The Ant Larvae of the Subfamily Ponerinae: Supplement[1]

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ABSTRACT

Earlier studies on the larvae of the Ponerinae were published by the authors in 1952 and 1957. The present supplement contains descriptions of the larvae of 25 additional species in the genera *Acanthoponera, Amblyopone, Anochetus, *Belonopelta, Euponera, Gnamptogenys, Leptogenys, *Myopopone, Onychomyrmex, *Paranomopone, Ponera, Prionopelta, *Psalidomyrmex, Rhytidoponera, *Thaumatomyrmex, Trapeziopelta,* and *Typhlomyrmex.* Genera marked with an asterisk are new to the authors' collection and are characterized here for the first time. Necessary revisions are made in earlier descriptions and additional references to the literature are cited. The body profiles of ponerine larvae are classified into 8, mandible shapes into 20, and tubercles into 9 generalized types. The least specialized profile is that of *Myrmecia;* the most specialized are those of *Platythyrea* and *Proceratium. Myrmecia* also has the least specialized mandible shape; the most specialized is probably that of *Proceratium.* The taxonomic value and the possible functions of the tubercles are discussed. A new key is given to the mature larvae in the authors' collection, based mostly on body profile and mandible shape.

Subsequent to the publication of our article "The Ant Larvae of the Subfamily Ponerinae" (1952) we have received from other myrmecologists so much additional material that it seems desirable to publish a supplement.

The purposes of this supplement are (1) to characterize the genera acquired since our previous publication; (2) to describe species in such genera; (3) to describe additional species in previously studied genera; (4) to revise our published characterizations as required by new material; (5) to cite additional references in the literature; (6) to classify body pro-

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files, mandible shapes and tubercles; and (7) to revise our key to the genera.

We have described in this article 5 genera (*Myopopone, Paranomopone, Thaumatomyrmex, Belonopelta, Psalidomyrmex*) and 25 species which we have acquired since 1952. Including these, we have studied 93 species in 35 genera in this subfamily.

Genus ***Myrmecia*** F.

Freeland 1958, p. 5–9:—Larvae were usually kept in batches according to size. There were generally 3 size-groups. Small larvae were allowed to remain in the egg mass after hatching; they usually consumed nearby eggs, which the workers sometimes held while the larvae ate. Larger larvae (i.e., after they were about ⅓ grown) were abundantly fed with whole insects.

Haskins and Haskins 1950, p. 465–8:—Young larvae are markedly adhesive and during the earlier instars are in packets. Larvae are fed with pieces of insects. They are not fed by regurgitation from the crops of the workers. This would seem to preclude trophallaxis, but it should be noted that the larvae apparently produce abundant dermal exudates, which are avidly licked by the adults. The licking begins soon after hatching and continues throughout the larval stage. The larvae have well-developed musculature and powerful mandibles. Although well tended by the workers, they are capable of limited locomotion. They sometimes kill and devour sister larvae and have even been observed to attack their adult nurses. When ready to spin cocoons the larvae are covered with earth, which is essential for the spinning process.

Myrmecia forficata F.—Wheeler 1907, p. 15; 1926, p. 44: Reference to Forel 1890.

Myrmecia gulosa F.—Wheeler 1926, p. 44: Referred to Brues 1919.

Myrmecia regularis Crawley.—Haskins and Wheldon (1954) reported ingluvial feeding of larvae.

Myrmecia sanguinea F. Smith.—Bernard 1951, Fig. 944 on p. 1043: After Wheeler 1918 (but labeled *M. gulosa*).

Myrmecia vindex F. Smith.—Haskins and Wheldon (1954) reported ingluvial feeding of larvae.

Myrmecia (Promyrmecia) mandibularis F. Smith.—Haskins and Wheldon (1954): An isolated female reared larvae halfway to maturity by ingluvial feeding.

Myrmecia (Promyrmecia) pilosula F. Smith.—Haskins and Haskins 1950, Fig. 3 on p. 471: photograph of a larva in side view.

Genus ***Mystrium*** Roger

REVISION.—Anterior surface of mandible produced into a medial blade which bears the medial teeth.

Emery 1904, p. 114:—Le larve "portano soltanto peli semplici."

Genus ***Stigmatomma*** Roger

REVISED GENERIC CHARACTERIZATIONS.—Shaped somewhat like a slender crookneck squash. Body hairs short to long, simple, slightly curved. Cranium with angulate lateral borders; upper half semicircular in anterior view. No hairs on head. Labrum small, short and broad; posterior surface spinulose, the spinules near the ventral border isolated, the remainder grouped in short transverse arcuate rows. Mandibles stout, heavily sclerotized, subtriangular in anterior view; apical tooth curved medially and posteriorly; from the anterior surface a blade extends medially and bears several small medial teeth. Labial palp a low rounded elevation.

Stigmatomma pallipes (Haldeman).—Fig. 1. REVISION—Delete description of mandibles and replace with: Mandibles stout, heavily sclerotized, subtriangular in anterior view; apical tooth curved medially and posteriorly; from the anterior surface a blade extends medially and bears several small medial teeth. [We have also revised (Fig. 1b) our previous drawing of the larva in side view.]

Creighton 1950, p. 32:—Fragments of small insects are "fed directly to the larvae, again a primitive habit, without recourse to regurgitation."

Emery 1904, p. 114:—Le larve "portano soltanto peli semplici."

Haskins 1939, p. 31; 1951 p. 435:—The relationships between larvae and workers are of a primitive sort. The larvae are active and able to take care of themselves. They will attack and devour any arthropod fragments scattered within reach and also their sister larvae and occasionally workers. When mature they are able to spin a thick tough cocoon without the assistance of the workers, although the latter may attempt to help. (See also Michener and Michener 1951, p. 143.)

Wilson 1958, p. 25:—The larvae feed directly on whole centipedes, without previous dismemberment.

Genus ***Amblyopone*** Erichson

REVISION.—Add: Shaped somewhat like a crookneck squash. Head small.

Amblyopone australis Erichson.—VERY YOUNG LARVA: Length (through spiracles) about 2 mm. Similar to the mature larva except as follows: Slenderer; thorax and first abdominal somite forming a neck which is only a little narrower than the remainder of the abdomen; body without a lateral welt. Posterior end narrowly rounded. Anus ventral. Body hairs moderately sparse, fewer on the ventral surface; simple; 0.025–0.145 mm long, the longer ones flagelliform. Head large. Labrum without median notch or lateral bosses; spinules fewer and smaller. Mandibles shorter and stouter, subtriangular and curved medially and posteriorly; all teeth short and acute. Maxillae with the spinules shorter and finer; palp a small button with 5 sensilla, 1 of which bears a tall digitiform structure; galea a subcone. Labial palp a low knob with 5 sensilla (1 encapsulated and 4 with a spinule each, 1 of which is tall and digitiform). (Material studied: numerous larvae from New South Wales, courtesy of B. B. Lowery.)

Haskins and Haskins 1951: The adults seem incapable of distributing ingluvial food either to one another or to the brood. Larvae are fed entirely on

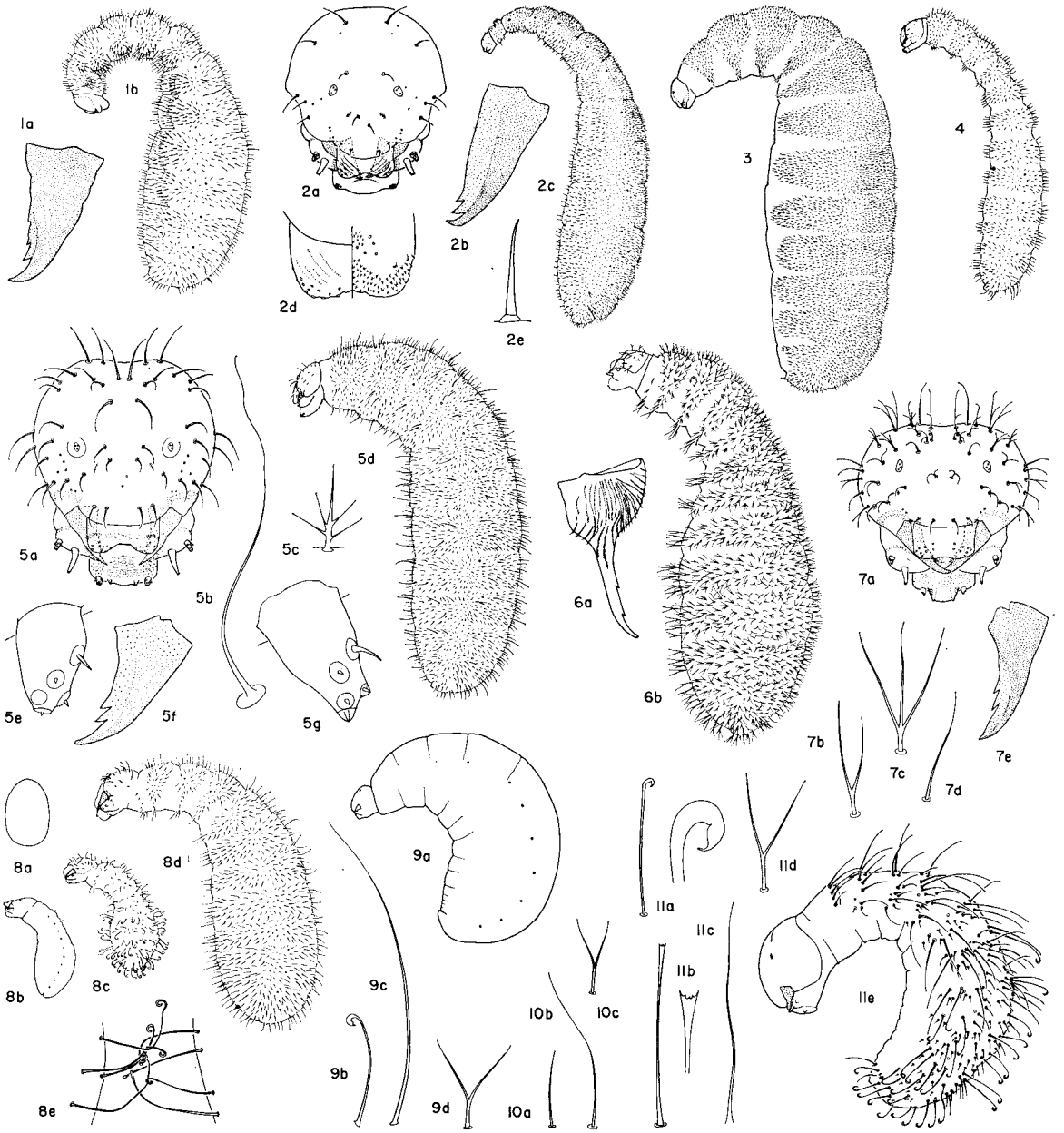

FIG. 1.—*Stigmatomma pallipes:* a, left mandible, anterior view, ×185; b, larva, side view, ×12. FIG. 2.—*Myopopone castanea:* a, head, anterior view, ×47; b, left mandible, anterior view, ×111; c, larva, side view, ×6; d, labrum (right half, posterior view; left half, anterior view), ×139; e, body hair, ×139. FIG. 3.—*Paraponera clavata:* larva, side view, ×4. FIG. 4.—*Prionopelta opaca:* immature larva, side view, ×22. FIG. 5.—*Paranomopone relicta:* a, head in anterior view, ×67; b and c, 2 types of body hairs, ×278; d, larva, side view, ×15; e, left labial palp, anterior view, ×333; f, left mandible, anterior view, ×139; g, left maxillary palp, anterior view, ×333. FIG. 6.—*Typhlomyrmex pusillus:* a, right mandible, anterior view, ×235; b, larva, side view, ×67. FIG. 7.—*Acanthoponera* (*Anacanthoponera*) sp.: a, head, anterior view, ×71; b-d, 3 types of body hairs, ×278; e, left mandible, anterior view, ×139. FIG. 8.—*Rhytidoponera tasmaniensis:* a, egg, ×16; b, first-instar larva, side view, ×16; c, second-instar larva, side view, ×16; d, young larva, side view, ×16; e, entangled hairs on dorsa of 2 larvae, ×96. FIG. 9.—*R. mayri:* a, sexual (?) larva, side view, ×8; b-d, 3 types of body hairs, ×85. FIG. 10.—*R. cristata:* a-c, 3 types of body hairs, ×44. FIG. 11.— *R. cerastes:* a, hooked hair of very young larva, ×85, and tip (enlarged), ×350; b, body hair of mature larva with frayed tip, ×85, and tip (enlarged) ×350; c and d, simple and bifid hairs of mature larva, ×85; e, very young larva, side view, ×28.

fragments of insects and other arthropods. They are active and frequently attack and even kill and devour sister larvae when food is scarce. Also they may attack the adult nurses. Newly hatched larvae adhered in packets and were constantly licked by colony-founding queens. Larvae were placed on or near food as it was brought in. As the larvae developed they were allowed to lie separate on the floor and became an important source of food for the queens, which spent much time in rasping and pinching them. Approximate life cycle: egg, 1 month; larva, 2 to 3 months; pupa, 1½ months. Fig. 1 on p. 438—photograph of young larvae.

