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# Ant Larvae of the Subfamily Formicinae: Second Supplement[1,2]

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ABSTRACT

The present supplement contains descriptions of the larvae of 16 species in the genera *Acanthomyops, Myrmecorhynchus, Opisthopsis, Polyrhachis,* and *Camponotus* (Hymenoptera: Formicidae). Tribes are characterized. References to recent literature are cited. The body profiles of formicine larvae are classified into 8, and the mandible shapes into 9 generalized types. The least specialized profile is that of *Melophorus;* the most specialized are profiles of *Myrmelachista* and *Camponotus.* All formicine mandible shapes are specialized, but the most specialized are those of *Myrmelachista, Plagiolepis,* and *Oecophylla.* A revised key is given to the mature formicine larvae available for study, based mostly on body profile and mandible shape.

The purposes of this supplement are: (1) to describe the larvae of the species of formicines acquired subsequent to the preparation of our 1st supplement (1968); (2) to revise our published characterizations as required by the new material; (3) to cite recent references in the literature; (4) to classify body profiles and mandible shapes; and (5) to revise our key to the formicine larvae. Including this supplement, we have studied a total of 130 species in 26 genera of the subfamily Formicinae.

## Genus *Acanthomyops* Mayr

*Revised Description.*—Anus with anterior and posterior lips, the latter the larger. Three types of body hairs occur: (1) simple; (2) 2- or 3-branched; (3) denticulate. A larva may have denticulate hairs only or all 3 types. Antennae small. Head hairs few and moderately long. Three types of head hairs occur: (1) simple; (2) 2- or 3-branched; (3) denticulate. A larva usually has only denticulate head hairs or simple and branched head hairs. Mandibles subtriangular in anterior view; width (at base) ca. ⅔ length; medial border strongly convex and bearing a few denticles on the distal half; lateral border feebly convex.

### *A. mexicanus* (Wheeler)

*Immature Larva.*—Length (through spiracles) ca. 3.4 mm. Similar to *A. subglaber* (Emery) (Wheeler and Wheeler 1953: 155) except in the following details. Head hairs stout, denticulate. Posterior surface of labrum with 6 sensilla. Mandibles with the apical tooth longer and more curved. Maxillary palp with 1 apical, 2 subapical, and 2 lateral sensilla.

*Material Studied.*—Four larvae from Mexico, courtesy of Dr. M. W. Wing.

### *A. subglaber* (Emery)

(Fig. 1)

This genus was considered a subgenus of *Lasius* in Wheeler and Wheeler (1953), hence we did not draw a typical mature worker larva.

## Genus *Myrmecorhynchus* Ern. André

### *M. carteri* Clark

*Worker Larva.*—Length (through spiracles) ca. 4.5 mm. Similar to *M. emeryi* Ern. André, except in the following details. Body hairs of 2 types: (1) 0.036–0.12 mm long, mostly 2- or 3-branched (rarely 4- to 6-branched), the base short and the branches long, on all somites; (2) 0.036–0.054 mm long, with long shaft and 2–6 short apical branches, a few on the ventral surface of abdominal somites I and II. Labrum somewhat broader than long, posterior surface with 6 small sensilla.

*Queen Larva.*—Length (through spiracles) ca. 9.5 mm. Similar to the worker larva, except in the following details. Head very small; body more swollen, with distinct lateral longitudinal welts. Anus ventral. Gonopod vestiges on abdominal somites VIII and IX. Entire integument with minute spinules in short transverse rows. Body hairs 0.075–0.3 mm long, with short base and long slender branches. Cranium transversely subelliptical in anterior view. Head hairs more numerous and reduced to mere spinules. Labrum with the breadth twice the length, narrowed ventrally.

*Male Larva.*—Length (through spiracles) ca. 6.2 mm. Similar to queen larva, except in the following details. Body less swollen and head relatively larger. Integument of venter of prothorax with a few minute spinules in short transverse rows. Body hairs of 2 types: (1) as in the queen, except shorter; (2) 0.027–0.072 mm long, with a stout base and a few short terminal denticles, numerous on prothorax, a few near the venter of meso- and metathorax. Posterior surface of labrum with 6 large and 16 small sensilla.

*Material Studied.*—Numerous larvae from Canberra, Australia, courtesy of the Reverend B. B. Lowery.

## Genus *Opisthopsis* Emery

### *O. rufithorax* Emery

Length (through spiracles) ca. 4.8 mm. Similar to *O. haddoni* Emery, except in the following details.

[1] Hymenoptera: Formicidae.
[2] Received for publication June 4, 1969.

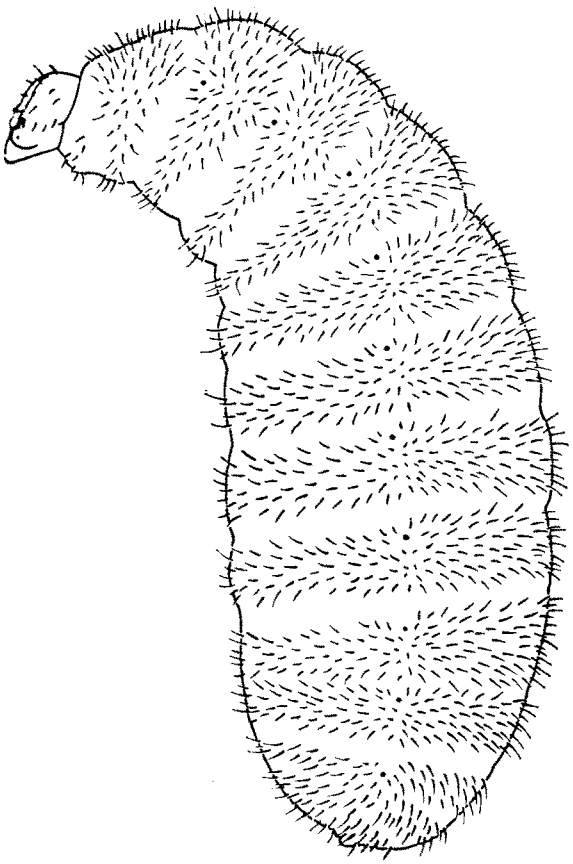

FIG. 1.—*Acanthomyops subglaber*. Mature larva in side view, ×39.

