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The Larvae of the Fungus-Growing Ants

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Fungus-growing ants have for many years attracted the attention of myrmecologists and other biologists because of their extremely interesting habit of cultivating fungi for food. Certain species (especially in the genus *Atta*) have received serious consideration from the economic entomologists, for they rank high among the destructive insects of the tropics. These leaf-cutters are also noticed by laymen because of their habit of making trails along which they travel while carrying in their mandibles the pieces of leaves they have cut; this habit has earned for them the name of parasol ants.

The fungus-growers belong to the tribe Attini of the subfamily Myrmecinae. This tribe musters at present nearly 300 species, subspecies and varieties which are commonly grouped in nine genera — *Myrmicocrypta, Apterostigma, Mycocepurus, Cyphomyrmex, Sericomyrmex, Trachymyrmex, Acromyrmex, Pseudoatta* and *Atta*. Some myrmecologists have at various times included *Proatta* and *Blepharidatta* in the tribe and others have elevated certain subgenera to generic rank.

The Attini are mostly restricted to the Neotropical Realm, but four genera (*Cyphomyrmex, Trachymyrmex, Acromyrmex* and *Atta*) range northward into the southern United States, while one of these (*Trachymyrmex*) is found as far north as a line running from southern Illinois to Long Island.

In this article I have described the larvae of twenty species and subspecies representing seven genera. In addition I have included all the references to attine larvae that I have been able to find in the literature.

Tribe Attini F. Smith

Larvae commonly swathed with mycelium from the fungus garden. Head on the ventral surface of the body often at a considerable distance from the anterior end. Body short, very stout, plump, bean-shaped, subreniform in profile; slightly compressed; somewhat narrowed near the middle; depth greatest at the middle and decreasing slightly and equally toward each end; ends large, subequal and broadly rounded; dorsal profile (occiput to anus) extremely long, crescentic; ventral profile (anus to gula) relatively short and concave. Anus ventral and usually at some distance in front of the posterior end; with one or two prominent lips. Vestigial legs near the posterior border of each thoracic segment. Segmentation indistinct. Spiracles 10 pairs, small, arranged in J-shaped or crescentic rows. Integument usually smooth. In most genera the body is almost naked and the few hairs are largely restricted to the ventral surface. Typically body hairs are short (0.03-0.16 mm), simple,

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slender, flexous, tapering gradually to an acute tip; longest on the thorax and shortest near the anus.

Head somewhat broader than long. Genae often produced into a more or less conspicuous lobe. Antennae small to moderately large; three sensilla each. Mouth parts small. Head hairs usually sparse and concentrated on the lower part of the head below the antennae; typically simple, slightly curved and tapering gradually to an acute tip.

Labrum a thick flap or a subhemispherical lobe; very small; spinulose.

Mandibles small, short, stout and feebly sclerotized; typically with the apical portion curved medially, with the surfaces covered with sharp spinules and with a single elongate, acute apical tooth.

Maxillae reduced; mostly long, narrow and adnate to the head except for a free apical lobe; spinulose (at least in part).

Labium small, short, mostly concealed in front view; two anteriorly projecting bulges separated by a median depression; each lobe bearing typically a cluster of sensilla which represents the palp.

Bischoff, 1927, p. 122: "Eine reine Pflanzenkost dürften normalerweise nur die pilzzüchtenden Attinen ihren Larven bieten."

Forel, 1928 (Vol. I), p. 517: "The larvae of the *Attini* (*Myrmicinae*) like the adults are fed on the products or 'turnip cabbages' of the fungi cultivated by their ☿." (=1922, p. 136: "Les larves des *Attini* (*Myrmicinae*) sont nourries comme les adultes par les produits ou 'choux-raves' des champignons cultivés par leur ☿.")

Weber, 1945, p. 4: "The larvae and naked pupae are commonly swathed in mycelium from the fungus garden but the workers may clean them on occasion."

Wheeler and Bailey, 1920, p. 253: "A recent study by the senior author of various Attine larvae, belonging to the genera *Atta, Trachymyrmex, Cyphomyrmex, Sericomyrmex,* and *Apterostigma,* shows that their mouthparts are beautifully adapted for the methods of feeding described by Tanner and Huber. The mandibles are short, stout and acute, and except in *Apterostigma,* covered with numerous sharp spines, so that the delicate egg-shell or the thin walls of hyphal filaments or of kohlrabi spherules can be held and firmly squeezed and at the same time perforated with many small openings, thus allowing the liquid contents to be rapidly expressed and trickle into the mouth."

Wheeler, 1928, p. 201: The Attini "uniformly feed, both as larvae and adults, on the mycelium of particular fungi." The larval mouth parts are "beautifully adapted for puncturing the hyphae and imbibing their protoplasmic contents. . . . The feeding of the larvae among the Attini is quantitative, although the possibility of an administration of saliva to certain larvae and their conversion into queens as a result of such treatment, cannot be altogether excluded." (See also Wheeler, 1937, p. 50.)