Amblyopone longidens Forel.—Length (through spiracles) about 4.5 mm. Very similar to *A. australis*, except in the following details: Body hairs slightly shorter (0.075–0.175 mm long), with some stout spinelike hairs at the posterior end of the body. Occipital outline of the head flatter and broader. Labial palp a skewed peg with 3 apical sensilla (each with a spinule) and 2 lateral sensilla (1 with a spinule and 1 large and digitiform). (Material studied: 36 larvae from New South Wales, courtesy of B. B. Lowery.)

Genus ***Myopopone*** Roger

Shaped somewhat like a slender crookneck squash. Body hairs short, simple, slightly curved. Head small. Cranium with angulate borders; upper half semicircular in anterior view. Head hairs few, short, simple. Labrum small, short and broad, feebly bilobed; posterior surface spinulose, the spinules isolated or in very short rows. Mandibles stout, subtriangular in anterior view; apical tooth sharp-pointed, curved medially and posteriorly; from the anterior surface a blade extends medially and bears 2 acute subapical teeth. Labial palp represented by a cluster of 5 sensilla.

Myopopone castanea (F. Smith).—Fig. 2. Length (through spiracles) about 10 mm. Shaped somewhat like a slender crookneck squash; thorax and first 2 or 3 abdominal somites forming a long slender curved flexible neck; the remainder of the abdomen straight and somewhat stouter; anus posteroventral. Leg vestiges present. Thirteen differentiated somites. Integument spinulose, the spinules minute and in short arcuate rows. Body hairs short (0.025–0.15 mm), simple, slightly curved, moderately numerous, uniformly distributed, longest on the thorax and the ventral surface of the abdomen. Head very small; in anterior view the sides of the cranium are angulate while the upper half is semicircular; integument with a few sensilla. Head hairs few, simple, short (0.05–0.075 mm), slightly curved. Antennae moderately large, each with 3 sensilla. Labrum small, breadth 1½× length, bilobed; anterior surface of each lobe with 12 sensilla on or near the ventral border and 5 oblique grooves (ridges?); posterior surface spinulose, the spinules rather large and isolated or in very short rows; posterior surface of each lobe with about 7 sensilla, 4 of which may be contiguous. Mandibles stout, heavily sclerotized, subtriangular in anterior view; apical tooth sharp-pointed, curved medially and posteriorly; from the anterior surface a blade extends medially and bears 2 acute subapical medial teeth. Maxillae with the apex paraboloidal and rather densely spinulose, the spinules isolated and rather large; palp a short irregular projection with 2 apical and 3 basal sensilla (1 basal encapsulated, the others bearing a spinule each); galea digitiform, with 2 apical sensilla, each bearing a spinule. Labium with the basal portion of the anterior surface densely spinulose, the spinules isolated and rather large; palp represented by a cluster of 5 sensilla; opening of sericteries a long transverse slit. Hypopharynx densely spinulose, the spinules isolated and rather large. (Material studied: 3 larvae from the Philippine Islands, courtesy of Dr. J. W. Chapman.)

Genus ***Paraponera*** F. Smith

Paraponera clavata (Fabricius).—REVISION.—Anterior surface of mandible produced into a medial blade which bears medial teeth. [We have also revised (Fig. 3) our previous drawing of the larva in side view.]

Genus ***Platythyrea*** Roger

Platythyrea inermis Forel.—REVISION.—Anterior surface of mandible produced into a medial blade which bears medial denticles.

Genus ***Paranomopone*** Wheeler

Neck stout and curved ventrally; body only a little stouter, straight and subcylindrical. Spiracles small. Body hairs of 2 types: (1) short, moderately stout, with fine branches all in one plane; (2) long, simple, flagelliform. Antennae small, each on a low convexity and bearing 3 sensilla, each of which bears a small spinule. Head hairs simple, moderately long and moderately numerous. Labrum short, broad and deeply bilobed; posterior surface spinulose, the spinules shorter and in shorter rows ventrolaterally, the rows and spinules becoming longer dorsomedially. Mandibles subtriangular in anterior view, with a large apical tooth which is curved medially; with a medial blade which bears 2 subapical teeth.

Paranomopone relicta Wheeler.—Fig. 5. Length (through spiracles) about 4.7 mm. Thorax and first abdominal somite forming a rather stout neck which is curved ventrally, the remainder of the abdomen moderately stout, straight and subcylindrical; posterior end rounded. Segmentation indistinct. Anus posteroventral. Leg and wing vestiges present. Spiracles small. Body hairs abundant, short to moderately long. Of 2 types: (1) short (0.04–0.12 mm), moderately stout, with very fine branches (0.004–0.036 mm long), all the branches in one plane; (2) long (0.13–0.24 mm), simple, flagelliform. Integument with numerous minute spinules in transverse rows on the ventral surface of the thorax and the anterior abdominal somites. Occipital border feebly impressed. Head hairs simple, moderately long (0.07–0.13 mm) and moderately numerous. Antennae small, each on a low convexity and bearing 3 sensilla, each of which bears a small spinule. Labrum

short, breadth twice the length, strongly bilobed; anterior surface of each lobe bearing 5 sensilla; ventral border with 2 or 3 sensilla on each lobe and a few rather long spinules near the middle; posterior surface spinulose, the spinules shorter and in shorter rows ventrolaterally, becoming longer dorsomedially; posterior surface with 2 or 3 sensilla near the middle of each lobe. Mandibles heavily sclerotized, subtriangular in anterior view; with a large apical tooth which is curved medially; anterior surface with a medial blade bearing 2 subapical teeth. Maxillae bulging laterally, the apex conoidal and directed ventromedially; the apex sparsely spinulose, the spinules rather long, in short arcuate rows which are arranged in longitudinal rows, with the spinules directed ventrolaterally; palp a short peg with 5 sensilla (each bearing a spinule); galea digitiform, with 2 apical sensilla. Labium with the anterior surface spinulose, the spinules rather coarse and isolated ventrally and laterally, becoming smaller and assembled in short rows medially and dorsally; palp a low irregular projection with 5 sensilla (4 with a spinule each and 1 encapsulated); opening of sericteries wide and salient. Hypopharynx spinulose, the spinules arranged in arcuate rows.

VERY YOUNG LARVA: Length (through spiracles) about 2.1 mm. Generally similar to mature larva except in the following details: Hairs restricted to prothorax. Entire integument spinulose. Antennae not mounted on an elevation. Mandibular teeth shorter and more acute.

(Material studied: Numerous larvae from Queensland, courtesy of Dr. W. L. Brown.)

Genus ***Prinopelta*** Mayr

Prionopelta modesta Forel.—Length (through spiracles) about 1.6 mm. Indistinguishable from the larvae of *Prionopelta punctulata.* (Material studied: 9 larvae from Mexico, courtesy of Dr. E. O. Wilson.)

Prionopelta opaca Emery.—Fig. 4. IMMATURE LARVA.—Length (through spiracles) about 2.3 mm. Very similar to *Prionopelta punctulata,* except in the following details: Very slender; diameter greatest at abdominal somite VI; head only slightly less than the thorax in diameter. Longest hairs mostly restricted to posterior segments. Head hairs shorter (0.009–0.024 mm long). Fingerlike projection on maxillary palp about twice as long. (Material studied: 24 larvae from New South Wales, courtesy of B. B. Lowery.)

Prionopelta punctulata Mayr.—CORRECTION.—The galea bears 2 apical sensilla.

Genus ***Typhlomyrmex*** Mayr

REVISION.—Add: Thorax moderately stout and bent ventrally; slightly constricted at first abdominal somite; remainder of abdomen stout and ovoidal.

Typhlomyrmex pusillus Emery.—Fig. 6. MATURE LARVA.—Length (through spiracles) about 2.6 mm. Generally similar to *T. robustus,* except in the following details: Thorax moderately stout and bent ventrally; slightly constricted at first abdominal somite; remainder of abdomen stout and ovoidal. Ventral surface of thorax and first 3 abdominal somites with a few minute spinules in short transverse rows. Mandibles with the apical tooth a little shorter and blunter; spinules longer. Maxillae with minute spinules in short arcuate rows; palp with 3 apical and 2 lateral sensilla. (Material studied: 7 larvae from Argentina, courtesy of Dr. W. L. Brown.)

Typhlomyrmex robustus Emery.—REVISION.—Anterior surface of mandible produced into a narrow blade which bears the medial teeth. Galea with 2 apical sensilla.

Genus ***Stictoponera*** Mayr

See *Gnamptogenys.*

Genus ***Acanthoponera*** Mayr

Acanthoponera (*Anacanthoponera*) sp.—Fig. 7. YOUNG LARVA—Body hairs numerous, short (0.036–0.11 mm), uniformly distributed, 1–4 branched (usually bifid), branching near the base. Integument with minute spinules in a few short transverse rows on the ventral surface of the thorax. Cranium transversely subellipitical in anterior view; the occipital outline impressed at the middle. Head hairs moderately numerous; 0.012–0.096 mm long; simple or bifid (rarely trifid), branching near the base. Antennae small, each with 3 sensilla, each of which bears a spinule. Labrum feebly bilobed; breadth twice the length; anterior surface of each lobe with 6 sensilla; ventral border of each lobe with 6 sensilla; posterior surface densely spinulose, the spinules rather long and in numerous transverse rows. Mandibles heavily sclerotized, narrow, with the base slightly dilated; apex narrowed abruptly to form a small sharp tooth; lateral portion thickened posteriorly, medial portion thin and bladelike and bearing 2 sharp-pointed medial teeth. Maxillae moderately swollen; palp an irregular projection with 2 apical and 3 lateral sensilla, each bearing a spinule (1 of which is rather long); galea digitiform with 2 apical sensilla. Labium with numerous rather long spinules on the anterior surface; palp a short peg bearing 2 apical and 3 lateral sensilla, each with a spinule (1 of which is rather long); opening of sericteries wide and salient. (Material studied: 4 larvae from Victoria, Australia, labeled "*Anacanthoponera imbellis*?", courtesy of Dr. W. L. Brown.)

Genus ***Holcoponera*** Mayr

Brown (1958, p. 216) concluded that the larval differences which we found (1952) between *Holcoponera* and *Gnamptogenys* are too slight to warrent separating them. He has included the former genus in the latter. See below under *Gnamptogenys.*

Brown (1958, p. 229) regarded *H. brasiliensis* as a synonym of *Gnamptogenys striatula.* We have said (1952, p. 124) that the larva of *H. brasiliensis* is similar to *striatula.* We are therefore dropping it from our list.

Genus *Chalcoponera* Emery

We have previously (1952, p. 658) stated that the larvae of *Rhytidoponera* and *Chalcoponera* were difficult to separate and characterize. We agree with Emery (1911) and Brown (1958) that they should be in the same genus (*Rhytidoponera*).

Genus *Rhytidoponera* Mayr

REVISION.—Body hairs of 2 to 5 types (including simple and bifid).

Rhytidoponera aspera (Roger).—Apparently very similar to *R. cristata,* except in the following details: Body hairs shorter. Of 3 types: (1) bifid, 0.135–0.25 mm long, the longest flagelliform; (2) simple, about 0.3 mm long; (3) 0.115–0.165 mm long, with blunt multifid tip. Integument of body with short rows of minute spinules on the ventral surface of the anterior somites and the dorsal surface of the posterior somites. Head hairs short (0.04–0.07 mm), with multifid tip. Labrum nearly twice as broad as long. Anterior surface of the labium with most spinules long and in short arcuate rows. (Material studied: 2 damaged larvae from New South Wales, courtesy of B. B. Lowery.)

Rhytidoponera cerastes Crawley.—Fig. 11. SEMIPUPA.—Length (through spiracles) about 10.9 mm. Very similar to *R. cristata* except in the following details: Body hairs of 3 types: (1) simple, 0.15–0.42 mm long, on all somites, the most numerous type; (2) short (0.025–0.125 mm), with multifid tip, a few on each somite but numerous on the dorsal surface of the thorax; (3) bifid, 0.15–0.25 mm long, a few on the lateral surfaces of the thorax and abdominal somites I and II. Width of labrum 3 times the length. Mandibles with the base more dilated, the medial teeth closer together and the apical tooth longer. Spinules on the anterior surface of the labrum mostly in short arcuate rows.