With the simple hairs on the ventral surface. Antennae moderately large. Labrum with the breadth 1½ the length; feebly bilobed. Maxillary and labial palps with 4 apical and 1 subapical sensilla.

*Material Studied.*—Numerous larvae from New South Wales, courtesy of the Reverend B. B. Lowery.

## Genus *Polyrhachis* F. Smith

In all the descriptions for *Polyrhachis* we have compared the larvae with the larva of *P. hookeri* Lowne (Wheeler and Wheeler 1953: 206) unless otherwise indicated; only differences are given here.

### *P. lamellidens* F. Smith

Length (through spiracles) ca. 7.7 mm. Thorax stouter, ventral profile of abdomen flatter. Entire integument spinulose, the spinules minute and arranged in subtransverse rows. Cranium circular in anterior view. Body hairs longer, moderately numerous, of 3 types: (1) 0.14–0.18 mm long, 2- to 4-branched; (2) ca. 0.23 mm long, simple; (3) ca. 0.19 mm long, uncinate, a few on abdominal somites IX and X. Head hairs moderately numerous, 0.072–0.14 mm long, simple, with long slender tip. Posterior surface of labrum with ca. 16 sensilla near the middle. Mandibles with the apex much shorter and more rounded. Maxillae with the apex digitiform.

*Material Studied.*—Two larvae from Japan, courtesy of Mr. A. C. F. Hung.

### *P. (Campomyrma) hecuba* Forel

Length (through spiracles) ca. 7.2 mm. Body hairs of 2 types: (1) 0.036–0.11 mm long, 2- to 6-branched, the branches very long and slender, numerous, generally distributed; (2) 0.054–0.14 mm long, with stout shaft which bears denticles, sparse, except numerous on abdominal somite X and on either side of the praesaepium. Head hairs numerous, 0.05–0.1 mm long, denticulate or 2- to 4-branched. Anterior surface of labrum with ca. 13 hairs, ventral border with ca. 9 sensilla; posterior surface with 6 sensilla. Mandibles with the apical tooth stouter and more curved.

*Material Studied.*—Six larvae from Canberra, Australia, courtesy of the Reverend B. B. Lowery.

### *P. (Myrmhopla) hippomanes* F. Smith

Length (through spiracles) ca. 5.8 mm. Stouter. Body hairs of 2 types which are about equally abundant: (1) 0.072–0.09 mm long, palmately 3- to 6-branched, the branches very long and slender; (2) 0.07–0.14 mm long, with heavy shaft and numerous denticles. Head hairs moderately numerous, 0.072–0.11 mm long, each roughened with a few minute denticles. Labrum with 15 hairs and 7 sensilla on the anterior surface; posterior surface with 6 large and 6 small sensilla. Mandibles with the apical tooth stouter.

*Material Studied.*—Two larvae from Japan, courtesy of Mr. A. C. F. Hung.

### *P. (M.) simplex* Mayr

Length (through spiracles) ca. 5.7 mm. Integument largely spinulose, the spinules minute and in short transverse rows. Body hairs of 3 types: (1) 0.11–0.23 mm long, with stout shaft bearing a few denticles; (2) ca. 0.72 mm long, palmately 4- to 9-branched, fewer on the posterior abdominal somites; (3) ca. 0.25 mm long, stout, uncinate, a few in a transverse row across the dorsum of abdominal somites VII and VIII. Head hairs moderately numerous, 0.072–0.14 mm long, denticulate. Labrum more narrowed ventrally; posterior surface with 4 sensilla. Mandibles with the apical tooth slightly stouter.

*Young Larva.*—Length (through spiracles) ca. 2.7 mm. Body hairs of 3 types: (1) 0.072–0.18 mm long, simple to 4-branched, generally distributed; (2) ca. 0.4 mm long, slender and whip-like, a few on the dorsal and lateral surfaces of the thorax and abdominal somites I–VI; (3) 0.09–0.2 mm long, stout and uncinate, a few in a transverse band across the dorsum of abdominal somites VI–VIII. Head hairs and labrum as in mature larva. Mandibles with the apical tooth shorter, more acute and curved. Labium deeply bilobed.

*Material Studied.*—Two larvae from Japan, courtesy of Mr. A. C. F. Hung.

### *P. (M.) wheeleri* Mann

Length (through spiracles) ca. 9 mm. Entire in-

tegument with minute spinules in short transverse rows. Body hairs of 2 types: (1) 0.054–0.11 mm long, palmately 6-branched, on all somites; (2) 0.07–0.3 mm long, furnished with minute denticles, on the dorsal surface of the thorax and abdominal somites I–VI and IX and on all surfaces of abdominal somite X. Labrum with the anterior surface bearing 12 hairs and 6 sensilla; ventral border with 10 sensilla. Mandibles with the apical tooth stouter.

