The Ant Larvae of the Subfamily Ponerinae—Part II

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Reprinted from
THE AMERICAN MIDLAND NATURALIST
Vol. 48, No. 3, pp. 604-672, November, 1952

University of Notre Dame Press
Notre Dame, Indiana

The Ant Larvae of the Subfamily Ponerinae — Part II[1]

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Tribe PONERINI Forel

Genus CENTROMYRMEX Mayr

Neck short and stout. Nine differentiated somites. Body beset with a very large number (about 400) of spine-like tubercles,[2] which are so slender as to simulate body hairs; surface of tubercles beset with several fine denticles; base occasionally bearing two long extremely fine hairs. Body hairs restricted to ventral surface. Antennae large. Ventral notch of labrum wide, deep and sclerotized. Posterior surface of labrum with about 20 sensilla. Mandibles straight; basal half of medial and posterior surfaces roughened with scales (?); on the posterior surface these are arranged in transverse rows; on the medial surface they are imbricated and each scale is produced ventrally into a spinule.

Centromyrmex feae Emery.—Plate I, figs. 1-10. Shaped somewhat like a crook-neck squash; thorax and first abdominal somite forming a short stout curved neck; remainder of abdomen stout and subovoidal. Diameter greatest at the sixth abdominal somite; diminishing gradually toward the anterior end. Posterior end rounded. Anus ventral. Nine differentiated somites. Body furnished with numerous (about 370) spine-like tubercles, some of which are mounted on low elevations; tubercles uniformly distributed, slender, acuminate; typically with several fine denticles projecting obliquely from the sides; bases slightly swollen; some tubercles are bifurcate; length of tubercles 0.035-0.23 mm; the smallest tubercles lack denticles and have the basal half swollen and the apical half greatly attenuated; the largest tubercles have each two long (0.09 mm) flexuous and extremely fine hairs arising near the base. No tuber-

1 Part I appeared in Vol. 48 of this journal, pages 111-144. 1952.

2 We have had some doubts about the appropriateness of the term tubercle. Webster's *Collegiate Dictionary* defines it as "a small knoblike prominence or excrescence, esp. on an animal or plant; a nodule . . . *Med.* A small rounded morbid growth in an organ or in the skin." Thus there is a definite connotation of roundness with which few ponerine tubercles could qualify. 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 knob-like (i.e., rounded). So apparently entomological usage takes care of all types of ponerine protuberances, although it must be stretched somewhat to include the spine-like structures of Centromyrmex. But, in any event, myrmecological usage definitely sanctions the term. Müller (1886) used *Tuberkeln* in German when referring to the rounded protuberances of mature Pachycondyla larvae; the subconical structures on the young were called merely *Erhebungen.* Emery in 1899 used *sporgenze segmentali o tubercoli del tegumento* in Italian when referring to both the rounded and the pointed projections of several genera. In the *Genera Insectorum* (1911) Emery used the French *tubercules.* Wheeler first used *tubercles* in 1900 in "A Study of Some Texan Ponerinae" (his second paper on ants) and he was still using it in 1922.

cles on the midventral surface. Body hairs very few; limited to the ventral surface; 4-6 per somite; simple, flexuous, short (0.06-0.16 mm). Integument spinulose on the ventral surface; spinules exceedingly minute and arranged in short transverse rows. Cranium subhexagonal, broader than long, the dorsal corners rounded; occipital border slightly concave. Head hairs few, rather short (0.07-0.12 mm), simple, slightly curved. Antennae large low rounded convexities, bearing three sensilla each. Labrum broader than long (1¾X); narrowed at base; lateral borders sinuate; strongly bilobed due to a wide and deep median notch in the ventral border; surface of notch heavily sclerotized; the anterior surface of each lobe with a low rounded eminence bearing several large sensilla and a few minute hairs. Posterior surface of labrum densely beset with minute spinules; on the middle half the spinules are arranged in long transverse rows; on the lateral quarters the rows are short, arcuate and oblique; with about 20 sensilla arranged in two irregular rows. Mandibles moderately stout and heavily sclerotized; straight; subtriangular in anterior view; base only slightly dilated; apical tooth short, moderately stout, round-pointed, slightly curved medially and posteriorly; two short rather stout blunt teeth on the inner border; inner and posterior surfaces of basal half roughened with scales (?); on the posterior surface these are arranged in transverse rows; on the inner surface they are imbricated and each scale is produced ventrally into a spinule; anterior surface with longitudinal striae. Maxillae conoidal; spinulose, with the spinules minute and mostly in short arcuate rows, but a few on the anterior surface coarser and isolated; palp a subcylindrical peg with four sensilla on its flattened end—one finger-like, one discoidal and two bearing a spinule each; galea twice as long as palp, finger-like, bearing two apical sensilla. Labium subhemispherical; spinulose, the spinules minute and arranged in long transverse rows on the anterior surface, but elsewhere in short arcuate rows; on the anterior surface near its base there is a conspicuous transverse welt, which is semicircular in profile and whose spinules are in long transverse rows; palp a subcylindrical peg with four sensilla on its flattened end—one finger-like, two paxilliform and one bearing a spinule; opening of sericteries wide and salient. Hypopharynx densely spinulose, the spinules long, fine and arranged in transverse rows. (Material studied: numerous larvae from Java and Indochina.)

Wheeler, 1936, p. 207: "slender, tuberculate larvae."

Centromyrmex sp. (in Bolivia).—Mann, 1934, p. 189: "In the chambers of the ants' home I noticed on the top of each larva the body of a decapitated termite. Near by were little piles of dead termites to provide a second helping."

Genus ODONTOPONERA Mayr

Integument of body with fine ridges forming a reticulate pattern, the ridges bearing at irregular intervals minute spinules. Tubercles moderately numerous (about 100); subconical; of two types—(1) short, stout and blunt, and (2) long and slender with an expanded base and having at or near the tip 0-3 minute acute projections and/or spinule-bearing sensilla; integument of tubercles with numerous encircling rows of minute spinules; no hairs. Body hairs very few and exceedingly minute. Posterior surface of labrum with

eight or nine sensilla on each half. Mandibles elongate and narrow; not curved posteriorly and only slightly curved medially; base not dilated; basal half of posterior surface with short arcuate ridges arranged in transverse rows; each ridge usually bearing one or two spinules, which are pointed ventrally. Maxillary spinules rather long and slender; galea twice as long as palp.

Odontoponera transversa (F. Smith).—Plate I, figs. 11-19. Thorax and first abdominal somite forming a short slender neck which is bent ventrally; neck usually straight; remainder of abdomen voluminous and subelliptical in profile; posterior end rounded, produced ventrally into a post-anal boss. Anus ventral. A peculiar ventrolateral integumentary structure on either side of abdominal somites II-VIII. Eleven differentiated somites. Leg vestiges present. Body furnished with approximately 100 subconical tubercles which are 0.05-0.25 mm long and arranged in irregular rows, one row around the middle of each somite; no tubercles on the ventral surface; shorter tubercles stout and blunt; the longer are quite slender, with an expanded base and have at or near the apex 0-3 minute acute projections and/or spinule-bearing sensilla; integument of tubercles with numerous encircling rows of minute spinules. Body hairs very few and exceedingly minute (about 0.009 mm); widely scattered, mostly on ventral surface. Integument of body with fine ridges forming a reticulate pattern, the ridges bearing at irregular intervals minute spinules. Cranium as long as broad; slightly narrowed ventrally; subtrapezoidal in anterior view but with the occipital angles rounded; integument (except on front and clypeus) beset with exceedingly minute spinules which are uniformly distributed, arranged irregularly and either isolated or in groups of two to four. Head hairs few, short (0.045-0.72 mm), stout; tapering gradually throughout most of their length, then rapidly to the point; the tip may be slightly hooked; constricted near the base. Antennae moderately large, each bearing three sensilla. Labrum twice as broad as long; lateral borders sinuate; bilobed due to a deep median incision in the ventral border; near the ventral border of each lobe there is a low convex prominence on the anterior surface, which bears several sensilla and a few minte hairs; middle half of posterior surface densely spinulose, the spinules minute and mostly arranged in long transverse rows; lateral quarters with a few short scattered arcuate rows of minute spinules; ventral border spinulose; posterior surface with eight or nine sensilla scattered irregularly on each lobe. Mandibles elongate and narrow; nearly straight; heavily sclerotized; base not dilated; not arcuate posteriorly; apical tooth long, slender and curved medially; with two rather stout blunt-pointed subapical teeth on the inner border; posterior surface of basal half with short arcuate ridges arranged in transverse rows; each ridge usually bears one or two spinules which point ventrally. Maxillae with the apex paraboloidal and spinulose, the spinules rather long and slender and arranged in short transverse arcuate rows; palp a subcylindrical peg with several sensilla on its rounded distal end; galea finger-like, with two apical sensilla. Labium prominent; anterior surface densely spinulose, the spinules near the center fine and grouped in short transverse rows, the others coarser and isolated; on the anterior surface near its base there is a conspicuous transverse welt, which is semicircular in profile and whose spinules are arranged in numerous short transverse rows; posterior surface less densely spinulose; palp a subcylindrical peg with several

sensilla on its flat apical end; opening of sericteries wide and salient. Hypopharynx densely spinulose, the spinules slender and in transverse rows. (Material studied: a dozen larvae from the Philippine Islands.)

In younger larvae the neck is longer and more slender and the tubercles are more conspicuous.

Genus DINOPONERA Roger

Neck short and stout. Leg vestiges conspicuous and tuberculate. Body beset with numerous (160) mammiform tubercles; each with 6-25 short flexuous hairs arranged in an irregular circle near the base; often a second circle nearer the apex. Body hairs very few and exceedingly minute. Integumentary spinules on the tubercles arranged in short arcuate rows which form a reticulate pattern. Head small. Cranium transversely subelliptical in anterior view; a third broader than long; a shallow median longitudinal furrow from the occiput to the level of the antennae. Mandibles strongly arcuate posteriorly but only slightly curved medially, with two apical teeth; only one tooth on the medial border. Maxillae densely furnished with long coarse spinules; palps are subcylindrical pegs, with the end flattened and bearing two sensilla each; galea only a little longer than palp.

Dinoponera grandis mutica Emery.—Plate II, figs. 1-8. Shaped somewhat like a crook-neck squash; thorax and first abdominal somite forming a short stout strongly curved neck; remainder of abdomen voluminous and nearly straight, its dorsal profile somewhat curved, ventral serrate and nearly straight; ventral surface somewhat flattened. Thoracic somites separated dorsally by deep intersomitic furrows. Posterior end rounded. Anus ventral. Leg vestiges conspicuous and tuberculate. Thirteen differentiated somites. Body thickly beset with approximately 160 mammiform tubercles distributed (on each half) as follows: prothorax (anterior third)—one small dorsal and two small lateral; prothorax (posterior two-thirds)—a medium-sized double dorsal, a medium-sized double lateral and a very small ventrolateral; mesothorax—a large double dorsal, a large lateral and a very small ventrolateral; metathorax—a large double dorsal, a medium-sized lateral and a small ventrolateral; abdominal somite I—a large double dorsal, a double lateral (upper large, lower small) and a small ventrolateral; II—two large dorsal, two lateral and a small ventrolateral; abdominal somites III-VIII have each a vestigial dorsolateral, three large lateral and a small ventrolateral; IX—three small lateral and one small ventrolateral; X—one large ventrolateral; no tubercles on entire midventral surface or on middorsal surface of abdomen. Hairs on tubercles short (0.03-0.37 mm), simple flexuous; 6-25 on each tubercle; arranged in an irregular circle near the base of each tubercle; often a second circle nearer the apex. Body hairs very few and exceedingly minute (about 0.009 mm). Integument mostly spinulose; spinules exceedingly minute; usually arranged in rows; on the tubercles the rows are short and arcuate and form a reticulate pattern. Head small; cranium transversely subelliptical in anterior view; a third broader than long; occipital border broadly rounded and feebly notched at the middle; a median longitudinal furrow extending from this notch to the level of the antennae. Antennae a pair of low conoidal elevations, each bear-

ing three or four sensilla. No hairs on head. Labrum short and broad; breadth twice the length; narrowed at the base; lateral borders convex; ventral border with a shallow depression; anterior surface with two ventrolateral clusters of sensilla and minute hairs (each cluster on a low rounded convexity) and coarse isolated spinules near the ventral and lateral borders. Middle half of posterior surface densely spinulose, the spinules minute but relatively long and slender and arranged in long transverse rows; lateral to the above area the spinules are very sparse, much shorter and grouped in short arcuate rows; near the lateral borders the spinules are isolated, coarse and larger; lateral and ventral borders with coarse isolated spinules; posterior surface with three sensilla on each end of the depression in the ventral border. Mandibles moderately stout; heavily sclerotized; strongly arcuate posteriorly; with two apical teeth which are round-pointed and slightly curved medially; the single tooth on the inner border is acute and rather short. Maxillae large and lobose; apex densely beset with long coarse spinules; palp a slender subcylinder, with two sensilla on the flat apex; galea finger shaped, scarcely longer than the palp and bearing on its apex one or two sensilla. Labium with its anterior surface densely beset with isolated coarse spinules; palp cylindrical, with two sensilla on its flat apex; opening of sericteries broad. Hypopharynx densely beset with fine spinules in transverse rows. (Material studied: the damaged integument of a single larva about 20 mm long, from Brazil, and a photograph.)

Mann, 1916: "A larva probably immature, in alcohol measures 13 mm. in length. The body is thick and the neck short. All the segments are distinct, with fine, short hairs. The head is glabrous, from above a little broader than long; the mandibles are long and acuminate. The thorax and abdomen are tuberculate, the tubercles very large and prominent, rounded above, each bearing a small sensory papilla at the middle. Each segment has three of these large tubercles laterally, and a smaller, less conspicuous one basally" (p. 409). Plate 7, fig. 55, an "immature (?) larva" in side view.

Genus DIACAMMA Mayr

Neck long and slender. Body beset with tubercles. Integumentary spinules abundant and conspicuous. Cranium subcircular in anterior view; its integument granular. Labrum short and broad; breadth more than twice the length. Mandibles falciform; distal third long, slender and directed medially; with or without a small tooth on its medial surface; the surface of the stout base is roughened with short arcuate transverse spinulose ridges. Maxillae densely furnished with long coarse spinules; integument of base granular; integument of galea rugose. Anterior surface of labium densely beset with long slender sharp spinules; posterior surface granular.

Wheeler, 1910: "The larvae . . . have prominent, pointed, or rounded tubercles which probably have a protective function" (p. 74). "Larvae furnished with rows of tubercles" (p. 233). On page 234 he mentions a possible function of such tubercles—defending the larvae from one another.

Diacamma australe (Fabricius).—Plate II, figs. 9-18. Shaped somewhat like a crook-neck squash; thorax and first abdominal somite forming a long slender neck, which is strongly bent ventrally; remainder of abdomen stout, straight and elongate-ellipsoid. Posterior end rounded. Anus ventral. Leg vestiges and vestigial gonopods conspicuous. Thirteen differentiated somites. Spiracles small. Body sparsely beset with approximately 72 tubercles, distributed (on each half) as follows: prothorax—a lateral, ventrolateral and a ventral; mesothorax and metathorax—each with a lateral and a ventrolateral; abdomen I—a small lateral; II—two lateral; III-VII—each with two lateral and one ventrolateral; VIII—a dorsolateral, three lateral and a ventrolateral; IX—a dorsal, a dorsolateral, two lateral and a ventrolateral; X— a terminal. Tubercles paraboloidal; each crowned with a number of minute conoidal papillae, girdled near its middle with a zone of reticulate markings and bearing near its base two small hairs (about 0.06 mm long). No tubercles on ventral surface and only one pair on the dorsal. Near each abdominal spiracle and each ventral tubercle there is a peculiar integumental structure of unknown function. Body hairs very few, limited to ventral surface; simple, slightly curved or flexuous; those on the ventral surface of two sizes—0.06 mm and 0.2 mm. Integument densely spinulose; spinules about 0.013 mm long and arranged in short rows of 2-4; rows transverse, except near the tubercles where they are arranged in concentric circles. Cranium subcircular in anterior view; integument granular with minute (0.005 mm) isolated paraboloidal and conoidal tubercles, except on the gula, where it is thickly beset with larger elliptical elevations. Hairs of head few, simple, short, slightly curved, uniformly scattered; constricted at the base; apex acuminate; length about 0.14 mm (except clypeal 0.06 mm). Antennae with three sensilla each. Labrum short and very broad (breadth $2^1/_3$X the length); ventral border concave, finely spinulose and furnished with numerous sensilla; ventral corners rounded; lateral borders sinuate; anterior surface with a few spinules in short arcuate rows near the ventral border; in each ventrolateral area of the anterior surface a low convexity bearing a few minute hairs and several sensilla. Posterior surface of labrum spinulose, the spinules of the middle $^2/_3$ minute and arranged in transverse rows; lateral sixths with coarser isolated spinules; very few scattered sensilla. Mandibles falciform; base broad and stout; distal third long, slender and directed medially, bearing a small sharp tooth on its medial surface and terminating as a long, slender apical tooth; the stout base has its surfaces roughened with short transverse arcuate spinulose ridges. Maxillae paraboloidal; densely spinulose, the spinules long, slender and sharp-pointed; integument of base granular like that of the cranium; palp a slender subcylindrical peg with four sensilla on the apex; galea a longer, rugose, finger-like projection with two sensilla on the tip. Labium subhemispherical; integument of posterior surface granular like that of the cranium; anterior surface densely spinulose, the spinules long, slender and sharp-pointed; palp a rather slender subcylindrical peg, with four apical sensilla, one of which is paraboloidal; opening of sericteries wide and salient, with three conspicuous projections. Hypopharynx densely beset with fine spinules in transverse rows. (Material studied: five larvae from Queensland.)

Diacamma scalpratum (F. Smith).—Plate II, figs. 19 and 20. In general, similar to *australe,* but differing in the following particulars: Tubercles twice as numerous (160) and arranged in regular rows, one row around the middle of each somite; no tubercles on midventral surface. Tubercles stout and conoidal, bearing 2-6 simple hairs about 0.1 mm long and (on the apex) a long slender smooth slightly curved spine; base densely spinulose, the spinules minute and arranged in regular encircling rows; length of tubercle (including spine) 0.23-0.45 mm, the largest on the thorax. Body hairs moderately numerous and uniformly distributed; short (length about 0.15 mm); apex acuminate. Integumental spinules much smaller. Integument of cranium roughened with minute papillae, which are isolated or in short rows of three or more; lateral to antennae papillae replaced by spinules; integument of gula like that of frons. Head hairs moderately numerous; rather stout and blunt-pointed; only two on clypeus; length about 0.22 mm. Lateral sixths of posterior labral surface with fine spinules in short arcuate rows. Mandibles longer and less curved medially. Palps and galea longer. (Material studied: four larval integuments from India.)

Diacamma rugosum viridipurpureum Emery.—Plate II, figs. 21-24. Fundamentally similar to *scalpratum* but differing in the following characters: Tubercles about half as long; length (including spine) 0.15-0.23 mm; apical half of spine roughened with minute denticles, basal half smooth; hairs 1-3, which are about 0.08 mm long. Body hairs very few, widely scattered, short (0.1-0.16 mm), blunt-pointed, with the tip fuzzy. Integumental spinules in short rows which form a reticulate pattern. Integument of cranium as in *australe,* except that of gula, which has minute spinules in short transverse rows. Head hairs acuminate apically. Mandibles without a medial tooth. Spinules on labium fewer and coarser. (Material studied: two larval integuments from the Philippine Islands.)

The young larva (4 mm long) appears to have more tubercles than the adult, but this is due to the relatively larger size of the tubercles (0.1-0.2 mm long); actually the number is approximately the same. The tubercles have the shape of a tall cone; the spine of the mature tubercle of the next-instar integument appears to form the axis of the cone. Each tubercle bears two hairs but no spinules. Body hairs rather stout and about 0.1 mm long; straight or slightly curved or kinked; apex branched or sometimes fuzzy. Integumental spinules about 50% longer than in the mature larva. The labium has a curious median projection from its anteroventral surface; this process is finger-like and long (0.27 mm) and slender (basal diameter 0.07 mm); the distal third is bent forward at a small but distinct angle (artifact?); surface uniformly spinulose, the spinules minute, long and slender. On either side of this median process (but on a more posterior level) there is a prominent hemispherical boss; its surface is glabrous except for a few basal spinules. Is the median process associated with the sericteries, as Emery (1899, p. 5) maintained? We do not know the answer; but we can detect no apical opening; furthermore the silk duct of the next-instar larva is conspicuous and its opening is between the bosses at some distance posterior to base of the process

and has no apparent connection with the latter. (Material studied: a single specimen from the Philippine Islands; the integument of this young larva contains the integument of the next-instar larva.)

Diacamma rugosum vagans (F. Smith).—Generally similar to *r. viridipurpureum,* but differing in these respects: the tubercles are about half as long (0.075-0.15 mm); body and head hairs are shorter; integument granular, but many of the granules bear a spinule. (Material studied: two integuments from the Philippine Islands.)

Diacamma rugosum geometricum (F. Smith).—Banks, 1904: "White grubs, which are shaped very much like a long-necked gourd, the head being at the smaller end" (p. 9). Fig. 1c, larva in side view.

Emery, 1899: "Nella forma generale del corpo, le larve . . . rassomigliano piuttosto a quelle della *Ponera stigma:* la parte addominale è poco rigonfiata, e i limiti dei segmenti sono distinti. Sopra ciascuno di essi si trova una serie trasversale, irregolare di tubercoli conici, ineguali che, nelle larve più sviluppate, portano da uno a quattro peli. Nelle piccole larve, i tubercoli sono piccoli, subcilindrici e senza peli; negli stadi intermedi passano per una forma acuminata con pochi peli. Nelle larve giovani di questa specie, il labbro inferiore offre, in avanti, una vistosa sporgenza conica, alquanto curvata in su e relativamente maggiore nelle più piccole larve. Questa sporgenza corrisponde alla papilla mediana o filiera, del margine labiale. Nelle larve maggiori, essa è molto ridotta e poco appariscente. Le mandibole sono foggiate diversamente da quelle della *Ponera* e *Odontomachus,* ed hanno forma arcuata con punta acutissima" (p. 5). (Quoted in part by Wheeler, 1900a, p. 19.) Pl. I, fig. 3: *a,* a large larva, apparently immature; *b,* head of younger larva in side view; *c,* same in anterior view; *d,* head of very young larva in side view; *e,* end of abdomen of same; *f,* tubercles of this larva greatly magnified; *g,* tubercles of medium-sized larva. (Emery's figure *b* is reproduced by Berlese, 1925, Fig. 825C on p. 846; figures *b* and *c* by Escherich, 1906, Fig. 31 = 1917, Fig. 37A.)

Wheeler, 1900a, p. 15 (referring to Emery, 1889): "Mandibles powerfully developed for ant-larvae, the anterior portion of the body long and slender and folded over the abdominal portion, and . . . covered with rows of peculiar tubercles beset with more or less prominent hairs."

Genus MEGAPONERA Mayr

Elongate and very slender; subcylindrical; slightly curved ventrally; no distinct neck. No tubercles or bosses. Body practicaly naked; with only a very few widely scattered and exceedingly minute hairs. Cranium subtrapézoidal in anterior view; broader than long. Antennae small. No hairs on head. Labrum very short and broad; breadth 3X length; ventral border convex. Mandibles long and falciform; base dilated; apical half very slender, sharp-pointed and strongly curved medially; no medial teeth; inner surface of base with few minute spinules irregularly arranged. Apex of maxillae densely furnished with long slender flexuous spinules. Hypopharynx cordate; finely spinulose ridges forming a reticulate pattern.