VERY YOUNG LARVA—Length (through spiracles) about 2.5 mm. Body C-shaped; diameter of thorax less than that of head. Body hairs few; absent from the ventral surface. Of 2 types: (1) 0.125–0.4 mm long, simple or with frayed tip, on all somites; (2) 0.115–0.275 mm long, stout and terminating in a single stout hook or an enlarged flattened tip, on abdominal somites III–X. Integument with minute spinules in transverse rows. Head hairs lacking. Each antenna a cluster of 3 sensilla on a slight elevation. Mouth parts similar to those of mature larva.

(Material studied: 20 larvae from Northern Australia, collected by W. Bateman, courtesy of W. L. Brown.)

Rhytidoponera convexa (Mayr).—Whelden 1958, p. 80: Description of hairs; larvae held together by a "tangle of rather coarsely looped fibres"; internal anatomy.

Rhytidoponera cristata (Mayr).—Fig. 10. REVISION.—Anterior surface of mandible produced into a wide medial blade which bears the medial teeth. [The engravings of our drawings of the hairs of this species were defective; we are publishing them again herewith.]

Rhytidoponera croesus Emery.—SUBMATURE LARVA.—Length (through spiracles) about 4.5 mm. Very similar to *R. cristata,* except as follows: Body hairs (1) 0.15–0.28 mm long, bifid (rarely trifid), the longest with flexuous tip; (2) 0.18–0.26 mm long, few, simple, flagelliform, on the ventral surface of the anterior abdominal somites; (3) 0.1–0.18 mm long, stout, slightly curved, with short-bifid tip, on the posterior somites. Head hairs 0.036–0.135 mm long, slightly curved and with the tip frayed. Each antenna a slender peg with 3 sensilla, each bearing a stout spinule. Mandibles similar to *R. impressa.* Labial palp a short, skewed peg with 5 sensilla (3 apical, 1 subapical, 1 lateral), 4 with a spinule each.

IMMATURE LARVA.—Length (through spiracles) about 2.75 mm. Similar to the submature larva (above) except in the following details: Diameter of thoracic spiracles half that of the abdominal spiracles. Body hairs (1) 0.09–0.2 mm long, bifid, the longest flagelliform, the most numerous type; (2) 0.036–0.25 mm long, with simple or frayed tip, on the ventral and lateral surfaces of the anterior abdominal somites; (3) 0.16–0.2 mm long, with swollen recurved hook at the tip, on the posterior abdominal somites. Head hairs slightly shorter (0.03–0.1 mm long). Labrum shorter and more rounded. Mandibles with the teeth shorter. Maxillae spinulose and with the apex sharp-pointed. Labium shorter and more rounded; palp a slight elevation with 5 sensilla.

(Material studied: 21 larvae from New South Wales, courtesy of B. B. Lowery.)

The young larvae are held together in clusters by their hooked hairs.

Rhytidoponera impressa (Mayr).—REVISION.—Anterior surface of mandible produced into a wide medial blade which bears the medial teeth. Labrum rather large; subrectangular, breadth 1½× the length. Maxillary palp with 5 sensilla; galea with 2 apical sensilla. [Page 125, line 6, "length" should be substituted for "width."]

Rhytidoponera mayri Emery.—Fig. 9. SEXUAL (?) LARVA (READY TO MOLT).—Length (through spiracles) about 7.3 mm. Body very stout, diameter greatest at abdominal somites III and IV, dorsal profile long and C-shaped, ventral profile short and J-shaped. Anus ventral. Diameter of thoracic spiracles half that of the abdominal. *Outer integument:* Body hairs moderately numerous, short to long. Of 3 types: (1) most numerous, 0.025–0.525 mm long, simple, the longest with fine flexible tip, on all somites; (2) few, about 0.05 mm long, with the tip bifid; (3) 0.075–0.19 mm long, stout and terminating in a single stout hook, on dorsal and lateral surfaces. *Inner integument:* Body hairs numerous. Of 2 types: (1) bifid, 0.15–0.275 mm long, on thorax and abdominal somites I–VIII; (2) simple, 0.15–0.225 mm long, on abdominal somites VI–X, most numerous posteriorly; no hooked hairs seen. Both integuments spinulose, with the spinules minute and in short transverse rows. Head hairs few, scattered, with the tips simple, bifid or trifid. Spinules on the labium small and in short transverse arcuate rows. Otherwise as

in *R. cristata.* (Material studied: 8 larvae from South Australia, courtesy of Dr. W. L. Brown.)

Rhytidoponera metallica F. Smith.—SUBMATURE LARVA.—Length (through spiracles) about 4.4 mm. Probably very similar to *R. cristata,* except as follows: Abdomen not so swollen. Body hairs shorter (1) 0.096–0.15 mm long, on the thorax and abdominal somite I, the least abundant type; (2) about 0.2 mm long, flagelliform, on the ventral surface of abdominal somites I–VI; (3) 0.075–0.15 mm long, simple, rather stout, on all somites. Head hairs with the tip simple or with short denticles. Antennae each a short peg with 3 apical sensilla, each bearing a stout spinule. Labial palp with 5 sensilla.

VERY YOUNG LARVA.—Length (through spiracles) about 1.5 mm. Similar to the submature larva except as follows: Of nearly uniform diameter, decreasing gradually from the fifth abdominal somite to the anterior end and more rapidly to the posterior end which is narrowly rounded. Anus terminal. Body hairs of 2 types, with intergrades: (1) 0.02–0.18 mm long, simple, the longest flagelliform, on all somites, but becoming sparse posteriorly; (2) 0.036–0.126 mm long, with the tip swollen, hooked and often tightly curled, on the lateral surfaces of abdominal somites III–X and on the ventral and dorsal surfaces of abdominal somites V–X. Integument spinulose, the spinules minute and in short transverse rows. Head hairs few, 0.02–0.076 mm long, with the tip simple or frayed. Antennae each a low subcone, with 3 apical sensilla each bearing a short spinule. Mandibles subtriangular, short and stout, with the apex curved medially; apical and subapical teeth short and sharp-pointed, proximal tooth blunt; not divided into 2 portions as in the mature larva. Maxillary palp a skewed peg. Labial palp a cluster of 5 sensilla on a slight elevation.

(Material studied: 138 larvae from New South Wales, courtesy of B. B. Lowery.)

The young larvae are held together in clusters by their hooked hairs. Of the 138 larvae from Sydney, New South Wales, 4 bore eucharid planidia, 1 each on the ventral surface at the junction of the head and the prothorax. One planidium is attached to a larva with hooked hairs and 3 are on more mature larvae (without hooked hairs).

Rhytidoponera tasmaniensis Emery.—Fig. 8. YOUNG LARVA.—Length (through spiracles) about 3.25 mm. Generally similar to *R. cristata,* except as follows: Body decreasing gradually in diameter from the fifth abdominal somite to the anterior end and more rapidly to the posterior end, which is rounded. Body hairs shorter: (1) 0.075–0.15 mm long, bifid; (2) 0.15–0.225 mm long, flagelliform; (3) about 0.11 mm long, with simple or frayed tip. Head hairs 0.07–0.11 mm long, with the tip simple or frayed. Each antenna a short peg with 3 sensilla, each with a relatively long spinule. Maxillary palp with 5 sensilla.

VERY YOUNG LARVA.—Length (through spiracles) about 1.4 mm. Generally similar to the above except in the following details: Body hairs moderately abundant. Of 2 types: (1) on all somites, 0.05–0.15 mm long, simple or with a stout multifid tip, grading into (2) 0.036–0.16 mm long, ending in a thickened recurved hook, on the ventral surface of all abdominal somites, the dorsal surface of abdominal somites V–X, and the lateral surfaces between. Head hairs 0.04–0.12 mm long, with the tip simple or slightly frayed. Mandibles relatively shorter, apical and subapical teeth acute and curved medially, proximal tooth rounded; mandible lacking the division into 2 parts seen in the mature larva. Maxillary palp and galea shorter and stouter.

FIRST INSTAR LARVA.—Length (through spiracles) 0.85–1.35 mm. Head very large. Posterior end pointed. Anus subterminal. Thoracic spiracles smaller than abdominal. One pair of hairs on the dorsum of each thoracic somite, about 0.036 mm long. Head rounded. No head hairs seen. Antenna represented by a cluster of 3 sensilla, each bearing a minute spinule. Labrum short, width 2× length, a slight median impression of the ventral border, 4 sensilla on the ventral border of each half. Mandibles subtriangular, the sides nearly equal; with the apical and subapical teeth short and sharp-pointed, proximal tooth represented by a rounded swelling; no spinules seen. Maxilla small and rather sharp-pointed; palp a small knob with 5 sensilla; galea a short frustum with 2 apical sensilla. Labium small, short and wide; palp represented by a cluster of 5 sensilla.

(Material studied: numerous larvae from New South Wales, courtesy of B. B. Lowery.)

The young larvae are held together in clusters (Fig. 8e) by their hooked hairs. One such cluster (in a vial of alcohol) comprises 26 individuals.

Of the 298 larvae from Sydney, New South Wales, 3 bore eucharid planidia, 1 each on the ventral surface at the juncture of head and prothorax. One planidium is attached to a larva in a cluster and 2 are on more mature larvae (without the hooked hairs).

Rhytidoponera victoriae (Ern. André).—IMMATURE LARVA.—Length (through spiracles) about 3.6 mm. Similar to *R. impressa* except in the following details: Head hairs simple or with bifid tip. Breadth of labrum twice the length. (Material studied: 9 larvae from Victoria, Australia, courtesy of Dr. W. L. Brown.)

Genus ***Emeryella*** Forel

See *Gnamptogenys.*

Genus ***Ectatomma*** F. Smith

We concur in Brown's opinion (1958) that the genus *Ectatomma* should be restricted to the former subgenus *Ectatomma.* Our subgeneric description should, therefore, become the generic description. For the fate of the other former subgenera, see *Gnamptogenys.*

Emery 1904, p. 114:—Le larve "portano soltanto peli semplici."

Ectatomma tuberculatum (Olivier).—REVISION.—Anterior surface of mandible produced into a medial blade which bears the medial teeth.

Genus *Gnamptogenys* Roger

Body hairs short to moderately long, simple to multifid, frequently 2- to 4-branched. Head hairs few, usually simple, minute to short. Antennae minute, peglike, each bearing 3 stout apical spines. Labrum large; slightly broader at the base than long; ventral corners strongly rounded; an excision at the middle of the ventral border; posterior surface spinulose, the spinules minute but increasing in length toward the ventral border and arranged in definite rows which radiate from the dorsolateral angles, the rows continuous on the basal ⅔ but broken into short arcuate components on the distal third. Mandibles large, elongate, rather narrow; basal half moderately dilated; distal half with its lateral border thickened and its medial border blade-like; apical tooth rather long and slender; medial teeth smaller; basal ⅔ to ¾ of anterior surface beset with numerous spinules arranged in longitudinal rows; spinules mostly minute but along and near the lateral border of the middle portion they are exceedingly long.

In 1952 we noted (p. 657) that "Emeryella, Stictoponera, Ectatomma (Poneracantha), E. (Parectatomma), E. (Gnamptogenys) are so similar that they can be separated only by differences of a sort that distinguish species elsewhere" and that (p. 660) these 3 subgenera of *Ectatomma* "more closely resemble the genus *Emeryella* than their congeneric subgenus *Ectatomma.*" Body hairs, antennae, shape of mandibles and mandibular spinules were the characters upon which we based our conclusion. Brown (1958, p. 206) referred to our above findings and stated (p. 207): "My own studies, based on adult characters, are in good agreement with the larval findings." We are, therefore, following Brown and placing these genera and subgenera in the genus *Gnamptogenys.*

Gnamptogenys hartmanni (Wheeler).—Length (through spiracles) about 4.8 mm. Generally similar to *G. bispinosum* (Emery), except in the following details: Body hairs mostly bifid and a few simple. Mandibles with the apical and subapical teeth longer. Anterior surface of the labium with the spinules mostly fine and in short arcuate rows. (Material studied: 12 larvae from Louisiana, courtesy of H. W. Echols.) (Formerly in *Ectatomma.*)

Gnamptogenys menadensis (Mayr). — Length (through spiracles) about 6.6 mm. Similar to *Gnamptogenys* sp. from Kalabit Country, North Borneo, except in the following details: Shorter body hairs 0.08–0.15 mm long, 2- to 4-branched; longer body hairs 0.15–0.31 mm long, simple, on abdominal somites VIII-X. Four hairs on the clypeus. Hypopharynx with a few scattered minute spinules. (Material studied: 3 larvae from the Philippine Islands, courtesy of Dr. J. W. Chapman.) (Formerly in *Stictoponera.*)

Gnamptogenys striatula (Mayr).—CORRECTION.—Maxillary palp with 5 sensilla; galea with 2 apical sensilla. (Formerly in *Holcoponera.*)

Gnamptogenys strigata (Norton). — Length (through spiracles) about 2.2 mm. Similar to *G. striatula* except in the following details: Thorax and abdominal somite I slenderer. Body hairs mostly 2- or 3-branched, but simple and 4-branched also present. Antennae more slender. (Material studied: 6 larvae from Mexico, courtesy of Dr. E. O. Wilson.) (Formerly in *Holcoponera.*)

Genus *Thaumatomyrmex* Mayr

Body with numerous (about 146) slender spirelike tubercles; surface of tubercles with a few rows of denticles; each spire capped with a sensillum bearing a spinule. No body hairs. Head long; mouth parts large. No head hairs. Antennae small. Mandibles subtriangular in anterior view; apical tooth sharp-pointed, constricted basally, with a medial flange; subapical tooth narrowly round-pointed and constricted basally; proximal tooth broadly rounded in anterior view; in medial view all teeth compressed and sharp.