*Material Studied.* — Three damaged integuments from the Solomon Islands.

## Genus *Camponotus* Mayr

In all the following descriptions for *Camponotus* we have compared the larvae with the larvae of *C. noveboracensis* (Fitch) (Wheeler and Wheeler 1953: 183) unless otherwise indicated; only differences are given here.

### *C. (Colobopsis) etiolatus* Wheeler

Length (through spiracles) ca. 4 mm. Similar to *C. mississippiensis* M. R. Smith, except in the following details. Cranium shorter and wider. Head hairs more numerous. Antenna a small low elevation. Labrum nearly twice as broad as long, not so narrowed ventrally; with 10 sensilla on the ventral border; posterior surface with 10 sensilla. Maxillary palp a tall cone with the apical fourth narrowed abruptly and sharp pointed.

*Very Young Larva.*—Length (through spiracles) ca. 1.5 mm. Similar to the mature larva but with the mouth parts more rounded.

*Material Studied.*—Numerous larvae from Texas, G. C. and J. Wheeler no. 233.

### *C. (C.) gasseri* Forel

(Fig. 2)

Fig. 2 is drawn from a preserved larva which has retained the pellet in the praesaepium. See also Wheeler and Wheeler (1953) p. 180, 183, 188, and 189.

### *C. (Myrmaphaenus) yogi* Wheeler

Length (through spiracles) ca. 8.2 mm. Body hairs somewhat less numerous and shorter: (1) 0.054–0.072 mm long; (2) 0.09–0.18 mm long. Head hairs simple or bifid, shorter, 0.036–0.126 mm long. Labrum without the small median lobe. Lateral border of the mandible straight.

*Material Studied.* — Six larvae from California, courtesy of Mr. R. R. Snelling.

### *C. (Myrmentoma) anthrax* Wheeler

Length (through spiracles) ca. 5.2 mm. Body hairs of 2 types: (1) 0.036–0.18 mm long, mostly 2- or 3-branched; (2) 0.11–0.25 mm long, with heavy shaft, the apex with a single hook or bifid or multifid. Head hairs simple, bifid, or trifid, 0.054–0.14 mm long.

*Young Larva.*—Length (through spiracles) ca. 1.9 mm. Praesaepium present. Entire integument spinulose. Body hairs moderately numerous, short to long, of 3 types: (1) 0.04–0.18 mm long, uncinate, in a row around the middle of each somite; (2) 0.036–0.09 mm long, slender and flexuous, a few on the thorax, numerous on the abdomen; (3) 0.036–0.09 mm long, bifid or trifid, on all surfaces of thorax. Head hairs numerous, 0.036–0.072 mm long, simple or uncinate. No chiloscleres; labrum with the breadth twice the length. Mandibles subtriangular, slightly broader than long, lateral outline convex; apical tooth acute and moderately long. Maxillary palp a short peg with 4 apical and 1 lateral sensilla; galea slightly longer and more slender than palp, with 2 apical sensilla. Labium with a few short rows of minute spinules; palp a cluster of 5 sensilla. Opening of sericteries a transverse slit.

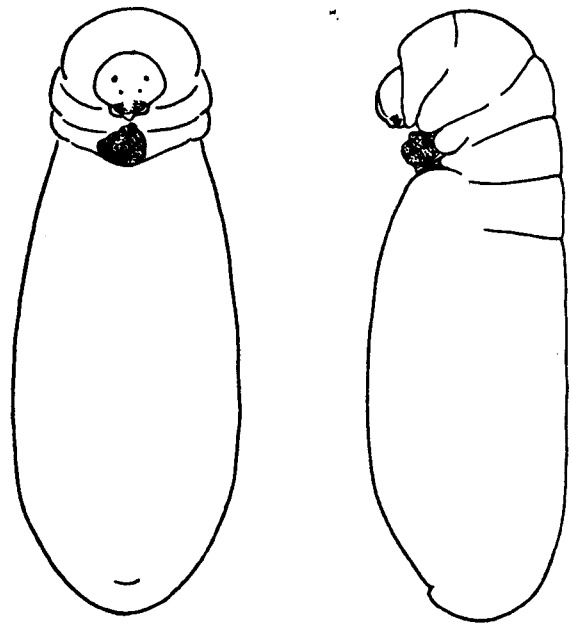

FIG. 2.—*Camponotus (Colobopsis) gasseri.* Larva in ventral and side views (hairs omitted) to show pellet in praesaepium. ×15.

*Material Studied.*—A dozen larvae from California, courtesy of Mr. R. R. Snelling.

### *C. (Myrmophyma) capito* Mayr

Length (through spiracles) ca. 9.3 mm. Body hairs of 1 type: 0.036–0.12 mm long, simple, bifid, or trifid, the longest with alveolus and articular membrane. Head hairs more numerous, 0.075–0.15 mm long, mostly simple, a few bifid. Labrum with the breadth more than twice the length; no midventral lobe; anterior surface with 8 hairs; posterior surface with 6 large and 6 small sensilla. Mandibles much narrower apically; with straighter and longer apical tooth. Maxillae with the apex shorter and stouter.

*Material Studied.*—Sixteen larvae from Canberra, Australia, courtesy of the Reverend B. B. Lowery.