Wheeler, 1937: Attine workers place "malaxated tufts of fungus bromatia within reach of the larval mouth parts" (p. 36). "The feeding habits of

both the adults and larvae are much simpler than those of many less specialized ants, because each species cultivates only a particular species of fungus and under normal conditions has no other diet. The bearing of this fact on the trophogenic hypothesis of caste determination is apparent when we consider that the larvae of all stages are scattered through the gardens and like the adults subsist only on bromatia, or hyphal swellings" (p. 46). "It is doubtful . . . whether the colony-founding mother feeds the larvae of her first brood in the same manner [as that employed in well established Attine colonies.] . . . It is more probable that the larvae of the incipient colony eat the mycelium directly and that larval feeding in this very early phase of colony development may really represent an ancient phylogenetic stage which persists throughout the life of the colony in Sericomyrmex and other primitive genera." (pp. 49-50).

KEY TO THE GENERA OF ATTINE LARVAE

1. Body hairs tapering gradually; straight, slightly curved or flexuous; with the tips unbranched 2
   Body hairs not as above ..... *Acromyrmex*
2. Head hairs numerous and uniformly distributed ..... *Atta*
   Head hairs few and mostly restricted to lower part of head 3
3. Head with conspicuous genal lobes; apical portion of mandibles curved medially 5
   Head without genal lobes; mandibles not curved 4
4. Head outline indefinite; 16 short head hairs, mandibles spinulose ..... *Myrmicocrypta*
   Head outline distinct; 10 long head hairs; mandibles with very few spinules or none ..... *Apterostigma*
5. Mandibles with two apical teeth ..... *Sericomyrmex*
   Mandibles with one apical tooth or none 6
6. With one hair on each genal lobe ..... *Cyphomyrmex*
   With several hairs on each genal lobe ..... *Trachymyrmex*

Genus MYRMICOCRYPTA F. Smith

Head near anterior end. Body nearly straight, subcylindrical, only moderately stout. Body hairs restricted to thorax and vicinity of anus. Integument of body spinulose. Head indistinctly separated from prothorax; no spinules or hairs above the level of the antennae; no genal lobes; hairs moderately long. Labrum a thick flap. Mandibles small; apical portion conical, not curved medially; spinules moderately numerous. Maxillae exposed; with very few spinules; palp and galea subconical. Labium exposed; palp subconical.

M. urichi Weber.—Plate I, figs. 1-8. Head on the ventral surface of the body near the anterior end. Body subcylindrical, moderately stout, somewhat compressed; nearly straight, but with the ends slightly curved ventrally; a slight constriction at the first abdominal segment; ends large, subequal and broadly rounded. Prothorax slightly arched (in profile) above and slightly inflated below. Terminal segment directed ventrally; anus ventral, with prominent lips. On either side of the prothorax, near the head, there is a dark-staining (with acid fushsin) structure of unknown nature and function. Segmentation indistict. Spiracles small. Body nearly naked; hairs restricted to the ventral surface, most abundant on the prothorax, with very few on the meso- and metathorax and a cluster around the anus. Body hairs short

(0.04-0.06 mm), simple, tapering, nearly straight. Integument of body with minute spinules arranged in rows to form a reticulate pattern. Head broader than long; occipital border broadly rounded; lateral and ventral boundaries indistinct; integument spinulose below the antennal level, the spinules arranged in short rows. Head hairs 16, simple, slightly curved, tapering rapidly, acute, 0.06 mm long. Antennae moderately large; each with three sensilla. Labrum very small; short and thick; spinulose. Mandibles small and feebly sclerotized; divided into two distinct parts — a stout base and a smaller acute conical apex; the anterior surface of the base is beset with many sharp spinules. Maxillae small and lobose; each with four relatively long hairs; palp a slender subconical projection with several lateral spinules, galea a subconical, spinulose protuberance. Labium subhemispherical; coarsely spinulose; a pair of spinulose lobes projecting forward from the anterior surface; with several hairs; palp a slender subconical process with several lateral spinules. (Material studied: several specimens collected in Trinidad by Dr. N. A. Weber.)

M. spinosa Weber.—Similar to *M. urichi.* (Material studied: two larvae from British Guiana.)

M. guianensis Weber.—"Pupae were naked but the larvae had tufts of mycelia on their integument." (Weber, 1946, p. 129)

Genus APTEROSTIGMA Mayr

Head near anterior end. Body hairs limited to prosternum and vicinity of anus. Integument spinulose on the head and around the anus. No genal lobes. Head hairs relatively long; four above the antennal leval and six below. Mouth parts extremely small, apparently vestigial. Labrum a thick flap. Mandibles with the apical portion subconical and not curved medially; few spinules or none. Maxillae exposed; spinulose; palp and galea represented by clusters of sensilla. Labium exposed.

Wheeler and Bailey (1920, p. 253) state that the mouth parts in this genus "are beautifully adapted for the methods of feeding described by Tanner and Huber. The mandibles are short, stout and acute."

