

The Larvae of the Army Ants (Hymenoptera: Formicidae): A Revision

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ABSTRACT: This complete revision of our previous articles on the larvae of army ants (Dorylinae) is the immediate result of the acquisition of much new material. The larvae of 22 species in the genera *Aenictus*, *Cheliomyrmex*, *Dorylus*, *Eciton*, *Labidus* and *Neivamyrmex* are described. Genera are keyed and characterized and each is assigned a specialization index. Feeding behavior is discussed. This study does not support the separation of Old World and New World army ants into separate subfamilies.

When we published our first paper on the larvae of the army ants (1943) our collection comprised representatives of six genera. Of four genera (*Aenictus*, *Cheliomyrmex*, *Eciton* and *Labidus*) we had an abundance of good material. For *Neivamyrmex* [then called *Eciton (Acamatus)*] we had only damaged larvae. In *Dorylus* we had seen one male each of two species (*D. wilverthi* and *D. molesta*) and four damaged worker larvae of *D. wilverthi*. Since the male larvae were superficially unlike any other ant larvae and since we were not permitted to prepare them for study under the microscope, they were of no use to us in comparison with other genera. The worker larvae of *Dorylus* were so different from other doryline genera that we have since been haunted by the suspicion that they might have been prey.

During the intervening 40 years we have received only one addition to our collection (*Eciton vagans*) and we have published two revisionary notes (Wheeler and Wheeler, 1964, 1974).

Recently Dr. W. H. Gotwald sent us a splendid collection of *Dorylus* larvae. We have also received additional material of *Neivamyrmex*, which is acknowledged in the appropriate places. So much new material makes it advisable for us to do an extensive revision of the larvae of the army ants. Since *Aenictogiton* is known only from males and we have never seen larvae of *Nomamyrmex*, we cannot include them in this study.

We have referred to our previous articles (Wheeler, 1943; Wheeler and Wheeler, 1964, 1974) on Dorylinae. Our earlier references to the literature in those articles have not been repeated here. This revision will necessitate changes in our 1976 monograph on pages 46, 75, 96 and 104.

The use of our specialization index is fully treated in Wheeler and Wheeler (1976, pp. 86–88 and 104–105).

In this revision the characters common to each higher taxon are given in the description of that taxon only and are not repeated in the lower taxa as we have done in our previous papers.

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Historical Notes

Emery in the "Genera Insectorum" (1910) and W. M. Wheeler (1922) placed army ants in the subfamily Dorylinae, which they divided into tribes: Dorylini, Ecitoni (or Ecitonini) and Leptanillini. Later W. M. Wheeler (1923, p. 335) raised the Leptanillini to subfamily rank.

Borgmeier (1955, p. 57) split the remaining Dorylinae into Dorylini (*Dorylus*), Aenictini (*Aenictus*), Aenictogitonini (*Aenictogiton*, known only from males), Cheliomyrmecini (*Cheliomyrmex*), Ecitonini (*Eciton*, *Labidus*, *Neivamyrmex* and *Nomeamyrmex*). Schneirla (1971, p. 9) and Gotwald (1979) concurred (omitting *Aenictogiton*).

In dissonance to this harmony (omitting *Aenictogiton*, which is now regarded as a ponerine) are Brown's (1973), Snelling's (1981) and Gotwald's (1982) separation of the army ants into 2 subfamilies: Dorylinae for the Old World genera (*Dorylus* and *Aenictus*) and Ecitoninae for the New World genera (all the others).

Subfamily Dorylinae

Profile myrmecioid (i.e., elongate and rather slender; curved ventrally; without a differentiated neck; diameter diminishing gradually from the middle of the abdomen to anterior end and more rapidly to posterior end). Somites distinct. Leg vestiges conspicuous as slightly raised bosses. Spiracles small; decreasing in diameter posteriorly. Integument spinulose. Antenna large; a slightly elevated boss; with 2 sensilla, each bearing a spinule; located at or near midlength of cranium. Mouth parts small and with few or no spinules. Labrum and clypeus not clearly distinguishable from each other. Mandible vestigial; amblyoponoid (i.e., subtriangular in anterior view; without a blade; straight or with apex slightly curved medially; with or without denticles on medial border); feebly sclerotized.

The specialization index for the subfamily is 26.

OBSOLETE: Wheeler (1943). Characterization and key. Also all characterizations of tribes Wheeler (1943) and Wheeler and Wheeler (1974).

Gotwald (1982) devotes about 1½ pages to the larvae, including quotations from our previous descriptions.

Rettenmeyer (1961, p. 610): a species of mite in the family Parasitidae is known to be parasitic on adult and larval New World army ants.