Megaponera foetens (Fabricius).—Plate I, figs. 20-25. Elongate and very slender; subcylindrical; slightly curved ventrally; no distinct neck; diameter greatest at the seventh abdominal somite, decreasing gradually to the anterior end and more abruptly to the posterior end, which is rounded. Anus ventral. Vestigial legs and gonopods present. Thirteen differentiated somites. Body practically naked; a very few exceedingly minute (0.009 mm long), widely scattered hairs. Integument densely beset with exceedingly minute spinules arranged in transverse rows. Integumental structures of unknown nature and function are located on the ventrolateral surfaces of each somite; on the abdomen such structures are also found in the dorsolateral regions and in the intersegmental furrows. Cranium subtrapezoidal, broader than long; occipital corners broadly rounded. No head hairs. Antennae small, with three sensilla each. Labrum very short; breadth 3X length; lateral borders sinuate; ventral border convex, beset with a few sensilla and numerous fine spinules; on the anterior surface near each ventrolateral corner there is a low convexity which bears several sensilla; middle half of anterior surface spinulose, the spinules minute and arranged in transverse rows, a few sensilla and minute hairs scattered among these spinules; median half of posterior surface thickly beset with long parallel transverse ridges, each bearing a row of exceedingly minute spinules, the lateral quarters with short transverse rows of much longer spinules; a few scattered sensilla on the lateral quarters of the posterior surface. Mandibles long and falciform; base dilated; apical half very slender, sharp-pointed, strongly curved medially; inner surface of base with a few minute spinules irregularly arranged. Maxillae with the apex paraboloidal and densely spinulose, the spinules extremely long, slender and flexuous, those on the apex twice as long as those on the sides; palp a rather stout subcylindrical peg, with five sensilla on the blunt-pointed apex; galea finger-like, with two apical sensilla. Labium with the anterior surface densely spinulose, the spinules mostly coarse and isolated, but near the center smaller and grouped in short transverse rows; palp a subcylindrical peg, with four or five apical sensilla; opening of sericteries wide and salient. Hypopharynx cordate; with finely spinulose ridges forming a reticulate pattern. (Material studied: a dozen larval integuments from the Belgian Congo.)

Wheeler, 1918: "The larva is cylindrical, covered with a very tough, opaque, grayish, hairless skin and furnished with long, falcate mandibles" (p. 299). Fig. 3*A*, nearly adult larva in side view; *B*, head in anterior view (p. 300).

Wheeler and Bailey, 1920: "The transverse ridges [of the trophorhinium] are still represented by a reticulate areolation like that of the general integument, except that the meshes are drawn out transversely" (p. 269). Pl. III, fig. 18, a photomicrograph of some of the mouth parts.

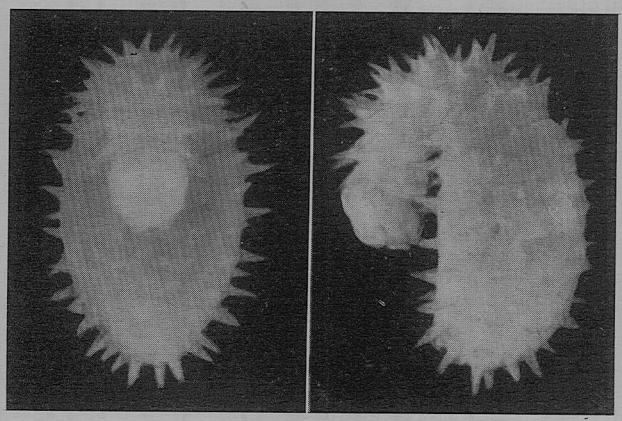
Wheeler, 1922: "The larvae are grayish white, long and subcylindrical, and only slightly curved, with strongly marked segments and with smooth, remarkably tough integument, which is quite hairless in all stages, a condition which I have never observed in any other ant larva. The head is very large, rounded, strongly chitinized, and terminal, with long, acute, falcate, edentate

mandibles, minute vestiges of antennae, and very prominent tactile sensillae on the maxillae and labium. The size of the head and mandibles shows that the larvae are fed on pieces of termites and not with regurgitated liquid food, and the strong integument is evidently an adaptation to exposure to the air and light and to the exigencies of frequent and protracted transportation in the powerful denticulate jaws of the workers. The nudity of the integument indicates that even the very young larvae are carried singly and not in bunches held together by interlocking hairs as in most other species of ants" (pp. 68-69). Fig. 8 on p. 68 = Wheeler, 1918, Fig. 3. On page 56 Wheeler states that the larvae of Megaponera are hairless.

Genus NEOPONERA Emery

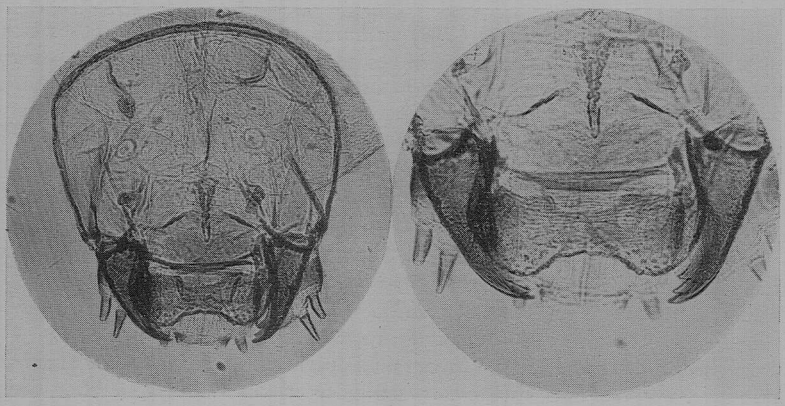
Neck stout and moderately long. Tubercles numerous (140); elongate, slender, subconical; with a few short hairs on the sides; integument roughened with minute spinules in transverse rows; a few apical or subapical sensilla and/or minute hairs. Body hairs minute. Dorsal to each antenna near the occipital border there is a prominent boss bearing a few sensilla and a minute hair. Anterior surface of clypeus roughened with sensilla and minute bosses; rest of cranium spinulose (or partly so). Antennae with a basal disc. Labrum with transverse ridges on the ventral border of the notch; lateral borders of labrum with appressed scales, some of which are produced into spinules. Mandibles narrow and somewhat elongate; some of basal half roughened with minute spinules, which are isolated or in short arcuate rows. Maxillae densely spinulose, the spinules coarse, stiff and sharp-pointed; palp and galea arising close together on a low lateral lobe; galea scarcely longer than palp. Labium densely spinulose, the apical spinules long, coarse, stiff and sharp-pointed.

Neoponera obscuricornis latreillei Forel.—Plate III, figs. 15-17 and 19.



Text fig. 1. *Neoponera obscuricornis* Emery.—Left, young larva, ×14; right, side view of same, ×14. (Photographs by E. L. Krause.)

Shaped somewhat like a crook-neck squash; thorax and first two abdominal somites forming a stout moderately long neck, which is strongly bent ventrally; remainder of abdomen moderately stout, nearly straight, subcylindrical; ventral surface flattened and posterior end somewhat flattened, so that their profiles meet at right angles. Anus ventral and surrounded by tubercles. Leg vestiges present. Thirteen differentiated somites. Spiracles mounted on small papillae. Body thickly and conspicuously beset with approximately 140 elongate, slender subconical tubercles which are 0.2-0.5 mm long (longest on the sides) arranged in 12 longitudinal rows and apportioned thus: thoracic somites, 10 each; abdominal somites I-VIII, 12 each; IX, 10; X, 6. The most dorsal tubercle on each side of abdominal somites IV-VI is reduced to a vestige; no tubercles on middorsal and midventral surfaces of abdomen and none on midventral of thorax; integument of tubercles roughened with minute (but relatively stout) spinules arranged in short transverse rows; each tubercle bearing several lateral hairs, which vary in number, size (0.002-0.036 mm) and location; a few apical or subapical sensilla and/or minute hairs. Body hairs exceedingly few, widely scattered, minute (0.015 mm long), straight and slender. Integument spinulose, the spinules minute, stout and in short rows. Cranium subhexagonal in anterior view; somewhat broader than long; dorsal to each antenna near the occipital border there is a prominent boss bearing a few sensilla and a single hair; integument of front and most of clypeus roughened with numerous minute bosses; remainder of cranium bearing minute spinules which are isolated or in short rows. Hairs of head few, minute (0.02-0.036 mm long), scattered, simple, slightly curved. Antennae a pair of low rounded eminences, each bearing three sensilla and mounted on a disc. Labrum short; breadth twice the length; strongly bilobed due to a wide median incision of the ventral border; anterior surface with a low boss (bearing several sensilla and a few minute hairs) on each ventrolateral area; ventral border of notch with transverse ridges; lateral borders of labrum with appressed scales, some of which are produced into spinules. Posterior surface of labrum: middle 2/3 spinulose, the spinules minute and arranged in numerous parallel transverse rows; lateral sixths with spinules coarse and isolated or in short arcuate rows; five or six sensilla in an irregular row extending obliquely upward from each side of the notch. Mandibles narrow and somewhat elongate; heavily sclerotized; apical tooth curved medially and posteriorly, slender in anterior view, its medial surface concave; two subapical teeth on the medial border; basal half partly spinulose, the spinules minute and isolated or in short arcuate rows. Maxillae with the apex paraboloidal and densely spinulose; spinules moderately long, coarse, stiff, sharp-pointed, in arcuate rows; palp and galea arising close together on a low lateral lobe; palp subcylindrical, slightly curved, the apex rounded and bearing four sensilla (one large and button-like); galea scarcely longer than palp, slender, subconical, bearing two apical sensilla. Labium with the anterior surface densely spinulose; apically the spinules are long, coarse, stiff, sharp and isolated; basally they are minute and arranged in short transverse rows; on the anterior surface near its base there is a conspicuous transverse welt, which is semicircular in profile and whose spinules are



Text fig. 2. *Neoponera obscuricornis latreillei* Forel.—Left, photomicrograph of integument of head in anterior view, ×42; right, photomicrograph of integument of mouth parts, ×70.

arranged in transverse rows; palp a frustum bearing five apical sensilla (one of which is button-like); opening of sericteries wide and salient, with three projections. Hypopharynx densely spinulose, the spinules fine and arranged in long parallel transverse rows. (Material studied: 21 larval integuments from Brazil, British Guiana and Panama Canal Zone.)

Neoponera apicalis (Latreille).—Plate III, fig. 13. Similar to *latreillei*, except in the following characters: Tubercles with several (typically four) longer (0.05 mm) lateral hairs; apex flat and bearing a sensillum or a minute hair; two small tubercles on abdominal somite III and two vestigial each on IV-VII. Cranium with a broad low rounded longitudinal ridge extending from the middle of the occipital border to the level of the antennae; vertex, genae and gula spinulose, the spinules minute and isolated or in short rows, but variable as to size and arrangement. Maxillary spinules on anterior surface mostly isolated, those on the posterior surface in short transverse arcuate rows. (Material studied: 12 larval integuments from Colombia and Costa Rica.)

Neoponera villosa (Fabricius).—Plate III, figs. 11, 12, 14 and 18. Similar to *latreillei*, except in the following characters: Tubercles shorter (0.11-0.38 mm); those on the thorax predominantly long, with the basal half cylindrical and the apical half conical; those on the abdomen predominantly short and conical; terminating in a short acute apical spine. Body hairs longer (0.027-0.072 mm). Integument of occiput spinulose, the spinules minute, those near the middle in short transverse rows, the lateral isolated. Bosses on anterior surface of labrum less prominent, with fewer sensilla. Maxillary spinules on the anterior surface in short transverse arcuate rows, those on the posterior surface isolated. (Material studied: four larval integuments from British Guiana.)

Neoponera villosa inversa (F. Smith).—Emery (1904) and Wheeler (1928a and 1928b, p. 205) discuss mermithergates of this ant and infer that the nematode larvae were parasitic in the ant larvae.

Genus PACHYCONDYLA F. Smith

Body beset with numerous (118) mammiform tubercles, each with a circle of 5-10 hairs around the base; no spinules on tubercles (except on prothoracic). Young larvae have the tubercles surmounted by a stout acuminate subconical spine. Body hairs minute and restricted to ventral surface. Labrum short; ventral border concave; numerous (24) sensilla on posterior surface. Mandibles elongated and rather narrow; base stout but not dilated; surface of basal ⅔ partly spinulose, the spinules minute and in short arcuate rows. Maxillary palp and galea arising close together (but not from a lateral lobe).

Wheeler, 1910: "The larvae . . . have prominent, pointed, or rounded tubercles which probably have a protective function" (p. 74). "Larvae furnished with rows of tubercles" (p. 233). On page 234 he mentions a possible function of such tubercles—defending the larvae from one another.

Wheeler, 1928b, p. 233: "In certain Ponerinae (Pachycondyla) which are primitive, wasplike ants, the larvae when fed produce a salivary secretion which is licked up by the nurses."

Pachycondyla striata F. Smith.—Plate III, figs. 1-10. Shaped somewhat like a crook-neck squash. Thorax and first abdominal somite forming a long slender neck which is strongly curved ventrally; remainder of abdomen voluminous and subellipsoidal, its ventral profile nearly straight, its dorsal profile curved, its flattened ventral surface separated from its convex dorsal surface by a rounded ventrolateral longitudinal welt. A ventral welt across the anterior portion of the prothorax. Posterior end round-pointed. Anus ventral. Leg vestiges and vestigial gonopods present. Thirteen differentiated somites. Spiracles mounted on low papillae. Body beset with numerous (approximately 118) mammiform tubercles, which are arranged in 10 longitudinal rows and apportioned thus: prothorax, 10 (one pair vestigial); meso- and metathorax, 8 each; abdominal somites I-IV, 10 each; V-VII, 10 each (the dorsal pair vestigial); VIII, 10; IX, 8; X, 4; none on midventral surface. Around the base of each tubercle is a circle of 5-10 hairs which are simple, nearly straight, constricted at the base and 0.04-0.23 mm long. Body hairs few, simple, straight, minute (0.05 mm long), limited to ventral surface. Integument of tubercles smooth, except on the prothoracic where it is spinulose. Integument of prothorax and of midventral surface elsewhere spinulose, the spinules minute and isolated or in short rows. Cranium subhexagonal in anterior view, the dorsal corners rounded; as broad as long, broadest just below the antennal level; vertex and upper half of genae spinulose, the spinules minute and isolated or in short rows. Hairs of head few, short (0.035-0.088 mm), simple, nearly straight. Antennae a pair of low convexities, circular in outline and bearing three sensilla each. Labrum short, breadth 1¾X length; bilobed due to the wide shallow concavity of the ventral border; lateral border sinuate; ventrolateral borders spinulose; the anterior surface of each lobe bears about 20 sensilla and three minute hairs. Posterior surface of labrum: middle ⅔ densely spinulose, the spinules minute and arranged in numerous short subparallel transverse rows; lateral sixths sparsely spinulose, the spinules coarser and isolated or in short rows; a dozen sensilla on each lobe.

Mandible elongate and rather narrow; base stout but not dilated; apical tooth slender, acute, curved medially and posteriorly; two (rarely three) stout subapical teeth on the medial border; basal ⅔ partly spinulose, the spinules minute and arranged in short arcuate rows; sometimes a few minute blunt denticles on the medial border proximal to the subapical teeth. Maxillae with the apex paraboloidal and densely spinulose, the spinules short (longer apically), slender, sharp-pointed and isolated on the anterior surface, in short arcuate rows on the posterior surface; palp and galea arising close together on the lateral surface; palp a subcylinder bearing four or five sensilla on its flat apex; galea finger-like and bearing two apical sensilla. Labium: middle third of the anterior surface sparsely spinulose, the spinules in short rows; lateral thirds densely spinulose, the spinules isolated; spinules sharp-pointed, mostly long; on the anterior surface near the base there is a conspicuous transverse welt, which is semicircular in profile and whose spinules are arranged in transverse rows; on the posterior surface the spinules are minute and arranged in short arcuate rows; palp a moderately stout subcylinder, with four or five sensilla on its flat opex; opening of sericteries wide and salient, with three projections. Hypopharynx densely spinulose, the spinules in numerous transverse rows. (Material studied: numerous larvae from Panama Canal Zone.)

In young larvae (2.5-6 mm long) each tubercle is surmounted by a subconical spine about 0.12 mm long. This spine has a stout base but narrows rapidly to an acuminate apex; it may be straight or slightly curved. The base of the tubercle is encircled by a row of stiff slightly curved hairs about 0.14 mm long. A 6-mm larva which is ready to moult shows a mature tubercle inside each immature tubercle; the basal hairs of the former are gathered together in a bunch and inserted into the cone of the latter.

Eidmann, 1936, p. 35: "Die Larven gleichen völlig denen von *Pachycondyla harpax* Fabr., wie sie von Wheeler (1910, p. 74) abgebildet wurden. Die jungen Larven sind bedeckt von Warzen, die mit einer kräftigen, stachelartigen Spitze gekrönt sind, deren Basis von Borsten umstellt ist. Bei den älteren Larven sind die Warzen abgeflacht und ohne den stachelartigen Fortsatz, tragen aber an ihrer Peripherie in ringförmiger Anordnung Borsten. Die Mandibeln der Larven sind in allen Stadien sehr kräftig entwickelt und zweispitzig. Sie lassen auf eine Ernährung mit festen Substanzen, wahrscheinlich erbeuteten Insekten schliessen."

Pachycondyla crassinoda (Latreille).—The tubercles number approximately 112. The tubercle hairs are curved and are mostly longer and more numerous. The head hairs are coarser and constricted at the base. Otherwise as in *striata*. (Material studied: four larvae from British Guiana.)

Myers (1931, p. 276) records the rearing of *Kapala cuprea* Cameron from cocoons of *crassinoda*. Presumably the eucharid larva was parasitoid in the ant larva.

Pachycondyla fuscoatra Roger.—Emery (1904) and Wheeler (1928a & 1928b, p. 205) discuss a mermithergate of this species and infer that the nematode larva was parasitic in the ant larva.

Pachycondyla harpax (Fabricius).—Tubercle hairs shorter; fewer sensilla

on anterior surface of labrum; no denticles on medial border of mandibles; spinules on mandibles in longer rows; maxillae with the spinules shorter and arranged in short arcuate rows on both anterior and posterior surfaces; medial spinules of labium longer and more abundant. Otherwise as in *striata*. (Material studied: two larvae from British Guiana.)

Pachycondyla harpax montezumia F. Smith.—Similar to *harpax*. (Material studied: seven larvae from Texas.)

Wheeler (1900a) described the larva of *montezumia* (but cited it merely as *harpax*) as "neither as slender as those of Leptogenys nor as robust as those of Odontomachus. The ventral surface of the abdomen is distinctly flattened. The head resembles that of Odontomachus, especially in the shape of the labrum and mouth-parts. There is a striking difference between the tubercles of the very young and the adult larva. In the former the tubercles are nearly or quite straight, and somewhat longer and more pointed than those of Leptogenys. They lack the terminal bristle. The bristles about the base are somewhat irregular in their insertion. In the adult larva the tubercles are reduced to large more or less flattened bosses, encircled with a regular row of numerous, rather long bristles. In the stages between those figured the gradual flattening of the juvenile spine-like tubercles can be traced through the successive moults" (pp. 17-18). Fig. 8 on p. 19: *b*, a young larva in side view; *c*, tubercle of same; *d*, mature larva in side view; *e*, head of same in anterior view. Refigured: Wheeler, 1910, Fig. 40 on p. 74.)

In the same paper Wheeler gave an account of feeding (1900a, p. 24): "Among the larvae were several pieces, one or two segments long, of a recently killed myriopod (Scutigera). Into these pieces the larvae, some of which were nearly full-grown, had inserted their heads and were devouring the softer tissues! . . . In another nest . . . I observed the larvae . . . lying on their backs, devouring the pieces of some insect which I could not identify." (Repeated by Wheeler, 1910, pp. 234-235.) (Referred to by Forel, 1923, p. 118 = 1928, vol. II, p. 300.)

Wheeler (1901a) described *montezumia* larvae as "shaped like the well-known cucurbitaceous product known as the 'crook-necked squash,' and covered with hairy tubercles" (p. 1008). But this paper deals primarily with the extraordinary phorid larvae commensal with the ant larvae: "Each of these seemed to wear about its neck a huge collar, — a sort of Elizabethan ruff, — consisting of a curled larva. That this could not be another ant-larva was apparent from a moment's examination. In all cases it almost completely encircled the ant-larva in the region of the first abdominal, or in some cases the metathoracic, segment. The posterior end was provided with a sort of disk, which adhered so tightly that both larvae could be killed in alcohol without separating" (p. 1008).

"As soon as the ants had been transferred to the Lubbock nest they were given a number of young larvae of *Camponotus sansabeanus*. These they soon proceeded to malaxate with their mandibles, twirling the morsels about in the mean time with their fore legs and lapping up the exuding juices with their tongues. Finally they deposited the crumpled and pulpy remains of the

Camponoti on the trough-like ventral surfaces of their larvae, which had been previously placed on their backs in a rough chamber dug in the earth of the nest. This chamber was immediately under the glass roof-pane, so that further developments could be closely observed with a pocket lens. Each ant-larva at once stretched forth its head eagerly and began to devour the viands with which it had just been provided. At the same moment the dipteron larva, too, as if sniffing the odor of the fresh food, unwound its tapering neck from the ventral surface of its host, and, without shifting the attachment of its posterior end, at once plunged its mandibles into the food. Under the lens both larvae could be seen greedily dining side by side till the last particle of the Camponotus larva had been consumed or prematurely removed by the worker ants.

"When the ant-larvae were huddled close together, a collar-like larva was sometimes observed to reach over and help itself from the food supply of a neighbor; but even when thus compelled to crane its neck to the utmost, it never shifted the attachment of its caudal end. Sometimes when there was no food within reach it would tweak with its sharp little jaws the sensitive hide of a neighboring ant-larva, till the latter squirmed with pain. It would sometimes even tweak its own host, as if to make it wriggle and perhaps thereby incite the worker ants to bring a fresh supply of provisions.

"The following day two living myriopods (Lithobius) were placed in the nest. During the morning hours they were killed by the Pachycondyla workers, shorn of their many legs, cut up into pieces of convenient length, malaxated, and fed to the larvae as on the preceding day. And again I was able to witness the strange banquet—the dwarf reaching down from the shoulders of the ogre and helping himself from the charger formed by the trough-like belly of his host. The same observation was repeated on several successive days. Pieces of various ant-larvae, beetle-larvae, Lithobius, Scutigera, Oniscus, —all were served up to the ant-larvae and partaken of with great relish by the dipteron larvae as well. There could be no doubt that the latter were true commensals, — perhaps the most perfect commensals, in the original meaning of the term, to be found in the whole animal kingdom!

"As one of the smallest Pachycondyla larvae, scarcely one-fourth grown, bore a very small dipteron larva, it is, perhaps, safe to say that the ant-larva acquires its commensal at a very early age. The two then grow up together, so that there is always a certain relation between the two kinds of larvae—large Pachycondyla larvae bearing large commensals, and *vice versa*. The worker ants lick and cleanse the commensals at the same time that they are caring for their own larvae. This is usually done just after meals" (pp. 1009-1010).

"First, the peculiar habits of the phorid show clearly that the ponerine method of feeding the larvae with comminuted insects is not only the typical but the only method employed by these ants, for such a commensal would certainly starve if the Pachycondyla larvae were carefully fed like the larvae of Camponotus and Formica, by regurgitation of liquid food from the mouths of the workers. The phorid profits by a peculiarity in the behavior of its

host, and thereby demonstrates—by one of Nature's experiments—that *Pachycondyla harpax* cannot feed its young by regurgitation" (p. 1015).

"The larvae bearing the commensals were certainly as large and healthy as any others in the nest, and produced perfectly normal pupae, which in the cases observed all lacked the imaginal disks for the wings and were therefore of the worker type. Whether the presence of the commensals by reducing the amount of food even to a slight degree could inhibit the development of queen larvae and thereby convert them into workers, involves a problem as interesting as it is difficult to solve in the present stage of our knowledge" (p. 1015).

Wheeler's classic illustration (1901a, Fig. 1 on p. 1009) shows the host larva lying on its back with the phorid larva wrapped around its neck. This figure has been repeated by Brues (1946, Fig. 7), Brun (1924, Fig. 51), Escherich (1902), Forel (1921b, Fig. 35 = 1928, Vol. I, Fig. 39) and Kellogg (1905, Fig. 759).

The phorid was later described by Brues (1903) as *Metopina pachycondylae*. "The larvae live as commensals with the larvae of the ant *Pachycondyla harpax Fabr.*" (p. 384).

Wheeler in 1907 (p. 44-49) repeated "in a slightly altered form" his 1901 account and published a photograph (Pl. V, fig. 69; repeated Wheeler, 1910, Fig. 243 on p. 407) of Pachycondyla and Metopina larvae.

Wheeler, 1918, pp. 295-296: "I was able to show that their peculiar tuberculate larvae are not fed with regurgitated food, like the larvae of more specialized ants, but with pieces of insects (1900). . . . An unpublished note, the significance of which I did not appreciate at the time, refers to *Pachycondyla* and was recorded while I was studying the behavior of its extraordinary Phorid commensal, *Metopina pachycondylae* (1901). It runs as follows:

" 'As soon as the fragments of insects are placed on the larva's trough-like ventral surface, the latter is sometimes inundated with a copious, colorless liquid, which is at once eagerly lapped up by the attendant nurse.'