A. collare angulatum Weber.—Plate I, figs. 9-17. Head on ventral surface near anterior end. Body short, very stout, plump, bean-shaped; slightly narrowed at the middle; ends large subequal and broadly rounded; abdominal segments lengthened dorsally and shortened ventrally to such an extreme degree that the anus is ventral to the second abdominal spiracles. On either side a short, narrow, dark-staining (with acid fushsin) structure extends from the genae onto the prothorax; its nature and function unknown. Postanal lip prominent. Segmentation indistinct. Spiracles small; arranged in a J-shaped row. Body naked except for four hairs on the prosternum and a cluster around the anus. Body hairs slender, tapering, slightly curved, rather short (0.06-0.12 mm). Integument smooth except around the anus where minute spinules are arranged in short rows. Head somewhat broader than long; narrowed above, widest at the level of the labrum; occipital border short, impressed at the middle; sides strongly curved; integument furnished with

minute spinules which are grouped in short rows on the frontal and clypeal regions, but single elsewhere; gula inflated into a median ventral swelling. Head hairs sparse (10), simple, relatively long (0.2 mm). Antennae moderately large; each with three minute sensilla. Mouth parts greatly reduced. Labrum very small; short, broad and thick; rounded distally; a pair of sensilla on the anterior surface; anterior surface and distal edge furnished with papillae; posterior surface spinulose near the distal border, the spinules arranged in short transverse rows. Mandibles very small and feebly sclerotized; the relatively large base bearing a small acute conical apical tooth; no spinules. Maxillae lobose, subtriangular in anterior outline; integument with minute papillae arranged in short rows; palp represented by a cluster of several sensilla; galea represented by two sensilla on the medial surface. Labium transversely subelleptical in anterior view; on each side a paraboloidal lobe projecting anteriorly and bearing a cluster of three sensilla, which represents the palp; surface roughened with minute papillae arranged in short arcuate rows. Hypopharynx with minute papillae arranged in transverse rows. (Material studied: two larvae from Panama Canal Zone.)

A. mayri Forel.—Similar to *A. angulatum*. (Material studied: four larvae from Costa Rica.) Weber (1945, p. 35): "The larvae are heavily coated with the same type of mycelium as grows in the garden." Weber (1946, p. 137): "The larvae were covered with mycelium."

A. tramitis Weber.—Plate I, fig. 18. Resembles *A. angulatum* except in the mandibles. These are much smaller than in *angulatum*; triangular in anterior view; apical portion subconical, blunt-pointed; a few spinules on the lateral surface. (Material studied: two larvae from Panama Canal Zone.)

A. urichi Forel.—"Larvae were embedded in the mycelium." (Weber, 1946, p. 138.)

Genus CYPHOMYRMEX Mayr

Body hairs restricted to thorax, first three abdominal segments and vicinity of anus. Genal lobes moderately large, one hair on each. Head hairs relatively long. Labrum a thick flap. Mandibles with the apical portion strongly curved medially; spinules moderately numerous. Maxillary palp a subcylindrical peg; galea represented by a cluster of sensilla.

Wheeler and Bailey (1920, p. 253) state that in this genus "the mouthparts are beautifully adapted for the methods of feeding described by Tanner and Huber. The mandibles are short, stout and acute, and . . . covered with numerous sharp spines, so that the delicate egg-shell or the thin walls of hyphal filaments or of kohlrabi spherules can be held and firmly squeezed and at the same time perforated with many small openings, thus allowing the liquid contents to be rapidly expressed and trickle into the mouth."

C. rimosus Spinola.—Plate II, figs. 1-6. Head on the ventral surface of the body at a considerable distance from the anterior end. Body short, very stout, plump, bean-like; slightly compressed; ends large, subequal and broadly rounded; dorsal profile extremely long, crescentic; ventral profile relatively short and convex; a midventral triangular projection on the first abdominal

segment. Anus ventral and quite far forward; with prominent lips. Segmentation indistinct. Spiracles small; arranged in a crescentic row; diminishing progressively in size from anterior to posterior. Body nearly naked; a few hairs on the ventral surface of the six anterior segments and a cluster around the anus. Body hairs simple, short (0.03-0.07 mm), flexuous or slightly curved or straight. Head broader than long; occipital border broadly rounded; genae bulging into antero-ventral lobes; integument spinulose on clypeus and adjacent portion of front; naked except for a transverse row of eight long (0.05-0.1 mm) simple, slightly curved or flexuous hairs. Antennae moderately large; each with three sensilla. Labrum small and thick; breadth twice the length; distal outline strongly curved; anterior and posterior surfaces spinulose; posterior spinules in groups of one to four and arranged in short transverse rows. Mandibles small, short, stout, thick; feebly sclerotized; surfaces coarsely spinulose; apical portion strongly curved medially and terminating in several large sharp spinules; no apical tooth. Maxillae feebly developed; adnate to head except for a small subconical apical lobe; not spinulose; palp a cylindrical peg tipped with a rounded transparent cap; galea not peg-like but represented only by a cluster of four or five sensilla on the distal surface of the maxilla. Labium short, scarcely visible from in front; subhemispherical, covered with spinules arranged in short transverse rows; palp represented by a cluster of four or five sensilla on the distal surface. (Material studied: several specimens from Panama.)

Young Larva. Plate II, fig. 3. Length 0.62 mm. Head relatively very large; on the ventral surface near the anterior end. Posterior end of body bent ventrally at right angles and forming an obtuse conoid with the anus on its anterior surface. Remainder of body straight and subcylindrical; ends rounded. First abdominal sternum produced into a thick transverse flap. Segmentation distinct on the ventral surface, indistinct dorsally. Spiracles in a J-shaped row. Body hairs 0.05-0.09 mm long. In other respects, similar to mature larva. (Material studied: a few larvae from Panama.)