Key to the Genera of Dorylinae

- 1a. Combined clypeus and labrum bulging anteriorly; maxillary and labial palps represented by 7–15 isolated sensilla *Dorylus*
- 1b. Not as above 2
- 2a. Mandible without medial denticles; labial palp represented by 6 sensilla on a sclerotized base *Cheliomyrmex*
- 2b. Mandible with medial border finely erose; cranium subquadrate in anterior view *Labidus*
- 2c. Mandible with 1–6 medial denticles 3
- 3a. Maxillary palp represented by 5–12 sensilla on a sclerotized base .. *Eciton*
- 3b. Not as above *Aenictus* and *Neivamyrmex*

Genus *Aenictus* Shuckard

Anus terminal. Integument sparsely spinulose, the spinules minute, isolated or in short rows. Body hairs moderately numerous to rather sparse, uniformly dis-

tributed, short, unbranched, smooth, slightly curved or flexuous. Cranium widest at genal bulge. Head hairs moderately numerous, moderately long, unbranched, smooth, slightly curved. Mandible amblyoponoid, with 2–5 medial denticles. Maxilla small, appearing adnate; palp an irregular knob bearing 5 sensilla; galea a frustum bearing 2 apical sensilla. Labial palp represented by 3 contiguous sensilla; opening of sericteries a short transverse slit.

The specialization index is 24.

OBSOLETE: Wheeler (1943), Wheeler and Wheeler (1964, 1974): characterizations.

Aenictus laeviceps (F. Smith)

Fig. 1. Length (through spiracles) about 3.8 mm. Body profile myrmecioid; posterior end rounded and with a minute terminal knob. Anus terminal. Integument sparsely spinulose, the spinules minute and isolated or in short transverse rows. Body hairs moderately numerous, uniformly distributed, unbranched, smooth, slightly curved, short (0.025–0.075 mm long). Cranium subtrapezoidal in anterior view; widest just below antennal level; with pronounced genal bulges; integument with a few short rows of minute spinules. Antennae just below mid-length of cranium. Head hairs moderately numerous, unbranched, smooth, slightly curved, moderately long (0.038–0.075 mm). Labrum subrectangular, breadth twice length; anterior surface with a few sensilla near ventral border; ventral surface with a few sensilla near middle; posterior surface with 4 sensilla. Mandible with minute teeth near middle of medial border. Maxilla small, appearing adnate, apex conoidal and spinulose; palp an irregular knob with 5 sensilla; galea a frustum with 2 apical sensilla. Labium prominent; anterior surface with short to long arcuate rows of spinules dorsally; palp represented by 3 contiguous sensilla; opening of sericteries a short transverse slit. (Material studied: numerous larvae from Philippines.)

OBSOLETE: Wheeler (1943), Wheeler and Wheeler (1964, 1974): descriptions and figures.

Aenictus aratus Forel

SUBMATURE: Length (through spiracles) about 3.4 mm. Similar to *A. laeviceps* except as follows. No minute knob on posterior end. Body hairs rather sparse. Head subhexagonal in anterior view; broader than long; widest at genal bulge; lateral margins sinuate. Labrum feebly bilobed. (Material studied: numerous larvae from Philippines, labeled *A. a. nesiotus* var. *fraterculus*.)

OBSOLETE: Wheeler (1943): description and figures.

Aenictus gracilis Emery

Length (through spiracles) about 3.8 mm. Similar to *A. laeviceps* except in the following details. Head slightly longer than broad. Head hairs less numerous. (Material studied: numerous larvae from Philippines, labeled *A. martini*.)

OBSOLETE: Wheeler (1943): description.

Aenictus ceylonicus (Mayr)

Fig. 2. Length (through spiracles) about 3.2 mm. Similar to *A. laeviceps*. (Material studied: 10 larvae and semipupae from Queensland, labeled *A. turneri*, courtesy of Dr. W. L. Brown.)