"I should now describe this behavior in the following words: As soon as the fragments are placed on its ventral surface, the larve discharges from its salivary glands a supply of secretion which is sometimes very abundant. This secretion, by means of a strong proteolytic ferment which it contains, digests the food extraintestinally and thus enables the larva to swallow and assimilate it, and at the same time serves in part as an agreeable draught for the nurse. The strong mandibles of the Ponerine larvae are used for comminuting the insect food and thus preparing it for the action of the saliva."

Wheeler (1923a, pp. 24-25 = 1923b, pp. 221-223) has given a condensed summary of his earlier (1901) observations on Pachycondyla and Metopina and reproduced his 1907 photograph as Fig. 86 on p. 23 (= Fig. 86 on p. 222).

Wheeler (1928b, p. 254) refers to the Metopina larva as a myrmecocleptic and gives a brief abstract of his 1901 observations.

Brues (1946, p. 41) gives a brief summary of Wheeler's 1901 observations

and reproduces (Fig. 7) the classic figure. He uses the generic name Cataclinusa instead of Metopina.

Brun (1924) repeats (as Fig. 51, p. 167) Wheeler's 1901 figure and states that "die Larven gewisser kleiner Fliegen (*Phoridae*) legen sich als lebende Halsbänder rings um den Nacken der Ameisenlarven an, um bei deren Fütterung mitzuprofitieren."

Forel (1921b, p. 119 = 1928, vol. I, p. 311) gives a brief summary of Wheeler's observations and reproduces the classic figure (Fig. 35 = Fig. 39).

Kellogg (1905, p. 540, based on Wheeler, 1900) discusses the feeding of *P. harpax montezumia* (see under Leptogenys below).

Pachycondyla sp.—Müller, 1886, pp. 90-91: "Der Kopf trägt wohlausgebildete Mandibeln, kurze stummelförmige Taster. Der Körper, an seinem vorderen Ende schlank, nach hinten stark verdickt, zeigt breite, scharf abgesetzte Bauchplatten. Die Segmente sind tief geschieden, jedes typisch gebaute trägt 10 Tuberkeln, flache Erhebungen, von denen jede mit einem Kranz von 8-10 Chitinborsten umstellt ist. Neben diesen Larven findet sich noch eine zweite Form, vielleicht die jüngeren Tiere; dieselben sind stets kleiner, unterscheiden sich bei gleicher Kopfbildung und gleichem Gesamthabitus durch die Bildung der Tuberkeln, welche verhältnismässig lange konische Erhebungen ohne Kranz von Chitinborsten sind. Sie finden sich in grösserer Anzahl (14 oder 16?) auf den typischen Segmenten. Beiderlei Larven tragen fast stets das vordere Körperende weit ventralwärts eingebogen." Fig. 2 shows a larva in side view, Fig. 3 a head in anterior view (p. 91).

The larvae described in the preceding paragraph were regarded by Müller and by Forel (1891, p. 163) as heteromorphic Eciton larvae, but they are most probably Pachycondyla larvae which had been taken in a raid. See Emery, 1900, p. 513; Wheeler and Long, 1901, pp. 168-172; G. C. Wheeler, 1943, p. 330.

Genus BOTHROPONERA Mayr

Abdomen robust, depressed, elliptical in ventral view. Integument densely spinulose, the spinules long, with conical base and needle-like point, arranged in rows which in some places form a reticulate pattern. Tubercles few (10-38); restricted to sides of thorax and abdominal somites I or III-V; subconical; smooth or with the basal half spinulose; a few apical and/or subapical sensilla or with an apical hair. Body hairs few and minute. Head subglobular. Antennae mounted on discs. Head hairs minute. Mandibles with the base slightly enlarged; the apical half with a thickened outer edge and an inner blade off the anterior surface; basal half of posterior surface spinulose.

Wheeler (1918, p. 299 and 1922, p. 71) uses larval (as well as adult) differences to justify treating Bothroponera as a genus instead of a subgenus of Pachycondyla.

Bothroponera sublaevis Emery.—Pl. II, figs. 26-30. Thorax and first abdominal somite forming a moderately long and rather stout neck, which is strongly folded over toward the ventral surface; remainder of abdomen robust, depressed, elliptical in ventral view; a low rounded longitudinal welt on each side. Leg vestiges conspicuous; each a minute rounded pit at the bottom of

a larger rounded pit; wing (?) rudiments and vestigial gonopods conspicuous. Tubercles very few (10); subconical; squat to elongate; length 0.035-0.18 mm; basal half spinulose; with a few apical and/or subapical sensilla, some of which may bear a minute hair. Tubercles are found only on the lateral surfaces and are distributed thus on each half of the larva—prothorax 2, mesothorax 1, metathorax 1, first abdominal somite 1. Body practically naked; hairs very few, widely scattered, minute (length 0.03 mm). Integument densely spinulose; spinules long (0.018 mm), with stout conical base surmounted by a needle-like point; arranged in rows, which in some places form a reticulate pattern. Head moderately large, subglobular, practically naked; hairs moderately numerous but minute (length 0.006-0.018 mm). Antennae low rounded elevations, each mounted on a disc and bearing three sensilla. Labrum short; breadth twice the length; lateral borders convex, ventral sinuate; anterior surface with two ventrolateral clusters of about 20 sensilla and six minute hairs each. Posterior surface of labrum spinulose; spinules arranged in transverse subparallel rows on the medial ⅔; lateral sixths with coarser isolated spinules near the ventral border; very few sensilla. Mandibles with the basal half slightly dilated; apical half with a thickened lateral part from the anterior surface of which a blade extends medially; posterior surface of basal half with minute isolated spinules. (Material studied: two damaged integuments from Queensland.)

Wheeler, 1918: The larva of *sublaevis* has "a very broad elliptical body, with a short, stout neck, strongly folded over onto the ventral surface, which is somewhat concave. The integument is also hairless and of a peculiar opaque, gray color. The sides of the three thoracic segments and first abdominal segment are furnished with fleshy tubercles and the mouthparts are very highly developed. It is placed on its back by the nurses and fed with fragments of insects deposited on its trough-like ventral surface as in our North American Ponerinae" (p. 299). Fig. 4 on page 302: A, larva in ventral view; B, larva in side view; C, head in anterior view; D, head in side view. (Figures repeated by Wheeler 1922, Fig. 9 on p. 70; on page 56 he states that the larvae of Bothroponera are hairless.)

Bothroponera sp.—Pl. II, fig. 25. Tubercles few (38); subconical, squat to elongate; 0.026-0.16 mm long; the apex with a pit from the bottom of which arises a minute hair, which projects from the opening; with 0-3 subapical sensilla; spinules variable (from almost none to many on the basal half). Tubercles on the sides of the body only and distributed thus: five on each side of prothorax; one on each side of mesothorax and of the metathorax; a cluster of four on each side of abdominal somites III, IV and V. Integumentary spinules as in *sublaevis*. Body practically naked; hairs very few, widely scattered and minute (length 0.018 mm). Head as in *sublaevis* Labrum as in *sublaevis*, except lateral borders sinuate and the anterior surface of each lobe with about 12 sensilla and two minute hairs. Mandibles with the base slightly enlarged; apical half with a thickened lateral border and a median blade; the thickened outer edge terminates in a long and rather stout apical tooth, which is strongly curved medially and posteriorly, and bears one

or two subapical teeth on its anterior surface; blade terminates ventrally in a blunt apical tooth and sometimes has also a smaller subapical tooth on the inner border; posterior surface of basal half spinulose, the distal spinule exceedingly minute and arranged in transverse rows, the proximal coarser and isolated. Maxillae large; apex paraboloidal and densely spinulose, the spinules long, slender, curved, and sharp-pointed, shorter basally; palp a subcylinder with flat apex, which bears four sensilla, one of which is button-like; galea subconical, slightly curved, with two apical sensilla. Labium small; densely spinulose, the spinules long, slender, sharp-pointed and arranged in transverse rows; palp short and subcylindrical, with four apical sensilla, one of which is button-like; opening of sericteries wide and salient. Hypopharynx cordate; densely spinulose; the spinules arranged in a reticulate pattern. (Material studied: two damaged integuments from Queensland.)

Bothroponera soror Emery.—Eidmann (1944, p. 433) has compared this larva with *sublaevis:* "Von ihr unterscheidet sich die Larve von *B. soror* nicht unwesentlich. Vor allem ist die ventrale Einkrümmung des Vorderkörpers nicht so auffallend. Sie liegt zwar auch wie bei jener im Bereich des ersten Abdominalsegmentes, erreicht aber nur eine Abbiegung von etwa einem rechten Winkel. Ferner ist das larvale Abdomen bei weitem nicht so stark verbreitert wie bei *sublaevis,* sondern hat, wie bei den meisten Ameisenlarven, annähernd runden Querschnitt. Auch fehlen die fleischigen Fortsätze an den Seiten der 4 ersten Körpersegmente. Dafür ist die Larve jedoch stark bedornt; die einzelnen Dornen stehen auf warzenförmigen Erhöhungen." Fig. 6: E (p. 432), "erwachsene Larve"; F, head in anterior view. This larva is so different from those we have studied that we question whether it belongs in this genus at all.

Haskins (1941, p. 213) reported that the larvae of *B. soror* were fed with cut-up insect food. He found the life cycle to be: egg 15 days, larva 15 days, pupa one month.

Genus EUPONERA Forel

It is not possible to characterize the larvae of this genus as a unit, because they fall into two very distinct types. Neither is it possible to characterize the subgenera, because larval taxonomy is not at all correlated with current adult taxonomy. Different species of the same subgenus may belong to different types, while species of different subgenera may belong to the same type.

TYPE I.—Shaped somewhat like a crook-neck squash; thorax and first abdominal somite forming a long slender neck, which is strongly bent ventrally; remainder of abdomen rather plump. Tubercles numerous (136); subconical, short and stout to long and slender; dorsal tubercles on abdominal somites III-VI reduced to low rounded bosses; each tubercle with minute spinules arranged in numerous transverse rows and 1-3 minute hairs near the apex. Clypeal integument not spinulose. Mandibles narrow and elongate; slightly curved; base only slightly dilated; basal half spinulose, the spinules minute and arranged in short arcuate rows.

This group includes *E.* (*Mesoponera*) *constricta* and *E.* (*Trachymesopus*)

stigma; also—to judge from Emery's figures—*E.* (*M.*) *caffraria.*

TYPE II.—Elongate and slender; subcircular in cross section; diameter greatest at the sixth and seventh abdominal somites, decreasing gradually toward the anterior end and only slightly toward the posterior end; thorax and one or two abdominal somites somewhat curved ventrally; remainder of abdomen straight; no clearly defined neck. Tubercles numerous (166); typically long, slender and finger-like, encircled by several rows of minute spinules; they may bear on the apex an exceedingly minute hair. A certain number of abdominal somites (two, three or five) have the dorsal pair of tubercles doorknob-shaped, i.e., a stout stalk enlarging gradually to a distal bulb; a few minute spinules on the stalk and two exceedingly minute hairs on the bulb. Clypeal integument spinulose. Mouth parts large. Mandibles elongate, narrow and slightly curved; base only slightly dilated; basal half spinulose, the spinules minute and arranged in short arcuate rows.

This group includes *E.* (*Trachymesopus*) *gilva;* also—to judge from published descriptions and figures—*E.* (*Trachymesopus*) *sauteri, E.* (*Mesoponera*) *leveillei* and *E.* (*Brachyponera*) *solitaria.* This group show more affinity to Ponera than to its alleged congeners of Type I.

Wheeler (1910, p. 233) characterizes the larvae of Trachymesopus (but under the name of Pseudoponera) as "furnished with rows of tubercles."

Euponera (*Mesoponera*) *constricta* (Mayr).—Plate IV, figs. 1-7. Shaped somewhat like a crook-neck squash; thorax and first abdominal somite forming a long slender neck, which is strongly bent ventrally; remainder of abdomen rather plump, its dorsal profile moderately convex, its ventral straight; dorsal and ventral surfaces separated by a low rounded longitudinal welt; posterior end rounded. Anus ventral. Leg vestiges present. Thirteen differentiated somites. Spiracles mounted on low papillae. Body beset with numerous (136) tubercles, distributed as follows: 10 on each thoracic somite; 12 each on abdominal somites I-VIII; eight on IX; two on X. Tubercles on neck and on posterior end are long, slender and subconical; those on the rest of abdomen are shorter, stouter and more rounded apically; the most dorsal tubercles on abdominal somites III-VI are reduced to low rounded bosses; none on midventral surface. Integument of tubercles spinulose, the spinules minute and arranged in numerous transverse rows. Each tubercle bears 1-3 minute (0.006 mm long) hairs near the apex. Body hairs very few, simple, minute (0.012-0.022 mm long), on ventral surface only. Integument of ventral surface with minute spinules in transverse rows; rest of body integument very densely spinulose, the spinules minute but not in rows. Head (with mouth parts) oval in anterior view; integument of genae and dorsal part of cranium (down to level of antennae) with rather short rows of minute spinules. Head hairs few, slender, slightly curved, slightly constricted at base, short (0.045 mm). Antennae rather large, subcircular, convex; each with three sensilla. Labrum short, breadth 1¾X the length; bilobed due to a wide median incision in the ventral border; lateral borders sinuate; anterior surface of each lobe with a ventrolateral cluster of ten sensilla and two minute hairs. Posterior surface of labrum densely beset with fine spinules; those on

the middle half in numerous long subparallel transverse rows; those on the lateral quarters in short arcuate rows; four sensilla in a curved row extending obliquely upward from each side of the notch. Mandibles moderately sclerotized; elongate and narrow, with the base only slightly dilated; moderately curved medially and posteriorly; with one slender apical and two acute subapical teeth; surface of basal half spinulose, the spinules minute and arranged in transverse slightly curved rows. Maxillae conoidal; densely spinulose; spinules minute, short, slender, in short transverse rows; palp a subcylindrical peg, with four apical sensilla (one button-like); galea slender and subconical, with two apical sensilla. Labium densely spinulose; spinules in transverse rows, coarse on the anterior surface, minute on the posterior; on the anterior surface near the base there is a conspicuous transverse welt which is semicircular in profile and whose spinules are arranged in transverse rows; palp a short subcylindrical peg, its apex flat and bearing four sensilla (one button-like); opening of sericteries wide and salient, with three projections. Hypopharynx with numerous transverse subparallel rows of minute sharp spinules. (Material studied: two larvae from British Guiana.)

Euponera (*Mesoponera*) *caffraria* (F. Smith).—Emery, 1899, p. 5: "La parte posteriore del corpo è molto più rigonfiata e i suoi segmenti sono affatto indistinti. I tubercoli cutanei sono piccoli, acuti, subspiniformi e molto meno numerosi." Pl. I, fig. 2a, larva in side view; 2b, head enlarged, in side view.

Wheeler, 1900a, p. 15 (referring to Emery, 1899): "Mandibles powerfully developed for ant-larvae, the anterior portion of the body long and slender and folded over the abdominal portion, and . . . covered with rows of peculiar tubercles beset with more or less prominent bristles."

Euponera (*Mesoponera*) *leveillei* Emery.—Eidmann, 1936, pp. 35-36: "Sie sind am ganzen Körper mit Ausnahme des Kopfes ringsum mit langen fingerförmigen Höckern besetzt. Diese sind an der Spitze abgerundet und manchmal etwas verdickt und tragen auf ihrer ganzen Oberfläche mikroskopisch kleine Dörnchen, die besonders auf den distalen Teilen der Höcker eine regelmässig ringförmige Anordnung zeigen. Die Spitze trägt in der Regel einige grössere Dornen. Ausserdem befindet sich auf der Dorsalseite des 4. und 5. Abdominalsegments je ein Paar grosser, gestielter, knopfförmiger Auswüchse, ähnlich wie sie von Wheeler (1910, p. 75) bei der Larve von *Ponera coarctata* ssp. *pennsylvanica* Buckl. gefunden wurden. Ferner haben die Larven auf dem Prothorax unmittelbar hinter den Mundteilen auf jeder Seite 2 knopfförmige stumpfe Höcker und 2 Reihen ähnlicher Gebilde auf der Ventralseite des 2.-6. Abdominalsegments . . . Die knopfförmigen Papillen . . . halte ich für Exsudatorgane." Pl. I, fig. II 1 shows a larva in side view; fig. II 2 a tubercle enlarged.

Euponera (*Trachymesopus*) *gilva* (Roger).—Plate IV, figs. 8-16. Elongate and slender; subcircular in cross section; diameter greatest at the sixth and seventh abdominal somites, decreasing gradually toward the anterior end and only slightly toward the posterior end, which is rounded; thorax and one or two abdominal somites somewhat curved ventrally; remainder of abdomen straight; no clearly defined neck. Anus ventral. Leg vestiges present. Thir-

teen differentiated somites. Spiracles on small papillae. Body bristling with numerous (156) long (0.035-0.12 mm) slender finger-like nearly straight tubercles arranged in longitudinal rows and distributed as follows: 10 on the prothorax; 12 each on mesothorax and metathorax; 14 each on abdominal somites I and II; 12 each on III-VII; 14 each on VIII and IX; 6 on X. None on midventral surface. Each tubercle is encircled by several rows of minute spinules and may have on the apex an exceedingly minute hair (about 0.006 mm long) as well as a few spinules. In addition, the dorsum of each abdominal somite III-VII bears a pair of doorknob-shaped tubercles; each tubercle has a stout stalk which enlarges gradually to a distal bulb; shape of bulb variable in preserved specimens; the surface of the stalk bears a few minute scattered spinules; two exceedingly minute hairs on the bulb. Body hairs few, short (about 0.03 mm long), simple, restricted to the ventral surface. Integumentary spinules on the ventral surface only; minute; in short transverse rows. Cranium subhexagonal in anterior view; all corners rounded; clypeus bulging, sharply delimited by furrows; a median rounded ridge from the dorsal border of the clypeus, fading dorsally; integument of clypeal bulge spinulose, the spinules in short tranverse rows; isolated spinules on the median ridge, the vertex and the genae. Mouth parts large and conspicuous. Head hairs few but variable in number and arrangement; stout at base, apex acuminate; slightly curved near the tip or straight; short (0.035-0.07 mm long). Antennae moderately large, each with three sensilla. Labrum moderately large; breadth 1.4X length; bilobed due to a wide deep median incision of the ventral border; lateral borders sinuate; ventral border with a few spinules and four sensilla on each lobe; anterior surface with a cluster of six sensilla and two minute hairs on each lobe. Most of posterior surface densely spinulose, the spinules minute and arranged in numerous long sinuate transverse subparallel rows; ventrally and laterally the rows are broken into arcuate components; from either side of the notch a row of four sensilla extends obliquely upward and outward. Mandibles large and heavily sclerotized; narrow and elongate; base scarcely enlarged; apex slightly curved medially; apical tooth small, round-pointed; two moderately large round-pointed subapical teeth on the medial border; basal half with short transverse arcuate rows of exceedingly minute spinules. Maxillae large, conoidal, with the base constricted; apical half spinulose, the spinules minute, those near the apex in short rows, the others isolated; palp a slender cylinder with four apical sensilla, one bearing a long spine, the others a spinule; galea finger-shaped, with two apical sensilla. Labium large and prominent; spinulose, the spinules minute; those on the anterior surface in short transverse rows on the medial half, isolated on the lateral quarters; those on the posterior surface isolated distally and in short rows basally; on the anterior surface near its base there is a conspicuous transverse welt, which is semicircular in profile and whose spinules are arranged in short transverse rows; palp a subcylindrical peg, with four apical sensilla, two of which bear a spinule each, one a spine, while the fourth is button-like; opening of sericteries wide and salient, with three projections. Hypopharynx densely spinulose, the spinules minute and arranged in numerous long transverse

rows. (Material studied: eighteen larvae from Alabama, collected by Dr. W. S. Creighton.)

Haskins, 1931, p. 512: "Immediately upon hatching the larva is removed from the egg-mass and allowed to lie singly on the chamber floor. Not infrequently the ova and hatched larvae are kept in separate chambers, and a rough division of the larval brood according to size is usual, but not rigidly maintained. The larvae are fed with bits of solid food in the usual Ponerine fashion, and are active and athletic, and wholly entomophagous. They are surprisingly sensitive. Not infrequently, when food was introduced at the entrance to an artificial nest, larvae uncurled and stretched their long necks in search of it. It is possible that this action resulted from an association of light, perceived through the general integument, with the fact of food as previously experienced. The adults of the colony spend much time in licking the larvae for exudates and also apparently for saliva. This food, indeed, seems normally to constitute the entire diet of the callows for the first few days. The adults frequently pinch the larvae vigorously about the neck and abdomen, apparently to hasten and encourage the flow of exudates. When mature, the larvae are carefully covered entirely with earth in the usual manner, and spin at once. The earth is removed as soon as the first sheet of silk is completed, and the cocoon is cleaned within a short time." The life cycle is given (pp. 512-513) as egg 30-31 days, larva 22-35 days and pupa 31-33 days.

Euponera (*Trachymesopus*) *sauteri* (Wheeler).—Teranishi, 1927 (translated from the Japanese by two university students): "This larva, closely related to Ponera, has glutinous tubercles on the dorsal surface of abdominal somites III to VII inclusive, one pair on each somite. In addition there is a pair of bristle-capped tubercles on the dorsal surface of each somite and two pairs on each lateral surface. All other somites, except the most anterior, have two pairs on the dorsal surface and two pairs on each lateral surface. The first somite has only one pair of bristle-capped tubercles on the dorsal surface; like the others it has two pairs on each lateral surface. The number and function of the glutinous dorsal tubercles do not change as the larva matures. The neck region of the larva is long and hook-shaped.

"The above species was formerly known as a Pseudoponera in the genus Pachycondyla until C. Emery (Genera Insec., Ponerinae, p. 84, 1911) classified it under Trachymesopus in the genus Euponera. After studying the position of the glutinous dorsal tubercles in the young larva of *sauteri*, I fully agree with Emery in separating it from Pachycondyla, but I am not convinced that it should be placed in Euponera" (p. 298).

"The neck and mouth parts are well developed because these larvae reach for their own food, which is placed near them by the workers" (p. 300). "The function of the glutinous dorsal tubercles is to attach the larva to the walls or ceiling of the nest" (p. 297). "At present it is believed that the bristle-capped tubercles prevent the larvae from eating each other" (p. 300). Fig. 4 on p. 299—a nearly full-grown larva in side view.

Euponera (*Trachymesopus*) *stigma* (Fabricius).—Similar to *Mesoponera constricta* but differing in the following respects: The tubercles number the

same (136) but are distributed differently: 12 on each thoracic somite; 14 each on abdominal somites I and II; 12 each on III and IV; 10 each on V-VIII; 6 on IX; 2 on X. Integumentary spinules on ventral surface only. Head hairs exceedingly minute (about 0.009 mm long). Lateral borders of labrum convex. Mandibles with dorsal subapical tooth stouter. Maxillary palp with two apical and one button-like subapical sensilla. Labial palp with four apical and one subapical sensilla. Hypopharynx cordate. (Material studied: numerous larvae from British Guiana and Costa Rica.)

The young larva (length 2 mm) of this species is only slightly curved ventrally and has the posterior part only slightly enlarged. There is no differentiated neck. The posterior end is round-pointed and directed ventrally. The number and distribution of the tubercles is the same as in the mature larva; those on the prothorax and mesothorax and on the venter of the abdomen are conoidal; those on the metathorax and on the lateral longitudinal welts are paraboloidal; those on dorsum of the abdomen are subhemispherical. There is a rounded transverse welt on the dorsal surface of each abdominal somite IV-VII.

Euponera (*Trachymesopus*) *stigma* var. *quadridentata* (F. Smith).—Emery, 1899, pp. 4-5: "Il corpo ha una porzione anteriore più sottile, coi segmenti ben distinti e una posteriore rigonfiata, in cui non si vedono limiti distinti tra i segmenti, il loro numero essendo indicato dalle stigme e, negli stadi più inoltrati, dalle sporgenze segmentali o tubercoli del tegumento. Come in generale, nelle larve degli Imenotteri, le stigme sono al numero di 10 paia e mancano nel 1° segmento che segue il capo, nonchè nei due ultimi segmenti della regione addominale. Nello stadio più giovane, si vedono solo deboli accenni dei tubercoli cutanei; ritengo che questo stadio debba corrispondere alle larve di prima schiusa e che lo stadio seguente, di poco più grande, sia quello che segue la prima muta. In esso appariscono, già ben distinti, parte dei tubercoli; questi si fanno successivamente più numerosi e sporgenti, a misura che la larva cresce. La mie figure faranno riconoscere la loro distribuzione e la grandezza relativa. Osservati a forte ingrandimento, i tubercoli più acuti della regione toracico hanno forma conica, troncata all'apice e portano ciascuno alcuni brevi peli. Del resto, il corpo di queste larve è quasi totalmente destituto di peli.