Weber, 1945, referring to *C. rimosus*: "The larvae appeared to have a scanty, diffuse, whitish mycelial envelope as in *Atta* larvae" (p. 7-8). "The sexual pupae and larvae were covered with whitish mycelial masses" (p. 8). "Larvae of different sizes up to the large, mature worker size as well as several pupae were covered with a network of mycelium" (p. 11).

C. rimosus comalensis Wheeler.—Indistinguishable from *C. rimosus s. str.* (Material studied: a few specimens from Texas.)

Wheeler, 1907, p. 773: "Several of the larvae and pupae that had been injured while the colony was being captured were eaten with avidity not only by the workers but also by the males and winged females."

C. strigatus Mayr.—Plate II, figs. 7-8. Resembles *C. rimosus* except in the following details: No preanal lip. No flap projecting from first abdominal sternum. Body hairs restricted to a few on the sterna of the anterior segments and a few on the pre-anal sterna; length 0.03-0.14 mm. Clypeus and front not spinulose. Head hairs 0.14 mm long. Labrum very small, very broad

and very short; breadth four times the length; distal border slightly convex; lateral borders sinuous, continued distally into a spinule at each corner; posterior surface with a few coarse spinules on the middle third; no spinules on the anterior surface. Mandibles with a typical apical tooth. (Material studied: several specimens from Panama Canal Zone.)

Young Larva. Length 0.67 mm. Resembles young larva of *C. rimosus* except in the following details: Posterior end of body bent ventrally at right angles and forming an acute conoid with the anus on its anterior surface. Segmentation distinct except near the posterior end; intersegmental furrows deeply impressed on the ventral surface. Body hairs 0.03-0.14 mm long. Mandibles with a typical apical tooth. (Material studied: a few specimens from Panama Canal Zone.)

C. olitor Forel.—Apparently similar to *C. strigatus*. (Material studied: a single damaged larva from Panama Canal Zone.)

C. bigibbosus Emery.—"The larvae were swathed in mycelia." (Weber, 1946, p. 123.)

C. bigibbosus faunulus Wheeler.—"Larvae and pupae were covered with mycelium." (Weber, 1946, p. 124.)

C. bigibbosus tumulus Weber.—"Larvae and pupae were covered with the mycelium." (Weber, 1946, p. 127.)

C. (Mycetophylax) brittoni littoralis Weber.—Weber (1945, p. 25) mentions "a large larva covered with mycelia."

Genus SERICOMYRMEX Mayr

Head on ventral surface near anterior end; ventral profile relatively longer than in most Attini; first spiracle larger than the others. Genal lobes prominent. Head hairs moderately long to very long; few or none above the level of the antennae. Labrum subhemispherical. Mandibles moderately stout; subtriangular in anterior view; base broad and thick; narrowed apically; with the apical portion only slightly curved medially; two apical teeth; spinules moderately numerous. Maxillary palp short, stout, subcylindrical; galea represented by two sensilla.

Wheeler and Bailey (1920, p. 253) state that in this genus the "mouthparts are beautifully adapted for the methods of feeding described by Tanner and Huber. The mandibles are short, stout and acute, and . . . covered with numerous sharp spines, so that the delicate egg-shell or the thin walls of hyphal filaments or of kohlrabi spherules can be held and firmly squeezed and at the same time perforated with many small openings, thus allowing the liquid contents to be rapidly expressed and trickle into the mouth."

S. wheeleri Weber.—Plate II, figs. 9-13. Head on ventral surface near anterior end. Body short, very stout, plump, bean-like; ends large subequal and broadly rounded; dorsal profile very long, C-shaped; ventral profile short and bent ventrally at the posterior third; anus ventral, near posterior end. On either side a short, slender, dark-staining (with acid fuchsin) structure extends from the gena on to the prothorax; its nature and function unknown. Seg-