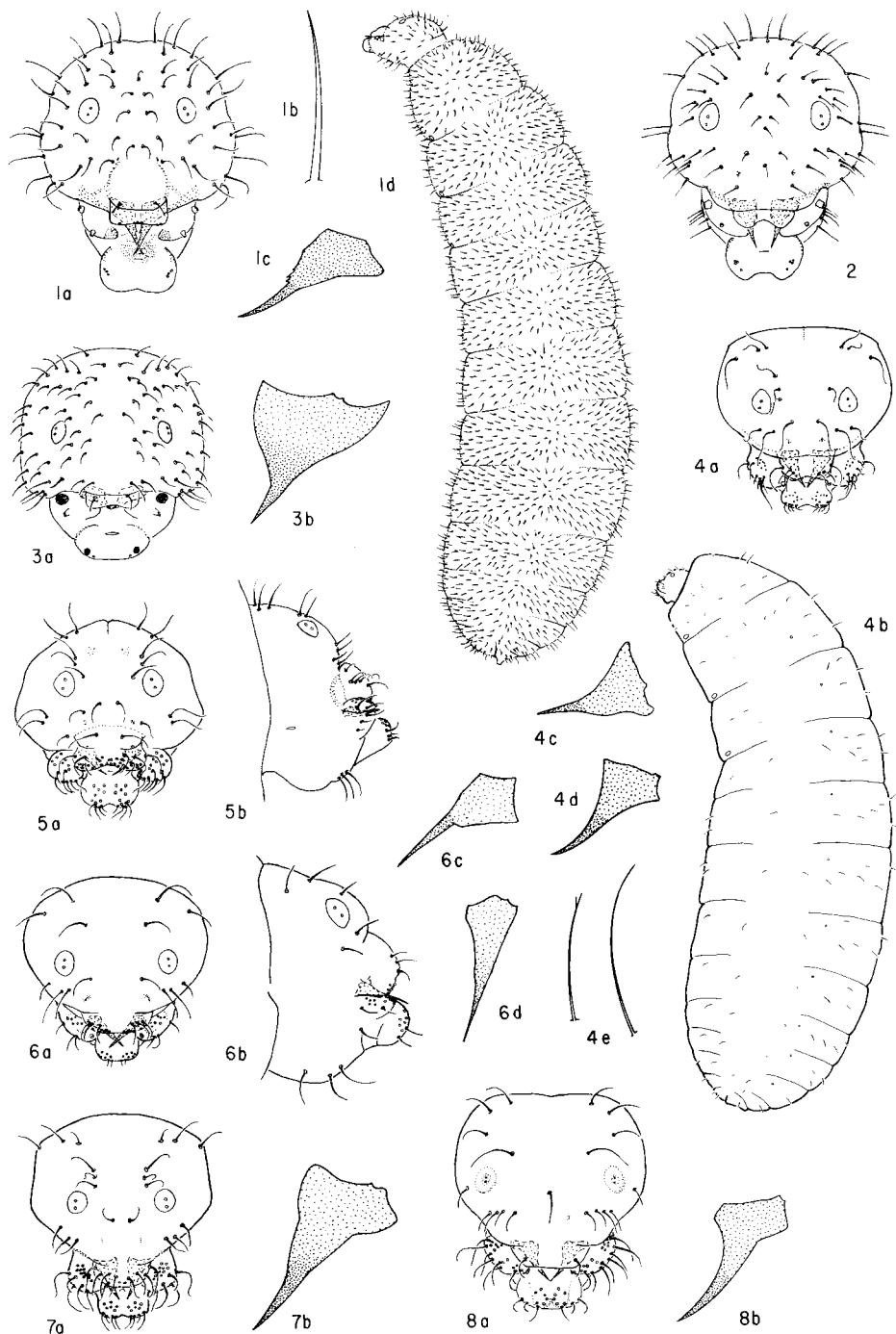


Fig. 1. *Aenictus laeviceps*. a, Head in anterior view, $\times 81$; b, body hair, $\times 333$; c, left mandible in anterior view, $\times 172$; d, larvae in side view, $\times 24$. Fig. 2. *Aenictus ceylonicus*. Head in anterior view, $\times 91$. Fig. 3. *Cheliomyrmex megalonyx*. a, Head in anterior view, $\times 57$; b, left mandible in anterior view, $\times 267$. Fig. 4. *Dorylus (Anomma) molesta*. a, Head in anterior view, $\times 45$; b, larva in side view, $\times 9$; c, left mandible in lateral view, $\times 133$; d, left mandible in anterior view, $\times 133$; e, two types of

OBSOLETE: Wheeler and Wheeler (1964): description.

Genus *Cheliomyrmex* Mayr

Anus terminal. Integument densely spinulose, the spinules rather large and in arcuate rows, the rows on ridges. Body hairs sparse, mostly on the dorsal surface; unbranched, short, smooth, slightly curved. Labrum short and feebly bilobed; ventral and posterior surfaces with a few rows of minute spinules. Mandible amblyoponoid but without medial denticles. Maxilla appearing adnate; palp a cluster of 13–17 sensilla on a sclerotized base; galea a small frustum bearing 2 apical sensilla. Labium with a few short rows of spinules basally; palp a cluster of about 6 sensilla on a sclerotized base; opening of sericteries a short transverse slit.

The specialization index is 27.

OBSOLETE: Wheeler (1943), Wheeler and Wheeler (1974): generic characterizations.

Cheliomyrmex megalonyx W. M. Wheeler

Fig. 3 and Wheeler and Wheeler (1974), Fig. 1. Length (through spiracles) about 5.8 mm. Anus terminal. Integument densely spinulose, the spinules rather large and in short rows, the rows on ridges. Body hairs sparse, unbranched, smooth, short (0.05–0.1 mm). Cranium semicircular in anterior view. Antennae located just below midlength of cranium. Head hairs moderately numerous, unbranched, smooth, slightly curved, short (0.05–0.1 mm). Labrum feebly bilobed; anterior surface with 1 or 2 hairs and 4 sensilla; ventral surface with 6 sensilla and a few rows of minute spinules; posterior surface with 4 small sensilla and a few short rows of spinules. Mandible without denticles on medial border. Maxilla appearing adnate; palp a cluster of 13–17 sensilla on a sclerotized base; galea a small frustum bearing 2 apical sensilla. Labium with a few short rows of spinules dorsally; palp a cluster of 6 sensilla on a sclerotized base; opening of sericteries a short transverse slit. (Material studied: numerous larvae from British Guiana.)

OBSOLETE: Wheeler (1943): description and figures.

Genus *Dorylus* Fabricius

Anus terminal. Integument densely spinulose. Body hairs sparse, mostly unbranched, smooth, slender. Head hairs few, unbranched, smooth, flexuous and moderately long. Labrum and clypeus bulging anteriorly and not clearly distinguishable from each other. Mandible amblyoponoid but without medial denticles. Maxilla large and lobose; bearing several long hairs; palp represented by 7–15 isolated sensilla; galea a small frustum bearing 2 apical sensilla. Labium bearing several conspicuous ventral hairs; each palp represented by 10–15 isolated sensilla. No spinules on mouth parts, except on posterior surface of labrum; opening of sericteries a short transverse slit.

body hairs, $\times 170$. Fig. 5. *D. (A.) nigricans*. a, Head in anterior view, $\times 48$; b, head in lateral view, $\times 48$. Fig. 6. *Dorylus (Alaopone)* sp. a, Head in anterior view, $\times 95$; b, head in lateral view, $\times 95$; c, left mandible in lateral view, $\times 267$; d, left mandible in anterior view, $\times 267$. Fig. 7. *Dorylus (D.)* sp. a, Head in anterior view, $\times 67$; b, left mandible in anterior view, $\times 333$. Fig. 8. *Dorylus (Rhogmus)* sp. a, Head in anterior view, $\times 70$; b, left mandible in anterior view, $\times 185$.