### *C. (M.) nigroaeneus* F. Smith

Length (through spiracles) ca. 5.8 mm. Body hairs of 2 types: (1) 0.036–0.072 mm long, 2- or 3-branched; (2) shorter (ca. 0.12 mm long), on each

somite (including thorax), a few on the dorsal and lateral surfaces, uncinate (except a few simple on thorax). Head hairs very numerous, shorter (0.045–0.14 mm long), mostly bifid, a few simple or 3-branched, with long branches. Labrum without a midventral lobe; anterior surface with 5 hairs and 16 sensilla on or near the ventral border; posterior surface with 6 large sensilla. Mandibles with the apical tooth longer and straighter; subapical medial border more erose.

*Material Studied.*—Numerous larvae from Canberra, Australia, courtesy of the Reverend B. B. Lowery.

### *C. (Tanaemyrmex) festinatus* (Buckley)

Length (through spiracles) ca. 6.3 mm. Body hairs of 3 types: (1) 0.036–0.072 mm long, 2- or 3-branched, on all somites, the most numerous type; (2) ca. 0.14 mm long, uncinate, stout, on thorax and abdominal somites I–VIII; (3) 0.036–0.11 mm long, tip simple or with many short denticles, the only type on abdominal somite X, some on abdominal somite IX. Head hairs shorter, 0.054–0.09 mm long, mostly with a few minute denticles, a few deeply bifid with very slender branches. Labrum lacking midventral lobe, with 5 sensilla on or near each ventrolateral border and 4 elevated sensilla on the ventral border; posterior surface with 17 sensilla.

*Very Young Larva.*—Length (through spiracles) ca. 2.7 mm. Praesaepium present. Body hairs of 2 types: (1) 0.054–0.11 mm long, uncinate, the most conspicuous type, a few on each somite; (2) 0.036–0.11 mm long, simple or bifid, with long slender tips, on all somites. Head hairs mostly uncinate, ca. 0.075 mm long; a few bifid or simple, 0.036–0.072 mm long.

*Material Studied.*—A dozen larvae from Texas, G. C. and J. Wheeler no. 214.

### *C. (T.) ocreatus* Emery

Length (through spiracles) ca. 11 mm. Uncinate body hairs much shorter (ca. 0.075 mm long). Cranium subpentagonal, widest just above the mandibular level. Head hairs shorter, 0.075–0.15 mm long, twice as numerous. Labrum with the breadth twice the length; 6 projecting sensilla on the ventral border; posterior surface with 6 large and 12 small sensilla.

*Very Young Larva.*—Length (through spiracles) ca. 2.6 mm. Body hairs of 2 types: (1) 0.036–0.11 mm long, simple or palmately 2- to 4-branched; (2) 0.072–0.16 mm long, with alveolus and articular membrane, with heavy shaft and recurved tip which becomes curled toward the posterior end of the body. Head hairs 0.054–0.16 mm long, simple to 6-branched.

*Material Studied.*—A dozen larvae from Arizona, courtesy of Mr. R. R. Snelling.

## Recent Literature on Formicine Larvae

### *Gigantiops destructor* (F.)

Kempf and Lenko (1968: 212–3) used our descriptions of this genus and species (Wheeler and Wheeler 1953: 170–1, 180, 211) to support their conclusion that *Gigantiops* is closer to the Formicini than to the Camponotini, but in a separate tribe.

### *Camponotus herculeanus* (L.)
### *C. noveboracensis* (Fitch)

Sanders (1964, Fig. 1, p. 896) gave lengths of larvae from nests in various months.

### *C. pennsylvanicus* (DeGeer)
(Black carpenter ant)

Newman (1967: 102) provided a photograph of larvae.

### *Lasius flavus* (F.)

Newman (1967) provided photographs of sexual larvae (p. 21) and young larvae (p. 44).

### *Myrmecocystus* spp.

Snelling (1968: 17) stated that the fluids stored in the repletes are "largely stored for the use by the adult members of the colony, little or none being fed to the larvae. Larval food consists mainly, if not entirely, of dead insects brought to them by the foraging ants." In observation nests, if only honey-water is supplied, the larvae are rarely fed by the workers and eventually die. "On the other hand, if dead insects are supplied to the colony, these are placed with the larvae which feed directly on the fragments."

### *Formica rufa* L.

Newman (1967: 7) published data on the life cycle: egg 13 days, larva 8 days, pupa 15 days.

### *Formica* sp.

Costello (1968: 80) published an excellent photograph of larvae.

## TRIBES OF FORMICINAE

The names, inclusions, and arrangement of the tribes of Formicinae in Emery's "Genera Insectorum" (1925) are quite different from those proposed by W. M. Wheeler (1922) and the 2 schemes are irreconcilable. We have therefore dared to be eclectic, selecting features of both schemes and modifying them under the influence of larvae. Following is our plan; after the name of each tribe we have listed the genera that we have studied; in parentheses we have added the number of species studied in each genus.

Myrmoteratini.—None.
Santschiellini.—None.
Melophorini.—*Melophorus* (2), *Diodontolepis* (1), *Notoncus* (3), *Prolasius* (1).
Formicini.—*Lasius* (6), *Acanthomyops* (4), *Myrmecocystus* (6), *Formica* (11), *Polyergus* (2).
Gesomyrmecini.—*Gesomyrmex* (2).
Gigantiopini.—*Gigantiops* (1).
Oecophyllini.—*Oecophylla* (2).
Myrmecorhynchini.—*Myrmecorhynchus* (2).
Plagiolepidini.—*Acropyga* (2), *Plagiolepis* (2).
Brachymyrmecini. — *Brachymyrmex* (1), *Prenolepis* (1), *Stigmacros* (3).