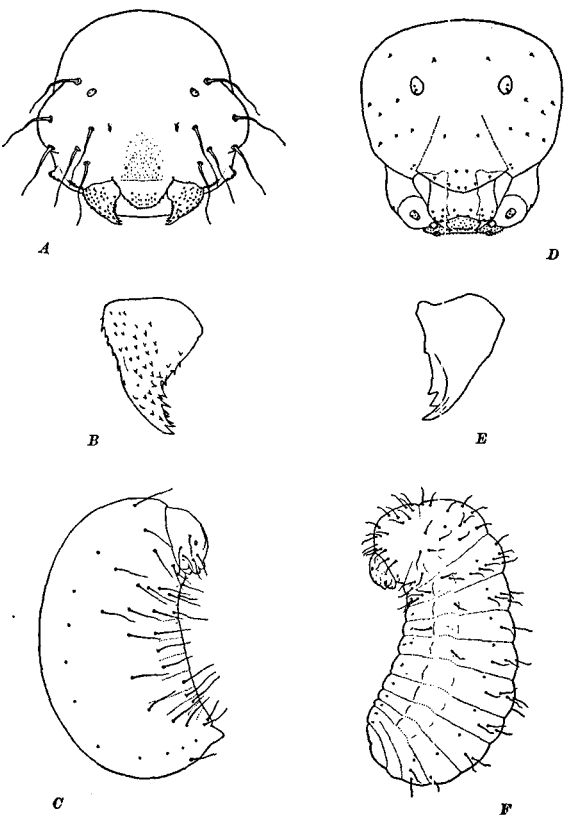
mentation indistinct. Spiracles small; size diminishing progressively from anterior to posterior; arranged in a crescent. Body nearly naked; hairs restricted to ventral surface of thorax and first four abdominal segments and two extremely minute hairs in front of the anus. Body hairs simple, slender, slightly curved, moderately long (0.06-0.14 mm). Head somewhat broader than long; subhexagonal in anterior view, but with all corners rounded; with a median longitudinal welt which widens ventrally. Head hairs 8-12; simple, slightly curved, moderately long (0.1 mm); all below the antennal level. Antennae small, each with three sensilla. Labrum subhemispherical; spinulose; a few sensilla on the anterior surface. Mandibles small, moderately stout, subtriangular in anterior view; base broad and thick; narrow toward the apex, which is slightly curved medially and posteriorly and which terminates in two long slender teeth; moderately spinulose, the spinules coarse and sharp-pointed. Maxillae feebly developed; adnate to the head, except for a small apical lobe; not spinulose but with several minute hairs; palp a short stout peg tipped with a rounded transparent cap; galea represented by two sensilla. Labium subhemispherical, short, scarcely visible from in front; palp represented by a cluster of sensilla on the distal surface. Hypopharynx with spinules in transverse rows. (Material studied: several specimens from British Guiana collected by Dr. N. A. Weber.)

S. amabilis Wheeler.—Text fig. 1, figs. A-C. Head on the ventral surface near the anterior end. Body short, very stout, plump, bean-like; ends large, subequal and broadly rounded; dorsal profile very long and C-shaped; ventral profile much shorter than dorsal but still relatively long and only slightly concave. Anus ventral, near posterior end; postnatal lip conoidal. Segmentation indistinct. Spiracles small, the first larger than the others; arranged in a crescent. Body hairs mostly restricted to the ventral and lateral surfaces, a few dorsal; long (0.2 mm), simple, tapering, flexuous. Integument sparsely and minutely spinulose. Head about as broad as long; occipital border strongly rounded; genal lobes moderately large and prominent; clypeus sparsely and minutely spinulose. Head hairs like body hairs; one pair above the antennal level, five pairs below. Antennae very small; each with three sensilla. Labrum small, subhemispherical, spinulose. Mandibles small, moderately stout, subtriangular in anterior view; base broad and thick; narrow toward the apex which is slightly curved medially and which terminates in two small acute teeth; moderately spinulose, the spinules coarse and sharp-pointed. Maxilla feebly developed; adnate to the head; except for a small apical lobe; palp a short stout subcylindrical peg; galea represented by two sensilla. Labium short, subhemispherical, scarcely visible from in front; palp represented by a cluster of sensilla on the distal surface. (Material studied: several specimens from Panama Canal Zone.)

The differences between *amabilis* and *wheeleri* are much greater than those usually found among congeners. They differ markedly in body shape; in the postanal lip; in the size, shape and arrangement of hairs on the head and body; in the spinules on the integument; and in the shape of the head. In fact, *amabilis* more closely resembles Trachymyrmex than its own congener *wheeleri*.

Wheeler, 1925, p. 158: "The ants placed their eggs, larvae and pupae on the fungus-covered surfaces and in the crypts. . . . Since I never saw the workers administering hyphae or 'kohlrabi' to the larvae, . . . I infer that the latter when hungry merely reach out and crop the fungus. The larvae are short, thickset and beset with sparse, long, flagellum-like hairs. The head is large and subrectangular, bearing small, acute mandibles covered with acute points. This type of mandible, which I find to be peculiar to the Attini, seems to be adapted to puncturing the delicate fungus hyphae and expressing their juices."

Wheeler, 1937: "Some time after the larvae hatch they are carried by the workers to other parts of the garden and placed in contact with fresh masses of the fungus. Since the workers were never observed in the act of administering bromatia to the larvae, it was inferred that the latter merely



Text Figure 1.—*Sericomyrmex amabilis* Wheeler, Figs. A-C.—A, head in anterior view, ×62; B, right mandible in anterior view, ×185; C, larva in side view, ×21. *Megalomyrmex* (*Cepobroticus*) *symmetochus* Wheeler, Figs. D-F.—D, head in anterior view, ×93; E, right mandible in posterior view, ×185; F, larva in side view, ×15.

reach out and crop the food that is within reach of their mandibles" (p. 47). "It is . . . probable that the larvae of the incipient colony [in the higher Attines] eat the mycelium directly and that larval feeding in this very early phase of colony development may really represent an ancient phylogenetic stage which persists throughout the life of the colony in Sericomyrmex and other primitive genera" (pp. 49-50).

