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GEORGE C. WHEELER AND JEANETTE WHEELER

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THE LARVAE OF THE ANT GENUS *BOTHROPONERA*
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GEORGE C. WHEELER and JEANETTE WHEELER, *Laboratory of Desert Biology,
Desert Research Institute, University of Nevada, Reno, Nevada 89507*

ABSTRACT—The larvae of nine species of the ant genus *Bothroponera* (Ponerinae: Ponerini) are described and figured. These fall into three generically distinct groups on the basis of body profile, mandible shape and tubercles: (I) *sublaevis*, *denticulata*, and *piliventris*; (II) *mayri*; and (III) *sjostedti*. The remaining species cannot be grouped, because we have only semipupae of *cariosa* and only immature larvae of *porcata*, *pumicosa* and *soror*. The mature larvae of the five species are keyed. It is concluded that W. M. Wheeler was justified in using larval differences (among others) in separating *Bothroponera* from *Pachycondyla*.

The Paleotropical ant genus *Bothroponera*, which comprises about 35 species, is a member of the tribe Ponerini in the subfamily Ponerinae. It is widely distributed throughout the Ethiopian, Malagasy, Indomalayan, Papuan and Australian Regions. The monomorphic workers are small or medium-sized or large, black or dark brown, opaque or subopaque and usually strongly sculptured. They form small colonies under stones, in rather moist clayey soil; they are rather sluggish and do not sting readily, but instead exude from the posterior end a whitish frothy substance (Wheeler 1922:69). The larger species are highly predatory and termitophagous (Wheeler 1922:15). Arnold (1915 *vide* Wheeler 1936:182) claimed that "the economic value of the Ponerinae in tropical countries can hardly be overestimated, for it may be safely asserted that at least 80 percent of their food consists of termites, and they thereby constitute one of the chief checks to these pests in the tropics."

Since our earlier study of *Bothroponera* larvae (1952:621–623) was based on unsatisfactory material and since we now have satisfactory material in five species, we are starting over and revising completely.

Genus *Bothroponera* Mayr—Type I

Profile paraponeriform (i.e., thorax and AI forming a moderately long and rather stout neck, which is curved ventrally; remainder of abdomen stout and elongate-subellipsoidal). Anus ventral, with posterior lip. Body beset with 6–87 tubercles of 3 different kinds. Integument densely spinulose. Body hairs few, simple, minute to short, or none. Integument of cranium roughened with spinules or rugules or granules. Head hairs lacking. Antennae low knobs, each on a disc and bearing 3–5 sensilla. Anterior surface of labrum bearing numerous sensilla (30–56); posterior surface densely spinulose, with very few sensilla. Mandibles ectatomiform (i.e., subtriangular in anterior view, the distal half slightly curved

medially; with a distinct medial blade joining the body of the mandible in a smooth curve and bearing 2 medial teeth); with a few spinules on the basal half.

B. denticulata, *piliventris* and *sublaevis* belong to this type. Since we do not have mature larvae of *porcata*, *pumicosa* and *soror* and only semipupae of *cariosa* we cannot safely assign them to type, but suspect that they may be Type I.

***Bothroponera sublaevis* Emery**

(Fig. 1)