"Il capo è relativamente molto sviluppato e subgloboso; sotto il labbro superiore appariscono le mandibole, molto più grandi che non siano nelle larve di *Formica* e *Camponotus;* esse sono in buona parte scoperte nella loro faccia laterale, e sporgono in avanti, terminate con tre piccoli denti. . . . Le mascelle hanno alla loro faccia laterale due prolungamenti chitinosi conici, giallognoli, dei quali quello più vicino all'apice è più grande e diretto innanze. Il labbro inferiore ha due paia di simili coni più piccoli e più pallidi, e nel mezzo una papilla o filiera che riceve lo sbocco delle ghiandole della seta. Le parti boccali hanno del resto struttura quasi identica a quella che si osserva nella larva di *Odontomachus.*" (Wheeler, 1900a, p. 18, footnote: the third and fourth sentence quoted.) "La forma di queste larve e i tubercoli spiniformi che si trovano sulle più grandi di esse parvero anche a me singolari" (p. 4). Pl.

I, fig. 1a, b, c—three different stages in development of the larva, drawn to the same scale; d—a dorsal tubercle from the first somite, enlarged. (Fig. 1c copied by Berlese, 1925, Fig. 825B on p. 846.)

In this same article Emery quoted (p. 4) a note from Professor L. Biró concerning the same larvae: " 'Nelle gallerie del nido scavate nel legno putrido, si trovavano le larve dal lungo collo, coperte di spine singolari: abbandonate dai loro vigliacchi custodi, quelle larve sapevano difendersi da sè; quando qualche termite (il nido di queste trovavasi nello stesso legno) si avvicinava ad una di esse, questa batteva innanzi e indietro col suo collo di cigno e tosto veniva lasciata in pace.' " Wheeler (1910, p. 234), referring to the above, says that Biró "saw these larvae, when disturbed by some termites, move their long necks back and forth with sufficient force to drive away the intruders." Emery (1911, p. 53): "M. le Prof. Biró a observé à la Nouvelle-Guinée que les larves de *Euponera stigma*, Fabricius, en agitant leur col de cygne, étaient capable d'effrayer des termites qui voulaient en faire leur proie."

Wheeler (1900a, p. 15) refers to Emery's description, making the same comments as under *Eu.* (*M.*) *caffraria* above.

Euponera (*Brachyponera*) *lutea* (Mayr).—Wheeler, 1933, p. 99: "I have not seen the larvae of *lutea* devouring insect food and am therefore inclined to believe that they may be fed with liquids by regurgitation." This hypothesis has been confirmed by Haskins and Haskins (1950, p. 7).

Euponera (*Brachyponera*) *solitaria* (F. Smith).—Teranishi,, 1927 (translated from the Japanese by two university students): "There is one pair of glutinous tubercles on each of abdominal somites II-IV. The other somites have, instead of glutinous dorsal tubercles, a pair of bristle-capped tubercles on the dorsal surface and five on each lateral surface, whereas somites II-IV have five bristle-capped tubercles on each lateral surface only. When the larva is in the third instar (I am not certain about the exact age) the glutinous dorsal tubercles on the second abdominal somite disappear; those on the third and fourth move posteriorly and assume a different position. . . . Those of the third somite are larger than those of the fourth. Those of both somites are, however, shorter than those of the previous stage. The anterior portion of the body bends downward. . . . The abdominal somites are not very distinct" (p. 298). "The neck and mouth parts are well developed because these larvae reach for their own food, which is placed near them by the workers" (p. 300). "The function of the glutinous dorsal tubercles is to attach the larvae to the walls or ceiling of the nest" (p. 297). "At present it is believed that the bristle-capped tubercles prevent the larvae from eating each other" (p. 300). Fig. 2—second (?) instar larva in side view; Fig. 3—dorsum of abdominal somites II-V in side view (p. 299).

Genus CRYPTOPONE

Tubercles numerous; typically slender, elongate and subcylindrical; basal third slightly constricted, its integument smooth; distal ⅔ encircled by a few

rows of spinules; apex surmounted by a hemispherical cap which is encircled by a row of spinules. Doorknob-shaped tubercles also present. Body hairs moderately abundant. Body hairs and head hairs with the distal third denticulate. Cranium short; transversely subelliptical in anterior view. Antennae small. Labrum short; anterior surface with two minute hairs but no sensilla; ventral border with four sensilla on each lobe. Mandibles with a few arcuate rows of fine spinules on the basal half. Galea spinulose.

Cryptopone mayri Mann.—Plate III, figs. 20-26. Body beset with numerous tubercles, most of which are slender, elongate, subcylindrical (but with the basal third slightly constricted), encircled by a few rows of minute spinules (none on basal third) and having the apex surmounted by a hemispherical cap which is encircled by a row of spinules. There are also doorknob-shaped tubercles, somewhat similar to those of Ponera. Body hairs slender, straight and short (length about 0.045 mm), the distal third roughened with minute denticles. Cranium transversely subelliptical in anterior view. Head hairs moderately numerous, short (0.03-0.06 mm); distal third with minute denticles. Labrum short, breadth twice the length; bilobed due to a wide shallow median incision of the ventral border; lateral borders sinuate; ventral border with four sensilla on each lobe; the anterior surface of each lobe bears two minute hairs but no sensilla. Posterior surface of labrum with numerous subparallel transverse rows of minute spinules, except near the lateral borders where there are only a few scattered arcuate rows; two sensilla near the center of each lobe. Mandibles moderately sclerotized; slightly enlarged at base: curved medially; apex slightly curved posteriorly; apical tooth rather small, round-pointed, curved medially; two small, round-pointed subapical teeth arising from a narrow mesal blade; basal half with short transverse rows of minute spinules. Maxillae large, lobose, round-pointed; apex bearing minute spinules arranged in short rows; palp a subcylindrical peg, with a few isolated spinules on its surface and with three apical sensilla (two of which bear each a spinule); galea slender, elongate, subconical, with a few short transverse rows of minute spinules on its surface and with two apical sensilla. Labium narrow; anterior surface with numerous minute spinules arranged in short transverse rows; on the anterior surface near its base there is a conspicuous transverse welt, which is semicircular in profile and whose spinules are arranged in transverse rows; palp a subcylindrical peg with three apical and one subapical sensilla; opening of sericteries wide and salient with two projections. (Material studied: one head integument and fragments of body integument from the Solomon Islands.)

Genus PONERA Latreille

Without a sharply differentiated neck; thorax stout; abdomen scarcely enlarged. Integument of ventral surface finely spinulose; lateral and dorsal surfaces coarsely and conspicuously spinulose. Tubercles numerous (164-184), typically spire-like; each encircled by a few rows of minute spinules and surmounted by a long and rather stout spine-like hair. There are also on the dorsal surface of certain abdominal somites two to four pairs of doorknob-

shaped tubercles, one pair on a somite. Cranium suboctagonal in anterior view; its integument spinulose on the genae, vertex and middle of front. Antennae subhemispherical. Labrum with one to three sensilla on the ventral border of each lobe. Mandibles rather long and narrow; base only slightly dilated; apical half consisting of a thicker outer part and a narrow mesal blade; basal half sparsely spinulose, the spinules minute and in short transverse arcuate rows.

Donisthorpe (1915, p. 68 = 1927a, p. 69): "*Head* fairly large, with strong horny mandibles, body clothed with bristle capped tubercles, and four pairs of glutinous club-shaped tubercles, situated on the dorsal part of the sixth and following somites."

Wheeler, 1910: The larva of Ponera has "prominent, pointed . . . tubercles which probably have a protective function, and in addition to these . . . pairs of glutinous dorsal tubercles which . . . serve to attach the larva to the walls of the nest" (p. 74). "Larvae furnished with rows of tubercles" (p. 233). "Some of the species of *Ponera* also have long cylindrical dorsal tubercles which are glutinous at their ends and serve to anchor the larva to the walls of the nest" (p. 234). It is possible that the bristly tubercles "are used in defending the larvae from one another, for the larvae, like the adults, are highly carnivorous and when food is scarce probably attack one another" (p. 234).

Ponera coarctata pennsylvanica Buckley.—Plate V, figs. 18-21 and 28-32. Without a well differentiated neck; diameter greatest at the fifth and sixth abdominal somites, decreasing gradually toward the anterior end and more abruptly toward the posterior end; thorax and first two abdominal somites stout and curved ventrally, remainder of abdomen nearly straight; ventral surface slightly flattened and separated from the more rounded dorsal surface by a feebly developed longitudinal welt; posterior end rounded. Anus ventral. Thirteen differentiated somites. Body beset with numerous (156) tubercles distributed as follows: prothorax, 10; mesothorax, 12; metathorax, 12; abdominal somites, I, II, VII and VIII, 14 each; III-VI, 12 each; IX, 12; X, 6; none on the midventral surface. These tubercles are spire-like; each is encircled by a few rows of minute spinules and is surmounted by a rather long and stout spine which arises by an articulation from an apical depression; length (including spine) 0.04-0.11 mm. In addition, there is also a pair of doorknob-like glutinous tubercles on the dorsum of each abdominal somite III-VI; each consists of a stout column bearing an inflated knob; shape of knob variable; length about 0.11 mm. Body hairs few, simple, straight, minute to short (length 0.018-0.072 mm); limited to ventral surface. Head moderately large; cranium suboctagonal in anterior view; integument spinulose on the middle of the front (down to the level of the antennae), on the vertex and on the genae; spinules minute, mostly isolated but some in rows; mouth parts moderately large. Head hairs moderately numerous, short (0.035-0.07 mm), simple, slightly curved. Antennae moderately large; subhemispherical; each with three sensilla. Labrum: breadth 1¾ X length; strongly bilobed due to a wide deep incision of the ventral border; lateral borders sinuate;

near its ventral border each lobe bears on its anterior surface two minute hairs and about five sensilla; 1-3 sensilla on the ventral border of each lobe. Posterior surface of labrum densely spinulose; spinules minute; on the median half arranged in numerous subparallel transverse rows; on the lateral quarters sparser and in short arcuate rows; two or three sensilla near the middle of each lobe. Mandibles moderately sclerotized; rather long and narrow; base only slightly dilated; apical half consisting of a thicker outer part and a narrow inner blade; apical tooth prominent, strongly curved medially, slightly curved posteriorly; two stout subapical teeth arising from the blade; basal half sparsely spinulose, the spinules minute, in short transverse arcuate rows; on the posterior surface near the subapical teeth there are a few coarse spinules. Maxillae large; bulging at the sides; apex paraboloidal and densely spinulose; the spinules minute and in short arcuate rows; rest of surface sparsely and irregularly spinulose; palp a frustum, with four apical sensilla (three bearing each a spinule and one a small cone) and one button-like subapical sensillum; galea finger-like, with two apical sensilla, each bearing a spinule. Labium prominent; spinulose, the spinules arranged in short transverse rows, except at the sides, where they are isolated; palp a short frustum bearing four apical (each surmounted by a spinule) and one button-like subapical sensilla; opening of sericteries wide and salient, with three projections. Hypopharynx densely spinulose, the spinules minute, in long curved transverse rows. (Material studied: numerous larvae from Illinois, Michigan and New Hampshire.)

Young larvae resemble mature larvae, except that the head and tubercles are relatively larger and the body curvature is less.

Our observations on living larvae show that the glutinous tubercles are really sticky. When a single tubercle was touched with a dissecting needle it adhered to the latter so firmly that the larva (length about 1.8 mm) was picked up by merely lifting the needle; it remained thus suspended. A larva was caused to adhere to the ceiling of a glass cell by means of its four posterior tubercles.

Wheeler, 1900b, pp. 52-53: "The larva is clearly of the Ponerine type. . . . It is rather robust, with a large head succeeded by five distinct segments. The remaining segments, forming the swollen abdomen, are not distinctly marked off from one another. The body is furnished with outgrowths of three different types. The first of these is represented by a number of pointed bristles confined to the ventral surface of each segment. The second type is represented by several longitudinal rows of pointed tubercles, each of which, under a high magnification is seen to consist of a short distal spine and a long, tapering proximal base, directly continuous with the integument of the larva, and covered with transverse rows of serrated points. The distal spine is movably articulated with the proximal portion, and is so easily detached that it may be overlooked. The third type of projection is found only on the dorsal surface of the third to sixth abdominal segments as four pairs of club-shaped structures which are glutinous to the touch. That these are peculiar modifications of the tapering tubercles seems to be indicated by the fact that they

replace on either side in each of the four above-mentioned segments the more posterior of the two pointed projections seen in the thoracic, first and second, and seventh and eighth abdominal segments. The larva is usually kept on its back, so that the four pairs of glutinous tubercles act as suckers and fix it to the sides of the earthen chamber or to the glass of the artificial nest. The ants have to exert a slight effort in pulling the larva away from its attachment. The head . . . is broad, evenly rounded behind, and beset with short stiff bristles. The labrum is bilobed and does not extend beyond the tips of the powerful tridentate mandibles. The fleshy maxillae and labrum [labium] project somewhat beyond the mandibles, the former being provided with robust tactile cones, the latter with a prominent median tubercle on which opens the duct of the spinning gland. Comparison of the figures in this and my previous paper shows that the larva of *P. coarctata* is peculiar in lacking the circlets of bristles on the pointed projections and in possessing clavate adhesive tubercles on the dorsal surface of the abdomen.

"The larvae are fed in the very same manner as the larvae of the large Texan Ponerinae, *i.e.*, with pieces of food and not with liquid regurgitated by the ants. In confinement I did not succeed in inducing the ants to feed their larvae with fragments of insects, but they carried crumbs of moistened corn bread to them, and the larvae could be seen lying on their backs, attached by their glutinous dorsal tubercles, slowly consuming the morsels which had been placed on their flattened ventral surfaces. The fixation of the larva to the walls of the nest seems to be an adaptation for giving freer play to the head and slender neck during feeding." Fig. 4 on p. 52: *a*, larva nearly ready to pupate; *b*, bristle-capped tubercle of same; *c*, head in anterior view. Figure repeated by Wheeler, 1910, Fig. 41 on p. 75; by Escherich, 1906, Fig. 30 = 1917, Fig. 360).

Eidmann (1936, p. 36 and 1944, p. 438) refers briefly to the larva of *pennsylvanica;* he regards the fungiform tubercles as exudate organs.

Escherich (1917, p. 96-97) refers briefly to the four pairs of "keulenförmiger klebriger Fortsätze auf dem Rücken;" he regards them as organs of attachment ("Haftorgane").

Ponera coarctata (Latreille).—Donisthorpe (1927b, p. 72) records the staphylinid beetle, *Lamprinus saginatus* Gr. as a "hostile persecuted lodger" with the ant. "Both the adult beetle and their larvae devour the ants' eggs, larvae, and pupae."

Ponera foeda Forel.—Wheeler, 1901b, p. 200: "Larvae similar to those of *P. opaciceps.*"

Ponera japonica Wheeler.—Teranishi, 1927 (translated from the Japanese by two university students): "On the ventral side of the larva there are segments. On the dorsal surface of the fourth, fifth and sixth abdominal somites there are glutinous tubercles, one pair on each. Surrounding these dorsal tubercles and generally scattered over the body are numerous bristle-capped tubercles. At the anterior end the first and second somites bend directly downward. Behind this bend the thorax forms an arc. The above remarks refer to the young larva" (p. 298). "The neck and mouth parts are well

developed because these larvae reach for their own food which is placed near them by the workers" (p. 300). "The function of the glutinous dorsal tubercles is to attach the larva to the walls or ceiling of the nest" (p. 297). "At present it is believed that the bristle-capped tubercles prevent the larvae from eating each other" (p. 300). Fig. 1—first (?) instar larva (p. 299).

Ponera opaciceps Mayr.—Wheeler, 1901b, p. 199: The larvae resemble those of *coarctata* [*pennsylvanica*] except that they "have fewer pairs of dorsal adhesive tubercles."

Ponera sp.—Pl. V, fig. 33. Apparently similar in general to *pennsylvanica* but differing in the following characters: The spine-like tubercles are stouter; only two pairs of doorknob-like glutinous tubercles, which are located on abdominal somites IV and V. No integumentary spinules on the ventral surface. On either side of the ventral surface of the prothorax there is a large flap-like outgrowth; each bears a small hair and a sensillum but no integumentary spinules. These flaps are unique among the ant larvae we have studied. It is therefore unfortunate that a more precise identification cannot be made; we have no adult ants; our material includes only the damaged integuments of three larvae accompanied by the label "Ponera sp. N.S.W."

Ponera sp.—Pl. V, figs. 22-27. Generally similar to *pennsylvanica* but differing in the following respects: Spine-like tubercles more numerous. There are only 2 pairs of glutinous doorknob-shaped tubercles, one pair each on abdominal somites IV and V; they are much stouter; the integument of the stalk has several transverse rows of minute spinules. In addition there is a pair of ventrolateral projections on the prothorax; these are paraboloidal; each bears two hairs (about 0.045 mm long); they are not found on *pennsylvanica* but are in the same position as the flaps of the New South Wales species described above. The body integument has finer spinules on the ventral surface, while those on the dorsum are longer and more acuminate. Head hairs fewer and shorter. Integument of head not spinulose. Labrum twice as broad as long; lateral borders spinulose; each half of posterior surface with three or four sensilla near the base. Apical and subapical teeth of mandibles smaller; apical tooth less curved; no spinules near subapical teeth. Maxillae conoidal. Spinules on labium short but in longer rows.

A single living larva of this species was observed in an artificial formicary. The whole body glistened as if its integument was wet. The larva usually lay on its side, but when stimulated it rolled onto its belly, stretched its neck forward, applied its mouth parts to the filter paper (on which it was lying) and pulled itself forward by a shortening and hunching of the neck. The glutinous tubercles (on their stalks) were waved about in all directions. The knobs were filled with a clear fluid and their shape was changeable, apparently by means of pressure changes in this fluid. Once while creeping the knobs of the two posterior glutinous tubercles chanced to touch an overhanging bit of damp soil. The knobs adhered to the soil; the anterior end of the body was held suspended and consequently the larva was unable to progress; it wriggled vigorously but could not free itself.

The above observations and description are based on two larvae and two

semipupae found with workers in soil in flower pots in the Biology Department greenhouse at the University of North Dakota, Grand Forks, North Dakota, May 3, 1950 (No. 417) and May 24, 1950 (No. 418). Dr. M. R. Smith of the United States National Museum has kindly examined some of the workers and written us as follows: "The ants collected from your Department greenhouse on May 3 and 22 appear to be the same species of *Ponera*. They are, however, neither *coarctata* Latr. nor *coarctata pennsylvanica* Buckley. Those two forms are easily distinguished from your greenhouse specimens in that their heads are much more coarsely punctate and their petiolar nodes of an entirely different shape when viewed posterodorsally. I have compared your specimens with other determined forms in our collection, but have not found anything with which they are identical. Could your greenhouse form have been introduced? The ants are certainly different from all other recorded North American forms with which I am familiar. Thanks for the gift of the specimens. If I am ever able to name them I will write you."

Genus TRAPEZIOPELTA Mayr

Tubercles moderately numerous (about 90); subconical, with the apex rounded; each tubercle may bear one or two minute hairs and those on the abdomen have a few minute spinules on the apex; otherwise the integument is smooth. Head hairs exceedingly minute, mostly below the level of the antennae. Labrum subquadrate or subtrapezoidal (i.e., not bilobed); posterior surface with the spinules on the middle half (or third or $^3/_5$) rather long and arranged in short to moderately long transverse combs; posterior surface with 16 sensilla grouped in four clusters. Mandibles directed ventrally, completely exposed (or nearly so); long and slender; base only slightly enlarged; apical third strongly curved posteriorly and terminating in a long slender curved acute apical tooth; a few minute spinules on the inner surface, some longer, sharp-pointed and isolated, other exceedingly minute and in short transverse rows. Maxillary palp chair-shaped, the "seat" with two sensilla (one cup-shaped and one bearing a small cone), the apex with two apical sensilla (each bearing a spinule). Labial palp elongate (longer than maxillary palp), subconical, with the apical third skewed to one side, bearing two lateral (one button-like and one bearing a small cone) and two apical sensilla.

Trapeziopelta sp.—Plate IV, figs. 17-31. Shaped somewhat like a crookneck squash; thorax and first abdominal somite forming a long slender subcylindrical neck which is strongly bent ventrally; rest of abdomen swollen and subovoidal, its dorsal profile strongly convex, its nearly straight ventral and lateral profiles meeting at right angles; diameter greatest at the sixth abdominal somite. Leg vestiges present. Anus ventral. Thirteen differentiated somites. Body beset with 92 tubercles which are arranged in longitudinal rows on the dorsal and lateral surfaces (none ventral) and distributed as follows: six each on abdominal somites V, VI and IX; two on X; eight each on all other somites. Tubercles subconical, with the apex rounded; those on the thorax relatively slender and 0.075-0.17 mm long, those of the abdomen stouter and ranging in height from 0.075 to 0.19 mm; each tubercle may bear one or two minute (0.018 mm) hairs; the abdominal tubercles have a few

minute integumentary spinules on the apex. Body hairs few, simple, slightly curved, minute (length 0.018-0.07 mm); widely scattered, except on the rather densely hirsute dorsa of abdominal somites IV-VII. Dorsa of posterior abdominal somites and ventral surface of thorax spinulose; spinules exceedingly minute and arranged in short rows; on either side of each abdominal somite there is a dorsolateral and a ventrolateral integumentary structure of unknown nature and function. Head moderately large; cranium subhexagonal in anterior view, but with the occipital border strongly rounded; mouth parts moderately large. Head hairs few, simple, straight, exceedingly minute (length about 0.009 mm); mostly below the level of the antennae. Antennae rather large, elliptical, scarcely elevated; each with three sensilla. Labrum subquadrate; ventral corners rounded; on either side the anterior surface shows a low convexity bearing two minute hairs and about eight sensilla. Posterior surface of labrum densely spinulose; on the median half of the spinules are slender, acuminate and rather long and arranged in short to moderately long transverse combs; on the lateral quarters the spinules are smaller and arranged in short rows or isolated; two groups of sensilla at each side of the medial half—three in a cluster at the middle and five in a basal cluster. Mandibles directed ventrally; completely exposed (or nearly so); moderately sclerotized; long and slender; base only slightly enlarged; apical third strongly curved posteriorly and terminating in a long slender curved acute apical tooth; two short blunt subapical teeth on the inner border; a few minute spinules on the inner surface, some longer, sharp-pointed and isolated, others exceedingly minute and in short transverse rows. Maxillae large; apex conoidal and sparsely spinulose, the spinules coarse, sharp-pointed and isolated; palp chair-shaped, the "seat" with two sensilla (one cup-shaped and one bearing a small cone), the apex with two apical sensilla (each bearing a spinule); galea an elongate truncate cone with two sensilla on its flat apex. Labium wide and prominent; anterior surface spinulose, the spinules longer and in short rows mediobasally, shorter and isolated laterally and distally; on the anterior surface near the base there is a conspicuous transverse welt, which is semicircular in profile and whose spinules are arranged in short transverse rows; palp elongate (longer than maxillary palp), subconical, with the apical third skewed on one side, bearing two lateral (one button-like and one bearing a small cone) and two apical sensilla; opening of sericteries wide and salient with three projections. Hypopharynx densely and coarsely spinulose, the spinules arranged in transverse rows. (Material studied: two larvae—7 mm long—labelled "British N. Borneo E. Mjöberg.")

Trapezoipelta sp.—Labrum subtrapezoidal, slightly narrowed ventrally; slightly broader than long; anterior surface has six sensilla on each convexity; eight sensilla on the ventral border; posterior surface with combs on the middle third. Otherwise similar to the larvae described above. (Material studied: two semipupae—7 mm long—labelled "Mt. Dulit 3000 ft. Br. N. Borneo E. Mjöberg.")