Myrmelachistini. — *Myrmelachista* (2), *Paratrechina* (3).
Camponotini.—*Opisthopsis* (3), *Calomyrmex* (2), *Dendromyrmex* (1), *Echinopla* (1), *Polyrachis* (15), *Camponotus* (51).

## Characterization of the Tribes

### Tribe MELOPHORINI Forel

Profile melophoriform or formiciform (i.e., with the thorax and 1st abdominal somite forming a distinct neck, which is curved ventrally; remainder of body straight, subellipsoidal, and rather slender). Praesaepium lacking. No uncinate body hairs. Head small. Head hairs few and moderately long. Labrum bilobed; chiloscleres lacking. Mandibles notonciform, brachymyrmeciform, or polyrachiform. Anterior surface of labium with a median protuberance near the base.

### Tribe FORMICINI Forel

Profile formiciform. Praesaepium lacking. Body hairs short, sparse to moderately numerous; no uncinate hairs. Chiloscleres lacking. Mandibles formiciform, robust, medial border denticulate near base of apical tooth. Maxillae with the apex conoidal or paraboloidal and directed medially.

### Tribe GESOMYRMECINI Forel

Profile formiciform. No praesaepium. Body hairs sparse, simple, and exceedingly minute; no uncinate hairs. Antennae with 2 sensilla each. Chiloscleres lacking. Mandibles formiciform.

### Tribe GIGANTIOPINI Ashmead

Profile formiciform. Praesaepium lacking. Body hairs abundant, rather short and of 3 types: (1) simple, slender, and whip-like; (2) 2- to 4-branched; (3) moderately stout and denticulate; no uncinate hairs. Head hairs long, whip-like, and denticulate. Chiloscleres lacking. Mandibles camponotiform.

### Tribe OECOPHYLLINI Emery

Profile oecophylliform. Praesaepium lacking. Body hairs very few, minute, simple, acute. Antennae minute. Head hairs few, very short, simple, acute. Labrum small, bilobed; only 2 hairs on the anterior surface; chiloscleres lacking. Mandibles oecophylliform, very small. Maxillae broad and apparently adnate; palp and galea very small. Labium a small frustum; palps very small.

### Tribe MYRMECORHYNCHINI Wheeler

Profile myrmecorhynchiform. Praesaepium lacking. Body hairs sparse and short, of 2 types: (1) with the apex denticulate or with 2–6 short apical branches; (2) simple or 2- to 6-branched, with the distal portion very long, slender, and flexuous; no uncinate hairs. Head small. Antennae small. Head hairs few and short. Chiloscleres lacking. Mandibles brachymyrmeciform.

### Tribe PLAGIOLEPIDINI Forel

Profile formiciform. Praesaepium lacking. Without uncinate body hairs. Head hairs long. Chiloscleres lacking. Mandibles notonciform or plagiolepidiform.

### Tribe BRACHYMYRMECINI Emery

Profile brachymyrmeciform. Praesaepium lacking. Body hairs sparse; no uncinate hairs. Head hairs few. Labrum bilobed, without chiloscleres. Mandibles brachymyrmeciform or paratrechiniform. Maxillae lobose.

### Tribe MYRMELACHISTINI Forel

Profile myrmelachistiform or paratrechiniform (i.e., body plump, straight or nearly so, subellipsoidal, and without a neck; head applied to the ventral or anteroventral surface). Praesaepium lacking. No uncinate hairs. Head hairs few and short. Labrum bilobed; chiloscleres lacking. Mandibles myrmelachistiform or paratrechiniform.

### Tribe CAMPONOTINI Forel

Profile camponotiform. Praesaepium present, its floor spinulose. Body densely and uniformly covered with short hairs (except sparse on venter of the thorax and abdominal somites I and II). Five types of hair-shape occur in the tribe: (1) branched (typically with 2–6 branches, but there may be as many as 12); (2) simple, short, and slightly curved; (3) simple, long, and whip-like; (4) denticulate; (5) uncinate. One type, the branched in most species, is numerically predominant; other types are sparsely represented. Branched and simple hairs are generally the shortest, whip-like and uncinate hairs the longest; denticulate hairs are usually intermediate. Branched hairs are palmate and the plane of the branching is transverse. Typically a species has 3 of these 5 types, but the number of types ranges from 1 to 4; thus no species has all types. Head hairs are numerous. Head with a conspicuous naked area in the form of an inverted V. Four types of head hairs occur in the tribe: (1) branched (typically bifid or trifid, but there are also 4-branched hairs); (2) simple; (3) whip-like; (4) denticulate. A species usually has 2 of these types but may have 1, 3, or 4. Labrum subparabolic in anterior view; somewhat broader at the base than long; chiloscleres present; posterior surface with numerous (6–30) sensilla. Mandibles camponotiform. Maxillae swollen ventrolaterally; apex in the form of a slender cone which is directed medially; medial surface with rows of minute spinules. Anterior surface of labium spinulose.

## Significant Structural Characters

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

Among the **Formicidae, body shape** is the larval character which is most nearly constant throughout each genus. It is also the character which most closely correlates larval taxonomy with adult taxonomy. Therefore we have chosen body shape as the basic character for classifying the larvae of the Formicinae. The next most useful character is **mandible shape**. There are more kinds of mandible shapes than body shapes. Mandible shape also shows intrageneric and intraspecific variation.