Length (through spiracles) about 15 mm. Thorax and AI forming a moderately long and rather stout neck, which is curved ventrally; remainder of abdomen stout and elongate-subellipsoidal. Posterior end rounded. Lateral longitudinal welts low. Leg vestiges conspicuous, each a minute pit at the bottom of a larger pit; gonopod vestiges on AVII-IX; ~~leg and wing~~^{wing} vestiges present. Anus ventral with posterior lip. Eight vestigial tubercles on ventrolateral surfaces of thorax, distributed thus: TI 4, TII 2, TIII 2; about 0.024 mm tall. Integument densely spinulose; spinules long (about 0.018 mm), with stout conical base surmounted by a needle-like point; arranged in rows, which in some places form reticulate patterns. Body hairs few, simple, minute to short (0.04-0.18 mm), and widely scattered. Cranium suboctagonal in anterior view. Antennae low rounded elevations each mounted on a disc and bearing three sensilla. Integument of head roughened in a complicated pattern as follows: occiput with minute spinules in short transverse rows; frons (between antennae) granulose and rugulose; genae and upper clypeus rugulose. Head without hairs, but with a few sensilla, each of which bears a minute spinule. Labrum short, breadth twice the length; lateral borders convex; ventral border feebly concave; anterior surface with about 50 sensilla; posterior surface spinulose, the spinules arranged in transverse subparallel rows on the medial two-thirds, lateral sixths with coarser isolated spinules near the ventral border; posterior surface with a few sensilla. Mandibles with the basal half slightly dilated; distal half thickened laterally; from its anterior surface a blade extends medially and bears 2 subapical teeth; posterior surface of basal half with minute isolated spinules. Maxillae each narrowly round-pointed; all surfaces with numerous isolated spinules, which are longer ventrally; palp a peg bearing 5 apical sensilla; galea digitiform with 2 apical sensilla. Labium with the anterior surface densely spinulose, the spinules long and slender, isolated ventrally and in short rows dorsally; a transverse spinulose welt dorsally; palp a peg with 5 apical sensilla; opening of sericteries wide and salient. Hypopharynx densely spinulose, the spinules long and in short transverse rows, the rows so close together that the spinules overlap. (Material studied: 8 larvae from New South Wales, courtesy of Rev. B. B. Lowery, who reports a nauseating musty smell emanating from ants and larvae).

***Bothroponera denticulata* Kirby**

(Fig. 2)

Length (through spiracles) about 16.7 mm. Very similar to *B. sublaevis* except as follows. Tubercles 6, ventrolateral, a pair on each thoracic somite; each a stout subcone about 0.2 mm tall, bearing 3 apical sensilla. No body hairs. Gonopod vestiges on AVII-IX. Cranium transversely subelliptical; occipital border concave at the middle. Labrum short; a fourth broader than long; ventral border widely