The specialization index is 30.

OBSOLETE: Wheeler (1943): generic characterization.

Gotwald (1982, p. 187) (after Raignier). Young male larvae of *Anomma* differ from worker larvae in being more slender and making curling movements.

Dorylus (Anomma) molesta Gerstaecker

Fig. 4. Length (through spiracles) about 9 mm. Body profile myrmecoid; posterior end rounded. Spiracles minute. Integument spinulose, spinules isolated or in short rows, the rows on ridges; most prominent on venter of thorax. Body hairs very sparse and widely scattered; unbranched or with bifid tip; smooth, very slender, flexuous, short (0.1–0.2 mm long). Head small; cranium transversely subelliptical. Antennae just below midlength of cranium. Head hairs few, unbranched, smooth, flexuous, very slender, moderately long (about 0.1 mm). Labrum feebly bilobed; anterior surface of each lobe with 3 long hairs; medial portion of ventral surface with 14 sensilla; posterior surface with 4 sensilla medially and a few short rows of spinules. Mandible slender and curved medially. Maxilla large, lobose and bearing 6 slender, long (0.05–0.075 mm), flexuous hairs; palp represented by a cluster of 7–15 sensilla; galea a short frustum with 2 apical sensilla. Labium bilobed, each lobe bearing 4 distal hairs (0.025–0.05 mm long); palp represented by 12 sensilla; opening of sericteries a very short transverse slit. (Material studied: numerous larvae collected by Dr. W. H. Gotwald in Kenya and Dr. D. H. Kistner in Zambia.)

OBSOLETE: Wheeler (1943): description.

Dorylus (Anomma) nigricans Illiger

Fig. 5. Length (through spiracles) about 10 mm. Similar to *D. molesta* except as follows. Integument densely spinulose, the spinules rather large. Body hairs shorter (0.05–0.15 mm long). Cranium suboctagonal, broadest below antennal level. Antennae at midlength of cranium. Labrum bilobed, anterior and ventral surfaces with about 30 sensilla. (Material studied: numerous larvae from Ghana, collected by Dr. W. H. Gotwald.)

Dorylus (Anomma) wilverthi Emery

Apparently similar to *D. molesta*, except as follows. Body hairs shorter (0.05–0.075 mm long). Head hairs shorter (0.05–0.075 mm long). Labrum with 8 hairs on anterior surface; ventral surface spinulose, the spinules minute and in transverse rows. (Material studied: 4 damaged specimens from the Belgian Congo.)

OBSOLETE: Wheeler (1943): description and Figs. 1–6 on Pl I.

Dorylus (Alaopone) sp.

Fig. 6. SEMIPUPAE: Length (through spiracles) 3.8–4.8 mm. Similar to *D. molesta* except as follows. Mandible more slender. Labium smaller and with fewer hairs (4). (Material studied: numerous semipupae from Kenya, collected by Dr. J. Darlington, #429.)

Dorylus (Dorylus) sp.

Fig. 7. Length (through spiracles) 2.8–4.9 mm. Similar to *D. (A.) molesta* except in the following details. Body hairs 0.025–0.15 mm long. Head hairs few. Maxillary

palp represented by 10–16 sensilla. Labial palp represented by about 15 sensilla. [Material studied: numerous larvae collected by J. Darlington #38, #214 in Kenya; by D. H. Kistner #1854 (locality?); by J. M. Leroux #041676 in Ivory Coast.]

Dorylus (Rhogmus) sp.

Fig. 8. SEMIPUPAE: Length (through spiracles) 2.5–5.5 mm. Similar to *D. (A.) molesta*, except as follows. Body hairs shorter (0.04–0.15 mm long). Spinules rather long, isolated or in short rows. Cranium suboctagonal. Head hairs shorter (0.05–0.08 mm long). Antenna large, a slightly raised boss, with medial depression bearing 2 sensilla. Galea represented by 2 contiguous sensilla. (Material studied: numerous semipupae collected by Dr. W. H. Gotwald #GC054 in Ghana.)

Genus *Eciton* Latreille

Anus posteroventral. Integument densely spinulose, the spinules minute and in short transverse rows. Body hairs sparse to moderately numerous, short, unbranched, smooth and slightly curved. Cranium subhexagonal, widest at antennal level. Head hairs numerous, moderately long, unbranched, smooth, slender and flexuous. Labrum with spinules on ventral and posterior surfaces. Mandible with 4–6 medial denticles. Maxilla with 6 hairs; apex round-pointed, with a few rows of minute spinules; palp a cluster of 8–12 sensilla on a sclerotized base; galea a frustum with 2 apical sensilla. Labium with a few minute spinules; palp a cluster of 3 contiguous sensilla; opening of sericteries a long transverse slit. Hypopharynx with a few short rows of minute spinules.