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

**Body Shape.**—In our study of body shapes we have used only the profiles (i.e., outlines in side view), since dorsal and ventral views rarely show anything distinctive. Applying the technique just referred to, we found **8 generalized profiles** for the [redacted] (Fig. 3 and Appendix A). A simultaneous comparison of these 8 generalized profiles showed that they could be arranged in 3 groups on the basis of more superficial resemblances. We have not, however, attempted generalized diagrams of the 2nd order and we have not named these larger groups.

After the profiles were classified, the next question was: **which profile is unspecialized?** We selected melophoriform, because: (1) ***Melophorus* is generally regarded as the least specialized genus of the Formicinae**; (2) among the larvae of this genus no character shows extreme deviation from an average for all known ant larvae; (3) among larvae exhibiting melophoriform and formiciform profiles no character shows adaptation to any limited function or habit; (4) among larvae having these profiles the majority of characters are only moderately developed, in contrast to the extremes of the same characters in the subfamily.

The **melophoriform** profile resembles rather closely the **cetatommiform** profile, while the **formiciform** profile is similar to the **paraponeriform** (both in the Ponerinae); both of these profiles are among the less specialized ponerine profiles. Myrmechorhynchiform and brachymyrmeciform are like myrmiciform, an unspecialized myrmicine profile. Paratrechiniform suggests allomeriform, a rather specialized myrmicine profile. The most specialized formicine profiles are myrmelachistiform and camponotiform. We shall comment on this under "Specialization," following.

***Mandible Shape.***—The same generalizing procedures have been applied to the anterior view of the mandibles, using the apex and the anterior condyle as reference points for standardization (see Wheeler and Wheeler 1960: 102). The results of our generalizations are shown in Fig. 4 and Appendix B.

In the **Formicidae** the least specialized mandible shape is probably **aphaenogastriform** (in the Myrmicinae). It is narrow, subtriangular, and has 3 large subequal teeth—an apical and 2 medial. By this token **all formicine** mandible shapes are specialized. The most specialized are myrmelachistiform, plagiolepidiform, and oecophylliform.

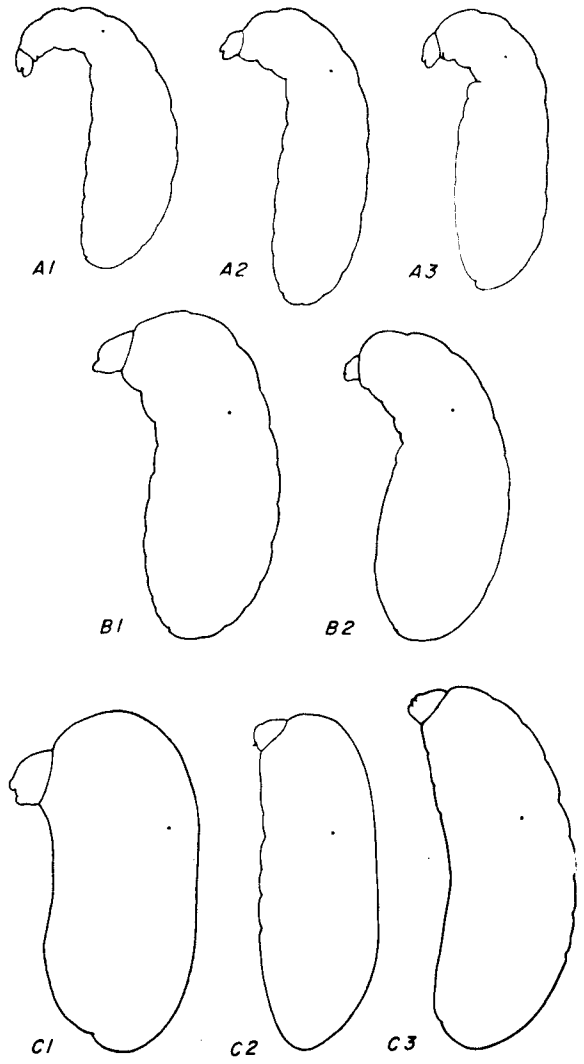


FIG. 3.—Generalized body profiles of formicine ant larvae. A1, melophoriform; A2, formiciform; A3, camponotiform; B1, brachymyrmeciform; B2, myrmecorhynchiform; C1, paratrechiniform; C2, myrmelachistiform; C3, oecophylliform.

The **myrmelachistiform** mandible shape resembles rather closely that of the subfamily **Dolichoderinae**, while the **brachymyrmeciform** is similar to the **messoriform** in the Myrmicinae. Other formicine mandible shapes are different from any in other subfamilies.

Heterogeneity.—We have discussed at length the heterogeneity of the Myrmicinae, Ponerinae, and Dolichoderinae (Wheeler and Wheeler 1960, 1964, 1966). **The adults of the Formicinae are less heterogeneous than those of the Myrmicinae.** Can the same be said of their larvae? To attempt an answer we have devised a simple index of heterogeneity: the