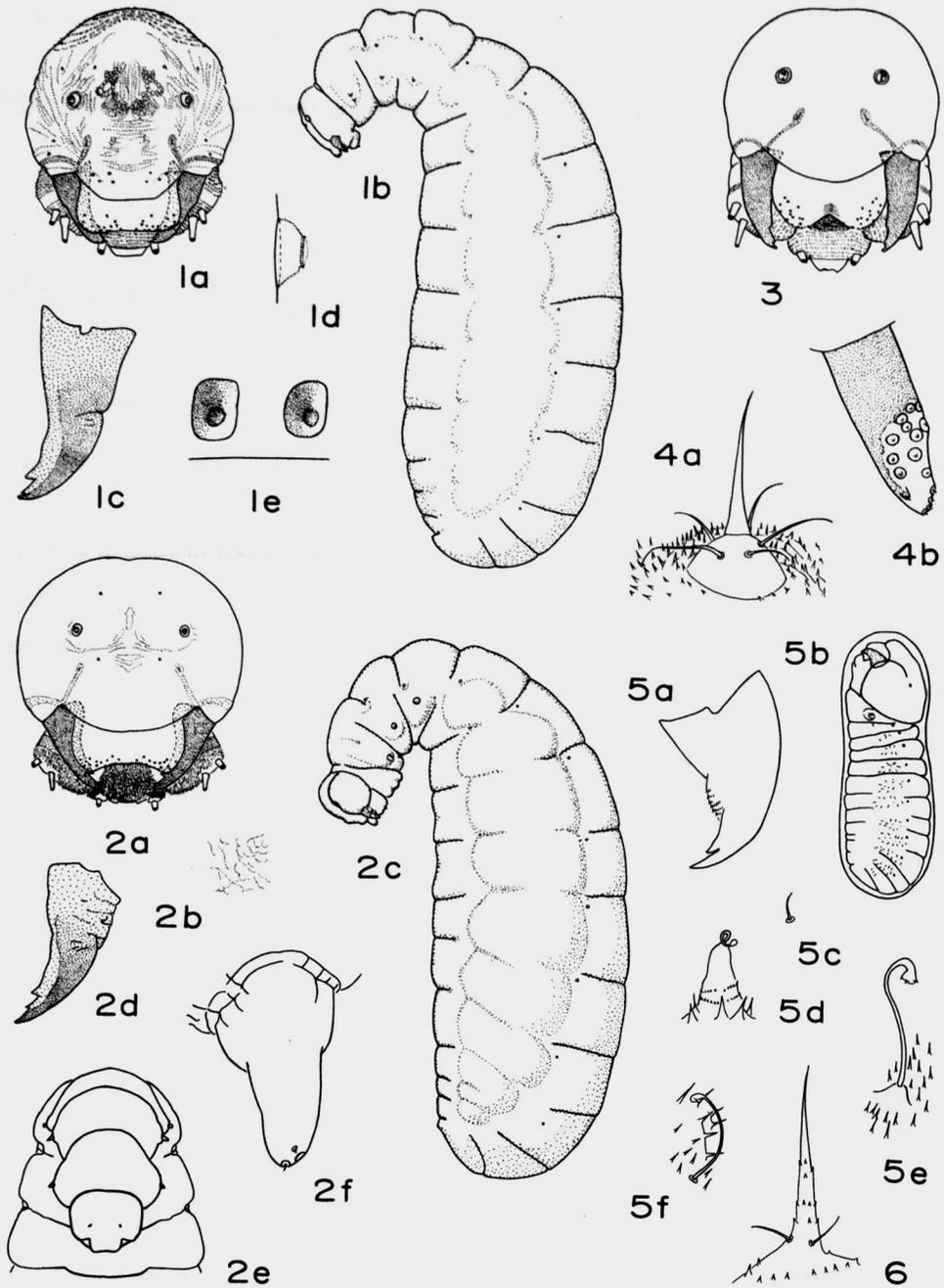


FIG. 1. *Bothroponera sublaevis* Emery: a, head in anterior view, $\times 20$; b, larva in side view, $\times 8$; c, left mandible in anterior view (shaded to show thickness), $\times 44$; d, mesothoracic leg vestige in optical section, $\times 133$; e, prothoracic leg vestiges in surface view, $\times 133$. Fig. 2. *B. denticulata* Kirby: a, head in anterior view, $\times 17$; b, rugae on head, $\times 56$; c, larva in side view, $\times 6$; d, left mandible in anterior view, $\times 31$; e, anterior end of larva to show tubercles, $\times 6$; f, left prothoracic tubercle in dorsal view, $\times 125$. Fig. 3. *B. piliventris* F. Smith:

concave. (Material studied: 3 larvae from Queensland, courtesy of Rev. B. B. Lowery).

Bothroponera piliventris F. Smith

(Fig. 3)

Length (through spiracles) about 15.7 mm. Similar to *B. sublaevis* except as follows. Tubercles arranged asymmetrically varying in number from 66 to 87; subconical from stout to spire-like, tallest about 0.2 mm, all with a single apical hair and without surface spinules; distributed thus: TI 20–26, TII 14–16, TIII 11, AI 7–9, AII 3–6, AIII 2–4, AIV 3–4, AV 2–3, AVI 2, AVII 2, AVIII 0–2, AIX 0–2, AX 0. Body hairs very few, widely scattered, minute (0.018 mm long), simple. Gonopod vestiges on AIX. Cranium subhexagonal but with the occipital corners strongly rounded. Antennae each with 4 sensilla. Labrum bilobed; ventral surface of each lobe spinulose, the spinules long and usually isolated. Mandibles with blunt teeth. Maxillae with the apex broadly rounded; each palp with 5–8 apical sensilla. Hypopharynx with the rows of spinules forming a reticulum. (Material studied: 8 larvae and 1 semipupa from South Australia, courtesy of Rev. B. B. Lowery.)

Genus **Bothroponera** Mayr—Type ?