Kempf 1954, p. 48:—"O comprimento varia de 2 a 4 mm. Em seu aspecto geral lembram a *Ponera coarctata pennsylvanica* Buckley . . . da qual difere pela ausência de cerdas minúsculas tanto na cápsula cefálica como no corpo. Outrossim faltam tubérculos glutinosos no dorso dos segmentos posteriores. A segmentação da parte posterior do corpo é pouco nítida. A configuração, o número e o arranjo dos tubérculos espiniformes são pràticamente os mesmos como em *P. coarctata pennsylvanica.*"

Thaumatomyrmex mutilatus Mayr.—Fig. 13. Length (through spiracles) about 4.5 mm. Probably shaped like a crookneck squash. Body furnished with numerous (about 146) tubercles distributed as follows: thoracic somites, 10 each; abdominal somites I–IV, 16 each; V, 15 or 16; VI–VIII, 14 each; IX, 8; X, 2. These tubercles are slender and spirelike and encircled with a few rows of spinules; each spire is capped with a sensillum bearing a spinule and fringed by integumentary spinules; height of spire 0.026–0.168 mm. No body hairs. Integument of body with a fine network of ridges which sometimes bear minute spinules. Head long; mouth parts large; cranium slightly longer than broad. Head hairs none. Antennae small, each with 3 sensilla each bearing a spinule. Labrum about as broad as long, narrowed ventrally, feebly bilobed; anterior surface with 9 sensilla near the ventral border of each lobe; posterior surface densely spinulose, the spinules rather large and arranged in rows, the rows long and transverse medially and dorsally, becoming shorter and arcuate laterally and ventrally; posterior surface with 4 scattered sensilla near the middle of each lobe. Mandibles stout, heavily sclerotized; subtriangular in anterior view; apical tooth large, sharp-pointed, with a medial flange which is narrowed at the base; subapical tooth narrowly round-pointed and constricted basally; proximal tooth broadly rounded in anterior view; in medial view all teeth compressed and sharp. Maxillae with the apex paraboloidal and densely spinulose, the spinules rather long and in short arcuate rows; palp a peg, with 1 large encapsulated subapical sensillum and 2 or 3 apical sensilla; galea digitiform with 2 apical sensilla.

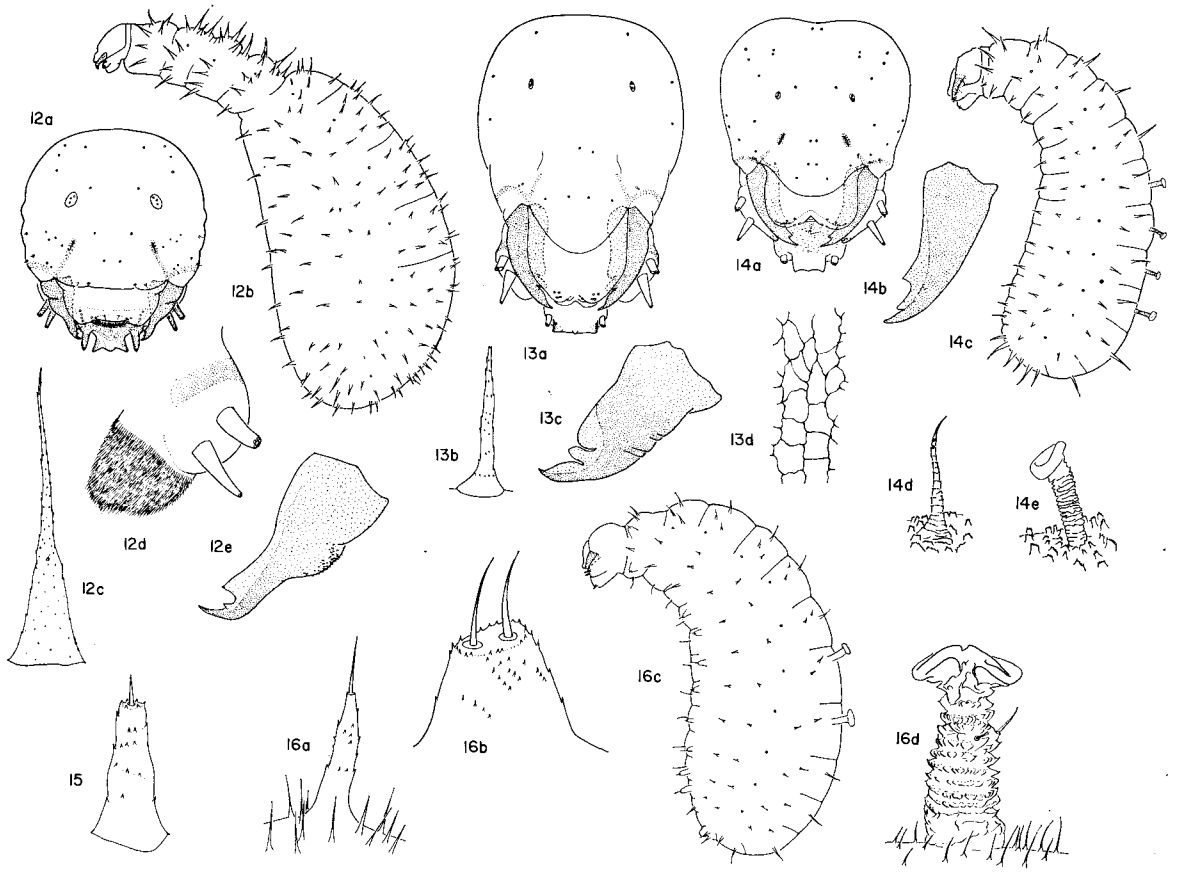

FIG. 12.—*Psalidomyrmex procerus:* a, head, anterior view, ×29; b, larva, side view, ×7; c, thoracic tubercle, ×95; d, left maxilla, anterior view, ×88; e, left mandible, anterior view, ×85. FIG. 13.—*Thaumatomyrmex mutilatus:* a, head, anterior view, ×95; b, thoracic tubercle, ×278; c, left mandible, anterior view, ×196; d, network of ridges on integument, ×278. FIG. 14.—*Belonopelta deletrix:* a, head, anterior view, ×71; b, left mandible, anterior view, ×139; c, larva, side view, ×19; d, thoracic tubercle, ×98; e, doorknob-like tubercle, ×98. FIG. 15.—*Trapeziopelta tasmaniensis:* dorsolateral thoracic tubercle, ×278. FIG. 16.—*Ponera opaciceps:* a, dorsolateral thoracic tubercle, ×350; b, ventrolateral thoracic tubercle, ×350; c, larva, side view, ×28; d, doorknob-like tubercle, ×139.

Labium narrow and spinulose, the spinules minute and in short transverse rows; palp a slender peg with 4 apical sensilla, 1 of which is encapsulated; opening of sericteries wide and salient. Hypopharynx densely spinulose, the spinules long and in transverse rows, the rows so close together that the spinules overlap. (Material studied: 3 damaged specimens from Brazil, courtesy of Dr. W. W. Kempf.)

Genus ***Proceratium*** Roger

REVISION.—We have referred to minute hairs on the head and body. We now regard them as sensilla each with a minute spinule.

Brown 1957, p. 115: Larvae fed on spider eggs.

Brown (1958, p. 245) referred to our description of the larvae.

Genus ***Centromyrmex*** Mayr

Centromyrmex feae (Emery).—REVISION.—Anterior surface of mandible produced into a medial blade which bears the subapical teeth. [Page 604, paragraph 2, line 7, delete "acuminate."]

Genus ***Odontoponera*** Mayr

Odontoponera transversa (F. Smith).—REVISION.—Anterior surface of mandible produced into a medial blade which bears the subapical teeth.

Genus ***Dinoponera*** Roger

Dinoponera grandis (Guérin).—Zahl 1959, p. 639: Colored photograph includes larvae. They are out of focus and no complete larva is shown, but the tubercles are evident.

Genus ***Diacamma*** Mayr

Diacamma australe (F.).—REVISION.—Anterior surface of the mandible with a very small medial blade.

Genus ***Megaponera*** Mayr

REVISION.—We have referred to exceedingly minute hairs on the body. We now regard these as sensilla each bearing a minute spinule. The body is therefore hairless.

Gantes 1949, p. 76:—"La larve de *Megaponera* est nue à tous les stades."

Genus ***Neoponera*** Emery

REVISION.—Page 613, line 9, ". . . produced with spinules." should read ". . . produced into spinules."

Neoponera obscuricornis latreillei Forel.—REVISION.—Anterior surface of mandible produced into a medial blade which bears the subapical teeth.

Genus ***Pachycondyla*** F. Smith

Wheeler (1921, p. 304) referred to Müller's mistake: Müller thought larvae of *Pachycondyla* were those of *Eciton*.

Pachycondyla harpax montezumia F. Smith.—Caullery (1952, p. 20-21) referred to Wheeler's (1901) account of the relationship between the larvae of *P. vorax* (sic!) and the larva of the fly *Metopina pachycondylae*, and reproduced Wheeler's classic figure.

Escherich (1906, p. 174 = 1917, p. 250) mentioned *Pachycondyla* and *Metopina* briefly and reproduced Wheeler's (1901) figure.

Michener and Michener (1951) mentioned very briefly larval feeding (p. 143) and *Metopina* (p. 234).

Pachycondyla striata F. Smith.—REVISION.—Anterior surface of mandible produced into a medial blade which bears the subapical teeth.

Genus ***Bothroponera*** Mayr

Michener and Michener 1951, p. 143:—A brief account of feeding.

Genus ***Euponera*** Forel

REVISION FOR TYPE I.—Shaped somewhat like a crookneck squash; thorax and first abdominal somite forming a long slender neck, which is strongly bent ventrally; remainder of abdomen rather plump. Tubercles numerous (136-186); subconical, short and stout to long and slender; each tubercle encircled by numerous rows of minute spinules and bearing, near the apex, 1 to 3 sensilla, each bearing a spinule; dorsal tubercles on abdominal somites III–VI or III–VIII reduced to low rounded bosses. Clypeal integument not spinulose. Mandibles narrow and elongate; slightly curved; base only slightly dilated; with at least a few spinules on the basal half.

Euponera (*Mesoponera*) *constricta* (Mayr).—REVISION.—Anterior surface of mandible produced into a medial blade which bears the subapical teeth.

Euponera (*Trachymesopus*) *gilva* (Roger).—REVISION.—Anterior surface of mandible produced into a medial blade which bears the subapical teeth.

Euponera (*Trachymesopus*) *clarki* Wheeler.—Length (through spiracles) about 4.2 mm. Generally similar to *Euponera* (*Mesoponera*) *constricta* but differing in the following details: Tubercles more numerous (186) and distributed as follows: 12 on each thoracic somite; 14 on abdominal somite I; 16 each on II–V and IX; 20 each on VI–VIII; 10 on X. Tubercles long and spirelike and capped by a spinule-bearing sensillum except as follows: on the dorsal surface of each abdominal somite III–VIII 1 pair of tubercles reduced to low contiguous elevations. Integument of tubercles beset with coarse isolated spinules. Integument of body sparsely spinulose. Integument of head not spinulose. Head hairs shorter and not constricted at the base. Antennae only moderately large. Subapical teeth of the mandibles round-pointed; spinules on the mandibles restricted to a small patch at the basal third of the medial surface. Maxillary spinules much longer. (Material studied: 6 larvae from South Australia, courtesy of Dr. W. L. Brown.) (Also called *Euponera* (*Brachyponera*) *rufonigra* Clark.)

Genus ***Belonopelta*** Mayr

Without a sharply differentiated neck; thorax stout; abdomen moderately swollen; posterior end broadly rounded. Integument of ventral surface with minute spinules arranged in transverse rows; on the lateral and dorsal surfaces there are numerous short ridges, each surmounted by a few minute spinules. Tubercles numerous (128); typically slender and spirelike; each encircled with rows of minute spinules and surmounted by a rather long, stout spine. There are also on the dorsal surface of abdominal somites III–VI 4 pairs of doorknob-shaped tubercles, 1 pair on each somite. Body hairs lacking. Head large and subcordate. Antennae minute. Head without hairs but with numerous sensilla. Mandibles rather long and narrow; base only slightly dilated; distal half with a narrow medial blade bearing 2 medial teeth; without spinules.