When the *amabilis* colony was host to the guest-ant *Megalomyrmex* (*Cepobroticus*) *symmetochus* Wheeler, Wheeler observed (1925, p. 162) that "the guest ants kept their brood in small clusters scattered throughout the garden and each cluster was cared for by a few workers. Although the ants and their brood were thus intermingled, the workers of each species lavished their attention exclusively on their own eggs, larvae and pupae and were never seen even to transport the progeny of the other species from one part of the garden to another."

"The larvae and pupae of the *Cepobroticus* can readily be distinguished from the *Sericomyrmex* brood. The larvae are more slender and more cylindrical and have smaller heads, with flat 3-toothed mandibles. The hairs on the body are more numerous, shorter and stouter, though rapidly tapering at their tips." (Wheeler, 1925, p. 163.)

I have prepared Text fig. 1 from type larvae to show some of the differences between host and guest.

S. harekulli arawakensis Weber.—Weber (1946, p. 142) has observed larvae covered with hyphae.

S. impexus Wheeler.—"Larvae in the nest were naked." (Weber, 1946, p. 142.)

S. urichi Forel.—"Both larvae and pupae are swathed in mycelium but the larvae may at times be partially to completely naked." (Weber, 1945, p. 43.)

Genus TRACHYMYRMEX Forel

Postanal lip conical. Body hairs on entire ventral surface. Genal lobes large and prominent; six hairs on each. Head hairs moderately long; mostly below antennal level, only a few above. Labrum subhemispherical. Mandibles densely spinulose; with apical portion strongly curved medially; one apical tooth. Maxilla with very few spinules; palp represented by a cluster of sensilla; galea by one or two sensilla.

Wheeler and Bailey, 1920, p. 253: "Mouthparts beautifully adapted for the methods of feeding described by Tanner and Huber. The mandibles are short, stout and acute, and . . . covered with numerous sharp spines, so that the delicate egg-shell or the thin walls of hyphal filaments or of kohlrabi spherules can be held and firmly squeezed and at the same time perforated with many small openings, thus allowing the liquid contents to be rapidly expressed and trickle into the mouth."

T. septentrionalis obscurior Wheeler.—Plate II, figs. 14-19. Head on the ventral surface at a considerable distance from the anterior end. Body short, very stout, plump, bean-shaped; slightly compressed; subelliptical in dorsal

view, but slightly constricted at the middle; dorsal profile very long and C-shaped, ventral short and nearly straight; ends large, subequal and broadly rounded. Anus ventral; near posterior end; with a conspicuous posterior lip which is surmounted by a small ventral conical projection. Spiracles small; in a crescentic row. Body mostly naked; hairs few; restricted to the ventral surface; simple, short (0.16 mm) and nearly straight. Head subquadrate in anterior view, but with the occipital angles broadly rounded; genae produced laterally into conspicuous subhemispherical lobes. Head hairs few; mostly below the antennal level; bases moderately stout, attenuated apically; slightly curved; moderately long (0.04-0.14 mm). Antennae small; each with three sensilla. Labrum small, subhemispherical, spinulose. Mandibles moderately large; very stout at the base but attenuating rapidly toward the apex which is strongly curved medially and which bears a long slender acute tooth; densely covered with coarse sharp spinules. Maxillae feebly developed; adnate to the head except for a small free apical lobe; the surface bearing a few spinules, a few sensilla and two minute hairs; palp a low elevation bearing two sensilla; galea a low elevation bearing one or two sensilla. Labium very small; concealed in anterior view; bearing a few minute hairs; palp a low rounded elevation which is densely spinulose and bears a few sensilla. Hypopharynx densely spinulose; spinules in short transverse rows. (Material studied; numerous larvae from Texas.)

Wheeler, 1907. An excellent photograph of the brood (Fig. 21 on p. 751). "The older larvae and young pupae . . . are always free from adhering hyphae, so that their surfaces are always smooth and glistening" (p. 752).

T. jamaicensis Ern. André.—Similar to *T. septentrionalis obscurior.* (Material studied: a single damaged specimen from Culebra Island.)

T. phippsi Weber.—Weber (1946) refers (p. 150) to "larvae with many tufts of hyphae on their integument" and figures (Fig. 3 and 4 on p. 121) an outline of a larva in side view and the mouth parts in side view.

Genus ACROMYRMEX Mayr

Body hairs short and stout; not restricted to ventral surface. Genal lobes large. Head hairs relatively short. Labrum subhemispherical. Mandibles densely spinulose; apical portion strongly curved medially; one apical tooth. Galea represented by a cluster of sensilla.

Bruch (1928, p. 345) describes the hairs as "una especie de ganchitos pardos, duros (quitinosos), formados por una pieza basal y dos ganchitos apicales divergentes en el ápice."