Bothroponera cariosa ~~F. Smith~~ **Emery**

(Fig. 4)

SEMI-PUPA. Length (through spiracles) about 10 mm. Similar to *B. sublaevis* except as follows. Tubercles 117, distributed thus: TI–AIII 10, AIV–AVII 8, AVIII 10, AIX 8, AX 6; each tubercle a conoid bearing a long apical spine and several basal hairs, tallest about 0.3 mm. Integument densely spinulose, the spinules long and isolated. Body hairs short (0.075–0.11 mm), simple, with flexuous tip, a few on each somite. Cranium semicircular in anterior view. Labrum bilobed, as broad as long, with the lateral borders sinuate. Mandibles with medial teeth smaller; apex strongly curved posteriorly; no spinules. Maxillae with the spinules isolated or in short rows; each palp a skewed peg with 10–13 sensilla. Each labial palp a skewed peg bearing 10 sensilla. (Material studied: 2 semipupae from South Africa, courtesy of Dr. W. L. Brown.)

Bothroponera porcata Emery

(Fig. 5)

YOUNG LARVA. Length (through spiracles) about 6.3 mm. Similar to *B. sublaevis* except as follows. Tubercles about 180, which are distributed thus: TI 9, TII–TIII 12, AI 14, AII 12, AIII 19, AIV 20, AV 25, AVI 21, AVII 19, AVIII about 10, AIX about 6, AX 0; shape grading from a stout subcone (with spinules in short rows around the base) bearing a peculiar apical hair, to the peculiar hair minus

←

a, head in anterior view, $\times 22$. Fig. 4. *B. cariosa* F. Smith: b, left maxillary palp in anterior view, $\times 185$; a, tubercle on semipupa, $\times 93$. Fig. 5. *B. porcata* Emery: a, left mandible in anterior view, young larva, $\times 77$; b, larva in egg, $\times 17$; c, body hair, young larva, $\times 185$; d, typical tubercle, young larva, $\times 185$; e, transitional tubercle with tall capitate hair, young larva, $\times 185$; f, capitate hair without tubercle, young larva, $\times 185$. Fig. 6. *B. pumicosa* Roger: tubercle, young larva, $\times 185$.

tubercle. Body hairs absent. Labrum with spinules on anterior surface. Opening of sericteries a transverse slit in a depression.

LARVA IN EGG. Length of egg about 1.9 mm; length of larva (through spiracles) about 2.1 mm. Similar to young larvae except as follows. Head very large and tilted backwards. Prothorax small and wedge-shaped. Diameter nearly uniform from mesothorax through AVIII. Anus ventral. Integument with appressed spinules. Body hairs of two types: (1) 0.027–0.11 mm long, in a cluster on the lateral surface of each somite except AX, hairs stout, with recurved tip and bulbous and spinose apex; (2) simple, 0.009–0.018 mm long, a few on the ventrolateral surfaces of each somite. Mandibles with the apical tooth longer and narrower, the subapical tooth farther from the apex, the proximal tooth represented by a narrow flange with short rows of spinules medially. Each maxillary palp a low knob; each galea a cone directed ventromedially. Labium short, represented only by a curved band. (Material studied: 11 larvae from New South Wales, courtesy of Rev. B. B. Lowery).

***Bothroponera pumicosa* Roger**

(Fig. 6)

YOUNG LARVA. Length (through spiracles) about 3.6 mm. Similar to *B. sublaevis* except as follows. Thorax and first abdominal somite folded ventrally; dorsal profile C-shaped; venter of AII–X flat. Tubercles 124; spine-like, about 0.13 mm tall, with a few basal hairs, integument with a few isolated spinules; distributed thus: TI–AIX 10, AX 4. Body hairs very few, widely scattered, except a small cluster on each ventrolateral surface of each thoracic somite; minute to short (0.009–0.27 mm long), simple, widely scattered. Head hairs few, moderately long (0.018–0.063 mm), simple. Labrum bilobed, about as long as broad. Mandibles with rows of minute spinules on the anterior surface. Each maxillary palp a stout cone with 9 sensilla. Each labial palp a low cluster of 6 sensilla; opening of sericteries a transverse slit in a depression. (Material studied: 2 larvae from South Africa, courtesy of Dr. W. L. Brown.)