Belonopelta deletrix Mann.—Fig. 14. Length (through spiracles) about 3 mm. Without a well differentiated neck, diameter greatest at abdominal somites IV–VII, decreasing gradually toward the anterior end; thorax and first 2 abdominal somites stout and curved ventrally, remainder of abdomen nearly straight; posterior end broadly rounded. Anus ventral. Leg vestiges present. Spiracles on small low elevations. Body beset with numerous (124) tubercles, which are slender and spirelike and encircled with rows of minute spinules; each is surmounted by a rather long stout spine and may also bear sensilla near the apex; height of tubercle (including spine) 0.09–0.18 mm. The tubercles are distributed as follows: prothorax, 12; mesothorax and metathorax, 10 each; abdominal somites I, II and VII, 12 each; III–VI and VIII, 10 each; IX and X, 8 each. In addition there is a pair of doorknob-shaped tubercles on the dorsum of each abdominal somite III–VI; each consists of a stout column (the surface of which is wrinkled), surmounted by a knob of variable shape; height about 0.18 mm. Body hairs lacking. Integument of the dorsal and lateral surfaces furnished with numerous short ridges, each surmounted by a few minute spinules; the ridges become lower toward the ventral surface; on the ventral surface (where the ridges are lacking) the spinules are arranged in transverse rows. Head large; subcordate; cranium (in anterior view) slightly broader than long; somewhat narrowed ventrally; occiptal outline impressed at the

middle; occipital corners rounded. Head without hairs but with numerous sensilla. Antennae minute, each mounted on a rounded protuberance and bearing 3 sensilla, each with a spinule. Labrum bilobed; breadth twice the length; anterior surface of each lobe with about 12 sensilla near the ventral border; posterior surface densely spinulose, the spinules in transverse rows; posterior surface with 7 or 8 sensilla on each half. Mandibles heavily sclerotized; narrowly subtriangular in anterior view; apex forming a short sharp tooth which is curved medially and posteriorly; anterior surface produced into a medial blade which forms 2 subapical teeth. Maxillae with the apex conoidal and bearing short rows of rather long spinules; palp a peg with 5 apical sensilla; galea digitiform with 2 apical sensilla. Labium with the anterior surface spinulose, the spinules rather long and arranged in short arcuate rows, which are—in turn—arranged in transverse rows; palp a short peg with 5 apical sensilla; opening of sericteries wide and salient. Hypopharnyx densely spinulose, the spinules rather long and in transverse rows; the rows so close together that the spinules overlap. (Material studied: 6 larvae from Mexico, courtesy of Dr. E. O. Wilson.)

Wilson 1955, p. 86:—"When the workers transported larvae, they cradled them between the concave masticatory borders [of the mandibles] and avoided using the needle-like apical teeth." The larvae "were very active; when disturbed they thrashed violently back and forth in the manner of injured earthworms, but showed no capacity for directed locomotion. Insect prey were fed to them in typical ponerine fashion on their 'laps', either entire or cut up into large pieces." A cicadellid "was placed entire across the laps of two large larvae lying side by side."

Genus *Simopelta* Mann

Wheeler and Wheeler, 1957, p. 191–192: A generic characterization.

Simopelta pergandei (Forel).—Borgmeier 1950: Description of young larva on p. 376 (translation in Wheeler and Wheeler 1957, p. 194). Fig. 12 on p. 375, young larva in dorsal view.

Wheeler and Wheeler, 1957: Description of young larva on p. 192 and 194. Fig. 1 on p. 193: young larva in ventral and lateral views; head in anterior view; mandible in lateral view; mouth parts in sagittal section; tubercle and adjacent bulb in section. CORRIGENDA: On page 191, paragraph 2, the last 3 sentences should be changed to read: Dr. Wirth has written us that "the complete series of abdominal spiracles and the lack of a posterior differentiated pair of spiracles indicate that they are not dipterous. I know of no Diptera higher than the Fungivoridae-Itonididae series which have a complete series of abdominal spiracles. Traces of the usual pair of apical spiracles are practically always found in the higher Diptera." On page 193, legend for Fig. 1, line 3: the first word should be "papillae" (not "spines").

Genus *Ponera* Latreille

REVISED DESCRIPTION.—Without a sharply differentiated neck; thorax stout; abdomen scarcely enlarged. Integument of ventral surface finely spinulose; lateral and dorsal surfaces conspicuously spinulose, the spinules either short and coarse or long and hairlike. Tubercle numerous (130–224); typically spirelike, each encircled by a few rows of minute spinules and surmounted by a rather long and stout spinelike hair. There are also on the dorsal surface of certain abdominal somites 2 to 4 pairs of doorknob-shaped tubercles, 1 pair on a somite. Mandibles rather long and narrow; base only slightly dilated; apical half consisting of a thicker outer part and a narrow medial blade; basal half sparsely spinulose, the spinules minute and in short transverse arcuate rows.

Forel 1920, p. 266: Chez les Ponerinae (*Ponera*) où les larves "sont pourvues de tubercules, elles sont assez indépendentes, très mobiles et dévorent seules les insectes que leur donnent les ouvrières (Wheeler)."

Ponera nitidula Emery.—YOUNG LARVA.—Length (through spiracles) about 2.7 mm. In general, similar to *P. coarctata pennsylvanica* Buckley, differing as follows: Tubercles numerous (224), distributed as follows: prothorax, 12; mesothorax, 16; metathorax, 20; abdominal somites I–III and VI–VIII, 20 each; IV and V, 18 each; IX, 14; X, 6. These tubercles are spirelike; length (including spine) 0.048–0.12 mm. In addition, there is a pair of doorknob-shaped tubercles on the dorsum of each abdominal somite IV and V; length about 0.168 mm. Body hairs shorter (0.012–0.044 mm long). Head hairs fewer and a little longer (0.088 mm long). (Material studied: 6 larvae from Mexico, courtesy of Dr. E. O. Wilson.)

Ponera opaciceps Mayr.—Fig. 16. MATURE LARVA.—Length (through spiracles) about 2.3 mm. Generally similar to *P. coarctata pennsylvanica* Buckley, but differing in the following details: Anus with a conspicuous posterior lip. Body beset with numerous (134) tubercles, which are slender, spirelike, encircled by a few rows of minute spinules, and surmounted by a rather long spine (or stout hair) which arises by an articulation from an apical depression; height (including spine) 0.06–0.1 mm. The tubercles are distributed as follows: each thoracic somite, 10; abdominal somites I, IV, V, and VIII, 10 each; II, III, VI, and VII, 12 each; IX, 6; X, 4. In addition there is a pair of doorknob-shaped tubercles on the dorsum of each abdominal somite IV and V; each consists of a stout column bearing an inflated knob; the column encircled by numerous rows of minute spinules and bearing 2 hairs 0.03 mm long; height (knob plus column) 0.12 mm. Integument similar to *Ponera* sp. found in the Biology Department greenhouse: with a dense covering of isolated long (0.01–0.03 mm), hairlike spinules on the dorsal and lateral surfaces. Integument of head without spinules. Head hairs fewer. Mandibles with the teeth narrower and more sharply pointed.

VERY YOUNG LARVA.—Length (through spiracles) about 0.66 mm. Posterior end pointed, diameter increasing to abdominal somites IV and V, then decreasing to the prothorax which is smaller than the

head. Tubercles as in the mature larva. Mouth parts rounded, but similar to those of the mature larva.

(Material studied: numerous larvae from Florida, courtesy of Dr. P. B. Kannowski.)

Ponera trigona opacior Forel.—Length (through spiracles) about 2 mm. Similar to *P. coarctata pennsylvanica* Buckley, except in the following details: Body stouter. Anus with a conspicuous posterior lip. Tubercles less numerous (130). Spirelike tubercles distributed as follows: thoracic somites and abdominal somites IV, V and VII, 10 each; I–III and VI, 12 each; VIII, 8; IX, 6; X, 4. Integument with a dense covering of isolated, long (0.01–0.03 mm), hairlike spinules on the dorsal and lateral surfaces. Body hairs slightly longer (0.05–0.08 mm long). (Material studied: 12 larvae from Georgia, courtesy of Dr. P. B. Kannowski.)

Genus ***Trapeziopelta*** Mayr

REVISION.—Tubercles 90–112. Head without hairs but with a few sensilla, each of which bears a minute spinule.

Trapeziopelta sp. REVISION.—Head without hairs but with a few sensilla, each of which bears a minute spinule. Page 636, line 14 ". . . half of the spinules . . ." should read ". . . half the spinules . . ."

Trapeziopelta tasmaniensis (Wheeler).—Fig. 15. Length (through spiracles) about 4.4 mm. Similar to *Trapeziopelta* sp., except in the following details: Body furnished with numerous (112) subconical tubercles, the tubercles 0.018–0.036 mm in diameter and 0.024–0.096 mm high, encircled by a few rows of denticles and surmounted by an apical hair about 0.018 mm long. Tubercles arranged as follows: each thoracic somite, 8; abdominal somites I–VI, 12 each; VII–VIII, 10 each; IX, 8; X, 4. Integument of body spinulose, the spinules in short transverse rows on the ventral surface, but isolated elsewhere. Hairs simple, short (0.018–0.11 mm long), slightly curved, a few on each somite. (Material studied: 5 larvae from Victoria, Australia, courtesy of Dr. W. L. Brown.)

Genus ***Psalidomyrmex*** Ern. André

Tubercles very numerous (356), slender and spinelike, with minute scattered spinules on the integument. Integument of body with minute scattered spinules. Body hairs lacking. Head without hairs but with numerous sensilla; head subcircular in anterior view. Labrum with a wide median impression of the ventral border. Mandibles rather long and narrow; the basal half only slightly inflated and bearing a lateral bulge which is furnished with coarse isolated spinules; apical half slender, with a medial blade projecting from the anterior surface and bearing 2 subapical medial teeth, the proximal very large and the distal very small; apical tooth slender, acute and strongly curved medially.

Psalidomyrmex procerus Emery.—Fig. 12. Length (through spiracles) about 11.3 mm. Shaped somewhat like a crookneck squash; thoracic and first abdominal somites of about the same diameter, forming a long slender neck which is sharply demarcated; remainder of abdomen greatly inflated, with the dorsal profile convex, the ventral profile nearly straight and the posterior end broadly rounded. Anus ventral. Leg and gonopod vestiges present. Body furnished with numerous (356) tubercles which are spinelike and very slender; integument of tubercles with minute scattered spinules and 1 or 2 sensilla. The tubercles are distributed as follows: prothorax, 12; mesothorax, 14; metathorax, 16; abdominal somite I, 20; II, 24; III–VII, 40 each; VIII, 36; IX, 28; X, 6. Integument of body spinulose, the spinules minute and isolated. Body hairs lacking. Head subcircular in anterior view. Head without hairs but with numerous sensilla. Each antenna with 3 sensilla, each of which bears a spinule. Labrum short, breadth more than twice the length; ventral border with a wide median impression; anterior surface of each half with 7 sensilla near the ventral border; ventral border with 4 sensilla and a few rather long spinules; posterior surface densely spinulose, the spinules in rather long transverse rows; posterior surface with 5 sensilla on each half. Mandibles heavily sclerotized, rather long and narrow; the basal half only slightly inflated and bearing a lateral bulge, which is furnished with coarse isolated spinules; apical half slender, with a medial blade projecting from the anterior surface and bearing 2 subapical medial teeth (the proximal very large, the distal very small); apical tooth slender, acute, strongly curved medially and slightly curved posteriorly. Maxillae with the apex paraboloidal, directed ventromedially and densely spinulose, the spinules long (up to 0.02 mm), directed ventrally and arranged in arcuate rows; palp long, subcylindrical, with 5 apical sensilla (4 with a spinule each and 1 encapsulated); galea digitiform, with 2 apical sensilla. Labium spinulose, the spinules small and in short rows medially, large and isolated laterally, long and in transverse rows on a welt basally; palps long and subcylindrical, with 4 apical sensilla; opening of sericteries wide and salient, with 3 projections. Hypopharynx densely spinulose, the spinules in numerous transverse rows. (Material studied: numerous larvae from the British Cameroons, collected by B. Malkin, courtesy of W. L. Brown.)

Genus ***Onychomyrmex*** Emery

Brown 1954, p. 25: "Development of legionary habits has brought about structural modifications of larvae and adult workers and females ('dichthadiiforms') showing a remarkable convergence with corresponding doryline phases."

Brown 1960, p. 179: "The larva also shows no features that seem to contradict an amblyoponine affinity (Wheeler, 1916; G. C. and J. Wheeler, 1952: 637), although the Wheelers consider it to show specialization in the direction of the Cerapachyinae larva."