Trapezoipelta sp.—Generally similar to the larvae described first above but differing in the following characters: Tubercles fewer (88) and distrib-

uted as follows: eight each on prothorax and abdominal somites I-III; ten each on mesothorax and metathorax; six each in IV-VIII; four on IX; two on X. All tubercles similar, hemispherical, each bearing an exceedingly minute (about 0.006 mm long) hair. Body hairs exceedingly minute (length 0.009-0.018 mm); no dense patch on the dorsum. Integumentary spinules limited to ventral surface of thorax. Labrum with four sensilla on the ventral border; posterior surface with combs on the middle $^3/_5$; spinules on the outer fifths more numerous and in longer rows. Maxillary spinules shorter and in short transverse rows. (Material studied: one semipupa—6 mm long—labelled "Mt. Penrissen, Sarawak Altitude 2000 f. leg. Dr. E. Mjöberg.")

Tribe ONYCHOMYRMICINI Ashmead

Genus ONYCHOMYRMEX Emery

Moderately stout; constricted at the first abdominal somite; diameter increasing both anteriorly and posteriorly from this constriction; diameter greatest at the sixth abdominal somite. Thorax slightly bent ventrally; abdomen straight. Anus subterminal. No tubercles. Body hairs moderately abundant and uniformly distributed; head hairs very few. Antennae large, with 2-4 sensilla each. Labrum small; not bilobed; subtrapezoidal, narrowed below; several sensilla on or near the ventral and lateral borders; no hairs on the anterior surface; posterior surface sparsely spinulose, the spinules minute and in subparallel rows extending outward and upward from the middle; posterior surface with several sensilla near the ventral border and a median cluster near the base. Mandibles long and narrow; basal $^2/_5$ somewhat enlarged; distal $^3/_5$ very slender, with the apex strongly curved posteriorly (but not medially) and terminating in a slender curved acute apical tooth; two small blunt denticles on the mesal border; no spinules. Maxillae sparsely spinulose; palp a low elliptical elevation furnished with four sensilla (one a frustum, one bearing a finger-like process, and two with a spinule each). Labium with the anterior surface sparsely spinulose; palp a low elevation bearing four sensilla.

Wheeler, 1916, p. 47: "Slender, smooth and nontuberculate, with twelve very distinct postcephalic segments, the constrictions between which are everywhere deep and conspicuous, even at the posterior end of the body. Head short, rounded, with well-developed, slender, acute, falcate mandibles, destitute of teeth. Clypeus rather long, projecting. Antennae very small. Maxillary sensillae long and prominent. Head sparsely, remainder of body more densely and uniformly covered with short, straight, stiff hairs or bristles."

Whenever we examine a larva of Onychomyrmex, we are inclined to exclaim, "How did that get in here?" It certainly does not belong among the higher ponerine larvae. In fact, it hardly belongs among the Ponerinae at all. Apparently a somewhat similar attitude has been held toward the adults. True, the genus has usually been in the tribe Ponerini, but actually it has been *incertae sedis*. Emery in the "Genera Insectorum" says, "La place de ce genre singulier dans la section des Euponerinae et la tribu des Ponerini est provisoire. Tant que le mâle sera inconnu, l'on ne pourra prononcer un jugement fondé sur ses affinités véritables" (1911, p. 97). Wheeler (1916)

expresses a similar opinion but adds, "The larva of Onychomyrmex, in the very distinct segmentation of the body and in the structure of the head, seems to be of a rather primitive type and resembles the larvae of the Dorylinae (Eciton) and lower Ponerinae [now Cerapachyinae] (Acanthostichus, Cerapachys), but the larvae of ants have not been sufficiently studied to enable us to draw satisfactory conclusions concerning the phylogenetic relationships of the various genera" (p. 49).

Although we do not wish to draw any conclusions on phylogeny, we can nevertheless confirm the first part of Wheeler's statement. The larva of Onychomyrmex resembles doryline larvae in the following respects: body nearly straight, but with the anterior end slightly curved ventrally; segmentation distinct; spiracles small; body hairs short, simple and moderately abundant; labrum small; palps poorly developed, not peg-like; trophorhinium poorly developed. It differs from the Dorylinae in not being slender, subcylindrical and progressively attenuated toward the anterior end; in its better developed mandibles; and in having very few head hairs.

The larva of Onychomyrmex resembles the larvae of the Cerapachyinae in the following characters: body constricted at the first abdominal somite, the diameter increasing in both directions from this constriction (as in Eusphinctus and Lioponera, but not in Cerapachys); segmentation distinct; spiracles small; head hairs few, short and simple; labrum small; mandibles not heavily sclerotized; base of mandibles moderately enlarged, the rest long and slender; palps poorly developed, not peg-like; trophorhinium poorly developed. It differs from the cerapachyines in not being slender, nor subcylindrical nor evenly curved ventrally; in having simple body hairs; in not having the mesal borders of the mandibles serrate.

Ashmead (Can. Ent. 37: 382. 1905) regarded the genus Onychomyrmex as constituting a distinct tribe of Ponerinae (Onychomyrmicini). Wheeler (Bull. Am. Mus. Nat. Hist. 45: 638. 1922) gave it the same status in his "Keys to the Genera and Subgenera of Ants." In this we heartily concur; if it must be in the Ponerinae, it certainly should not be in the tribe Ponerini. It differs from the larvae of other genera of this tribe in not having a clearly differentiated neck which is strongly curved or bent ventrally; in lacking tubercles on the body; in having the body hairs moderately abundant (instead of few), in having 2-4 sensilla on each antenna instead of the typical three; in having a small labrum, which is not bilobed; in the shape of the mandibles and their lack of spinules; in the poorly developed palps, which are not peg-like; in the non-salient opening of the sericteries; in the poorly developed trophorhinium.

On the whole we find that the larva of Onychomyrmex shows a closer affinity to the Cerapachyinae than to any other group we have studied.

Onychomyrmex mjöbergi Forel.—Plate VI, figs. 1-7. Moderately stout; constricted at the first abdominal somite; diameter increasing both anteriorly and posteriorly from this constriction; diameter greatest at the sixth abdominal somite. Thorax slightly bent ventrally; abdomen straight; a low longitudinal welt on each side of the abdomen. Posterior end rounded. Anus subterminal. Leg vestiges present. Spiracles small. Segmentation conspicu-

ous, with deep furrows between the thirteen differentiated somites. No tubercles. Body hairs moderately numerous and uniformly distributed; simple, straight or slightly curved, rather stout, acute; short (about 0.035 mm). Integument of the anterior portion of the ventral surface of each thoracic somite with minute spinules in short transverse rows. Head moderately large and suboval; no integumentary spinules. Head hairs very few, widely scattered, simple, nearly straight, stout, acute; short (0.009-0.045 mm). Antennae large, elliptical, only slightly elevated; each with 2-4 sensilla. Labrum small, subtrapezoidal, narrowed ventrally; width about 1¼X length; about 14 sensilla on the ventral and lateral borders or near them on the anterior surface; posterior surface sparsely spinulose, the spinules minute and arranged in subparallel rows (of various lengths) extending obliquely outward and upward from the middle; posterior surface with a few scattered sensilla near the ventral border and a median cluster near the base. Mandibles long and narrow; moderately sclerotized; basal $^{2}/_{5}$ somewhat enlarged; distal $^{3}/_{5}$ very slender, with the apex strongly curved posteriorly (but not medially) and terminating in a slender curved acute apical tooth; two small blunt denticles on the mesal border; no spinules. Maxillae bulging laterally; apex conoidal and sparsely spinulose; spinules minute and arranged in short transverse rows; palp a low elliptical elevation furnished with four sensilla (one a frustum, two bearing each a small spine and one bearing a finger-like process); galea finger-like, with two apical sensilla. Labium with the anterior surface sparsely spinulose, the spinules coarse and isolated; palp a low elevation beset with four sensilla (one button-like and three bearing a spinule each); opening of sericteries wide but not salient, with three projections. (Material studied: numerous larvae from Queensland.)

Wheeler, 1916: Pl. 1, fig. 7—mature larva in side view; Pl. 2, fig. 1—head in side view, enlarged; Pl. 2, fig. 1a—mandible, enlarged; Pl. 2, fig. 2—head in anterior view.

Tribe LEPTOGENYINI Forel

Genus LEPTOGENYS Roger

Neck long and slender, strongly curved or bent ventrally; abdomen elongate, moderately slender, straight, subcircular in cross section. Tubercles numerous (134); mammiform; encircled by a subapical ring of 4-6 relatively long hairs; integument smooth. Tubercles of young larvae pointed. Integument of body densely spinulose. Head rather small; cranium subhexagonal in anterior view; slightly longer than broad; genae bulging at the middle; no integumentary spinules. Antennae large. Head hairs exceedingly minute. Labrum small and narrow, not bilobed; numerous (16-30) sensilla and/or minute hairs on anterior surface, posterior surface sparsely spinulose, the spinules in three patches; ventral border with conspicuous sensilla. Mandibles stout, elongate-subconical, with the apex rounded; a small subapical denticle which projects posteriorly; no apical or medial teeth; middle of mesal and posterior surfaces roughened with denticles. Maxillary palp chair-shaped, with two sensilla on the "seat" (one button-like and one bearing a small cone) and two on the apex (each bearing a spinule).

Wheeler (1903, p. 207) refers to the manner of carrying the larvae "by the neck, with the long slender body extending back between the legs of the worker" (as in *Cerapachys augustae* and Eciton).

Wheeler (1910): "The body [of Lobopelta] is more cylindrical" (p. 72). The larvae of Lobopelta "have prominent, pointed, or rounded tubercles which probably have a protective function" (p. 74). "Larvae furnished with rows of tubercles" (p. 233). On page 234 he mentions a possible function of such tubercles—defending the larvae from one another.

Leptogenys (*Leptogenys*) sp.—Plate VI, figs. 12-21. Shaped somewhat like a crook-neck squash; thorax and first abdominal somite forming a long slender neck which is strongly curved or bent ventrally; rest of abdomen elongate, moderately slender, straight, subcircular in cross section, the ventral surface only slightly flattened, the ventral profile straight, the dorsal slightly curved; posterior end rounded. Anus ventral. Leg vestiges present. Body beset with numerous (134) mammiform tubercles arranged in longitudinal rows and distributed as follows; prothorax, 8; mesothorax and metathorax, each with 10 (two of which are vestigial); abdominal somites I-VIII, 12 each; IX, 8; X, 2; none on ventral surface of thorax or midventral surface of abdomen; height of tubercles 0.07-0.09 mm (higher on abdomen); each tubercle encircled by a subapical ring of 4-6 relatively long (0.15 mm) simple curved hairs, which are constricted at the base; integument smooth. Body hairs very few, widely scattered, simple, straight or slightly curved, minute (about 0.009-0.04 mm long), restricted to the ventral surface. Integument of body densely spinulose; spinules on ventral surface of thorax and midventral surface of abdomen minute and in long transverse subparallel rows; elsewhere they are coarse and not in rows. Head rather small; narrow and elongate; cranium subhexagonal in anterior view, slightly longer than wide; genae bulging at the middle. Head practically naked; head hairs few, simple, minute (about 0.005 mm long), widely and irregularly scattered; no spinules. Antennae high on head; large subelliptical convexities; each with three sensilla. Labrum small; slightly broader than long; widest at the middle, narrowed above and below; anterior surface with about 20 sensilla; ventral border with six frustum-shaped projections each bearing an apical sensillum. Posterior surface of labrum with three spinulose areas—one mediobasal (but with a narrow extension down the middle) and two ventrolateral; spinules mostly minute and arranged in short arcuate rows; two clusters of sensilla (four in each) near the center. Mandibles moderately sclerotized; stout; elongate-subconical; apex rounded; on the posterior surface a small subapical denticle which projects posteriorly; no apical or medial teeth; middle third of mesal and posterior surfaces roughened with denticles. Maxillae conoidal; apical portion spinulose, the spinules isolated and thick-based; palp chair-shaped, with two sensilla on the "seat" (one button-like and one bearing a small cone) and two on the apex (each bearing a spinule); galea finger-like, with two apical sensilla. Labium large; anterior surface spinulose; on the anterior surface near its base there is a conspicuous transverse welt, which is semicircular in profile and whose spinules are arranged in short transverse rows; palp a subcylindrical peg

with the apical third skewed on one side, with two apical (each bearing a spinule) and two subapical (one button-like and one bearing a smaill cone) sensilla; opening of sericteries wide and salient, with three projections. (Material studied: five larvae from Barro Colorado Island, Panama Canal Zone, collected July 20, 1924, by G. C. Wheeler, No. 119; the drawing of the mature larva in side view is based on a specimen collected at Columbiana Farm, Santa Clara, Costa Rica, June 21, 1924, by G. C. Wheeler, No. 43.)

The young larvae of the above species have the body more slender and the posterior end more pointed. Apparently each tubercle is produced apically into a long slender sharp-pointed spine-like process which is very fragile and usually broken or lacking in preserved specimens.

Leptogenys (*Lobopelta*) *elongata* (Buckley).—Plate VI, figs. 8-10. In general like the above species of the subgenus Leptogenys, but differing in the following characters: Body hairs shorter, slenderer and more numerous. All integumentary spinules smaller, the more minute on the ventral and lateral surfaces, the larger on the dorsal. Labrum subtrapezoidal; width at base slightly greater than the length; strongly narrowed but greatly thickened ventrally; anterior surface with about 16 sensilla and/or minute hairs, which are scattered irregularly; from the ventral border project a pair of palp-like structure, each bearing two apical and two posterior sensilla. The mandibles have a longitudinal posterior blade from which the subapical denticle projects. Maxillary and labial palp with the apex more slender. (Material studied: a single damaged integument from Texas, supplemented by Wheeler's figures.)

Wheeler (1900a, p. 16) describes the larvae of the above species as "remarkably slender and scarcely flattened on the ventral surface. In the young larvae the tubercles are distinctly curved and pointed, without apical bristle, and with only a few rather short bristles encircling the base. In the adult larvae the tubercles are larger and shorter, with blunt or acuminate apex and with relatively longer and more numerous basal bristles. The head of the adult larva is remarkable for its length and the narrowness of the labrum, which is nearly as long as the slender mandibles and provided with a median tooth at its tip." Fig. 7 on p. 18: *a,* young larva and *b,* mature larva, in side view; *c,* head of mature larva in anterior view; *d,* tubercle of young and *e,* of mature larva. (This figure is repeated by Wheeler, 1910, as Fig. 39 on p. 73.) "These ants decapitated termite nymphs or cut off their abdomens and scattered these about among their larvae. . . . The larvae had inserted their long necks through the cut surfaces into the soft parts of the termites and were feeding exactly like the larvae of Pachycondyla" (p. 24; repeated 1910, p. 235).

Forel (1921a, Fig. 1A on p. 23 = 1928, Vol. I, Fig. 1A on p. 23): mature larva in side view (after Wheeler). On p. 23 (1921) he describes the larva as "allongée, très mobile, avec la peau couverte de tubercules, avec une tête bien marquée et fournie de mandibules ou pinces." (= 1928, Vol. I, p. 23; "long and very mobile and which has a skin covered with tubercles and a well-defined head furnished with mandibles or nippers.")

Forel (1923, p. 118 = 1928,Vol. II, p. 300) refers briefly to Wheeler's observations on feeding (see under Odontomachus below). On page 116

(= 1928, vol. II, p. 298) he cites Fig. 1A (1921a) to exemplify the larvae of the subfamily (see under Ponerinae below).

Kellogg (1905, p. 540) refers to Wheeler's observations on *L. elongata, Pachycondyla harpax montezumia* and *Odontomachus haematoda clarus:* "The larvae were fed simply by giving them pieces of freshly killed insects, which they chewed and devoured by means of their unusually well-developed mandibles. This method of larval feeding is more primitive (demands less care and manipulation on the part of the workers) than in the case of any other ants, — indeed of any other social insects, for even the wasps, which also feed their young pieces of insects, masticate these insect morsels thoroughly before turning them over to the tender larvae."

Wheeler (1918, p. 295): "I was able to show that their peculiar tuberculate larvae are not fed with regurgitated food, like the larvae of the more specialized ants, but with pieces of insects (1900)."

Leptogenys (*Lobopelta*) *neutralis* Forel.—Wheeler (1933, p. 87) refers to the "slender, long-necked, tuberculate larvae" (p. 87) and states (p. 88) that they are fed on entire or dismembered insects. Dealated females of *Crematogaster* (*Orthocrema*) *dispar* Forel. "had been cut in two at the petiole and only the succulent gasters given to the larvae, which inserted their slender necks into the opening at the anterior end."

Leptogenys (*Odontopelta*) *turneri* Forel.—Pl. VI, fig. 11. In general like the species of *Leptogenys s. str.* described above but differing in the following characters: Tubercles more elongate. The integumentary spinules, which are restricted to the ventral surface of the thorax, are minute and arranged in short transverse subparallel rows. Labrum long and narrow, the breadth at the base being only about seven-tenths the length; subtrapezoidal; lateral borders sinuate, with the distal third spinulose; ventral border rounded and bearing two clusters of three sensilla each; anterior surface with about 30 sensilla and/or minute hairs. Maxillae with the spinules between the palp and galea minute and in long transverse rows; palp with its apex more rounded and bearing five or six sensilla. (Material studied: seven larvae from Queensland.)

Tribe ODONTOMACHINI Mayr

Genus ANOCHETUS Mayr

Subgenus ANOCHETUS Mayr

Neck long and somewhat stout; abdomen straight and rather stout. Tubercles moderately numerous (92). The majority of the tubercles consist of a subconical base bearing 4-6 (usually 5) relatively long hairs; on this base is seated a much slenderer cone, which has mounted on its apex a heavy straight spine-like hair; integument of distal cone with short transverse rows of spinules. On the middorsal surface of the abdomen there are two circular structures, one on somite IV and one on V; they may be considerably elevated and pulley-like or thin discs or merely differentiated areas that are scarcely perceptible in profile; the integument of their dorsal surfaces is glabrous. No integumentary spinules on cranium. Each antennae a low convex area surmounted by a smaller rounded projection bearing three sensilla. Labrum a little broader

than long; bilobed due to a wide and moderately deep incision of the ventral border. Mandibles rather long and narrow, with the base slightly enlarged and the apex slightly curved medially; teeth small and round-pointed; basal half of anterior surface spinulose, the spinules minute and arranged in short transverse arcuate rows. Integument of galea beset with a few minute spinules.

Wheeler, 1910—"Larvae furnished with rows of tubercles" (p. 233). On page 234 he mentions a possible function of such tubercles—defending the larvae from one another.

Anochetus (*Anochetus*) sp.—Pl. V, figs. 1-11. Shaped somewhat like a crook-neck squash; thorax and first abdominal somite forming a long stout neck, which is bent ventrally; the rest of the abdomen straight and rather stout, its diameter greatest at the sixth abdominal somite, its ventral surface nearly flat and with a straight profile, its dorsal surface strongly rounded and with a curved profile; posterior end rounded. Anus ventral, with a conspicuous posterior lip. Leg vestiges present. Prothorax with a rounded swelling on each side, which bears a few minute hairs on its anterior face. Thirteen differentiated somites. Body beset with 92 tubercles distributed thus: Prothorax—10; mesothorax, metathorax and abdominal somites II, III, VI, VII and VIII—8 each; I, IV, V and IX—6 each; X—2; none on midventral surface nor on the dorsa of IV and V. A typical tubercle consists of a subconical base bearing 4-6 (usually 5) relatively long (0.18-0.25 mm) slender simple hairs, which are constricted at the point of attachment; on the apex of this basal cone is seated a much slenderer cone, which has mounted on its apex a heavy straight spine-like hair about 0.12 mm long; over-all length about 0.3-0.38 mm; integument of distal cone with short transverse rows of spinules. The ventrolateral tubercles on the thorax (one pair on each somite) are atypical: they are much smaller; they are not differentiated into two cones; and each bears only one or two hairs. On the middorsal surface of the abdomen there are two large discoidal elevations (one on somite IV and one on V); each might be compared to a pulley with one of its sides fused with the body wall; six or seven simple long (about 0.14 mm) slender hairs arise from the groove on each side (none from the front or back); integument of its dorsal surface glabrous. Body hairs very few; limited to ventral surface; widely scattered, except for a cluster on the prothorax; simple, straight and very short (0.018-0.07 mm); immediately in front of the anus there are a few longer hairs (0.108). Integument of ventral surface sparsely spinulose, the spinules exceedingly minute and mostly arranged in short transverse rows; rest of integument with fine grooves (?) which form a reticulate pattern; scattered irregularly along these grooves are a few exceedingly minute spinules. Head subpyriform in anterior view; cranium slightly broader than long; mouth parts prominent; gula moderately spinulose, the spinules minute and in short transverse rows. Head hairs few, simple, slightly curved, short (0.036-0.06 mm), widely scattered. Each antenna a low convex area surmounted by a smaller rounded projection bearing three apical sensilla. Labrum a little broader than long; narrowed at the base; bilobed, due to a wide and moderately deep incision of the ventral border; each lobe bearing on its ante-

rior surface a short hair and about six sensilla; lateral margins sinuate; posterior surface with numerous fine spinules arranged in short transverse rows (except on the lateral quarters where they are in short arcuate rows) and with two sensilla near the center of each lobe. Mandibles heavily sclerotized; subtriangular in anterior view; rather long and narrow; base slightly enlarged; apex slightly curved medially; apical and two subapical (on mesal surface) teeth small and round-pointed; basal half of anterior surface spinulose, the spinules minute and arranged in short transverse arcuate rows. Maxillae with the apex conoidal and spinulose; palp an elongate cylinder bearing four apical sensilla (one button-like, three bearing a spinule each); galea fingerlike, with two apical sensilla, its integument beset with a few minute spinules. Labium spinulose, the spinules coarse to fine and mostly isolated; on the anterior surface near the base there is a conspicuous transverse welt, which is semicircular in profile and whose spinules are arranged in short transverse rows; palp a slender truncate cone bearing four apical sensilla (one button-like, three bearing a spinule each); opening of sericteries wide and salient, with three projections. Hypopharynx spinulose, the spinules arranged in short transverse rows. (Material studied: seven immature larvae (4.8 mm long) labelled "Tobang Borneo 1300 m E. Mjöberg.")

We have two larvae (unaccompanied by their ants) labelled "Anochetus British Guiana." One is immature (4.8 mm long) and one mature (6.4 mm long). A comparison with our Borneo material shows that they are in the subgenus Anochetus, but there are differences. The immature larva differs from the Borneo specimens (described above) in having raised discs instead of "pulleys" on the dorsa of abdominal somites IV and V; the discs are about half as high, but their diameter is greater, in fact nearly equal to the length of the somite. In the mature larva these discs are depressed to mere circular areas which are scarcely perceptible in profile.

Subgenus STENOMYRMEX Mayr

Tubercles moderately numerous (94). The majority of the tubercles consist of a subconical base bearing 4-9 (usually 6) relatively long hairs; on this base is seated a much slenderer cone, which has mounted on its apex a heavy straight spine-like hair. On the middorsal surface of abdominal somite IV there is a pair of glabrous subcircular scarcely elevated areas; another pair of such areas on V. Gula densely spinulose. Each antenna a low convex area surmounted by a smaller rounded projection bearing three sensilla. Labrum short; breadth twice the length; subtrapezoidal, narrowed at the base; ventral border nearly straight. Mandibles falciform, with one or two denticles on the mesal face at the base of the long slender sharp-pointed apical tooth; middle third of anterior and posterior surfaces spinulose, the spinules minute and grouped in short transverse arcuate rows. Galea spinulose.