***Bothroponera soror* Emery**

(Fig. 7)

IMMATURE LARVA. Length (through spiracles) about 6.6 mm. Similar to *B. sublaevis* except as follows. Tubercles 84, distributed thus: TI 10, TII–AII 8, AIII–AIX 6, AX 0; tubercles spine-like, about 0.25 mm tall, with numerous spinules on the integument and a few hairs at the base. Gonopod vestiges on AIX. Integument of body densely spinulose, the spinules minute and in rows. Body hairs simple, long (0.094–0.19 mm), stout and nearly straight, generally distributed. Cranium transversely subelliptical. Head hairs few, simple, long (0.067–0.144 mm). Labrum bilobed; anterior surface of each lobe with 2 or 3 hairs and about 12 sensilla on or near the ventral border; ventrolateral corners with isolated spinules on anterior, ventrolateral and posterior surfaces. Mandibles with minute spinules in short rows on all surfaces of base. (Material studied: 5 larvae from Ghana and Congo, courtesy of Dr. W. L. Brown.)

Weber (1943:298): "The larvae were lying on their sides and feeding on pieces of an unidentifiable insect."

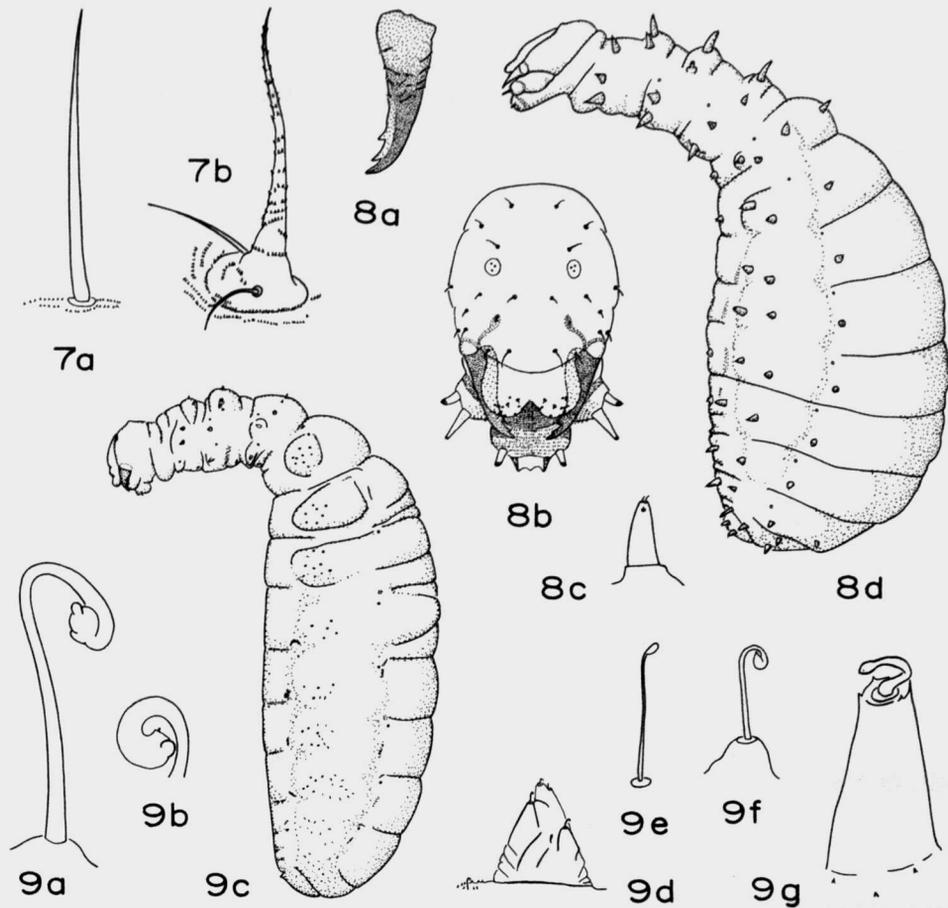


FIG. 7. *Bothroponera soror* Emery: a, body hair, young larva, $\times 185$; b, tubercle, young larva, $\times 185$. FIG. 8. *B. sjostedti* Mayr: a, mandible in anterior view, $\times 93$; b, head in anterior view, $\times 133$; c, tubercle, $\times 67$; d, larva in side view, $\times 22$. FIG. 9. *B. mayri* Emery: a, body hair, immature larva, $\times 370$; b, tip of body hair, immature larva in side view, $\times 370$; c, larva in side view, $\times 6$; d, multiple tubercle, $\times 370$; e, hair without tubercle, $\times 370$; f, hair with low tubercle, $\times 370$; g, typical tubercle with short capitate hair, $\times 370$.

Genus *Bothroponera* Mayr—Type II

Profile paraponeriform (i.e., thorax and AI forming a moderately long and rather stout neck, which is curved ventrally; remainder of abdomen stout and elongate-subellipsoidal); anus ventral, with posterior lip. Body beset with exceedingly numerous (300) tubercles, which vary from multiple subcones to a single frustum bearing an apical capitate hair. Body hairs few and minute; head hairs none. Mandibles ectatomiform (i.e., subtriangular in anterior view; the distal half slightly curved medially; with a distinct medial blade joining the body of the mandible in a smooth curve and bearing 2 medial teeth).