The specialization index is 24.

OBSOLETE: Wheeler (1943), Wheeler and Wheeler (1974): characterizations.

Audy et al. (1972): The females of the mite *Perperipes ornithocephala* Cross (Pyemotidae) inhabit the nests of *Eciton* and apparently mimic the larval ants among which they live. This is the only known case of mimicry of an ant larva.

“In the nomadic phase then the workers are increasingly occupied in grooming and feeding the brood. Army ant workers deliver food to their larvae much as do ponerines Morsels of booty, macerated as they are rolled about and squeezed between the jaws, tongue, and palps of the adult workers, become soft pellets which are laid upon larvae or larvae are laid upon them. The process of food preparation often begins with workers pulling against each other in pairs with a piece of booty in their jaws, evidently extracting juices with each new grip and pull. In keeping with the workers’ degenerate crops . . . and small gasters, their own food may be fluids more often than the tissues. The larvae, in contrast, feed voraciously and are often seen with their mouthparts applied to morsels or—increasingly as they grow—to whole pieces of booty.” (Schneirla, 1971, pp. 140–141.)

Eciton hamatum (Fabricius)

Fig. 9. Length (through spiracles) about 10.6 mm. Integument densely spinulose, the spinules moderately large and in transverse rows. Body hairs moderately abundant, short (0.075–0.2 mm), unbranched, smooth, slightly curved. Cranium subhexagonal, widest at midlength. Antennae located just below midlength of cranium. Head hairs moderately numerous, long (0.06–0.14 mm), unbranched, smooth, slightly curved; dorsal hairs directed downward, ventral upward. Labrum

small, transversely subrectangular; anterior surface with 10 sensilla; middle of ventral border with 4 sensilla; posterior surface spinulose near ventral and lateral borders, the spinules minute and in short rows; posterior surface with 6 sensilla near middle. Mandible with a few minute denticles on medial border. Maxilla with apex round-pointed; palp a cluster of 9–11 sensilla on a sclerotized base; galea a frustum with 2 apical sensilla. Labium with a sclerotized band laterally and posteriorly; palp a cluster of 3 sensilla; opening of sericteries a long transverse slit. Hypopharynx with a few short rows of minute spinules. (Material studied: numerous larvae from Panama.)

OBSOLETE: Wheeler (1943): description and all figures.

REFER to Wheeler and Wheeler (1964) for description of male larvae.

Akre reported (1968, p. 96) that the myrmecophilous histereid beetles *Euxenister wheeleri* Mann and *Pulvinister nevermanni* Reichensperger ate the larvae of this species.

Eciton burchelli Westwood

Length (through spiracles) about 9.2 mm. Similar to *E. hamatum* except in the following details. Head hairs numerous. Labrum subtrapezoidal, narrowed ventrally. Maxillary apex with a few short rows of minute spinules; palp a cluster of 8 sensilla. (Material studied: numerous larvae from Trinidad, courtesy of Dr. N. A. Weber.)

OBSOLETE: Wheeler (1943): description and figure.

REFER to Wheeler and Wheeler (1974) for description of immature larvae.

Akre reported (1968, p. 92) that the myrmecophilous beetles *Euxenister wheeleri* Mann and *E. caroli* Reichensperger ate the larvae of this species.

Eciton rapax F. Smith

Length (through spiracles) about 11.3 mm. Similar to *E. hamatum* except as follows. Integument with minute spinules. Body hairs sparse; lacking on venter, on intersegmental areas and around spiracles. Maxilla with apex spinulose, the spinules large and isolated or minute and in short rows; palp with 8–12 sensilla. (Material studied: numerous larvae from Ecuador, courtesy of P. Kazan.)

Eciton vagans (Olivier)

Length (through spiracles) about 9.6 mm. Very similar to *E. hamatum*. Mandible with apical tooth more slender. Galea taller. (Material studied: numerous larvae from Trinidad, courtesy of Dr. N. A. Weber and 10 larvae from Ecuador courtesy of P. Kazan.)

OBSOLETE: Wheeler and Wheeler (1974): description.

REFER to Wheeler and Wheeler (1974) for description of very young larvae.

Genus *Labidus* Jurine

Anus subterminal. Body hairs sparse to moderately numerous, unbranched, smooth, slightly curved, short. Cranium subquadrate. Mandibles in contact with each other at base; with medial border erose. Maxilla with apex paraboloidal; palp a skewed peg bearing 5–7 apical sensilla; galea digitiform, with 2 apical sensilla. Labial palp represented by 3 contiguous sensilla.