Anochetus (*Stenomyrmex*) *emarginatus* (Fabricius).—Plate V, figs. 12, 13 and 15-17. Prothorax with a rounded swelling on each side which bears a few hairs on its anterior face. Leg and gonopod vestiges present. Thirteen differentiated somites. Spiracles on minute papillae. Body beset with 94

tubercles, which are distributed thus: prothorax—10; mesothorax, metathorax and abdominal somites I-III and VI-VIII—8 each; IV, V and IX—6 each; X—2; none on ventral surface nor on dorsa of IV and V. Each tubercle consists of a subconical base bearing 4-9 (usually 6) relatively long (0.19-0.22 mm) slender simple hairs, which are constricted at the point of attachment; on this base is seated a much slenderer cone, which has mounted on its apex a heavy straight spine-like hair about 0.15 mm long; over-all length 0.25-0.4 mm. The ventrolateral tubercles on the thorax (one pair on each somite) are atypical: they are much smaller; they are not differentiated into two cones; and they bear only one or two hairs. On the middorsal surface of abdominal somite IV there is a pair of glabrous subcircular scarcely elevated areas; each area is fringed anteriorly, laterally and posteriorly (but not medially) by 5-8 short (about 0.07 mm) slender simple hairs; another pair of such areas on V. Body hairs few; mostly limited to ventral surface; widely scattered, except for a cluster on the prothorax; simple, slightly curved; length moderate (0.1 mm). Integument of dorsal surface with numerous long fine transverse grooves (?) and sparsely beset with spinules; ventral surface thickly beset with minute blunt spinules which are isolated or in short transverse rows. Cranium transversely subelliptical; gula densely spinulose, the spinules minute and arranged in short transverse rows. Head hairs few, simple, slightly curved, scattered, moderately long (0.07-0.1 mm). Each antenna a low convex area surmounted by a smaller rounded projection bearing three apical sensilla. Labrum short and broad; breadth more than twice the length; subtrapezoidal, narrowed at the base; ventral border nearly straight, spinulose and bearing several sensilla; anterior surface with minute spinules in transverse rows near the middle and near the ventral border, two hairs at each side of the spinulose area and a cluster of six sensilla near each ventral corner. Posterior surface of labrum with numerous fine spinules in short transverse rows, except near the lateral borders where the rows are irregularly arranged; two sensilla on each half. Mandibles falciform, with one or two denticles on the mesal face at the base of the long slender sharp-pointed apical tooth; moderately sclerotized; middle third of anterior and posterior surfaces spinulose, the spinules minute and grouped in short transverse arcuate rows. Maxillae with the apex conoidal and spinulose; palp an elongate cylinder with a fungiform sensillum arising from an apical pit, the rim of which bears three papillae; galea finger-like, its surface bearing spinules and its apex two sensilla (each with a spinule). Labium spinulose, the spinules coarse to fine and mostly isolated; on the anterior surface near the base there is a conspicuous transverse welt which is semicircular in profile and whose spinules are arranged in short transverse rows; palp a slender truncate cone with four apical sensilla (one button-like and three bearing a spinule each); opening of sericteries wide and salient, with three projections. Hypopharynx spinulose, the spinules in short transverse rows. (Material studied: four semipupae from British Guiana.)

Anochetus (*Stenomyrmex*) *emarginatus rugosus* Emery.—Plate V, fig. 14. Apparently similar to *emarginatus s. str.* but differing as follows: Body hairs longer (0.1-0.2 mm). On the dorsal surface of abdominal somites IV and V

the integument shows fine grooves (?) in a reticulate pattern; scattered irregularly along these grooves are a few exceedingly minute spinules. Head hairs longer (0.09-0.13 mm). Apical tooth of mandibles more acute. The maxillary palp (as well as the galea) has its surface spinulose. (Material studied: three damaged integuments from Brazil.)

Anochetus (*Stenomyrmex*) *emarginatus testaceus* Forel.—Apparently similar to *emarginatus s. str.* but differing as follows: Tubercles fewer (80); none atypical. Integumentary spinules mostly confined to the thorax. Head hairs shorter (0.05-0.07 mm). (Material studied: three damaged integuments from Puerto Rico.)

Genus ODONTOMACHUS Latreille

Neck long and rather stout; abdomen straight and somewhat swollen. Tubercles numerous (94-112). The majority of the tubercles consist of a subconical base bearing 3-14 relatively long hairs; on this base is seated a much slenderer cone, which has mounted on its apex a heavy straight spine-like hair; integument of distal cone with short transverse rows of spinules. On the middorsal surface of abdominal somite IV there is a pair of glabrous scarcely elevated areas; another pair of such areas on V. Gula spinulose. Antennae small. Labrum bilobed due to a moderately deep incision of the ventral border; breadth 1½X length. Mandibles moderately long and narrow; scarcely enlarged at base; only slightly curved; one apical and two subapical teeth on the mesal surface; all teeth rather large and prominent, heavily sclerotized, subequal, acute and round-pointed; surface of basal half roughened with short transverse arcuate spinulose ridges.

Clausen, 1940, p. 221: Kapala "appears to be most frequently associated with" Odontomachus. Eucharid larvae are parasitoid in ant larvae.

Wheeler, 1904, p. 767:"The larva of *Odontomachus* is much like that of the typical genus *Ponera*."

Wheeler, 1910: "Larvae furnished with rows of tubercles" (p. 233). On page 234 he mentions a possible function of such tubercles—defending the larvae from one another.

Odontomachus haematoda (Linnaeus).—Pl. VI, figs. 22-29. Shaped somewhat like a crook-neck squash; thorax and first abdominal somite forming a long and rather stout neck which is strongly bent or curved ventrally; rest of abdomen somewhat swollen, nearly straight, the ventral profile nearly straight, the dorsal slightly curved; posterior end rounded. Anus ventral. Leg, wing and gonopod vestiges present. Thirteen differentiated somites. Spiracles on minute papillae. Body beset with numerous (112) tubercles, distributed thus: 10 each on prothorax and abdominal somites I-III and VI-VIII; 8 each on mesothorax, metathorax, IV, V and IX; 2 on X. Of the tubercles just enumerated the following pairs are atypical: ventrolateral on each thoracic somite; dorsolateral on I-IX; dorsal on VI. No tubercles on midventral surface nor on the dorsa of IV and V. A typical tubercle consists of a subconical base bearing 3-6 relatively long (0.16-0.2 mm) slender nearly straight simple hairs, which are constricted at the point of attachment; on this

base is seated a much slenderer cone, which has mounted on its apex a heavy straight spine-like hair about 0.16 mm long; over-all height 0.38 mm; the distal cone bears a few minute spinules on its surface. The atypical thoracic tubercles are small paraboloids, bearing each two short (0.036 mm) hairs; the atypical tubercles on the abdomen are small cones, bearing each an apical hair 0.36 mm long; the pair on IX is represented only by two hairs each. On the middorsal surface of IV there is a pair of contiguous glabrous scarcely elevated areas which is irregularly fringed by about a dozen slender simple short (0.03 mm) hairs; a similar pair on V. Around each of these structures are a few minute spinules arranged in concentric rows; ventral and middorsal (except IV and V) surfaces of each abdominal somite with a patch of exceedingly minute spinules in short transverse rows. Body hairs very few; on ventral surface only; widely scattered, except for a cluster on the prothorax; simple, slightly curved, constricted at the base; very short (0.036-0.09 mm). Head moderately large; cranium transversely subelliptical in anterior view; mouth parts prominent; integument of gula with short transverse rows of minute spinules. Head hairs few, scattered, simple, slightly curved, constricted at the base, short (0.045-0.09 mm). Antennae small; each with three sensilla. Labrum bilobed due to a moderately deep median incision of the ventral border; breadth 1½X the length; constricted at the base; lateral borders sinuate; ventrolateral borders spinulose; ventral border with about six large and four small sensilla; anterior surface of each lobe with two small hairs and about seven sensilla. Posterior surface of labrum with numerous rather long transverse rows of fine spinules on the middle ⅔; lateral sixths with the rows short and scattered; spinules near the ventrolateral corners more numerous and isolated or in short arcuate rows; a cluster of sensilla near the center of each lobe. Mandibles moderately sclerotized; moderately long and narrow; only slightly curved medially and posteriorly; one apical and two subapical teeth on the mesal surface; all teeth rather large and prominent, heavily sclerotized, subequal, acute and round-pointed; surface of basal half roughened with short transverse arcuate spinulose ridges. Maxillae prominent; apex paraboloidal and densely spinulose, the spinules minute, some isolated, others in short transverse rows; palp a subcylindrical peg with four sensilla (one button-like and three bearing spinules) on its flat apex; galea finger-like, with a few scattered spinules near the base and two sensilla on the apex. Labium prominent; densely spinulose, the spinules minute; on the anterior surface the medial spinules are in short rows, the rest isolated; on the posterior surface they are in short transverse rows; palp a slender subcylindrical peg bearing four apical sensilla (one button-like and three bearing spinules); opening of sericteries wide and salient, with three projections. Hypopharynx cordate, with numerous fine spinules in long transverse rows. (Material studied: fourteen larvae from Costa Rica and Jamaica.)

Clausen (1941, p. 57) lists *Chalcura deprivata* (Walker) and *Schizaspidia convergens* (Walker) as parasitoid on this species in Ceylon. Presumably the eucharid larvae were parasitic on the ant larvae.

Eidmann, 1944: "Die Larven sind durch den dünnen, langen, fast

rechtwinklig abgebogenen Thorakalabschnitt ausgezeichnet, der wie ein langer Flaschenhals an dem ampullenartig verdickten Abdomen sitzt. Ihr Körper ist mit grossen Höckern bedeckt, die aus einem dicken Basalabschnitt bestehen, der ringsum mit langen Borsten besetzt ist und eine dünne spitze Papille mit langer Endborste trägt. Bei den Eilarven fehlt der beborstete Basalabschnitt dieser Höcker. Dagegen tragen sie auf der Dorsalseite des 4. und 5. Abdominalsegmentes je ein Paar knopfförmiger Papillen" (p. 438). Fig. 9 on p. 437 shows an egg, a very young larva ("Eilarve"), the tubercle of a mature larva (enlarged), a mature larva and a cocoon.

Emery, 1899: "Le larve di *Odontomachus haematoda* rassomigliano alle precedenti per la forma e per la mancanza di limiti esterni fra i segmenti addominali. I tubercoli sono disposti con ordine più regolare, in serie trasverse, sopra i singoli segmenti. Ciascuno di essi consta di un corpo rotondeggiante, nel mezzo del quale si eleva un prolungamento conico, terminato da un pelo; sulla parte basale ritondata, sono impiantati 4-5 peli, di rado un numero minore, che fanno corona al cono piligero centrale" (p. 5). Pl. I, fig. 4: *a*, mature larva in side view; *b*, thoracic tubercle (enlarged); *c*, mandibles and labrum in anterior view; *d*, maxilla and labium in anterior view.

Emery (1904) and Wheeler (1928a and 1928b, p. 205) discuss mermithergates of *haematoda* and infer that the nematode larvae were parasitic in the ant larvae.

Haskins and Haskins, 1950, p. 4: A young fertilized queen of this species, isolated in an artificial nest, "produced numerous eggs, hatched them, and evidently fed the resulting larvae with ingluvial food (although the process was difficult to observe) since they developed rapidly."

Wheeler, 1900a, p. 15 (referring to Emery, 1899): "Mandibles powerfully developed for ant-larvae, the anterior portion of the body long and slender and folded over the abdominal portion, and . . . with rows of peculiar tubercles set with more or less prominent bristles."

Odontomachus haematoda clarus Roger.—Wheeler, 1900a: "The young larva of *O. haematodes* is represented in Fig. 5, *a*, which shows the arrangement and character of the bristly tubercles and the neck-like anterior portion, consisting of the head, the three thoracic and the first two abdominal segments. The remaining eight abdominal segments are much enlarged and flattened ventrally. The larva is kept on its back, and the neck-like anterior portion rests against the flattened ventral surface. The shape of the tubercles, each of which is tipped with a rigid bristle and encircled with bristles, is shown in Fig. 5, *b*. The larva was about to moult, so that the tubercle of the succeeding cuticle is seen shining through the old one. The adult larva is shown in Fig. 6, *a*. Compared with that of the young larva, its head is very small in proportion to the body. This seems to be the universal rule in ant larvae. The head in dorsal view is represented enlarged in Fig. 6, *b*. The powerful dentate mandibles lie just below the outer edges of the bilobed labrum; still lower and projecting forward lies the labium, bearing on its tip the opening of the spinning gland (to be used in weaving the cocoon), and on either side two

peg-shaped tactile (?) organs. Similar but somewhat larger organs are seen on the edges of the maxillae, which protrude on either side below the mandibles. The ten tracheal stigmata, beginning on the mesothoracic and terminating on the eighth abdominal segment, are clearly shown in Fig. 6, *a*. The bristly tubercles are essentially the same in structure as those of the younger larva, but they are relatively shorter and smaller" (pp. 15-16). Fig. 5 on p. 16: *a*, young larva in side view; *b*, tubercle. Fig. 6 on p. 17: *a*, mature larva in side view; *b*, head in anterior view; *c*, tubercle.

"During the month of May I had frequent opportunity to see Odontomachus feeding its larvae in my artificial nests. These larvae are placed by the ants on their broad backs, and their heads and necks are folded over onto the concave ventral surface, which serves as a table or trough on which the food is placed by the workers. The following observations are transcribed from my notebook:

"May 13. This evening several house-flies, placed in the Janet nest of *O. haematodes*, were at once shorn of their legs, then decapitated, and finally their thoraces and abdomens were cut into smaller pieces and distributed among the larvae. One was given a fly's head, which it kept twirling around in a comical manner, while it devoured the brain through the small cervical orifice. Another was given a piece of a thorax with one of the wings still attached, another a piece of an abdomen, still another, a leg with a mass of muscle at its coxal end, etc.

"May 16. This evening a small homopterous insect was placed in the Odontomachus nest. One of the ants (A) snapped at it, disabled it, and then left it. A few moments later it was picked up by another ant (B) and carried into the chamber containing the larvae and pupae. Thereupon a third ant (C) took hold of it and began tugging at it with B till it was torn open, but not into pieces. B then placed it on the flat ventral surface of a medium-sized larva, which began feeding at once, moving the homopteron around with its jaws. After four minutes had elapsed, another ant (D) that had been standing near by, apparently much interested in the feeding, suddenly tore the morsel away and placed it on a small larva. This larva was permitted to feed ten minutes, closely watched during all this time by ant D and another (E) which had come up in the mean time. Then ant D tried to tear the morsel away from the small larva, but apparently unable to do so, it took up the larva with the morsel and dumped them both on the ventral surface of a large larva. This creature seized the homopteron and forced the small larva to release its hold and to drop to the ground. The large larva fed for fully twenty minutes, closely watched by ant D and two others (E and F). All of these ants tried at different times to wrench the morsel away from the larva, but failed. Suddenly a small ant (G) rushed up, tore it away, and ran off with it. By this time very little was left of the homopteron and I lost track of it.

"May 23. A few crumbs of cake, moistened with water, were placed in the Odontomachus nest at 11.7 P.M. A worker soon carried one of the crumbs into the breeding chamber and gave it to a large larva at 11.20. This larva fed but a few moments, but the cake was not removed till 11.35, when

it was carried into another chamber, then at once brought back and placed between three larvae, from one of which it had just been taken. The smallest of these three larvae nibbled at it for a short time, beginning at 11.40. But one minute later this larva was carried away by a worker, and the cake was taken by another worker and given to a small larva at 11.43. This larva, too, was soon carried away (at 11.48)), and the cake was taken to a large larva, which would have none of it. It was not removed, however, till 11.50. Then it was given by another worker to a large larva, which did eat some of it. At 11.51 the piece of cake, but little diminished in size after all its perambulations, was taken to another large larva. The ant remained over the larva holding the cake in place till 11.58 when another worker came up and ran away with the larva. While the larvae were feeding, the ants themselves could be plainly seen to partake of the cake from time to time. During the whole period of the above observations, and for some minutes later, *i.e.*, for over an hour, one little larva was permitted to feed without interruption on what seemed to be a piece of a house-fly" (pp. 24-26). (Repeated Wheeler, 1910, pp. 235-237.)

Wheeler, 1918, p. 295: "I was able to show that their peculiar tuberculate larvae are not fed with regurgitated food, like the larvae of more specialized ants, but with pieces of insects (1900). Concerning the feeding of the Odontomachus larva I published the following remark (p. 24):

" 'These larvae are placed by the ants on their broad backs, and their heads and necks are folded over onto the concave ventral surface, which serves as a table or trough on which the food is placed by the workers.' "

Escherich (1906, Fig. 30 = 1917, Fig. 36B) refigures Wheeler, 1900a, Fig. 5a.

Forel, 1923, p. 118: Wheeler "a entre autres observé en appareil comment les *Pachycondyla*, les *Lobopelta* et les *Odontomachus* ☿ apportent des insectes, mis en pièces par elles, à leurs larves qu'elles surveillent pendant que celles-ci dévorent ces proies. Quand une larve a à peu près terminé son repas, la pièce d'insecte est portée à une autre et ainsi de suite." (= Forel, 1928, Vol. II, p. 300: Wheeler "has observed among other things the way in which *Pachycondyla, Lobopelta* and *Odontomachus* in an apparatus bring their larvae insects which they themselves have cut into pieces, and watch the young creatures devour their prey. When one larva has nearly finished its meal, the piece of insect is carried to another, and so forth.")

Kellogg (1905, p. 540) refers to Wheeler's observations (1900a) on feeding the larvae (see under Leptogenys above).

Odontomachus haematoda erythrocephala Emery.—Very similar to *haematoda s. str.* The hairs on the tubercles are somewhat longer in *erythrocephala* and the spinules or the anterior surface of the labium are mostly in rows. (Material studied: seven larvae from Panama.)

Odontomachus haematoda insularis var. *pallens* Wheeler. — Clausen (1941, p. 57) lists *Kapala terminalis* Ashmead and *Kapala* sp. as parasitoid on this ant in Cuba. Clausen, 1940, p. 227: "The planidia of *K. terminalis* are usually found attached to the throat of the *Odontomachus* larvae, somewhat to one side. Transfer to the pupa is effected just prior to the first molt

of the parasite, and the appendages of the pupa never attain more than half their full length."

Odontomachus haematoda pubescens var. *bruneipes* Emery.—Eidmann, 1936, p. 37: "Die Larven sind ausgezeichnet durch den dünnen und langen, fast rechtwinklig abgebogenen Thoracalabschnitt, der wie ein langer Hals an dem ampullenartig verdickten Abdomen zu sitzen scheint. Der Körper ist bedeckt mit grossen Höckern, die aus einem dicken Basalabschnitt bestehen, der ringsum mit langen Borsten besetzt ist, und der wiederum eine dünne spitze Papille mit langer Endborste trägt. Die durchaus ähnlich gestaltete Larve der Stammform *Odontomachus haematoda* L. ist von Wheeler abgebildet worden."

Odontomachus affinis Guérin.—Borgmeier, 1920, p. 37: "Nur finden sich auf dem Tuberkel nicht mehr als 5 Härchen, die jedoch viel länger sind als bei *O. haematodes* und ungefähr bis zur Spitze des Dornes reichen, der aus der Mitte des Tuberkels hervorragt." "Für *O. haematodes* hat Wheeler nachgewiesen, dass sie ihre Larven mit Fleischnahrung füttert. Für *O. affinis* ist mir kein derartigen Fall bekannt. In den ersten 3 Monaten, in denen ich den Ameisen ausschliesslich Honig und Zuckerwasser reichte, wurden die Larven gefüttert wie die aller anderen Ameisen: durch Einpumpen der Nahrung. Aber auch hernach, als ich ihnen Termiten zu fressen gab, konnte ich keinen Fall beobachten, wie ihn Wheeler beschreibt."

Wheeler, 1933, p. 15: "Since 1900 I have found so many Ponerine ant-larvae feeding on pieces of insects that Father Borgmeier's (1920) negative observations on the Brazilian *Odontomachus affinis* are somewhat surprising. Though he fed his colonies on termites as well as honey and sugar-water, he was unable to detect any other method of feeding the larvae than by regurgitation."

Odontomachus biolleyi Forel.—Similar to *haematoda* but differing in the following details: all hairs shorter; tubercles shorter; anterior surface of median notch of labrum with a few scattered spinules; mandibles beset with fewer rows of fewer and finer spinules; apex of maxillae dilated and lobose. (Material studied: three semipupae from Costa Rica.)

Odontomachus chelifer (Latreille).—Similar to *haematoda* but differing in the following details: all hairs longer; hairs on tubercles more numerous (7-14). Tubercles taller. Integumentary spinules on the dorsal surface in short rows which are arranged in a concentric pattern around tubercles and spiracles; elsewhere in transverse rows. Six hairs on clypeus. Apex of maxillae dilated and lobose. (Material studied: a larva and a semipupa from Panama Canal Zone.)

Odontomachus rixosus F. Smith.—Similar to *haematoda* but differing as follows: Tubercles taller and less numerous (9-4) due to the lack of atypical tubercles on the abdomen; basal hairs more numerous (5-10). The rows of integumentary spinules are transverse on the ventral surface of the thorax; elsewhere they form a reticulate pattern. Six hairs on the clypeus. (Material studied: five integuments from Siam.)

Odontomachus ruficeps coriaria Mayr.—Dodd (1906, p. 123) records

Rhipipallus affinis Bingham "bred from the pupae" of this ant. Presumably the eucharid larvae were parasitoid on the ant larvae.

Odontomachus tyrannicus F. Smith.—Similar to *haematoda,* except in the following characters: All hairs longer. Tubercles less numerous (98); atypical abdominal tubercles lacking. No dorsal paired structures on the fourth and fifth abdominal somites; in place of each is a typical tubercle. Basal hairs of tubercles more numerous (5-9). Integumentary spinules on the dorsal surface in short rows which are arranged in a concentric pattern around tubercles and spiracles; elsewhere in transverse rows. No integumentary spinules on galea. (Material studied: eight larvae and four semipupae from Dutch New Guinea.)

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Subfamily PONERINAE Lepeletier

Shaped somewhat like a crook-neck squash; thorax and one or two abdominal somites forming a distinct neck which is curved or bent ventrally; rest of abdomen stout and straight, its ventral profile straight, its dorsal convex; ventral surface more or less flattened; usually with a longitudinal welt along each side. Posterior end rounded. Anus ventral or subterminal. Segmentation distinct, but often less so posteriorly; 7-13 differentiated somites, the majority showing 13. Leg vestiges present. Integument diverse—from smooth to densely spinulose; at least the ventral surface of the thorax is nearly always spinulose. Body furnished with either an abundant covering of hairs or with tubercles; in tuberculate larvae the hairs are few and most of them are on the tubercles. In hairy larvae the anterior portion of the prothorax is naked. Hairs typically simple, slightly curved, minute to short; straight, lash-like, denticulate or branched hairs occur in certain genera. Head on the anterior end of the body. Head shape varied. Antennae diverse in size and shape; each with three sensilla. Head hairs never numerous; minute to short; nearly always simple and slightly curved. Labrum mostly medium-sized to large, rarely small; short, breadth greater than length (mostly 1½-2X); usually bilobed due to a median incision of the ventral border; anterior surface furnished with sensilla and minute hairs; posterior surface provided with sensilla and densely spinulose, the spinules usually minute and arranged in rows which form characteristic patterns. Mandibles large for ant larvae; moderately to heavily sclerotized; somewhat broad to slender, mostly rather narrow, curvature usually rather slight; shape diverse; typically with a single apical tooth, which is curved medially, and two prominent subapical teeth on the mesal face; in most genera the surface is more or less spinulose. Maxillae prominent; apex paraboloidal or conoidal, and spinulose; palp and galea conspicuous, slender and paxilliform. Labium prominent, spinulose; palp conspicuous, slender and paxilliform; opening of sericteries wide and salient. Hypopharynx spinulose. Trophorinium elaborate. Carnivorous, feeding typically on insect prey provided by the workers. Active. Neck flexible and used in feeding, defense and limited locomotion.

LITERATURE ON THE SUBFAMILY

References on Feeding.—Bischoff, 1927, p. 87: "Bei den tiefstehenden Ponerinen werden den Larven tote Insekten und zerkautes Futter vorgelegt. Mit ihren verhältnismässig kräftigen, beweglich Mandibeln können sie diese Nahrung selbständig zu sich nehmen. Futter aus dem Kropf der Arbeiterinnen erhalten diese Larven im Gegensatz zu denen der anderen Unterfamilien der Ameisen nicht."

Brun, 1924, p. 95: "Seltener werden grösseren Larven auch mit Speichel durchtränkte Stücke erbeuteter Insekten . . . direkt zum Frasse vorgelegt. Bei den Ponerinen bildet nach den Beobachtungen Forels und Wheelers die einfachere und ursprüngliche Fütterungsart die Regel; daher sehen wir denn auch die Ponerinenlarven mit wesentlich kräftigeren Kieferstummeln ausgerustet. So verraten die Ponerinen auch in dieser Hinsicht, wie in so manchen andern biologischen Eigentümlichkeiten, noch sehr deutlich in Verharren auf verhältnismässig primitiver Entwicklungsstufe, eine Einfachheit der sozialen Sitten, die, im Verein mit einem gewissen Archaismus ihres morphologischen Gepräges, Forel mit Recht veranlasste, sie an den Anfang der phylogenetischen Entwicklungsreihe der Ameisenfamilie zu stellen."

Creighton, 1950, p. 29: "The workers collect other insects or small arthropods and these are cut to pieces and fed directly to the larvae. Regurgitation seems to play a much smaller part in the life of the colony than is the case in the higher subfamilies."