We have only *B. mayri* in this type.

Bothroponera mayri Emery
(Fig. 9)

Length (through spiracles) about 14 mm. Similar to *B. sublaevis* except as follows. Tubercles about 300; not arranged symmetrically; large and multiple (with apical sensilla) anteriorly, grading into a peculiar hair posteriorly; distributed thus: each thoracic somite with about 12, AI–AIII 16, AIV 24, AV 40, AVI 44, AVII 42, AVIII 36, AIX 28, AX 0. Body hairs absent. Cranium subcircular; sensilla numerous. Antennae with 5 sensilla each. Maxillary and labial palps with 7 sensilla each.

YOUNG LARVA. Length (through spiracles) about 10 mm. Similar to the mature larvae, except in the following details. Thorax forming a slender neck which is bent ventrally at a right angle; abdomen stout, dorsal profile C-shaped, ventral nearly straight; lateral longitudinal welts feebly developed. Tubercles about 200 and distributed thus—TI 18, TII 15, TIII 11, AI 12, AII 16, AIII 24, AIV 28, AV 18, AVI 18, AVII 26, AVIII 20, AIX 8, AX 2. Head longer than the diameter of any thoracic somite; AI greater in diameter than head length. Mandibles with the teeth shorter and stouter. Maxillary and labial palps short pegs. Opening of sericteries a transverse slit.

VERY YOUNG LARVA. Length (through spiracles) about 5.2 mm. Similar to young larva except in the following details. Thoracic spiracles half the diameter of abdominal spiracles. Abdominal tubercles replaced by heavy long hairs with curved, swollen spinulose tip. Tubercles 44, distributed thus: TI 16, TII 17, TIII 11; hairs AI 16, AII 22, AIII 26, AIV 24, AV 28, AVI 30, AVII–X 0. Body hairs very few, short (0.012–0.05 mm), simple. Each maxillary palp a low knob with 10 sensilla. Each labial palp a low cluster of 8 sensilla. (Material studied: 9 larvae from New South Wales, courtesy of Rev. B. B. Lowery.)