A. octospinosus (Reich).—Plate III, figs. 7-9. Head on the ventral surface at a considerable distance from the anterior end. Body short, very stout, plump, bean-like. Ends large and broadly rounded. Dorsal profile extremely long, C-shaped; ventral profile relatively short, concave. Anus ventral and at a considerable distance from the posterior end; posterior lip prominent. Segmentation indistinct. Body hairs numerous and uniformly distributed; resembling head hairs; extremely short (0.03-0.06 mm), rather stout,

the tips recurved or with two or more fine branches; apparently without alveolus, trichopore and articular membrane. Head a third broader than long; subtrapezoidal in anterior view, but with the occipital angles broadly rounded; genal lobes large but inconspicuous, scarcely protruding beyond the sides of the head. Head hairs short (about 0.05 mm), moderately abundant, uniformly distributed; resembling body hairs, but with alveolus, trichopore and articular membrane; base stout, tapering abruptly to a slender apical portion, the tip minutely bifid or trifid. Antennae small, each with three sensilla. Labrum small, subhemispherical, densely spinulose. Mandibles small, with moderately stout base; the more slender apical portion curved medially and terminating in a slender acute tooth; densely spinulose (except apical tooth), the spinules coarse and sharp. Maxillae reduced; long and narrow and adnate to the head except for a free apical lobe; coarsely spinulose; palp a short, stout, subcylindrical papilla; galea represented by two sensilla on a slight elevation. Labium small; mostly concealed by other mouth parts; spinulose, the spinules arranged in transverse rows; palp represented by two minute sensilla on a slight elevation. Hypopharynx spinulose. (Material studied: three larvae from British Guiana.)

Weber, 1945: "the pupae [in one observation nest] were covered densely with a white mycelium while the larvae were bare and glistening" (p. 65). "The larvae and pupae are commonly swathed in a mycelium" (p. 70).

Wheeler (1937, p. 49) reports that the feeding of the larvae of this species is very similar to that of *Atta cephalotes*. "A larva of *octospinosus* that was resting on its back was seen to receive a pellet of bromatia from a worker, to hold it in its mouth with the mandibles, and to eat it by abrading the surface while occasionally rotating it, without breaking off pieces." A minute larva in an incipient colony "seemed to be feeding on the fungus, as its ventral surface was curved into the mass of hyphae" (p. 50).

A. emilii Forel.—Similar to *A. octospinosus*. (Material studied: two larvae from British Guiana.)

A. lundi Guérin.—Plate III, figs. 1-6. Head on the ventral surface at a considerable distance from the anterior end. Body short, very stout and very plump, bean-shaped; somewhat compressed; narrowed at the middle; both ends large and broadly rounded; dorsal profile extremely long, C-shaped; ventral profile, very short and slightly concave. Anus ventral and at a considerable distance from the posterior end; postanal lip forming a tubercle. Segmentation indistinct. Spiracles small; arranged in a subcrescentic row. Body naked except for about 40 minute (length 0.027 mm) scattered spine-like hairs, which are stout, curved and rather bluntly pointed; none on ventral surface. Integument finely and reticulately rugulose [artifact?]; with minute spinules in short transverse rows on the prosternum. Head about a third broader than long; quadrangular; occipital border nearly straight; the middle of each side produced into a huge suborbicular genal lobe which projects conspicuously from the side of the head; shape of lobe somewhat variable; integument of head granulose [artifact?]. Head hairs few (about a dozen); except for an occipital pair, all are below the antennal level; only one on each genal lobe; head hairs

short (0.05 mm), stout, nearly straight, only slightly attenuated toward the apex which is blunt and spinulose. Antennae small; each with three sensilla. Labrum small, subhemispherical; partially retracted into head; spinulose distally. Mandibles moderately large, short and stout; distal portion attenuated somewhat and curved medially and backward to terminate in a slender, acute apical tooth; surfaces mostly covered with coarse sharp spinules. Maxillae elongate, narrow; mostly concealed behind mandibles; adnate to the head, except for a free apical lobe; basal half spinulose; palp a short, stout, subcylindrical peg; galea represented by two minute sensilla. Labium very short and very broad; concealed behind the other mouth parts; consisting mostly of two coarsely spinulose lobes separated by a deep impression; each palp represented by two adjacent sensilla. Hypopharynx spinulose. (Material studied: three larvae from Argentina.)

Bruch (1919): Colony-founding queens feed their eggs to larvae (*fide* Wheeler, 1933, p. 9).

A. coronatus globoculis Forel.—"Some of the larvae and pupae were free of the mycelium in this nest while others had a little. Ordinarily larvae and pupae are well swathed in mycelium." (Weber, 1946, p. 152.)

Genus PSEUDOATTA Gallardo

I have seen no larvae of this genus, but according to Bruch's description and photograph of two larvae in profile (1928, Pl. I, fig. 1) the body has the typical attine shape. The hairs on the head and body are flexuous and slightly curved; those on the dorsal surface are bifurcate at the tip; the hairs on the ventral surface of the thorax are much more abundant.

Bruch, 1928, p. 345: "Las larvas . . . son del tipo común de las larvas de podadoras del género *Acromyrmex*. Solamente su forma es algo más cilíndrica, poco menos estrechada hacia las extremidades y apenas menos encorvada. Sobre la cabeza y el cuerpo se destacan algunas setas parduscas, semiblandas y algo encorvadas, solamente alguna de éstas (sobre el dorso) son bifurcadas en el ápice; en la parte ventral del antecuerpo (tórax), estas setas son mucho más abundantes."

Wheeler, 1937, p. 54: "Pseudoatta is, as we should expect it to be, most closely related to its host genus, Acromyrmex. . . . The larvae of Pseudoatta, moreover, are described by Bruch as resembling those of Acromyrmex."