Forel, 1921a, pp. 23-24: "Wheeler surtout a bien montré que les ☿ ne leur dégorgent pas le contenu de leur propre jabot, mais qu'elles se contentent de déposer à côté d'elles des insectes morts ou autre pâtée que les larves savent ensuite dévorer seules-mêmes." (= vol. I, p. 24: "Wheeler in particular has shown that ☿ do not regurgitate the contents of their own crops to the larvae, but that they merely place beside them dead insects or other food which the larvae can afterwards eat on their own account."

Forel, 1921a, p. 134: "Elles nourrissent leurs larves directement en leur apportant des morceaux d'insectes ou de quelque autre comestible, que celles-ci doivent ronger elles-mêmes. Les *Ponerinae* donnent donc habituellement à manger aux larves, par un procédé plus primitif, qui est exceptionnel chez les autres fourmis. Les larves des *Ponerinae* ont une mobilité extraordinaire pour des larves de fourmis. Quand elles sont inquiétées, elles agitent leur long cou comme pour se défendre. Beaucoup d'entre elles ont des tubercules sur la peau." (= 1928, vol. I, p. 129: "They feed their larvae directly by bringing them pieces of insects or some other food, which the larvae have to gnaw for themselves. The *Ponerinae* therefore supply food direct to their larvae by a more primitive process, exceptional among the other ants. The larvae of the *Ponerinae* are remarkably mobile for ant-larvae. When they are disturbed, they move their long necks as though trying to defend themselves. Many of them have tubercles on the skin.")

Forel, 1922, p. 136: "Les larves des *Ponerinae* . . . se nourrissent des proies entières ou decoupées que leur donnent les ☿ sans les emboquer; elles sont assez mobiles et indépendantes pour manger seules." (= 1928, Vol. I, p.

516: "The larvae of the *Ponerinae* . . . feed on prey, whole or in fragments, which the ☿ supply to them without cramming. . . . They are sufficiently mobile and independent to eat alone.")

Forel, 1923, p. 116: "Wheeler a bien prouvé qu'elle dévore seule les proies mortes ou inertes que les ☿ ou les ♀ mettent à sa disposition. Cela paraît être le cas chez tous les *Ponerinae*." (= 1928, vol. II, p. 298: "Wheeler has actually proved that it devours unaided the dead or motionless prey which the ☿ or ♀ place at its disposal. This seems to be the case with all the *Ponerinae*."

Kellogg, 1905, pp. 540-541: a good abstract of Wheeler, 1900a, pp. 26-28.

Krausse, 1929, pp. 96-97: "Meist sind sie nur imstande flüssige Nahrung, die ihnen die Arbeiterinnen reichen, aufzunehmen. Doch können die Larven der Ponerinen und anderer Arten auch feste Nahrung, zerstückelte Insekten usw., selbständig fressen."

Wheeler, 1900a, pp. 26-28: "These observations lead us to several interesting reflections. First, it is certain that the feeding of the larva of the Ponerinae is of a far more primitive character than in any other ants in which this process has been studied. It is, in fact, even more primitive than the corresponding habit of the social wasps, which feed their larvae with masticated insect prey, for in the Ponerinae the prey is cut into a few pieces only, for the purpose of exposing the soft tissues and making them accessible to the mandibles of the larvae. Myriopods or large insects are disarticulated for this purpose, small insects are merely torn open. Leaving the question of systematic affinities out of consideration, the Ponerinae may be said to have habits of feeding the young intermediate between the habits of the solitary wasps, which provide their young with whole insects, and the social wasps, which masticate the food for their larvae. In this statement it may, perhaps, be more accurate to substitute the Bembecidae for the solitary wasps, since the Bembecidae, which feed their larvae from day to day with entire Diptera in a fresh condition, resemble the Ponerinae more closely than do the solitary wasps, which merely enclose their eggs with paralyzed larvae, spiders, grasshoppers, etc. From the condition of the Ponerinae to that of the more specialized ants, which feed their larvae with nothing but the liquid food regurgitated from their own crops or from their salivary glands, the transition is very abrupt. But there are many ants whose habits have not been studied, and some of these may yet be found to bridge this chasm.

"In the second place, the above-recorded observations seem to show that the Ponerine method of feeding the larvae is of a most capricious and irregular character. The quantity and quality of the food given to a particular larva, and the time it is permitted to feed, seem to be matters requiring no very strict regulation. The ants that feed the young rarely act in concert, but rather with a whimsical individualism that seems at times to border on the ridiculous.

"This irregular method of feeding suggests other considerations of a wider bearing. It is generally admitted that the polymorphism of the female sex in ants, *i.e.*, the occurrence of fertile females and of sterile females of one or more casts, is in some manner correlated with the feeding of the larvae developed

from fertilized eggs. In other words, the worker ants can control the production of individuals like themselves and of individuals like their queen. It is further maintained that these differences are effected by the quantity and quality of the food administered to the larvae at a certain period of their development; but here our knowledge ends. These data have been accumulated from the study of the specialized Myrmicine and Formicine ants of Europe and North America, and are supported by many valuable observations on the hive-bee. Now, while we can, perhaps, understand how these more specialized ants may manage to control the quantity and quality of liquid food regurgitated from their own crops and salivary glands, it is not so easy to understand how ants can exercise such control when they adopt a capricious method of feeding like that of the Ponerinae. Such a method can hardly produce clear-cut results; *i.e.*, either workers or fertile females. And a comparative study of the better known species of Ponerinae shows that in certain species at least there is no such sharp distinction between the sterile and fertile female as we find in the more specialized ants."

Wheeler, 1910, p. 234: "All Ponerine larvae, so far as observed, are fed with pieces of insect food. This method, which is undoubtedly very primitive, is also adopted by many specialized ants, but as a rule their larvae are given regurgitated food."

Wheeler, 1918, p. 299: In our North American Ponerinae the larva is "placed on its back by the nurses and fed with fragments of insects deposited on its trough-like ventral surface."

Wheeler, 1922, p. 56: "In the Ponerinae the larvae are nearly always fed with pieces of solid food, which is almost invariably animal matter."

References on Anatomy.—(Emery 1899, p. 8) describes the ponerine type of ant larvae: "con le mandibole robuste e sporgenti e con le appendici piligere dei segmenti del loro tronco."

Emery (1904b) describes the larvae of the Ponerinae as "piriformi o claviformi, con l'addome fortemente rigonfiato, tanto in quelle che portano soltanto peli semplici, come le larve di *Stigmatomma, e Ectatomma,* alle quali aggiungerò quella ancora inedita di *Mystrium,* quanto in quelle che sono fornite di tubercoli piligeri" (pp. 114-115). On page 115 he refers to "la forma tozza e panciuta delle larve di Ponerinae." On page 116 he divides the ponerine larvae into "due gruppi principali: nell'uno di essi che considero come relativamente primitivo, . . . le larve . . . non hanno tubercoli piligeri; comprende le tribù dei Myrmecii, Amblyoponii, Ectatommii, Proceratii e Platythyrei. Nell'altro gruppo, . . . le larve sono tubercolate; comprende tutte le Ponerinae non riferibili al gruppo precedente."

Emery, *Genera Insectorum,* 1911, p. 3: "Les larves des Ponérines ont une mobilité extraordinaire pour des larves de Fourmis. Quand elles sont inquiétées, elles agitent leur long cou comme pour se défendre." In the key to sections (p. 4), he employs larval (as well as adult) characters: "Proponerinae.—Larves uniformément poilues, sans tubercules piligères. . . . Euponerinae. —Larves pourvues de tubercules piligères." Later (p. 16) in characterizing the section Proponerinae: "Larve uniformément poilue, sans tubercules pili-

gères; les segments antérieurs formant un cou plus ou moins grêle, porté sur les segments abdominaux ventrus." For the section Euponerinae: "Larve hérissée de pointes ou de tubercules régulièrement disposés en séries transversales sur chaque segment, portant des poils isolés ou en couronne, d'un aspect tout à fait caractéristique. Ces larves ont un cou grêle" (p. 53).

Escherich, 1917, p. 95: "Bei den Larven der Ponerinen finden wir auf der Oberfläche in regelmässiger segmentaler Anordnung grosse Warzen oder Papillen, welche ihrerseits mit Stacheln, Borsten und kleine Zähnchen besetzt sind."

Forel, 1923, p. 116: "Nous avons vu . . . l'image de leurs larves mobiles, fort indépendantes, pourvues d'une bouche à bonnes mâchoires. Comparée à celles des autres sous-familles . . . elle a presque l'air d'une bête féroce auprès d'enfants au maillot." (= 1928, vol. II, p. 298: "Fig. 1A is an illustration of their mobile larvae, which are very independent and have mouths supplied with serviceable jaws. Compared with those of the other sub-families . . . it looks almost like some fierce animal by the side of children in swaddling-clothes.")

Wheeler, 1910, p. 233: "The great differences between the various tribes of Ponerine ants are reflected in the structure of their larvae. At least three different types may be distinguished among the species that have been studied by Emery . . . and myself . . .: 1. Smooth, thickset larvae, with short, sparse hairs and peculiar unpaired tubercles on the midventral surface of some of the abdominal segments (*Platythyrea*). 2. Smooth, slender larvae, with a rather dense covering of hairs (*Myrmecia, Stigmatomma, Parasyscia, Ectatomma*). 3. Larvae furnished with rows of tubercles which may be pointed or boss-like, tipped or merely encircled with stout hairs (*Pachycondyla, Ponera, Pseudoponera* [*Euponera*], *Leptogenys, Diacamma, Odontomachus, Anochetus*)."

Wheeler, 1920: ". . . rudiments of antennae (which are also present in the larvae of many other ants, notably in the Ponerinae)" (p. 47). "In many ants (Ponerinae)" the trophorhinium "may be used for comminuting parts of insects given directly to the larvae by the workers. . . . Many ant-larvae, notably those of the Ectatommiine Ponerinae . . ., also have elaborate but coarser stridulatory surfaces on the mandibles, so that the larva may be able to produce a variety of sounds and therefore apprise the nurses of more than one need or craving" (pp. 48-49).

Wheeler, 1922, p. 56: "Larvae with the mandibles powerfully developed for ant larvae; the anterior portion of the body long, slender and neck-like, folded over the swollen abdominal portion; the segments are either densely hairy all over or covered with rows of peculiar tubercles beset with more or less prominent bristles; the larvae of *Megaponera* and *Bothroponera* are hairless."

TRIBES

We have not found it feasible to characterize the tribes, chiefly because in most of them the sampling of genera is inadequate, but the following comments seem appropriate:

Tribe Cylindromyrmicini. Not represented in our collection.

Tribe Myrmeciini. We have one (Myrmecia) of the two genera, but it includes nearly all of the known species.

Tribe Amblyoponini. We have three of the six genera. Not sufficiently homogeneous to define.

Tribe Paraponerini. Only one genus.

Tribe Platythyreini. Only one genus.

Tribe Ectatommini. We have eight of the 15 genera. If Prionopelta is excluded, we can characterize the known genera by two traits: antennae small but projecting conspicuously from the head; their diameter not greater than their length; each bears three apical sensilla, each of which is surmounted by a conspicuous stout spinule; body hairs branched or at least denticulate.

Tribe Thaumatomyrmicini. Not represented.

Tribe Proceratiini. We have only one of the eight genera. The larvae of this one (Proceratium) are scarcely recognizable as ant larvae.

Tribe Dorylozelini. Not represented.

Tribe Ponerini. We have 12 of the 33 genera. If Megaponera is excluded, we can characterize the known larvae by only two traits: body furnished with tubercles which are not smoothly rounded bosses and are not restricted to the ventral surfaces; body hairs (other than those on tubercles) usually very few and small.

Tribe Onychomyrmicini. Only one genus (Onychomyrmex). As stated above, this genus shows more affinities with the Cerapachyinae than with the Ponerinae.

Tribe Leptogenyini. We have one (Leptogenys) of the two genera, but it includes nearly all of the known species.

Tribe Odontomachini. We have two of the four genera, but since these two include nearly all the known species, we feel justified in defining this tribe: Neck long and somewhat stout; abdomen straight and rather stout. Tubercles moderately numerous (92-112); the majority consisting of a subconical base bearing 3-14 relatively long hairs; on this base is seated a much slender cone, which has mounted on its apex a heavy straight spine-like hair; integument of distal cone with short transverse rows of spinules. On the middorsal surface of abdominal somite IV there is one or a pair of glabrous areas which may be almost flush or noticeably elevated; similar areas on V.

GENERA

In contrast to this tribal complexity stands the simplicity of the generic situation. Most genera may be readily defined by an adequate number of clear-cut characters. Among these characters are one or more which facilitate identification. In other words, it is easy to construct a key.

Nevertheless there are two groups of genera which constitute exceptions:

1. 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. It is interesting to note that Emery in the *Genera Insectorum* regarded Emeryella as very close to Gnamptogenys.

2. Rhytidoponera and Chalcoponera are likewise difficult to separate and characterize. In the *Genera Insectorum* they are both subgenera of the genus Rhytidoponera.

KEY TO THE GENERA OF MATURE PONERINE LARVAE IN OUR COLLECTION

1. Body without tubercles 2
   Body beset with tubercles 18
2. Body apparently naked (hairs about 0.009 mm long) ..... *Megaponera*
   Body hairs easily seen 3
3. Branched or denticulate body hairs present 4
   Body hairs all simple 13
4. Head hairs denticulate; body hairs whip-like, with the base denticulate ..... *Ectatomma* (*Ectatomma*)
   Not as above 5
5. Head hairs simple 6
   Head hairs branched 12
6. Mandibles with all spinules short 7
   Mandibles with some of the spinules longer and grouped in prominent combs 8
7. Mandibles with a deep and wide notch between the two medial teeth; apical tooth straight ..... *Rhytidoponera*
   Mandibles with a deep but narrow notch between the two medial teeth, apical tooth curved, narrow and sharp pointed ..... *Chalcoponera*
8. Body hairs all with long branches ..... *Stictoponera*
   Some body hairs with short branches (denticles) 9
9. Mandibles with all teeth blunt ..... *Emeryella*
   Mandibles with the medial teeth acute 10
10. Body hairs all with short lateral branches ..... *Ectatomma* (*Poneracantha*)
    Most body hairs with long branches 11
11. Antennae about as long as their diameter; body hairs mostly bifid ..... *Ectatomma* (*Parectatomma*)
    Antennae about twice as long as their diameter; body hairs mostly 4-branched ..... *Ectatomma* (*Gnamptogenys*)
12. Mandibles with some of the spinules longer and grouped in prominent combs ..... *Holcoponera*
    Mandibles with all spinules minute; mandible divided into a greatly inflated base and a very slender distal portion ..... *Typhlomyrmex*
13. Not distinctly differentiated into a more slender "neck" and a stouter "body" 14
    Differentiated into a more slender "neck" and a stouter "body" 16
14. Diameter least at the first abdominal somite; thorax swollen ..... *Onychomyrmex*
    Not as above 15
15. Hairs all short and slightly curved ..... *Myrmecia*
    Most hairs short, but some much longer and lash-like ..... *Prionopelta*
16. Mandibles with teeth on the anterior surface as well as the medial surface ..... *Stigmatomma*
    Mandibles with teeth on the medial surface only 17
17. Mandibles very narrow and elongate; body sparsely hairy ..... *Amblyopone*
    Mandibles broad and subtriangular; body densely hairy ..... *Paraponera*
18. Tubercles few (less than 50) and inconspicuous, restricted either to the ventral or to the lateral surfaces 19
    Tubercles numerous (80 to 400) and conspicuous 20
19. Tubercles restricted to ventral surface ..... *Platythyrea*
    Tubercles lateral ..... *Bothroponera*
20. Tubercles of two distinct types; mostly finger-like; a few pairs of conspicuous doorknob-shaped tubercles on the dorsal surface 21
    Tubercles not as above 23
21. Hairs denticulate ..... *Cryptopone*
    Hairs simple 22

22. Finger-like tubercles with a conspicuous apical spine-like hair ..... *Ponera*
Finger-like tubercles without apical spine ..... *Euponera* (*Trachymesopus*) *gilva*
23. Tubercles consisting of a subconical base bearing relatively long hairs and surmounted by a slender spinulose cone which bears on its apex a conspicuous spine-like hair (Tribe Odontomachini) 24
Tubercles not as above 27
24. With glabrous areas, partially fringed by hairs, on the dorsum of abdominal somites IV and V 25
Without such areas on the dorsum ..... *Odontomachus tyrannicus*
25. A single glabrous area on the dorsum of each of abdominal somites IV and V ..... *Anochetus* (*Anochetus*)
A pair of glabrous areas on the dorsum of each of abdominal somites IV and V .. 26
26. Mandibles with medial teeth subequal to the apical tooth ..... *Odontomachus* (except *O. tyrannicus*)
Mandibles with medial teeth reduced to denticles ..... *Anochetus* (*Stenomyrmex*)
27. Body beset with numerous rounded (but not mammiform) tubercles which are generally distributed (even on the dorsal surface); mandibles reduced and without teeth ..... *Proceratium*
Tubercles not as above; mandibles well developed 28
28. Tubercles mammiform 29
Tubercles not mammiform 31
29. Mandibles with a posterior denticle but without medial teeth; labrum narrow, not bilobed ..... *Leptogenys*
Mandibles with distinct medial teeth; labrum broad and bilobed 30
30. Mandibles with two apical and one subapical tooth; cranium short (a third broader than long) ..... *Dinoponera*
Mandibles with one apical and two subapical teeth; cranium as broad as long ..... *Pachycondyla*
31. Tubercles very numerous (350-400) and so slender as to simulate hairs ..... *Centromyrmex*
Tubercles less numerous (not over 200); not hair-like 32
32. Tubercles subconical 33
Tubercles not subconical 36
33. Tubercles with spinules confined to apex ..... *Trapeziopelta*
Tubercles encircled by rows of spinules 34
34. Tubercles with several lateral hairs; head hairs minute and inconspicuous ..... *Neoponera*
Tubercles with minute apical (but no lateral) hairs; head hairs short but conspicuous 35
35. Tubercles attenuated to a slender spire ..... *Odontoponera*
Tubercles not as above ..... *Euponera* (*Mesoponera*) *constricta* and *E.* (*Trachymesopus*) *stigma*
36. Tubercles paraboloidal, crowned with minute conoidal papilla ..... *Diacamma australe*
Tubercles consisting of an expanded base and a distal spine-like projection ..... *Diacamma scalpratum* and *D. rugosum* subspp

SPECIES

Concerning specific differences no general statement can be made. Thirteen of our genera are represented by only one species each. The others may be grouped according to the degree of differentiation of the species in our collection:

1. Species indistinguishable—Holcoponera, Chalcoponera, Ectatomma (*s. str.*).

2. Species scarcely distinguishable.—Myrmecia, Amblyopone, Stictoponera, Rhytidoponera, Proceratium, Pachycondyla.

3. Species easily distinguishable.—Ectatomma (*s. lat.*), Diacamma, Neoponera, Bothroponera, Euponera, Ponera, Trapeziopelta, Leptogenys, Anochetus, Odontomachus.

4. Specific differences of generic magnitude.—*Diacamma australe* vs. *D. rugosum* and *D. scalpratum*—on account of tubercles. The genus Ectatomma (*s. lat.*) presents a peculiar situation: subgenus Ectatomma vs. subgenera Poneracantha, Parectatomma and Gnamptogenys—on account of body hairs, antennae, shape of mandibles and mandibular spinules; in fact the last three subgenera more closely resemble the genus Emeryella than their congeneric subgenus Ectatomma. A similar situation obtains in the genus Anochetus: subgenus Anochetus vs. subgenus Stenomyrmex—on account of the labrum, mandibles and peculiar glabrous areas on the dorsa of abdominal somites IV and V; in fact the larvae of Anochetus *s. str.* are more like those of the genus Odontomachus than their own congeners of the subgenus Stenomyrmex. The situation in Euponera, which is considerably more complicated, is discussed above under the genus.

DISCUSSION

The larvae of the Ponerinae do not constitute as homogeneous a group as do the Dorylinae or the Cerapachyinae or the Attini, but this is perhaps to be expected since they are a much larger group. The nearest to a distinctive character is probably body shape; yet a fourth of the larvae studied are exceptional in this respect. We cannot select any one genus and call it typical; Centromyrmex may be as close as any. Certain genera are so aberrant that they can hardly be recognized as ponerines: Platythyrea, Prionopelta, Proceratiam, Megaponera and Onychomyrmex. Prionopelta, Megaponera and Onychomyrmex are more like dorylines or cerapachyines. Platythyrea and Proceratium are *sui generis*.

Among the typical ponerine larvae the most specialized of the nontuberculate genera occur in the tribe Ectatommini; among the tuberculate genera it is possibly Leptogenys.

Wheeler (1918, p. 295) considered the adults of *Myrmecia sanguinea* to be the most primitive of existing Formicidae. We believe that the same can be said of the larva, which we regard as primitive in every respect, but notably in the following details: body shape; short, simple and abundant hairs; few minute hairs on the head; size, shape and position of antennae; general size and shape of labrum; posterior labral spinules are not in rows but isolated; palp and galea peg-like and only moderately long; labial palp a low rounded elevation; opening of sericteries wide but not salient.

Other genera which are primitive—both in adult and larval stages—are Stigmatomma, Amblyopone, Mystrium and Paraponera. The first two show some advance in body shape in mandibles and in longer hairs. The larva of Paraponera is almost as primitive as that of Myrmecia; its body shape, however, is ponerine. Mosley (Bull. Soc. Ent. France 43: 190-194, 6 figs. 1938.) regards Mystrium as the possible ancestor of all Formicidae. It is most unfortunate, therefore, that our single larva is in such poor condition. From those

parts available, however, we judge it to be somewhat less primitive than Myrmecia.

It seems to us that the following phylogenetic hypothesis might be justified: The larva of Myrmecia represents the ancestral formicid type from which the higher ponerine larvae evolved by differentiation into a slender curved "neck" and larger "body." Before this differentiation occurred, a side branch was formed, the larvae of which became more attenuated posteriorly; this line led to the Cerapachyinae. A secondary offshoot from it gave rise through a straightening of the larval body to the Dorylinae.

SUMMARY

The larvae of 67 species in 31 genera are described and illustrated. References to ponerine larvae from the literature are cited, bringing the total number of species and genera considered up to 93 and 32 respectively. A bibliography is appended. The larvae of the Ponerinae do not constitute a homogeneous group and consequently are difficult to characterize as a subfamily. Most tribes cannot be characterized at present. Genera, on the other hand, are easy to distinguish and define. A key to the genera is included. Within genera, however, larval taxonomy is not closely correlated with adult taxonomy: in some genera the species show differences of generic magnitude; in others the differences are less striking, but the species are easily separated; in some the species are difficult to distinguish, while in a few they are indistinguishable. By way of contrast, a phylogenetic tree based on larval characters would be similar to that based on adult characters: Myrmecia is regarded as the most primitive and putatively ancestral to the Ponerinae (and in fact to all Formicidae); two lines of evolution culminate in the Ectatommini and in the Leptogenyini.

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EXPLANATION OF PLATES

PLATE I. *Centromyrmex feae* Emery, Figs. 1-10.—1, head in anterior view, ×56; 2, right half of labrum in posterior view, ×118; 3, body hair, ×121; 4, larva in side view, ×12; 5, right mandible in anterior view, ×121; 6, right mandible in posterior view, ×121; 7-10, four body tubercles, ×121.

Odontoponera transversa (F. Smith), Figs. 11-19.—11, head in anterior view, ×44; 12, integument of body, ×117; 13, left mandible in anterior view, ×60; 14, tubercle, ×117; 15, head hair, ×185; 16, larva in side view, ×10; 17, spinules of head in surface view, ×185; 18, spinules of head in profile, ×185; 19, ventrolateral organ of abdominal somite V, ×117.

Megaponera foetens (Fabricius), Figs. 20-25.—20, head in anterior view, ×22; 21, left mandible in anterior view, ×44; 22, body hair, ×370; 23, metathoracic leg vestiges in surface view, ×44; 24, lateral third of abdominal somite III in ventral view, ×22; 25, larva in side view, ×4.

PLATE II. *Dinoponera grandis mutica* Emery, Figs. 1-8.—1, head in anterior view, ×16; 2, two tubercle hairs, ×57; 3, right mandible in anterior view, ×33; 4, larva in side view, ×4; 5, spinules on integument of tubercle, ×115; 6, spinules on integument of prothorax, ×115; 7, spinules on integument between tubercles, ×115; 8, head, pro- and mesothorax in ventral view, ×11.