Genus Bothroponera Mayr—Type III

Profile pachycondyliform (i.e., shaped somewhat like a crookneck squash; thorax and AI forming a distinct long slender neck, which is curved ventrally; remainder of abdomen stout and subovoidal, but with ventral profile nearly straight). Body beset with 90 stout-conoidal tubercles. Integument densely spinulose. Body hairs few, simple, minute. Head large and elongate. Surface of cranium with faint rugules. Antennae small, each with 3 sensilla. Head hairs few, short, simple. Mandibles odontoponeriform (i.e., subtriangular in anterior view; narrow; distal third slightly curved medially; with a distinct medial blade arising from the anterior surface and bearing 2 medial teeth); with a few spinules on the basal half.

We have only *B. sjostedti* belonging to this type.

Bothroponera sjostedti Mayr
(Fig. 8)

Length through spiracles about 3.8 mm. Tubercles 90, distributed thus: TI 10, TII–AI 8, AII–VII 6, AVIII–IX 8, AX 4; tubercles moderately slender subcones, about 0.15 mm tall. Integument densely spinulose, the spinules minute (longer ventrally) and in numerous subparallel rows or in reticulate patterns. Body hairs few, simple, minute (0.035–0.075 mm long), mostly ventral. Head elongate; cranium subelliptical, slightly longer than broad; integument roughened with ridges and spinules. Head hairs few, short (0.027–0.045 mm), simple, slightly curved.

Antennae small, each a low elevation bearing 3 sensilla. Labrum bilobed; lateral borders sinuate; anterior surface of each lobe with 12 minute hairs and/or sensilla on or near the ventral border; posterior surface spinulose, the spinules arranged in transverse subparallel rows on the medial two-thirds, the lateral sixths with coarse isolated spinules near the ventral border; posterior surface with 3 sensilla near the middle of each lobe. Mandibles narrow and subtriangular in anterior view; distal half thickened laterally, from its anterior surface a blade extending medially and bearing 2 subapical teeth on its medial border; basal half with short rows of minute spinules on anterior, medial and posterior surfaces. Maxillae narrowly round-pointed; the spinules isolated, small and sparse basally, becoming long, dense and in short rows apically; each palp a slender peg with 5 apical sensilla; each galea tall and digitiform, with 2 apical sensilla. Labium moderately spinulose, the middle with short spinules in short transverse rows, becoming long and isolated laterally; each palp a frustum with 5 apical sensilla; opening of sericteries wide and salient. Hypopharynx densely spinulose, the spinules long and in short transverse rows, the rows so close together that the spinules overlap. (Material studied: 3 larvae from Ghana, courtesy of Dr. W. L. Brown).

KEY TO THE MATURE LARVAE OF *Bothroponera* IN OUR COLLECTION

In our previous studies of ant larvae we have not found enough distinct species in any one genus to justify a key to species. But we are now willing to try it in *Bothroponera*.

- 1a. Profile pachycondyliform; mandibles odontoponeriform; tubercles about 90 (TYPE III) **sjostedti**
- 1b. Profile paraponeriform; mandibles ectatommiform 2
- 2a. Tubercles about 300; on all somites except AX; tubercles varying from multiple subcones to frusta, each frustum bearing a single capitate hair (TYPE II) **mayri**
- 2b. Tubercles 6 to 87; not shaped as above (TYPE I) 3
- 3a. Tubercles 6-8; on thorax only 4
- 3b. Tubercles 60-87, grading from stout conoids to spire-like, on all somites except AX **piliventris**
- 4a. Tubercles 8 vestigial; body hairs few **sublaevis**
- 4b. Tubercles 6 stout subcones; body hairs none **denticulata**

DISCUSSION

Mayr described *Bothroponera* as a genus in 1862. In the "Genera Insectorum" (1911) Emery treated it as a subgenus of *Pachycondyla*. But in 1922 Wheeler restored it to generic rank on the basis of (1) larval differences, (2) differences in distribution (Paleotropical vs. Neotropical) and (3) peculiarities in the habits of *Bothroponera*. Our studies of 134 species in 41 genera of ponerine larvae convince us that Mayr and Wheeler were correct and that the latter was justified in using larval characters in evidence.

Although the 5 species of *Bothroponera* that we have studied are separable into 3 generically distinct groups, they are all generically distinguishable from the larva of *Pachycondyla*.

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