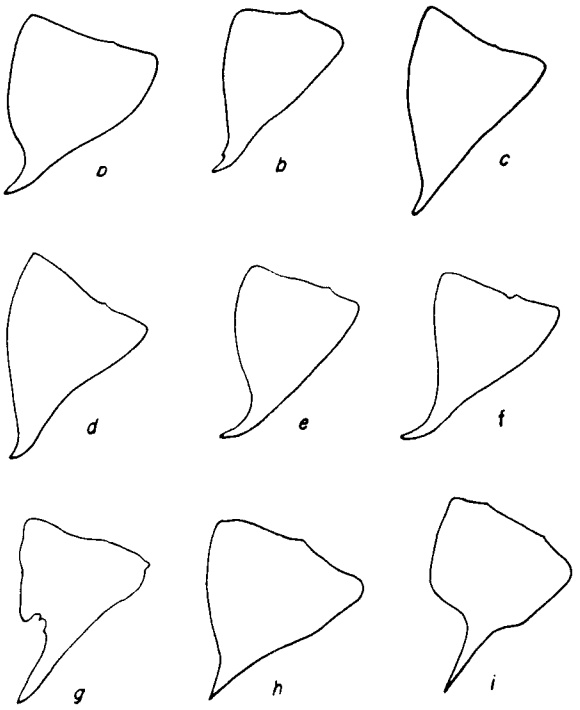


FIG. 4.—Generalized mandible shapes of formicine ant larvae. a, Formiciform; b, paratrechiniform; c, polyrachiform; d, camponotiform; e, notoniciform; f, brachymyrmeciform; g, plagiolepidiform; h, myrmelachistiform; i, oecophylliform.

ratio of the number of genera studied to number of types of body profile (or mandible shape). This ratio gives the average number of genera per type; the lower the index number, the greater the heterogeneity (see appendices). Our computations follow.

Profiles.—Myrmicinae: 57 genera/22 types = 2.59; Ponerinae: 26 genera/8 types = 3.25; Dolichoderinae: 10 genera/3 types = 3.33; Formicinae: 24 genera/8 types = 3.00.

Mandible Shapes.—Myrmicinae: 68 genera/30 types = 2.27; Ponerinae: 33 genera/20 types = 1.65; Dolichoderinae: 12 genera/1 type = 12.00; Formicinae: 26 genera/9 types = 2.89.

We were surprised to find the Formicinae as a whole so heterogeneous when we could not distinguish the genera within the tribes Camponotini and Formicini. However, if we separate the camponotiform and formiciform profiles and mandible shapes from the remainder of subfamily we find the following.

Profiles.—Camponotiform and formiciform: 17 genera/2 types = 8.50; other types: 13 genera/7 types = 1.86.

Mandible Shapes.—Camponotiform and formiciform: 12 genera/2 types = 6.00; other types: 13 genera/7 types = 1.86.

In other words, the Formicinae may be divided into a highly **homogeneous group (tribes Formicini, Camponotini, Gigantiopini, and Gesomyrmecini)** and a very **heterogeneous group** (the remaining tribes).

*Specialization.*—The most specialized formicine larvae are those of the tribes **Myrmelachistini and Camponotini.** Many of the species in these tribes inhabit **plant cavities.** The larvae of both tribes have the body elongate, straight, and subcylindrical; hairs are mostly minute or short. Both of these characters are possibly adaptations to life in plant cavities, particularly tubular cavities of small bore. A larva parked parallel and close to the wall would be less of a traffic hazard than a shorter larva parked crosswise or obliquely. These same characters are to be found also in the larvae of other ants that inhabit plant cavities, notably *Azteca* (Dolichoderinae), *Cataulacus, Crematogaster,* and *Cryptocerus* (Myrmicinae), and the Pseudomyrmecinae. *Camponotus* larvae have a neck, but it is short, stout, and strongly arched ventrally and posteriorly so that the cylindricality of the profile as a whole is scarcely affected.

We regard the Camponotini as even more specialized than the Myrmelachistini, because they possess 2 characters lacking in the latter tribe: chiloscleres and praesaepiun. Each chiloscleres is a hard brown spot on each lateral border of the labrum. **Chiloscleres are unique for the tribe Camponotini.**

The praesaepium is a shallow depression on the ventral surface of certain anterior abdominal somites, which is partly surrounded by welts to form a sort of trough. It is reminiscent of the trophothylax of pseudomyrmecine larvae and probably serves the same purpose (i.e., a receptacle for food) in a rudimentary way. The praesaepium attains its most elaborate form in the subgenus *Colobopsis;* see Fig. 2.

For a fuller discussion of chiloscleres and praesaepium, see Wheeler and Wheeler 1953: 180.

## Appendix A. Generalized Body Profiles (Fig. 3)

### Group A

(Thorax and 1st abdominal somite forming a distinct neck, which is arched ventrally; remainder of body elongate, straight, subelliptical and rather slender.)

**1. Melophoriform.** Neck moderately long and rather slender. Abdomen (exclusive of the 1st somite) elongate, somewhat swollen, with the dorsal profile convex and the ventral nearly straight. Genus: *Melophorus.*

**2. Formiciform.** Head directed ventrally. Neck short and stout; remainder of body with dorsal and ventral profiles slightly convex; diameter greatest at 4th abdominal somite, diminishing gradually toward either end. Genera: *Acanthomyops, Diodontolepis, Formica, Gesomyrmex, Gigantiops, Lasius, Myrmecocystus, Notoncus, Plagiolepis, Polyergus, Prolasius.*

**3. Camponotiform.** Neck short and stout. Remainder of body with the dorsal and ventral profiles nearly straight, the ventral depressed at the praesaepium. Diameter greatest at abdominal somites IV and V, decreasing but slightly toward either end. Posterior end rounded. Anus subterminal. Genera: *Calomyrmex, Camponotus, Echinopla, Opisthopsis, Polyrhachis.*

### Group B

(Short and stout; no neck.)