Onychomyrmex hedleyi Emery.—YOUNG LARVA.—Length (through spiracles) about 3.5 mm. Similar to *O. mjoebergi* Forel, except in the following details: Shaped somewhat like a crookneck squash, thorax and first abdominal somite curved ventrally

to form a slender neck, remainder of abdomen swollen. Body hairs 0.012–0.144 mm long, with the apical portion slender and flexible. Head with a very few sensilla and/or minute hairs (0.004–0.008 mm long). (Material studied: 10 larvae from Queensland, courtesy of Dr. W. L. Brown.)

Genus ***Leptogenys*** Roger

CORRECTION.—Tubercles numerous (about 130). Head without hairs but with a few minute sensilla.

Leptogenys (*Leptogenys*) *puncticeps* Emery.—SEMIPUPA.—Length (through spiracles) about 6.2 mm. Very similar to *Leptogenys* (*L.*) sp., No. 119, except in the following details: Tubercles 128, distributed as follows: prothorax and mesothorax, 8 each; metathorax and abdominal somites I and II, 10 each; III–VIII, 12 each; IX, 8; X, 2. Tubercles a little shorter (0.05–0.075 mm long). Posterior surface of labrum with 5 sensilla in each of the 2 clusters. (Material studied: 2 semipupae from cocoons, Barro Colorado Island, Panama Canal Zone, G. C. Wheeler No. 187, det. W. W. Kempf.)

Leptogenys (*Lobopelta*) *consanguinea* Wheeler.—Length (through spiracles) about 4.6 mm. In general similar to *Leptogenys* (*L.*) sp., except in the following details: Body tubercles 128; prothorax, 6; mesothorax, 8; abdominal somite I, 10. Integument of apical portion of tubercle spinulose. Head longer and narrower (widest at the occiput). Labrum with a pair of palplike structures as in *L.* (*Lobopelta*) *elongata*. Mandible as in *L. elongata*. Hypopharynx densely spinulose, the spinules minute and in short arcuate rows. (Material studied: 7 larvae from Mexico, courtesy of Dr. E. O. Wilson.)

Leptogenys (*Lobopelta*) *elongata* (Buckley).—Michener and Michener 1951, p. 143: Brief mention of feeding.

Genus ***Anochetus*** Mayr

Since *A.* (*A.*) *mayri* resembles the other species of subgenus *Anochetus* in some characters and subgenus *Stenomyrmex* in others, it is necessary to delete from our earlier article the subgeneric characterizations. Instead we offer the following generic description: Neck long and somewhat stout; abdomen straight and rather stout. Tubercles moderately numerous (about 90). The majority of tubercles consist of a frustum bearing 1–9 (usually 3–5) relatively long hairs; on this base is seated a spire, which has mounted on its apex a heavy spinelike hair. On the middorsal surface of abdominal somite IV there is a pair of glabrous, subcircular areas which may be considerably elevated and pulleylike or thin discs or merely differentiated areas that are scarcely perceptible in profile; similar structures on V; or there may be one such structure on IV and one on V. Each antenna is a low convex area surmounted by a smaller rounded projection bearing 3 sensilla. Integument of galea with a few minute spinules.

Anochetus (*Anochetus*) *mayri* Emery.—IMMATURE LARVA.—Length (through spiracles) about 2.1 mm. Similar to *Anochetus* (*Anochetus*) sp., except in the following details: Abdominal somite I with 8 tubercles; abdominal somite IX, 4. Hairs at the base of the tubercles fewer (1–4, usually 3), shorter (about 0.08 mm long); apical hair of tubercle shorter (about 0.07 mm long); overall length of tubercle less (about 0.13 mm long). On the middorsal surface of abdominal somite IV there is a pair of discoidal elevations, which are smaller and higher and with only 2 or 3 lateral hairs; a similar pair on V. Labrum twice as broad as long; anterior surface of each lobe with 2 hairs and a few short transverse rows of minute spinules. Shape of mandible as in *A.* (*S.*) *emarginatus*. (Material studied: 1 larva and 1 semipupa from Mexico, courtesy of Dr. E. O. Wilson.)

Anochetus (*Anochetus*) sp.—REVISION.—A typical tubercle consists of a frustum with 4–6 (usually 5) relatively long (0.18–0.25 mm) slender simple hairs, which are constricted at the point of attachment; on this frustum is a slender spire, which has mounted on its apex a heavy straight spine-like hair about 0.12 mm long; overall length of tubercle and spine 0.3–0.38 mm; integument of spire with short transverse rows of spinules. Anterior surface of the mandible produced into a medial blade which bears the subapical teeth. [Page 665, legend for Pl. V, Fig. 2 "left antenna in side view" should be changed to read "left antenna in medial view."]

Anochetus (*Stenomyrmex*) *emarginatus* (F.).—REVISION.—Each tubercle consists of a frustum with 4–9 (usually 6) relatively long (0.19–0.22 mm) slender simple hairs, which are constricted at the point of attachment; on this frustum is a spire which bears on its apex a heavy straight spine-like hair about 0.15 mm long; overall length of tubercle and spine 0.25–0.4 mm. Anterior surface of the mandible produced into a blade which bears the medial denticles.

Genus ***Odontomachus*** Latreille

REVISION.—Tubercles numerous (94–116); a typical tubercle consists of a frustum with 3–14 relatively long hairs; on this frustum is a spire with an apical straight, spinelike hair; integument of spire with short transverse rows of spinules.

Marcus (1953, p. 63–66) thought the hairs on the tubercles might be venomous (like those of certain caterpillars). A crude figure (p. 64) is labeled: "Corte sagittal de una larva de Eciton rapax, combinado." But it could not possibly represent a sagittal section. In the text the larvae are called *Eciton rapax*, but a correction slip pasted in the separate reads: "De los valiosos trabajos de George C. Wheeler, que permiten determinar las larvas de hormigas, me he convencido, que, los larvas transportadas por Eciton rapax no son las suyas, sino larvas raptadas de Odontomachus." Also in the German summary (p. 68) they are referred to *Odontomachus*.

Odontomachus haematoda (L.).—REVISION.—A typical tubercle consists of a frustum with 3–6 relatively long (0.16–0.2 mm), slender, nearly straight hairs, which are constricted at the point of attachment; on this frustum is a spire with an apical heavy straight spinelike hair about 0.16 mm long; over-all

height of tubercle and spine about 0.38 mm; integument of spire with a few minute denticles. Anterior surface of the mandibles produced into a small medial blade which bears the subapical teeth.

Odontomachus haematoda clarus Roger.—Michener and Michener 1951, p. 143: A brief account of feeding.

Odontomachus haematoda insularis Guérin.—Length (through spiracles) about 8.3 mm. Similar to *O. haematoda,* except in the following details: Body with numerous (116) tubercles; prothorax, 12; abdominal somite IX, 10. Apical tooth of mandible longer and more slender than subapical teeth. Maxillae and labium with longer spinules. (Material studied: numerous larvae from Florida, courtesy of Dr. P. B. Kannowski.)

LITERATURE ON THE SUBFAMILY

Bernard 1951:—"Larves eucéphales, carnivores; se nourrissant seules" (p. 1041). "Larves variables suivant les genres, mais habituellement primitives, à tête et pièces buccales très différenciées, poilue ou non. La trophallaxie paraît nulle ou rudimentaire: la larve dévore des fragments d'Insectes que les ouvrières ou la reine placent à sa proximité" (p. 1043).

Escherich 1906, p. 76 = 1917, p. 98:—"Manche Larven sind übrigens auch fähig, feste Nahrung zu verzehren. Bei den Ponerinen scheint dies sogar Regel zu sein, worauf schon die starke Entwickelung der Mundteile schliessen lässt. Nach den Beobachtungen Wheelers (1900) legen die Arbeiter dieser niederen Ameisen feste Nahrungsstücke, wie kleine tote Insekten oder Stücke von grösseren auf die flache, tellerförmige Bauchseite der Larven, von wo sie sich diese vermöge ihres langen, ventralwärts gebogenen Halses herholen, um sie zu verzehren."

Emery 1904, p. 114–5:—Le larve "delle vere Ponerinae sono piriformi o claviformi, con l'addome fortemente rigonfiato, tanto in quelle che portano soltanto peli semplici, . . . quanto in quelle che sono fornite di tubercoli piligeri."

Gantes 1949, p. 76:—Ponerine larvae compared with *Formica*: "La tête est plus grosse par rapport au corps: les pièces buccales très développées, les mandibules très grandes, les palpes sensoriels également."

Klots and Klots (1959, p. 281) have given a very brief account of feeding.

Michener and Michener 1951, p. 142:—The colony-founding queen leaves her nest to forage for food for her first brood.

TRIBES

The following is a synopsis (based on Emery 1911 and Wheeler 1922) of the sections, tribes, and genera that we have studied. The only ponerine tribes not represented in our collection are Cylindromyrmecini and Dorylozelini.

Section Proponerinae

Myrmeciini—*Myrmecia.*

Amblyoponini—*Mystrium, Stigmatomma, Myopopone, Amblyopone.*

Paraponerini—*Paraponera.*

Platythyreini—*Platythyrea.*

Ectatommini[2]—*Paranomopone, Prionopelta, Typhlomyrmex, Acanthoponera, Rhytidoponera, Ectatomma, Gnamptogenys.*

Thaumatomyrmecini[3]—*Thaumatomyrmex.*

Proceratiini—*Proceratium.*

Section Euponerinae

Ponerini—*Centromyrmex, Odontoponera, Dinoponera, Diacamma, Megaponera, Neoponera, Pachycondyla, Bothroponera, Euponera, Belonopelta, Simopelta, Cryptopone, Ponera, Trapeziopelta, Psalidomyrmex.*

Onychomyrmecini—*Onychomyrmex.*

Leptogenyini—*Leptogenys.*

Odontomachini—*Anochetus, Odontomachus.*

CHARACTERS

In our study of the larvae of the subfamily Myrmicinae (1960) we discussed the importance of various characters in taxonomy and described our techniques for generalizing about certain characters. We have applied the same reasoning and techniques to the larvae of the ponerines.

In the subfamily Ponerinae—as in the Myrmecinae—body shape is the character which is most nearly constant throughout the genus. It is also the character which most closely correlates larval taxonomy with adult taxonomy. Therefore we have chosen body shape as the basic character for classifying the larvae of the Ponerinae. The next most useful character is mandible shape. There are more kinds of mandible shapes than body shapes. Mandible shape also shows more intrageneric and intraspecific variation. Third in utility is the presence or absence of tubercles and the shape of the tubercles when present.

Other characters are less useful in separating genera and may be considered as primarily specific characters: integumentary spinules (location, pattern, abundance); hairs(shape, size, distribution, abundance); head shape; teeth of mandibles (size and shape); spinules on mandibles; other mouth parts (shape, spinules, sensilla). The species of a genus usually differ in characters which are both variable and quantitative.

BODY SHAPE

In our study of body shapes we have used only the profiles (i.e., outlines in side view), since dorsal and ventral views rarely show anything distinctive.

Applying the technique referred to above, we find 8 generalized profiles for the Ponerinae (Fig. 17 and Appendix A). A simultaneous comparison of the 8

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[2] "The larvae of the ectatommines are also relatively incompletely known, and before the pioneering work of the Wheelers on the ponerine larvae, . . . there was virtually nothing in print of any value for morphological or systematic purposes. The larval findings agree in most respects at the generic level with the new classification adopted here." (Brown 1958, p. 179.)

[3] It is our opinion that names of subfamilies and tribes based on generic names terminating in *-myrmex* (from the Greek *myrmex, myrmekos*) should be spelled -myrmecinae and -myrmecini (not -myrmicinae and -myrmicini), Emery and W. M. Wheeler to the contrary notwithstanding. Perhaps such spellings have been established by analogy with Myrmicinae, but the latter is derived from the generic name *Myrmica,* not from *Myrmex.*

generalized profiles showed that they could be arranged in 4 groups on the basis of more superficial resemblances. We have not, however, attempted generalized diagrams of the second order and we have not named these larger groups.

After the profiles were classified, the next question was: which profile is unspecialized? We selected myrmeciiform, because (1) *Myrmecia* has generally been regarded as the least specialized genus of ants; (2) among larvae of this genus and of other unspecialized ponerines (*Myopopone* and *Paraponera,* whose profiles approach myrmeciiform most closely) no character shows an extreme deviation from an average for all known ant larvae; (3) among larvae exhibiting myrmeciiform and paraponeriform profiles no character shows adaptation to any limited function or habit; (4) among larvae having these profiles the majority of characters are only moderately developed, in contrast to the extremes of the same characters in the subfamily. We believe that these larvae are unspecialized in the following characters: body shape; short simple abundant hairs; head without hairs (or with few hairs); size, shape and position of the antennae; general size and shape of the labrum; posterior labral spinules not in rows, but isolated; palp and galea peglike and only moderately long; labial palp a low rounded elevation; opening of sericteries wide, but not salient.