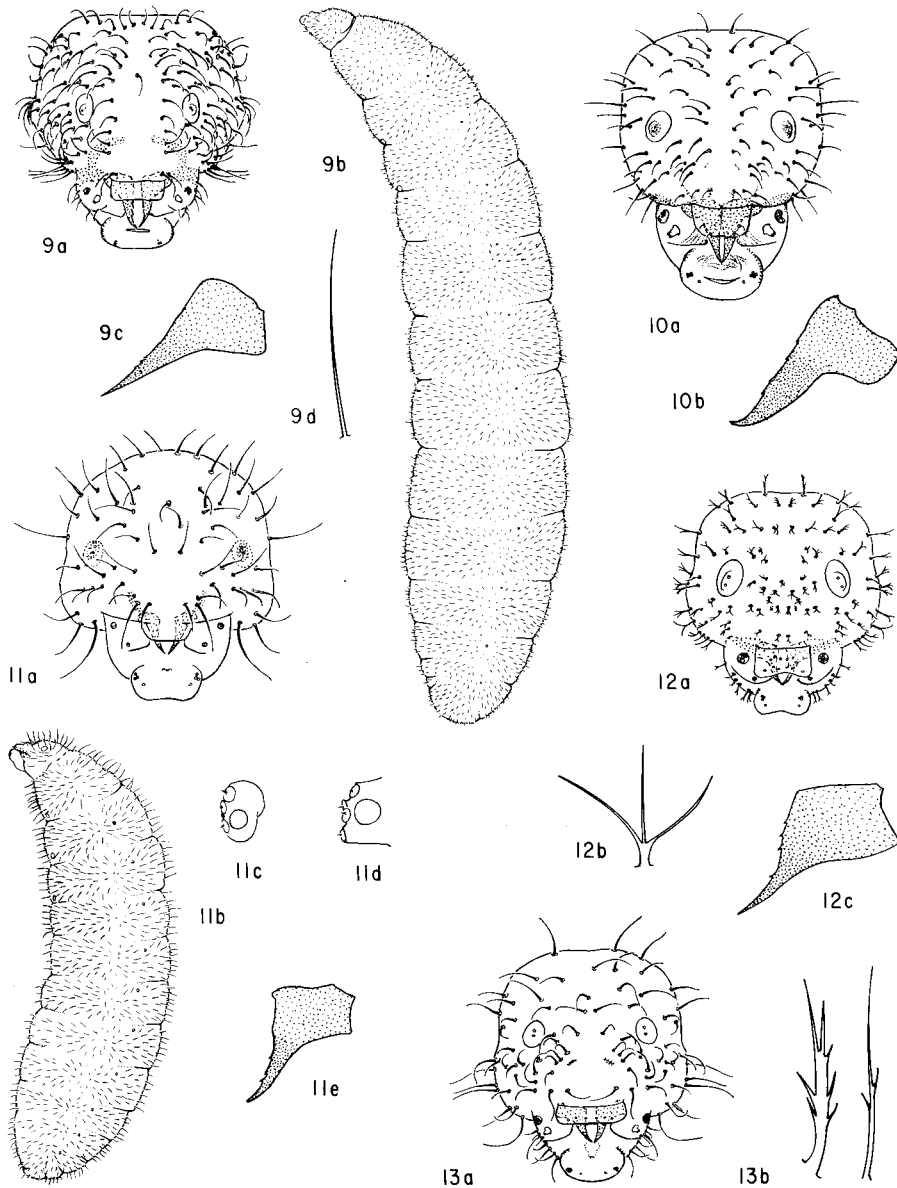


Fig. 9. *Eciton hamatum*. a, Head in anterior view, $\times 41$; b, larva in side view, $\times 10$; c, left mandible in anterior view, $\times 133$; d, body hair, $\times 339$. Fig. 10. *Labidus coecus*. a, Head in anterior view, $\times 60$; b, left mandible in anterior view, $\times 133$. Fig. 11. *Neivamyrmex postcarinatus*. a, Head in anterior view, $\times 85$; b, larva in side view, $\times 18$; c, left maxillary palp in anterior view, $\times 529$; d, left maxillary palp in side view, $\times 529$; e, left mandible in anterior view, $\times 267$. Fig. 12. *Neivamyrmex opacithorax*. a, Head in anterior view, $\times 67$; b, body hair, $\times 339$; c, left mandible in anterior view, $\times 267$. Fig. 13. *Neivamyrmex pilosus*. a, Head in anterior view, $\times 62$; b, two body hairs, $\times 339$.

The specialization index is 22.

OBSOLETE: Wheeler and Wheeler (1974): characterization.

Labidus coecus Latreille

Fig. 10 and Wheeler and Wheeler (1974), Fig. 3d. Length (through spiracles) about 7.4 mm. Integument densely spinulose, the spinules short and in arcuate rows, forming a reticulate pattern. Body hairs sparse, unbranched, smooth, slightly curved, short (0.038–0.125 mm). Antennae located just below midlength of head. Head hairs moderately numerous, unbranched, smooth, slightly curved, short (0.025–0.1 mm long). Labrum subtrapezoidal, narrowed ventrally; anterior surface with 8 sensilla and 4 small hairs (about 0.013 mm long); ventral surface spinulose, the spinules rather large and in short rows, and with sensilla medially; posterior surface spinulose, the spinules large and in rows; posterior surface with 8 sensilla middorsally. Mandible with medial border finely erose. Maxilla with apex spinulose, the spinules in arcuate rows forming a reticulate pattern; palp a skewed peg with 5–7 apical sensilla; galea digitiform, with 2 apical sensilla. Labium with a few spinules in short rows basally; palp represented by 3 contiguous sensilla; opening of sericteries a long transverse slit with protruding lips. (Material studied: 8 larvae from British Guiana, courtesy of Dr. N. A. Weber.)

OBSOLETE: Wheeler (1943): description and figures as *Eciton* (*Labidus*). 1974: descriptions and Fig. 3a, b, c.