Diacamma australe (Fabricius), Figs. 9-18.—9, head in anterior view, ×33; 10, left mandible in anterior view, ×73; 11, tubercle, ×92; 12, larva in side view, ×8; 13, integumentary pattern on gula, ×183; 14, integumentary pattern on cranium, ×183; 15, left galea in anterior view, ×95; 16, body hair, ×100; 17, body spinules in profile, ×185; 18, structure near spiracle on abdominal somite III, ×47.

Diacamma scalpratum (F. Smith), Figs. 19 and 20.—19, body hair, ×100; 20, tubercle, ×92.

Diacamma rugosum viridipurpureum Emery, Figs. 21-24.—21, body hair, ×100; 22, tubercle, ×100; 23, labium of young in anterior view, ×40; 24, labium of young in side view enclosing labium of next instar larva, ×40.

Bothroponera sp., Fig. 25, head in anterior view, ×44.

Bothroponera sublaevis Emery, Figs. 26-30.—26, left mandible in posterior view, ×47; 27, tubercle, ×92; 28, left metathoracic leg vestige and spinules, ×44; 29, body spinules in profile, ×185; 30, body hair, ×185.

PLATE III. *Pachycondyla striata* F. Smith, Figs. 1-10.—1, head in anterior view, ×28; 2, labrum in posterior view (right half only), ×61; 3, larva in side view, ×7; 4, right mandible in anterior view, ×61; 5, body hair, ×185; 6, tubercle hair, ×185; 7, immature tubercle enclosing mature tubercle, ×121; 8, mature tubercle in side view, ×57; 9, mature tubercle in surface view, ×57; 10, young larva in ventral view, ×7.

Neoponera villosa (Fabricius), Figs. 11, 12, 14 and 18.—11, abdominal tubercle, ×47; 12, thoracic tubercle, ×47; 14, right mandible in anterior view, ×47; 18, head in anterior view, ×32.

Neoponera apicalis (Latreille), Fig. 13, thoracic tubercle, ×47.

Neoponera obscuricornis latreillei Forel, Figs. 15-17 and 19.—15, integumentary spinules and body hair, ×185; 16, mature vestigial abdominal tubercle, ×47; 17, thoracic tubercle, ×47; 19, immature larva in side view, ×10.

Cryptopone mayri Mann, Figs. 20-26.—20, head in anterior view, ×80; 21, dorsal abdominal tubercle, ×108; 22, galea, ×233; 23, maxillary palp, ×233; 24, tubercle, ×167; 25, body hair, ×167; 26, left mandible in anterior view, ×185.

PLATE IV. *Euponera* (*Mesoponera*) *constricta* (Mayr), Figs. 1-7.—1, head in anterior view, ×33; 2, left mandible in anterior view, ×92; 3, larva in side view, ×13; 4, thoracic tubercle, ×106; 5, body hair, ×185; 6, abdominal tubercle, ×106; 7, dorsal abdominal tubercle, ×106.

Euponera (*Trachymesopus*) *gilva* (Roger), Figs. 8-16.—8, left maxilla in anterior view, ×118; 9, labrum in posterior view (right half only), ×118; 10, right mandible in anterior view, ×118; 11, head in anterior view, ×71; 12, labium and hypopharynx in side view, ×118; 13, body hair, ×125; 14, abdominal tubercle, ×119; 15, doorknob-shaped tubercle, ×137; 16, larva in side view, ×15.

Trapeziopelta sp. (labelled "British N. Borneo E. Mjöberg"), Figs. 17-31.—17, head in anterior view, ×44; 18, right mandible in anterior view, ×95; 19, right mandible in medial view, ×95; 20, left maxilla in anterior view, ×95; 21, left maxillary palp in ventral view, ×185; 22, left labial palp in anterior view, ×185; 23, dorsolateral integumentary structure, ×38; 24, two body hairs, ×191; 25, larva in side view, ×8; 26, labrum in posterior view, ×92; 27, a labral comb, ×333; 28, typical abdominal tubercle, ×44; 29, dorsal abdominal tubercle, ×44; 30, dorsal thoracic tubercle, ×44; 31, lateral thoracic tubercle, ×44.

PLATE V. *Anochetus* (*Anochetus*) sp. (labelled "Tobang Borneo 1300 m E. Mjöberg"), Figs. 1-11.—1, head in anterior view, ×47; 2, left antenna in side view, ×185; 3, typical tubercle, ×67; 4, left mandible in anterior view, ×73; 5 and 7, two body hairs, ×185; 6, ventrolateral thoracic tubercle, ×67; 8, larva in side view, ×11; 9, pattern and spinules of integument, ×130; 10, "pulley" on dorsum of abdominal somite IV or V, in side view, ×33; 11; "pulley" on dorsum of abdominal somite IV or V, in dorsal view, ×33.

Anochetus (*Stenomyrmex*) *emarginatus* (Fabricius), Figs. 12, 13 and 15-17.—12, head in anterior view, ×44; 13, right mandible in posterior view, ×92; 15, elevated area on dorsum of abdominal somite IV or V, in side view, ×33; 16, elevated area on dorsum of abdominal somite IV or V, in dorsal view, ×33; 17, body hair, ×67.

Anochetus (*Stenomyrmex*) *emarginatus rugosus* Emery, Fig. 14, palp and galea of left maxilla in anterior view, ×130.

Ponera coarctata pennsylvanica Buckley, Figs. 18-21 and 28-32.—18, head in anterior view, ×71; 19, right mandible in anterior view, ×118; 20, right mandible in posterior view, ×118; 21, larva in side view, ×19; 28, doorknob-like tubercle, ×185; 29, spire-like tubercle, ×185; 30, spinules on dorsal surface of abdomen in dorsal view and in profile, ×185; 31, spinules on ventral surface of abdomen in ventral view and in profile, ×185; 32, two body hairs, ×185.

Ponera sp. (North Dakota, greenhouse, No. 417), Figs. 22-27.—22, spinules on dorsal surface in profile, ×185; 23, spinules on ventral surface in ventral view, ×185; 24, spire-like tubercle, ×185; 25, doorknob-like tubercle, ×185; 26, body hair, ×185; 27, ventrolateral prothoracic projection, ×185.

Ponera sp. (from New South Wales), Fig. 33, head, pro- and mesothorax in ventral view to show flap-like projections, ×47.

PLATE VI. *Onychomyrmex mjöbergi* Forel, Figs. 1-7.—1, head in anterior view, ×95; 2, labrum in posterior view (right half only), ×185; 3, body hair, ×180; 4, left mandible in anterior view, ×111; 5, right maxillary palp in anterior view, ×367; 6, right mandible in medial view, ×111; 7, larva in side view, ×20.

Leptogenys (*Lobopelta*) *elongata* (Buckley), Figs. 8-10.—8, right mandible in medial view, ×117; 9, labrum in anterior view, ×117; 10, labrum in side view, ×117.

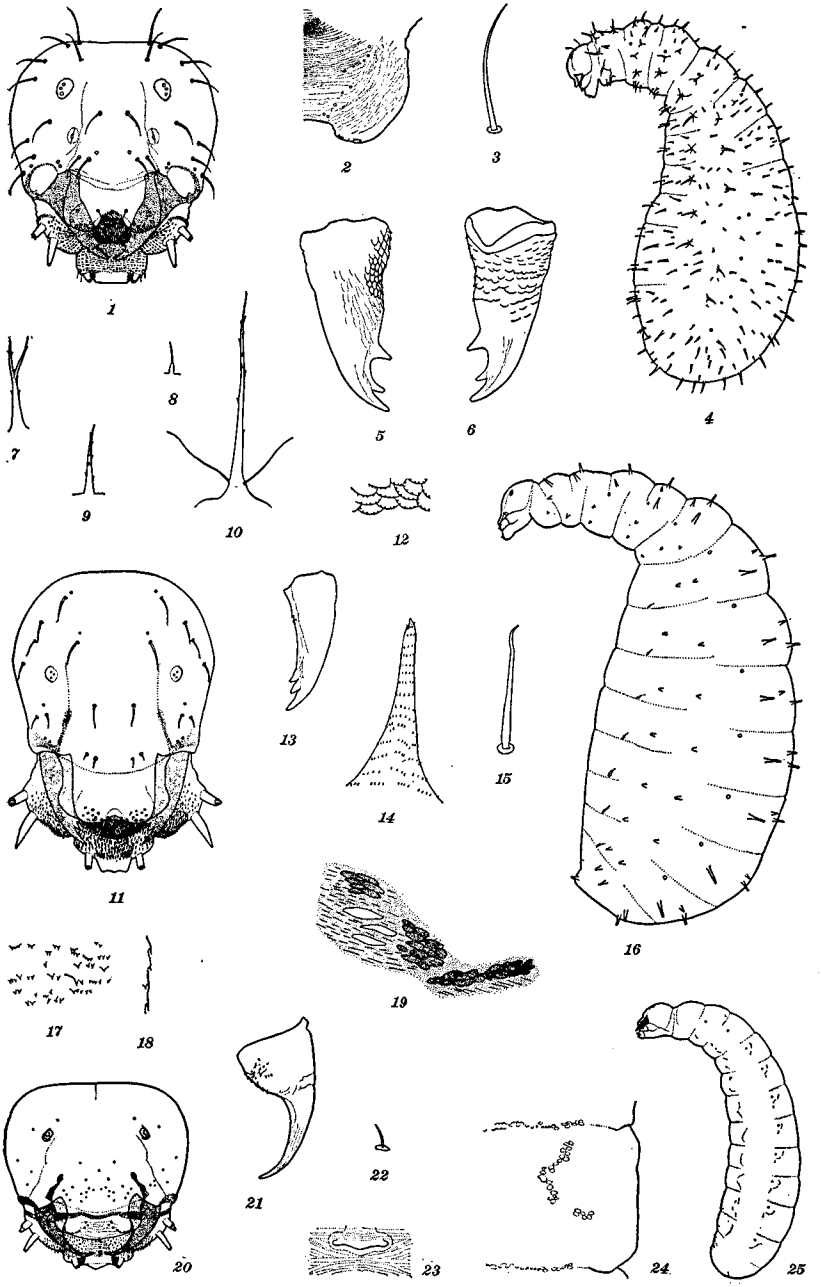
Leptogenys (*Odontopelta*) *turneri* Forel, Fig. 11, thoracic tubercle, ×72.

Leptogenys (*Leptogenys*) sp. (Panama Canal Zone, No. 119), Figs. 12, 13 and 15-21.—12, head in anterior view, ×77; 13, labrum in posterior view, ×117; 15, thoracic tubercle, ×72; 16, body hair, ×224; 17, abdominal tubercle, ×72; 18, right mandible in anterior view, ×117; 19, right mandible in posterior view, ×117; 20, right mandible in medial view, ×117; 21, right mandible in side view, ×117.

Leptogenys (*Leptogenys*) sp. (Panama Canal Zone, No. 43), Fig. 14, larva in side view, ×8.

Odontomachus haematoda (Linnaeus), Figs. 22-29.—22, head in anterior view, ×36; 23, typical tubercle, ×56; 24, atypical thoracic tubercle, ×56; 25, atypical abdominal tubercle, ×56; 26, larva in side view, ×11; 27, left mandible in anterior view, ×60; 28, body hair, ×231; 29, glabrous areas on dorsal surface of abdominal somite IV, in dorsal view, ×56.

PLATE I



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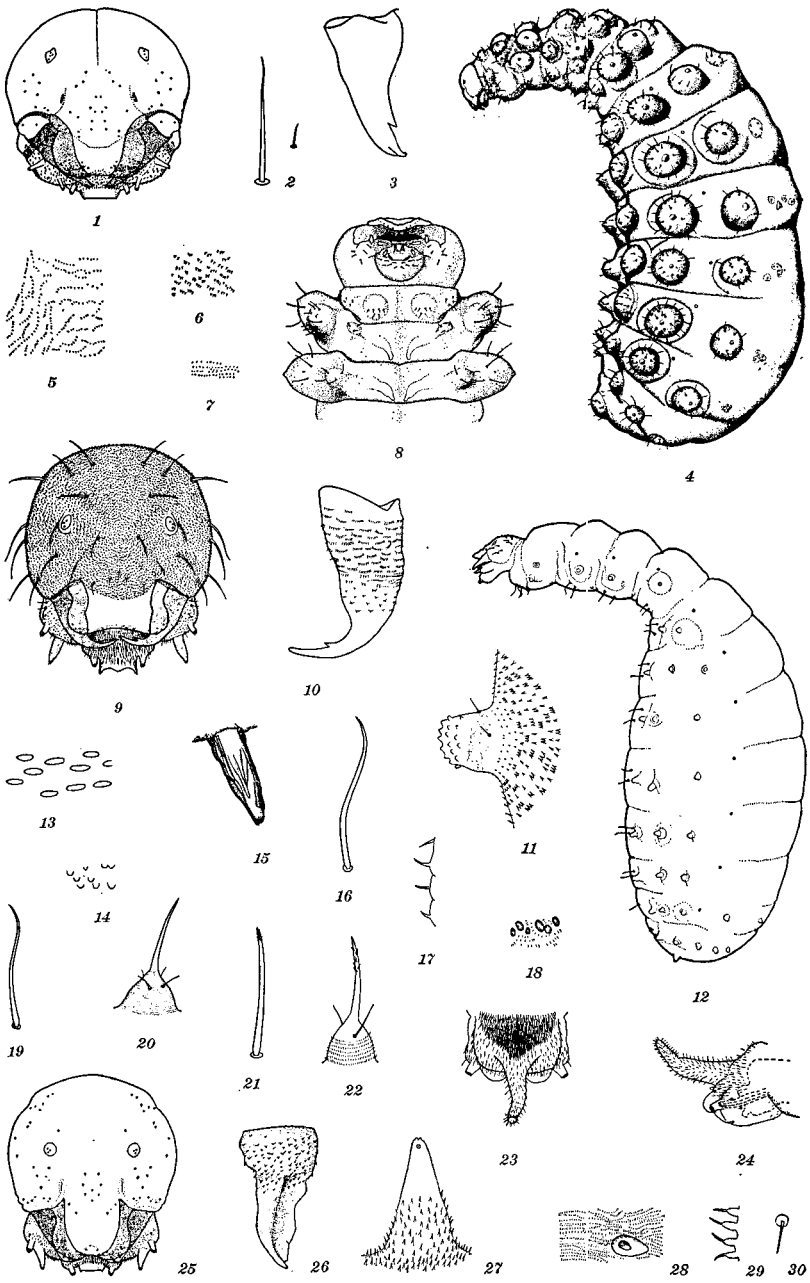
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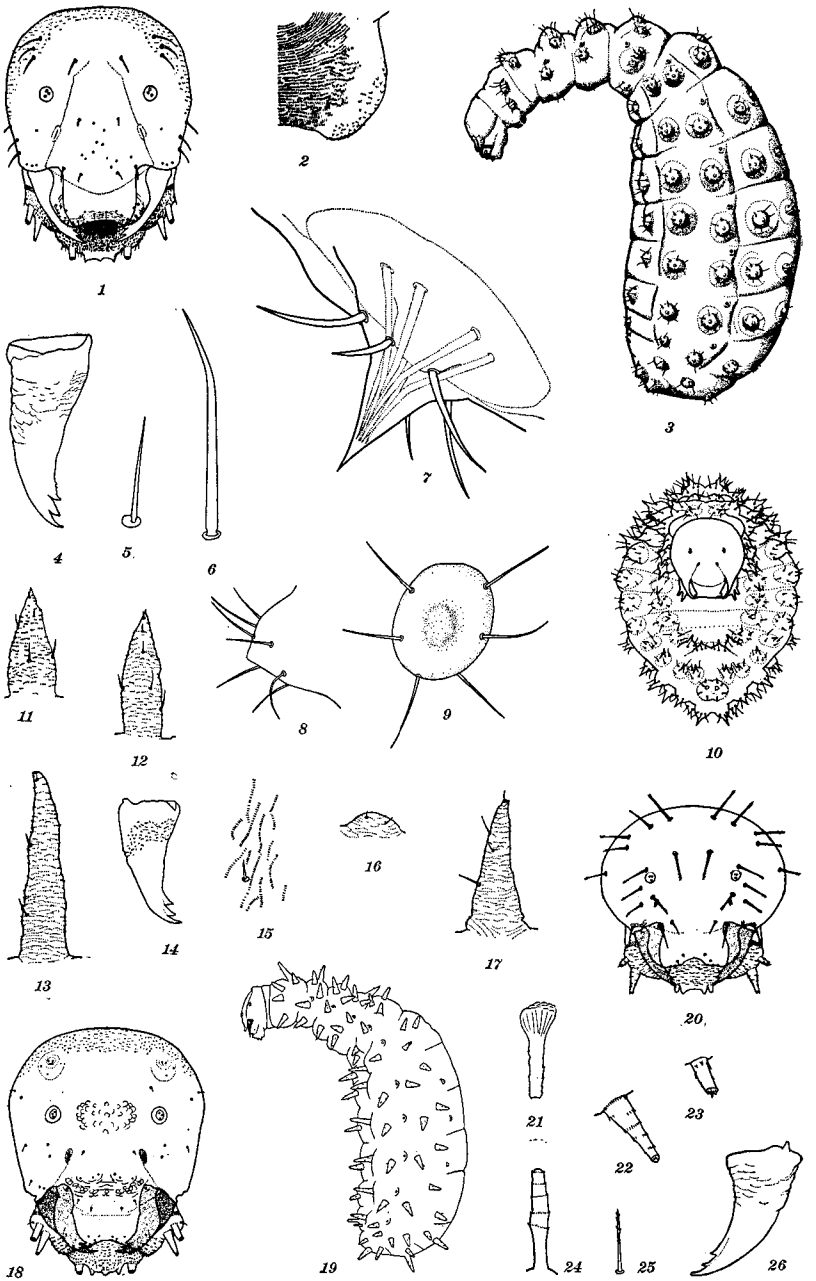
PLATE III



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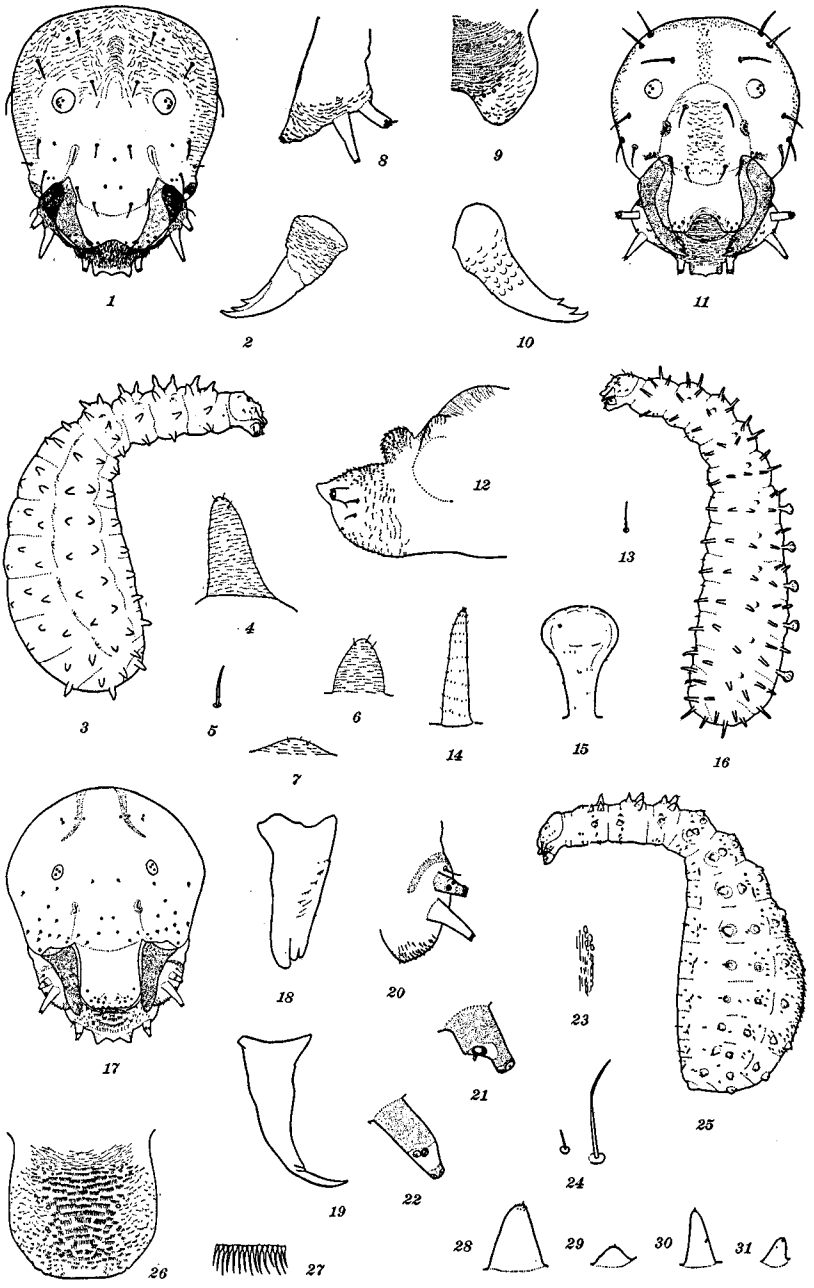
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Plate V

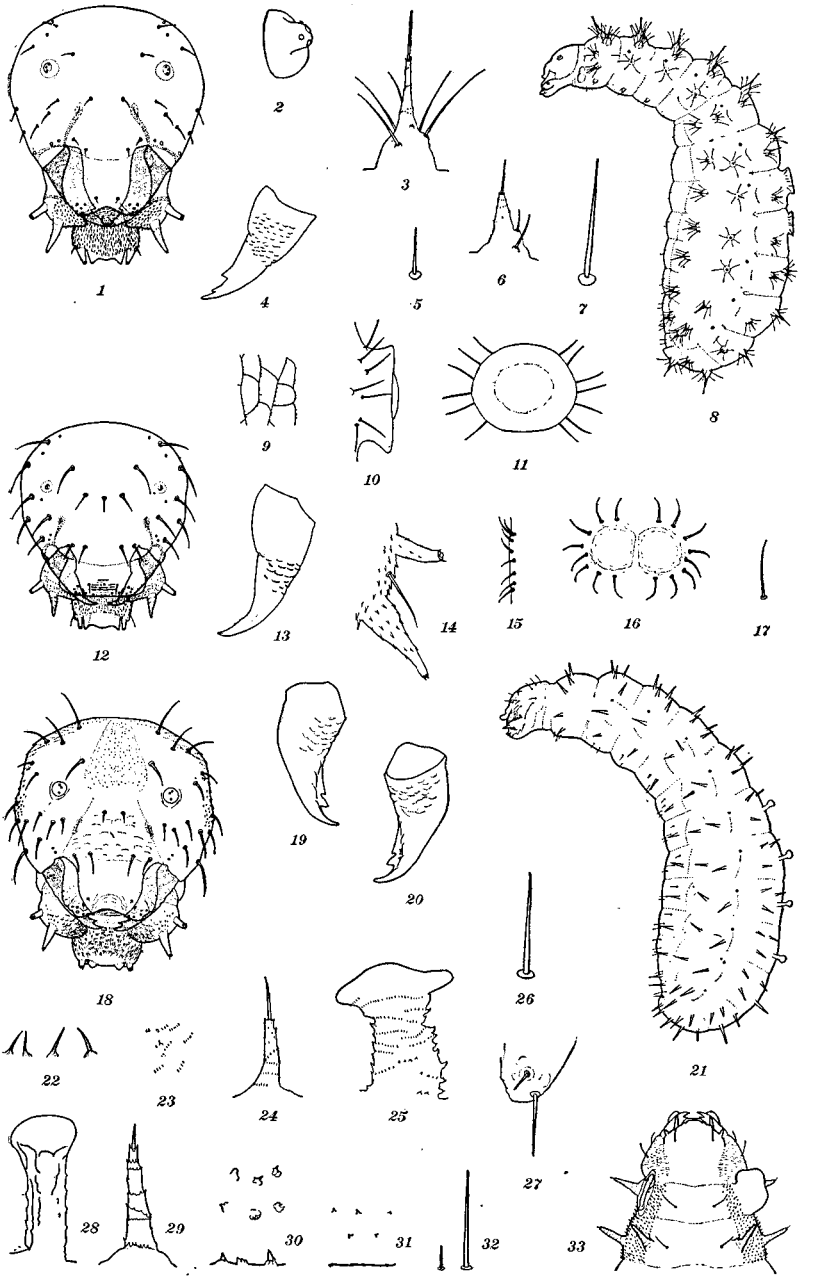
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PLATE VI