1. **Brachymyrmeciform.** Thorax curved ventrally. Head large. Genera: *Brachymyrmex, Prenolepis, Stigmacros.*

2. **Myrmecorhynchiform.** Thorax and 1st abdominal somite curved ventrally. Head small. Genus: *Myrmecorhynchus.*

### Group C

(Plump, straight or nearly so, subelliptical; no neck.)

1. **Paratrechiniform.** Plump, chunky, and subelliptical; anterior end broadly rounded; posterior end round-pointed; no neck; anterior end formed from the dorsa of prothorax and mesothorax; head ventral near the anterior end; anus posteroventral. Genus: *Paratrechina.*

2. **Myrmelachistiform.** Straight and subcylindrical; diameter nearly uniform back to the 5th abdominal somite, then tapering rather rapidly to the posterior end which is round-pointed; anterior end broadly rounded; head applied to the anteroventral surface; anus subterminal. Genus: *Myrmelachista.*

3. **Oecophylliform.** Sausage-shaped; slightly curved ventrally; terete, the diameter nearly uniform; anus posteroventral. Genus: *Oecophylla.*

## Appendix B. Generalized Mandible Shapes

(Fig. 4)

a. Formiciform. Very broad (width at base equal to the length exclusive of apical tooth); apex forming a slender, smooth, round-pointed, slightly curved tooth, which is sharply demarcated from the wide basal portion. No medial teeth. Medial border (excluding apical tooth) moderately to strongly convex; lateral border feebly convex or sinuate. Genera: *Acanthomyops, Formica, Gesomyrmex, Lasius, Myrmecocystus, Polyergus.*

b. Paratrechiniform. Subtriangular and rather narrow; apex forming a short slender curved sharp-pointed tooth; a small subapical tooth on the medial border. Genera: *Paratrechina, Prenolepis, Stigmacros.*

c. Polyrhachiform. Subtriangular, base broad (ca. ¾ the length); medial border slightly convex; basal half of lateral border nearly straight; apex forming a short, stout, straight, blunt tooth; no medial teeth. Genera: *Diodontolepis, Polyrhachis.*

d. Camponotiform. Subtriangular; base broad (ca. ¾ the length); medial border slightly convex; basal half of lateral border slightly convex, distal half slightly concave; apex forming a short stout curved blunt tooth; no medial teeth. Genera: *Calomyrmex, Camponotus, Dendromyrmex, Echinopla, Gigantiops, Opisthopsis.*

e. Notonciform. Width at base ⅔ the length; distal half narrowing rapidly to a curved apical tooth, which is moderately slender and moderately sharp; no medial teeth; medial border convex; lateral border nearly straight. Genera: *Acropyga, Melophorus, Notoncus.*

f. Brachymyrmeciform. Width at base ⅔ the length. Basal ⅔ subtriangular; narrowing rapidly to a moderately slender, curved, sharp-pointed, apical tooth; no medial teeth. Genera: *Brachymyrmex, Myrmecorhynchus, Prolasius.*

g. Plagiolepidiform. Basal half broad; distal half forming a long, slender, round-pointed tooth; a conspicuous jagged notch at the middle of the medial border. Genus: *Plagiolepis.*

h. Myrmelachistiform. Subtriangular; base broad (width ⅝ the length); distal fourth forming a slender, straight, sharp-pointed, apical tooth. Genus: *Myrmelachista.*

i. Oecophylliform. Width at base ¾ the length; basal ⅜ broad and subtrapizoidal; apical ⅖ forming a long, straight, slender, sharp-pointed tooth. Genus: *Oecophylla.*

## Appendix C. Revised Key to the Mature Worker Larvae of Formicinae in our Collection[3]

### Group A

Thorax and 1st abdominal somite forming a distinct neck which is strongly arched ventrally; remainder of body elongate, straight, subellipsoidal, and rather slender.

1a. Body melophoriform; mandibles notonciform ..... *Melophorus*
1b. Body camponotiform; chiloscleres present ..... Tribe Camponotini
1c. Body formiciform ..... 2
2a. Mandibles polyrhachiform ..... *Diodontolepis*
2b. Mandibles camponotiform; head hairs numerous, long, denticulate, and whip-like ..... *Gigantiops*
2c. Mandibles notonciform; head hairs few, short, the tips fuzzy ..... *Notoncus*
2d. Mandibles plagiolepidiform ..... *Plagiolepis*
2e. Mandibles brachymyrmeciform ..... *Prolasius*
2f. Mandibles formiciform ..... Tribes Gesomyrmecini and Formicini

### Group B

Short and stout; curved somewhat at the anterior end; no neck.

1a. Body brachymyrmeciform .. Tribe Brachymyrmecini 2
1b. Body myrmecorhynchiform ..... *Myrmecorhynchus*
2a. Mandibles brachymyrmeciform ..... *Brachymyrmex*
2b. Mandibles paratrechiniform ..... 3
3a. Long whip-like body hairs present ..... *Stigmacros*
3b. Without such hairs ..... *Prenolepis*

### Group C

Plump, straight or nearly so; subelliptical, no neck.

1a. Body paratrechiniform; mandibles paratrechiniform ..... *Paratrechina*
1b. Body myrmelachistiform; mandibles myrmelachistiform ..... *Myrmelachista*
1c. Body oecophylliform; mandibles oecophylliform ..... *Oecophylla*

[3] *Acropyga* and *Dendromyrmex* have been omitted from the key, the former because our material is immature, the latter because we have only damaged integuments.

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