Genus *Neivamyrmex* Borgmeier

Anus posteroventral. Integument densely spinulose, the spinules isolated or in short rows, the rows on ridges. Body hairs sparse to moderately numerous; short. Of 3 types: (1) unbranched, smooth, slightly curved; (2) unbranched and denticulate; (3) deeply 2–4-branched. Head widest at genal bulge. Head hairs long, moderately numerous. Of 3 types: (1) unbranched, smooth; (2) unbranched, with short denticles; (3) deeply 2–3-branched. Head widest at genal bulge. Head hairs long, moderately numerous. Of 3 types: (1) unbranched, smooth; (2) unbranched, with short denticles; (3) deeply 2–3-branched. Mandible with 1–6 denticles. Maxilla appearing adnate, apex narrowly rounded; palp a small knob bearing 5–7 sensilla; galea varying from 2 contiguous sensilla to a small frustum bearing 2 apical sensilla.

The specialization index is 29.

OBSOLETE: Wheeler and Wheeler (1974): characterization.

Neivamyrmex postcarinatus Borgmeier

Fig. 11. Length (through spiracles) about 2.4 mm. Body profile myrmecoid, with posterior end round-pointed. Anus posteroventral. Integument spinulose, the spinules minute but larger and more numerous posteriorly, isolated or in short rows. Body hairs numerous, unbranched, smooth, slightly curved, short (0.03–0.11 mm long) and stout; longest anteriorly. Cranium in anterior view with dorsal half semicircular, ventral half subtrapezoidal; widest at genal bulge, slightly wider than long. Antennae slightly below midlength of head. Head hairs moderately numerous; unbranched (rarely bifid), smooth, with stout base, slightly curved, long (0.025–0.075 mm). Mouth parts without spinules. Labrum short (breadth 3 times length); subtrapezoidal; with 8 sensilla near ventral border; posterior surface with 2 isolated sensilla. Mandible without medial denticles. Maxilla small, apex

narrowly rounded; palp a small irregular protuberance with 5 sensilla; galea a small frustum with 2 apical sensilla. Labium feebly bilobed; palp represented by 3 contiguous sensilla; opening of sericteries a short transverse slit. (Material studied: 2 larvae from Costa Rica, courtesy of J. Longino.)

Neivamyrmex harrisi (Haldeman)

Length (through spiracles) about 4.6 mm. Similar to *N. postcarinatus* except in the following details. Body and head hairs longer (0.1–0.18 mm long), with distal portion very slender and flexuous. Labrum feebly bilobed. Maxillary palp rarely with 7 sensilla. (Material studied: numerous larvae from Texas, courtesy of Dr. J. F. Watkins.)

Neivamyrmex nigrescens (Cresson)

Length (through spiracles) about 3.8 mm. Similar to *N. postcarinatus* except as follows. Integumentary spinules on ridges. Body hairs stout, short (0.038–0.075 mm long). Of 2 types: (1) unbranched; (2) 2- or 3-branched. Head hairs numerous; with stout base and flexuous tip; longer (0.05–0.11 mm long). Labrum with 10 sensilla on anterior surface, 6 on ventral surface and 10 on posterior surface; posterior surface sparsely spinulose, the spinules minute and in short transverse rows. Maxillary palp with 6 or 7 sensilla. Labium feebly bilobed; with a few rows of minute spinules basally. (Material studied: numerous larvae from Arizona, courtesy of Dr. J. F. Watkins.)

MALE: Wheeler (1943, p. 331) as *Eciton* (*Acamatus*) *schmitti*.

OBSOLETE: Wheeler (1943): description of worker and Figs. 29–33 as *E. (A.) schmitti*.

Petralia and Vinson (1979). Venter—description and SEM. “Workers placed the prey near larvae, which then attached themselves to this food and appeared to suck out the body fluids (Mirenda, pers. comm.)” (p. 390).

Neivamyrmex opacithorax (Emery)

Fig. 12. Length (through spiracles) about 4.6 mm. Similar to *N. postcarinatus* except as follows. Body hairs sparse; short (0.025–0.05 mm long); deeply 2- or 3-branched (rarely 4-branched). Cranium subtrapezoidal, with pronounced genal bulges. Head hairs moderately numerous; short (0.03–0.04 mm long); deeply 2- or 3-branched. Labrum with 10 sensilla on anterior surface, 4 on ventral surface and 10 on posterior surface. Mandible with 4–6 medial denticles. (Material studied: numerous larvae from Texas, courtesy of Dr. J. F. Watkins.)

Neivamyrmex pilosus (F. Smith)

YOUNG LARVA: Fig. 13. Length (through spiracles) about 3.4 mm. Similar to *N. postcarinatus* except as follows. Body hairs sparse, with several long stiff denticles apically, on a stout base. (Material studied: numerous larvae from Texas, G. & J. Wheeler #455.)

OBSOLETE: Wheeler (1943): description and Figs. 34–36 as *E. (A.) pilosum*.

Neivamyrmex texanus Watkins

Length (through spiracles) about 5.3 mm. Similar to *N. postcarinatus* except as follows. Body hairs may be 2- to 4-branched. Medial border of mandible with 6 small denticles. Maxillary palp represented by a compact cluster of 7 sensilla.

