiosos trabajos de George C. Wheeler, que permiten determinar las larvas de hormigas, me he convencido, que, las larvas transportadas por Eciton rapax no son las suyas, sino larvas raptadas de Odontomachus". In the German summary (p. 68): "Die Larven von Odontomachus besitzen Nesselhaare aenlich wie die Raupen (Fig. 51 u 52)."

### Subgenus **LABIDUS** Jurine

Borgmeier, 1955, p. 81:—"Annaehernd cylindrisch. Behaarung einfach. Tegument papillenartig. Labrum klein. Maxillarpalpen mit einigen Sensillen. Mandibeln laenglich, spitz, mit gezaehntem Innenrand."

**Eciton (Labidus) coecum** (Latreille)

Weber, 1941, p. 329:—"Larvae slender, curved, with numerous fine, simple hairs." Fig. 4 on p. 327, larva in side view (hairs not shown).

**Eciton (Labidus) hartigi** (Westwood)

Borgmeier, 1955, p. 136: "Annaehernd cylindrisch. Haare einfach. Tegument spinuloes. Mandibeln laenglich, spitz, ohne Zaehne am Innenrand." (Borgmeier placed this species in a separate genus, *Nomamyrmex*.)

Subgenus **NEIVAMYRMEX** Borgmeier

Borgmeier, 1955, p. 278:—Brief description after G. C. Wheeler (1943, called *Acamatus*.)

**Eciton (Neivamyrmex) nigrescens** (Cresson)

Schneirla, 1958:—The nomad-statary cycle of this species is similar to that of *Eciton s. str.* The nomadic phase is set off by the eclosion of a mature pupal brood and is maintained by stimulation from the next brood in the larval stage. In *Neivamyrmex*, however, this phase does not end abruptly with larval maturity but endures through the semipupal stage to end at pupation. This difference results from the fact that the worker larvae of *Neivamyrmex* do not spin cocoons. A worker brood was estimated to comprise 37,000 larvae.

Schneirla, 1961:—Sexual broods consist of approximately a thousand male larvae and a few queen larvae. These broods are over-stimulated and over-fed, which accelerates their growth; consequently larval development and the nomadic phase are shortened to about ten days. As in *Eciton s. str.* potential male and queen eggs are produced in response to a period of dry weather. Fig. 3 on p. 11, photograph of queen larva, body length 17 mm. Fig. 4 on p. 12, photograph of male larva, body length 15 mm. Duration (p. 13) of developmental stages (in days) of male brood (compared with worker brood, in parentheses): egg 2-3 (3-4); embryonic 2-3 (2-3); larva in statary phase 6-8 (2-7); larva in nomadic phase 10-12 (14-18); prepupa and pupa 20-21 (20-23); estimated total 42 (48).

**Eciton (Neivamyrmex) schmitti** Emery

Trabert, 1957, p. 299:—Brief reference to G. C. Wheeler, 1943.

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