The most specialized profiles are platythyreiform and proceratiiform.

MANDIBLE SHAPE

The same generalizing procedures have been applied to the anterior view of the mandibles, using the apex and the anterior condyle as reference points for standardization. (See Wheeler and Wheeler 1960, p. 102). The results of our generalizations are shown in Fig. 18 and Appendix B.

We conclude that the least specialized mandible shape is myrmeciiform. Specializations are extreme slenderness, posterior curvature of the apex and reduction of medial teeth.

TUBERCLES

In the "Genera Insectorum" Emery (1911, p. 4) divided the subfamily Ponerinae into 3 sections on the basis of larval and male characters. Section Prodorylinae is practically equivalent to the present subfamily Cerapachyinae and hence can be disregarded in this discussion. In section Proponerinae the larvae were characterized as *uniformément poilues, sans tubercules piligères,* while those in section Euponerinae were *pourvues de tubercules piligères.*

This division is of historical interest: it is Emery's second use of larval characters in formicid taxonomy. But is it still valid and useful? It is not particularly useful, since tribes adequately take care of the interval between subfamily and genus. It is valid only if 4 exceptions are allowed. Without knowing either the larvae or the males, Emery placed *Thaumatomyrmex* and *Proceratium* in the Proponerinae and *Onychomyrmex* in the Euponerinae; he had seen the male but not the larva of *Megaponera,* which he placed in the Euponerinae. We now know that the larvae of *Thaumatomyrmex* and *Proceratium* have tubercles, while those of *Megaponera* and *Onychomyrmex* lack them.[4]

Furthermore not all tubercles are piligerous. To be sure, those without obvious hairs usually have one or more sensilla, each of which may bear a spinule or minute hairlike structure, but we are not willing to dignify them with the term "hair" (although we have done so in the past).

What is really remarkable about Emery's division is that the larvae of only 9 ponerine genera had been described—6 tuberculate and 3 nontuberculate. We have studied the larvae of 38 genera in the subfamily Ponerinae and found only 4 (mentioned above) that do not conform to Emery's sectional classification.

The term "tubercle" is not particularly appropriate for these structures. The Latin *tuberculum* is the diminutive of *tuber,* which means swelling, hump, bulb, bump, or protuberance. Definitions in English dictionaries employ such nouns as "excrescence," "protuberance," and "nodule," modified by the adjectives "round," "rounded" or "knob-like." But not many ponerine tubercles can qualify for roundness. Torre-Bueno's "Glossary of Entomology," however, defines "tubercle" as a little solid pimple or small button. A pimple is pointed and a button may be knoblike. Seemingly, then, entomological usage takes care of all types of ponerine tubercles. Nevertheless the definition must be stretched to the breaking-point (or beyond) to include the spinelike tubercles of *Centromyrmex* and the "pulleys" of *Anochetus.* Be that as it may, myrmecological usage definitely sanctions the term. In 1886 Müller used *Tuberkeln* when referring (in German) to the rounded protuberances of mature *Pachycondyla* larvae; the conical structures on the young larvae were merely *Erhebungen.* Emery in 1899 used *sporgenze segmentali o tubercoli del tegumento* when referring in Italian to both rounded and pointed projections in 3 genera. In the "Genera Insectorum" (1911) he used the French *tubercules.* Wheeler first used "tubercles" in 1900 in "A Study of Some Texan Ponerinae" (his second article on ants) and he was still using it in 1922. In German Eidmann used *Warzen, Dörnchen, Fortsätze, Auswüchse,* and *Höcker.*

Of what use are these extraordinary structures? Not a great deal is really known, but 4 functions have been suggested:

1. Support. The customary resting position for ponerine larvae is on the side; the usual feeding position is belly-up. In either position the tubercles (which are largely confined to the lateral and dorsal surfaces) might prove beneficial by keeping most of the body surface away from the substrate. It is difficult to see any advantage in this in temperate zones, because ants can move their brood to those nest chambers which have a suitable humidity. In the

[4] Brown (1960) has recently moved *Onychomyrmex* to the tribe Amblyoponini, which is in the Proponerinae.

tropics, however, soil moisture may be so high that optimal conditions cannot be found; hence an airspace between body and substrate might be beneficial. At any rate, the Ponerinae are largely tropical.

2. Defense. Probably the greatest menace to a ponerine larva is her sister larvae. It is easy to believe that some of the hairy tubercles afford protection against cannibalism.

3. Attachment to ceilings. This is certainly probable in the case of the glutinous dorsal doorknobs; at least attachment can be readily observed in artificial formicaries. It would keep the larvae off the damp floors. (See 1 above.)

4. Trophallaxis. It has been suggested by W. M. Wheeler and others that tubercles may be exudate organs, which secrete onto their surfaces substances of which the workers are so fond that they tend the larvae for the "selfish" purpose of getting these exudates.

Tubercles such as we have been considering have been found among ant larvae in only 20 genera, all of which are in the higher Ponerinae. It is true that protuberances do occur elsewhere. A single caudal knob is found in *Platythyrea* (Ponerinae), in *Rhopalomastix* and *Acromyrmex* among the Myrmicinae, and in 4 dolichoderine genera (*Dorymyrmex, Engramma, Tapinoma, Technomyrmex*); there is a single middorsal row of tubercles in *Iridomyrmex itoi* (Dolichoderinae); lateral projections have been reported in *Crematogaster* (Myrmicinae). But none of these protuberances bears any resemblance to the ponerine tubercles.

In general a larva bears tubercles of only 1 kind, but 2 distinct kinds are found in 6 genera (*Anochetus, Belonopelta, Cryptopone, Euponera, Odontomachus* and *Ponera*). The number of tubercles per larva seems to be a generic characteristic, although it does vary within narrow limits among the species of a genus and even among individuals of the same species. The minimum number is 10 (*Bothroponera sublaevis*) and the maximum about 400 (*Centromyrmex*). The arrangement of tubercles usually follows a simple but definite pattern of longitudinal and transverse rows. No tubercles have been found on the midventral surface.

We have endeavored to classify and name the various shapes of ponerine tubercles and to illustrate each shape with a synthetic drawing; see Appendix C and Fig. 19. Only fully developed tubercles have been considered. One finds atypical tubercles on every larva, but they are obviously underdeveloped representatives of the typical form.

HETEROGENEITY

We have discussed at length (1960) the heterogeneity of the Myrmicinae—both adults and larvae. The adults of the Ponerinae are less heterogeneous than those of the Myrmicinae. Can the same be said of their larvae? To attempt an answer we have devised a simple index of heterogeneity: the ratio of the number of genera studied to the number of types of body profile (or mandible shape); this gives the average number of genera per type; the lower the index number, the greater the heterogeneity. (See appendices.)

Our computations follow:

Myrmicinae: 57 genera/22 profile types = 2.6 genera per type
Myrmicinae: 68 genera/30 mandible shapes = 2.3 genera per type
Ponerinae: 26 genera/8 profile types = 3.3 genera per type
Ponerinae: 33 genera/20 mandible shapes = 1.7 genera per type

We conclude therefore that both subfamilies are more heterogeneous in mandible shape than in body profile, the Ponerinae being more so by far. The Myrmicinae are more heterogeneous than the Ponerinae in profile, while the Ponerinae are the more heterogeneous in mandible shape.

APPENDIX A. GENERALIZED BODY PROFILES[5]

(Fig. 17)

GROUP A

1. Myrmeciiform. Not differentiated into neck and body; elongate and rather slender; diameter diminishing gradually from the fifth abdominal somite to the anterior end; anterior half strongly curved. Genus: *Myrmecia*. (*Myopopone* may belong here, but we cannot be sure because our material is damaged.)

GROUP B

Shaped somewhat like a crookneck squash; thorax forming a distinct neck, whose diameter is notably less than that of the abdomen and which is strongly bent or curved ventrally; first abdominal somite transitional to the remainder of the abdomen, which is stout or swollen.

1. **Paraponeriform.** Neck short and stout; body elongate, stouter, straight and subcylindrical. Genera: *Paranomopone, Paraponera.*

2. **Ectatommiform.** Neck long and slender; head small; abdomen ovoidal; anus subterminal. Genera: *Amblyopone, Ectatomma, Gnamptogenys, Rhytidoponera.*

3. **Pachycondyliform.** Neck long and slender; head large; abdomen subovoidal, but with the ventral profile nearly straight; anus ventral. [Except for *Stigmatomma*, all larvae of this type have tubercles (not shown on the profile).] Genera: *Anochetus, Centromyrmex, Diacamma, Dinoponera, Euponera* Type I, *Leptogenys, Neoponera, Odontomachus, Odontoponera, Pachycondyla, Psalidomyrmex, Stigmatomma, Trapeziopelta.*

GROUP C

Thorax curved or bent ventrally but not forming a distinct neck; abdomen only moderately swollen.

1. **Poneriform.** Not constricted at the first abdominal somite; ventral profile of abdomen nearly straight; anus ventral. [Tubercles present but not shown on the profile.] Genera: *Belonopelta, Euponera* Type II, *Ponera.*

2. **Onychomyrmeciform.** Constricted at the first abdominal somite; ventral profile of abdomen convex; anus subterminal. Genera: *Onychomyrmex, Typhlomyrmex.*

[5] The following genera which we have studied are not included here or in the key, because the material we have does not show adequate body profiles (the larvae are immature, the integuments are damaged, or the specimens are semipupae): *Acanthoponera, Bothroponera, Cryptopone, Megaponera, Mystrium, Prionopelta, Simopelta, Thaumatomyrmex.*

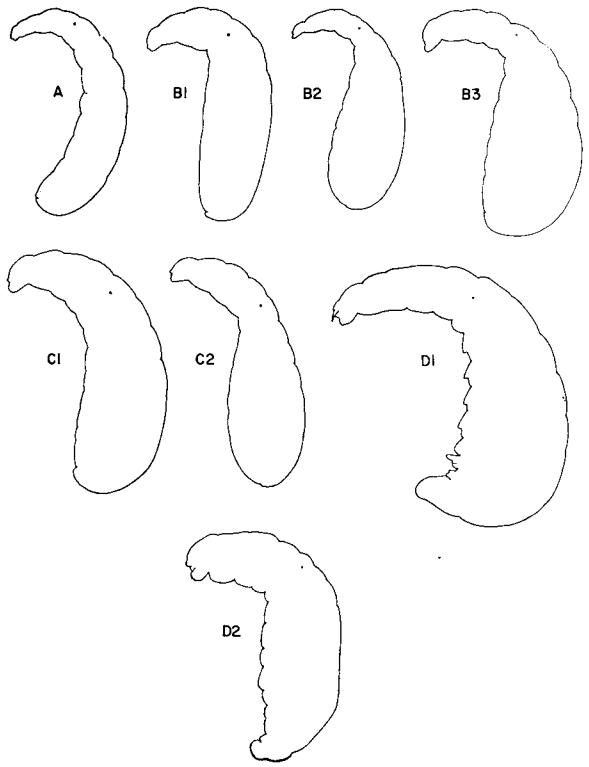

FIG. 17.—Generalized body profiles. *Group A,* myrmeciiform. *Group B*—1, paraponeriform; 2, ectatommiform; 3, pachycondyliform. *Group C*—1, poneriform, 2, onychomyrmeciform. *Group D*—1, platythyreiform; 2, proceratiiform.

GROUP D

Both ends directed ventrally; remainder of body straight and with a roughened (jagged or bumpy) ventral profile; thorax forming a distinct neck; terminal somite of abdomen stout and tail-like.