Labium feebly bilobed. (Material studied: 6 larvae from Texas, courtesy of Dr. J. F. Watkins.)

Discussion

Gotwald's (1982, pp. 187, 208) account is based on Wheeler and Bailey (1920 *nec* 1925) and Schneirla (1971). The former suspected that the larvae of *Eciton burchelli* were fed with large pellets composed of the rolled up soft parts of insects. These pellets were so compact that they retained their shape even in the larval gut. According to Schneirla, as the larvae grow larger they also feed with their mouth parts applied directly to whole pieces of prey. As the larvae mature the workers drop food on them, but more frequently they simply drop the larvae on the prey.

A study of doryline larvae presents an interesting paradox: Why do larvae of the world's most carnivorous ants have mandibles incapable of chewing solid food? The explanation was probably discovered by Schneirla (see above under *Eciton*). We speculate a little further: the larvae probably exude from the mouth an enzyme which digests the solid prey; the resulting liquid is sucked into the larval pharynx. The larval mouth parts are adapted for such sucking.

Taxonomic Conclusions

We have studied the larvae of 746 species in 199 genera and 51 of the 61 tribes and in all of the living subfamilies. Nevertheless we are unwilling to suggest how much weight should be given to larval characters in the taxonomy of ants. We will only go so far as to say that larval characters support—or fail to support—a certain change in classification. "Perhaps the problem is insoluble. In the end, the answer may be subjective based upon intuition based on experience." (Wheeler and Wheeler, 1979, p. 334.)

Larval characters will not support the recent classification of Brown (1973), Snelling (1981) and Gotwald (1982). The larvae are not separable into Old World and New World subfamilies. The larvae of *Dorylus* do show greater differences from the other genera than the latter do from each other, as is evident in our key. Those differences might support, but do not require, subfamilial distinction.

Our conclusion, based on known larvae, is that all army ants should be in one subfamily (Dorylinae) and should be divided into 4 tribes (Dorylini, Aenictini, Cheliomyrmecini and Ecitonini), with the qualification that Aenictini are separable only by geography from the Ecitonini.

Literature Cited

- Akre, R. E. 1968. The behavior of *Euxenister* and *Pulvinister*, histerid beetles associated with army ants. *Pan-Pacific Entomol.* 44:87–101.
- Audy, J. R., F. J. Radovsky, and P. H. Vercammen-Grandjean. 1972. Neosomy: radical intrastadial metamorphosis associated with arthropod symbioses. *J. Med. Entomol.* 9:487–494.
- Borgmeier, T. 1955. Die Wanderameisen der neotropischen Region. *Stud. Entomol.* Nr. 3. 717 pp., 87 pl.
- Brown, W. L. 1973. A comparison of the hylean and Congo-West Africa rain forest ant faunas. In B. J. Meggers et al. (eds.), *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*, pp. 161–185. Smithsonian Inst. Press, Washington, D.C.
- Emery, C. 1910. Fam. Formicidae, Subfam. Dorylinae. *Genera Insectorum Fasc.* 102:34 pp.
- Gotwald, W. H. 1979. Phylogenetic implications of army ant zoogeography. *Ann. Entomol. Soc. Amer.* 72:462–467.

- . 1982. Army ants. *In* H. R. Hermann (ed.), *Social Insects*, Vol. 4, pp. 157–254. Academic Press, New York.
- Petralia, R. S., and S. B. Vinson. 1979. Comparative anatomy of the ventral region of ant larvae, and its relation to feeding behavior. *Psyche* 86:375–394.
- Rettenmeyer, C. W. 1961. Behavior, abundance and host specificity of mites found on Neotropical army ants. XI Intern. Kongr. Entomol., Wien, 1960. Band 1:610–612, 1 pl.
- Schneirla, T. C. 1971. *Army Ants: A Study in Social Organization*. W. H. Freeman and Co., San Francisco. 349 pp.
- Snelling, R. R. 1981. Systematics of social Hymenoptera. *In* H. R. Hermann (ed.), *Social Insects*, Vol. 2, pp. 369–453. Academic Press, New York.
- Wheeler, G. C. 1943. The larvae of the army ants. *Ann. Entomol. Soc. Amer.* 36:319–332.
- Wheeler, G. C., and J. Wheeler. 1964. The ant larvae of the subfamily Dorylinae: supplement. *Proc. Entomol. Soc. Washington* 66:129–137.
- , and ———. 1974. Ant larvae of the subfamily Dorylinae: second supplement. *J. Kansas Entomol. Soc.* 47:166–172.
- , and ———. 1976. Ant larvae: review and synthesis. *Mem. Entomol. Soc. Washington* 7:1–108.
- , and ———. 1979. Larvae of social insects. *In* H. R. Hermann (ed.), *Social Insects*, Vol. 1, Chapter 7, pp. 287–338. Academic Press, New York.
- Wheeler, W. M. 1922. The ants collected by the American Museum Congo Expedition. *Bull. Amer. Mus. Natur. Hist.* 45:39–269, 22 pl.
- . 1923. *Social Life Among the Insects*. Harcourt, Brace and Co., New York. 375 pp.
- Wheeler, W. M., and I. W. Bailey. 1920. The feeding habits of pseudomyrmecine and other ants. *Trans. Amer. Phil. Soc. (Philadelphia)* (Art. 4): 235–279.