1. **Platythyreiform.** Thorax forming a long slender neck. Genus: *Platythyrea.*

2. **Proceratiiform.** Thorax forming a short stout neck; body surface beset with numerous rounded bosses (not shown on the profile.) Genus: *Proceratium.*

APPENDIX B. GENERALIZED MANDIBLE SHAPES

(Fig. 18)

GROUP I

Subtriangular in anterior view; with a medial blade arising from the anterior surface and bearing 2 medial teeth.

a. **Ectatommiform.** Apical half slightly curved medially; blade distinct and joining the body of the mandible in a smooth curve. Genera: *Anochetus* (*Anochetus*), *Belonopelta, Cryptopone, Ectatomma, Euponera, Gnamptogenys, Neoponera, Pachycondyla, Paranomopone, Ponera, Stigmatomma.*

b. **Myrmeciiform.** Straight and stout; blade distinct, joining the body of the mandible in an angulate line. Genera: *Myrmecia, Mystrium, Paraponera.*

c. **Odontoponeriform.** Base narrow; apical third slightly curved medially; blade distinct, joining the body of the mandible in an angulate line. Genera: *Odontoponera, Odontomachus.*

d. **Typhlomyrmeciform.** Basal half greatly dilated, distal half extremely narrow and straight; blade long and narrow. Genus: *Typhlomyrmex.*

e. **Psalidomyrmeciform.** Base with a pronounced lateral bulge; apical tooth strongly curved medially; blade distinct; subapical tooth minute, third tooth large. Genus: *Psalidomyrmex.*

f. **Thaumatomyrmeciform.** Stout; apical tooth large, sharp-pointed, with a medial flange which is narrowed at the base; medial tooth rounded; blade distinct. Genus: *Thaumatomyrmex.*

g. **Myopoponiform.** Narrow; blade indistinct; both medial teeth subapical. Genus: *Myopopone.*

h. **Centromyrmeciform.** Blade indistinct; proximal tooth at the distal third and directed medially. Genus: *Centromyrmex.*

i. **Rhytidoponeriform.** Basal two-thirds greatly inflated and terminating medially in a large tooth directed ventrally; distal third very narrow, terminating in a long apical tooth and bearing a small medial tooth; blade indistinct. Genus: *Rhytidoponera.*

GROUP II

With a distinct medial blade arising from the anterior surface; with or without medial teeth; shape diverse; if subtriangular, without conspicuous medial teeth.

a. **Bothroponeriform.** Subtriangular in anterior view; blade wide, its medial border sinuate and without teeth. Genus: *Bothroponera.*

b. **Diacammiform.** Falcate, with a stout base; blade short; apical tooth long, subapical tooth minute. Genus: *Diacamma.*

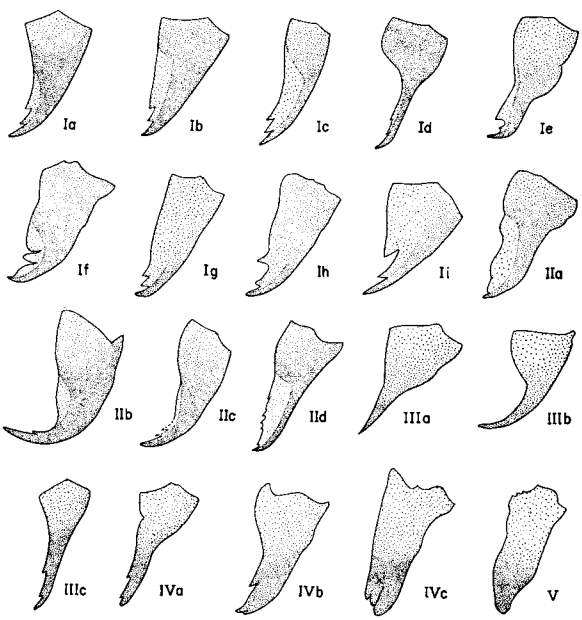

FIG. 18.—Generalized mandible shapes. *Group I*—a, ectatommiform; b, myrmeciiform; c, odontoponeriform; d, typhlomyrmeciform; e, psalidomyrmeciform; f, thaumatomyrmeciform; g, myopoponiform; h, centromyrmeciform; i, rhytidoponeriform. *Group II*—a, bothroponeriform; b, diacammiform; c, stenomyrmeciform; d, platythyreiform. *Group III*—a, proceratiiform; b, megaponeriform; c, amblyoponiform. *Group IV*—a, onychomyrmeciform; b, dinoponeriform; c, trapeziopeltiform. *Group V*—leptogenyiform.

c. **Stenomyrmeciform.** Falcate, with the base narrow; blade very narrow, toothless or with 2 minute medial teeth. Genus: *Anochetus* (*Stenomyrmex*).

d. **Platythyreiform.** Narrowly subtriangular in anterior view; apical tooth short and curved medially; distal half of medial border denticulate. Genus: *Platythyrea.*

GROUP III

Without a medial blade; shape diverse.

a. **Proceratiiform.** Subtriangular in anterior view, sharp-pointed; no medial teeth. Genus: *Proceratium.*

b. **Megaponeriform.** Falcate, with the base dilated; no medial teeth. Genus: *Megaponcra.*

c. **Amblyoponiform.** Elongate and very slender, distal two-thirds subcylindrical, base only slightly dilated; with 2 teeth on the medial border. Genera: *Amblyopone, Prionopelta.*

GROUP IV

Without a blade; distal portion strongly curved posteriorly; shape diverse.

a. **Onychomyrmeciform.** Elongate and narrow, base slightly dilated; apex not curved medially, terminating in a slender tooth; 2 denticles on the medial border. Genus: *Onychomyrmex.*

b. **Dinoponeriform.** Moderately stout, subtriangular in anterior view; with 2 apical teeth slightly curved medially; only 1 medial tooth. Genus: *Dinoponera.*

c. **Trapeziopeltiform.** Narrow, base only slightly enlarged; distal third strongly curved posteriorly and terminating in a long slender apical tooth; 2 short blunt subapical teeth on the medial border. Genus: *Trapeziopelta.*

GROUP V

Without a blade.

a. **Leptogenyiform.** Elongate subconical, with the apex rounded; a small subapical denticle which projects posteriorly; no teeth. Genus: *Leptogenys.*

APPENDIX C. GENERALIZED TUBERCLE SHAPES[6]

(Fig. 19)

I. SUBCONE

Subconical, varying from very slender (spirelike or digitiform) to stout; with or without a few lateral hairs; apex with 1–3 sensilla or hairs. Occurrence: *Belonopelta, Bothroponera, Euponera, Neoponera, Odontoponera, Ponera, Thaumatomyrmex, Trapeziopelta* (and possilby *Cryptopone*).

II. SPINE

Spinelike, very slender; base expanded; with or without 2 long, fine, flexuous basal hairs. Occurrence: *Centromyrmex, Psalidomyrmex.*

III. CONOID

Conoidal (=mammiform); 4–10 long, simple, slightly curved basal or lateral hairs. Occurrence: *Dinoponera, Leptogenys, Pachycondyla.*

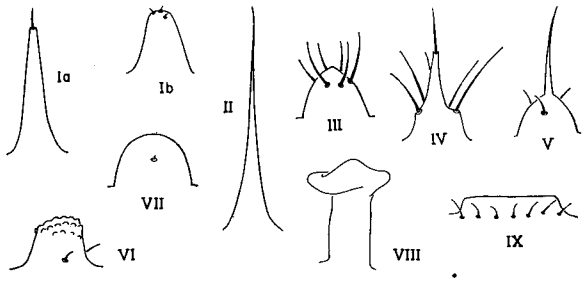

FIG. 19.—Generalized tubercle shapes. I, subcone (a, spirelike; b, stout); II, spine; III, conoid; IV, frustrum with spire; V, conoid with spine; VI, rounded frustrum; VII, hemisphere; VIII, doorknob; IX, discoid.

IV. FRUSTUM WITH SPIRE

A frustum surmounted by a spire; frustum with 1–14 long, simple, slender, slightly curved hairs; apex with a heavy, straight, spinelike hair. Occurrence: *Anochetus, Odontomachus.*

V. CONOID WITH SPINE

A conoidal base produced into a long slender curved spine; conoid with 1–6 simple hairs. Occurrence: *Diacamma rugosum, D. scalpratum.*

VI. ROUNDED FRUSTUM

A rounded frustum; with 2 small hairs near the base; apex with numerous minute, conoidal papillae. Occurrence: *Diacamma australe.*

VII. HEMISPHERE

Hemispherical; a few sensilla or minute hairs present. Occurrence: *Proceratium.*

VIII. DOORKNOB

Mushroom shaped; cap may have 2 sensilla. Limited to the dorsal surface of certain abdominal somites, a pair on each. Occurrence: *Belonopelta, Cryptopone, Euponera* Type II [=*E.* (*Brachyponera*) *sauteri, E.* (*B.*) *solitaria, E.* (*Trachymesopus*) *gilva, E.* (*T.*) *leveillei*], *Ponera.*

IX. DISCOID

Glabrous subcircular areas which may be considerably elevated and pulleylike or thin discs or merely differentiated areas that are scarcely perceptible in profile; limited to the dorsal surface of abdominal somites IV and V, 1 or a pair on each. Occurrence: *Anochetus, Odontomachus.*

KEY TO THE GENERA OF MATURE WORKER LARVAE OF PONERINAE IN OUR COLLECTION[7]

GROUP A

Not differentiated into a neck and body; elongate and rather slender; diameter diminishing gradually from the fifth abdominal somite to the anterior end; anterior half strongly curved.

[6] We have omitted *Simopelta* from the classification, because we have only young larvae in our collection and because the tubercles vary so much that it is not possible even to guess at the shape before preservation.

[7] See footnote 5.

1. Mandibles myrmeciiform (Ib) ..... ***Myrmecia***
2. Mandibles myoponiform (Ig) ..... ***Myopopone***

GROUP B

Shaped somewhat like a crookneck squash: thorax forming a distinct neck, whose diameter is notably less than that of the abdomen and which is strongly bent or curved ventrally; first abdominal somite transitional to the remainder of the abdomen, which is stout or swollen.

1. Body without tubercles ..... a
   - a_1. Body paraponeriform (B1) ..... b
   - a_2. Body ectatommiform (B2) c
   - a_3. Body pachycondyliform (B3) ..... ***Stigmatomma***
   - b_1. Body hairs all simple; head naked; mandibles paraponeriform (Ib) ..... ***Paraponera***
   - b_2. Body hairs of 2 kinds (simple and branched); head with simple hairs; mandibles ectatommiform (Ia) ..... ***Paranomopone***
   - c_1. Body hairs lashlike, with denticulate base; mandibles ectatommiform (Ia), with uniformly short spinules ..... ***Ectatomma***
   - c_2. Body hairs of more than 1 type, some branched; mandibles ectatommiform (Ia), some spinules long ..... ***Gnamptogenys***
   - c_3. Mandibles rhytidoponeriform (Ii) .. ***Rhytidoponera***
   - c_4. Mandibles amblyoponiform (IIIc) .... ***Amblyopone***
2. Body beset with tubercles ..... d
   - d_1. Tubercles of 1 shape ..... e
   - d_2. Tubercles of 2 shapes: frustiform with spire (IV) and discoidal (IX) ..... f
   - e_1. Tubercles subconical (I) ..... g
   - e_2. Tubercles mammiform (III) ..... h
   - e_3. Tubercles spine-like (II) i
   - e_4. Tubercles conoidal with spine (V) ..... ***Diacamma scalpratum, D. rugosum***
   - e_5. Tubercles rounded frusta (VI) ..... ***Diacamma australe***
   - f_1. Mandibles ectatommiform (Ia) ..... ***Anochetus (Anochetus)***
   - f_2. Mandibles stenomyrmeciform (IIc) ..... ***Anochetus (Stenomyrmex)***
   - f_3. Mandibles odontoponeriform (Ic) .. ***Odontomachus***
   - g_1. Mandibles odontoponeriform (Ic) .. ***Odontoponera***
   - g_2. Mandibles trapeziopeltiform (IVc) .. ***Trapeziopelta***
   - g_3. Mandibles ectatommiform (Ia) ..... j
   - h_1. Mandibles ectatommiform (Ia) ..... ***Pachycondyla***
   - h_2. Mandibles dinoponeriform (IVb) ..... ***Dinoponera***
   - h_3. Mandibles leptogenyiform (Va) ..... ***Leptogenys***
   - i_1. Mandibles psalidomyrmeciform (Ie) ..... ***Psalidomyrmex***
   - i_2. Mandibles centromyrmeciform (Ih) ..... ***Centromyrmex***
   - j_1. Tubercles with lateral hairs ..... ***Neoponera***
   - j_2. Tubercles lacking lateral hairs ... ***Euponera*** Type I

GROUP C

Thorax curved or bent ventrally but not forming a distinct neck; abdomen only moderately swollen.

1. Body poneriform (C1); with 2 types of tubercles: subconical (I) and doorknob (VIII) ..... a
   - a_1. Subconical tubercles with a conspicuous spinelike apical hair ..... b
   - a_2. Subconical tubercles without a spinelike apical hair ..... ***Euponera*** Type II
   - b_1. Head with hairs ..... ***Ponera***
   - b_2. Head without hairs ..... ***Belonopelta***
2. Body onychomyrmeciform (C2); without tubercles .. c
   - c_1. Mandibles onychomyrmeciform (IVa) ..... ***Onychomyrmex***
   - c_2. Mandibles typhlomyrmeciform (Id) ..... ***Typhlomyrmex***

GROUP D

Both ends directed ventrally; remainder of body straight and with a roughened ventral profile; thorax forming a distinct neck; terminal somite of abdomen stout and taillike.

1. Body platythyreiform (D1); dorsal and lateral surfaces without welts or tubercles; mandibles platythyreiform (IId) ..... ***Platythyrea***
2. Body proceratiiform (D2); tubercles hemispherical (VII); mandibles proceratiiform (IIIa) ..... ***Proceratium***

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