Genus ATTA Fabricius

Postanal lip subtriangular and flap-like. Body hairs mostly restricted to first four body segments and vicinity of anus. Posternum spinulose. Genal lobes small and inconspicuous. Head hairs numerous, uniformly distributed, relatively short. Labrum subhemispherical. Mandibles densely spinulose; apical portion strongly curved medially, one apical tooth. Maxilla with few spinules; palp represented by one sensillum, galea by a cluster of sensilla.

Forel, 1923, pp. 89-90: "Madame *Atta* alimente *directement* ses larves avec les oeufs qu'elle pond (adelphophagie directe). Elle chatouille la larva avec ses antennes, jusqu'à ce que celle-ci ouvre ses mandibules. Alors la ♀

pousse l'oeuf fraîchement pondu qu'elle saisit contre les mandibules de la larve, sur le ventre de cette dernière, et la larve le mange. Si la larve est petite et jeune, la ♀ donne ensuite le reste de l'oeuf à une seconde larve. Mais, si la larve est grande, elle déguste l'oeuf tout entier en trois à cinq minutes. [Huber] a observé ainsi 4 oeufs pondus administrés en deux heures à des larves, une fois même 8 dans le même laps de temps. Jamais H. n'a vu des ♀ donner à leur larves les choux-raves de leur jardin, ni les manger elles-mêmes. . . . Elle peut même élever sa couvée sans avoir de j. de ch., ce que [Möller] put observer une fois dans un nid artificiel jusqu'a l'éclosion des ☿. Dès que les premières petites ☿ de 2 à 3 mill. de long. sont écloses, la scène commence à changer, et les ☿ se chargent de soigner les nymphes. Elles continuent aussi pendant un certain temps à alimenter les larves et leur mère elle-même avec des oeufs pondus par cette mère commune."

Forel, 1928, Vol. II, p. 270: "But over and above this Huber managed to see how Madame *Atta* feeds her larvae *directly* with the eggs she lays (direct adelphophagy). She strokes a larva with her antennae until it opens its mandibles; she then seizes a new-laid egg and thrusts it against the larva's mandibles, and on to its gaster, whereupon it is eaten. If the larva is young and small, the ♀ then gives the rest of the egg to a second larva, but if it is large it consumes the whole egg in three to five minutes. Huber saw four eggs administered to various larvae in two hours, and on one occasion even eight in the same space of time. He never saw the ♀ eat kohlrabi clusters from their gardens or give them to their larvae. . . . She can also rear her brood without fungus, as Möller once managed to observe while watching an artificial nest till the workers were hatched. With the appearance of the first small ☿ (2-3 mm. long), the scene begins to change; the ☿ take charge of the nymphs, and for a certain length of time they also continue to feed the larvae and their common mother herself with the eggs she lays."

Weber, 1945, p. 7.—The larvae "have a scanty, diffuse, whitish mycelial envelope."

Hagen (1939, p. 32) states that staphylinid beetles "plunder the live young larvae of the nest."

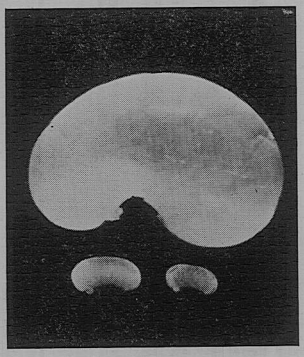
According to Wheeler (1910, p. 332-333) the colony-founding queen feeds her first larvae with her own eggs, thrusting them directly into their mouths. After the first workers emerge they continue to feed larvae with their mother's eggs. When the fungus-garden has begun to thrive larvae are fed "kohlrabi" by the workers.

Wheeler and Bailey (1920, p. 253) state that "the mouth parts are beautifully adapted for the methods of feeding described by Tanner and Huber. The mandibles are short, stout and acute, and . . . covered with numerous sharp spines, so that the delicate egg-shell or the thin walls of hyphal filaments or of kohlrabi spherules can be held and firmly squeezed and at the same time perforated with many small openings, thus allowing the liquid contents to be rapidly expressed and trickle into the mouth."

A. cephalotes (Linnaeus).—Plate III, figs. 10-16. Head on the ventral

surface at a considerable distance from the anterior end. Body short, very stout and plump, bean-shaped; slightly compressed; outline when viewed from above or below subelliptical but slightly narrowed at the middle; depth greatest at the middle, decreasing slightly and equally toward the ends; both ends large, subequal and broadly rounded. Dorsal profile extremely long, subcrescentic; ventral profile short, slightly concave. Anus ventral and at a considerable distance from the posterior end; with a conspicuous posterior lip. Segmentation indistinct. Spiracles small; in a subcrescentic row. Body nearly naked, having only a few minute (0.05 mm long) simple, slender, tapering hairs, which are largely restricted to the ventral surface of the thorax and the vicinity of the anus. Integument of prosternum with minute spinules. Head somewhat broader than long; suboctagonal in anterior view; a feebly developed genal lobe on each side near the middle; integument of gula spinulose. Head hairs moderately long (0.09 mm), moderately abundant, uniformly distributed, slender, tapering, slightly curved or flexuous. Antennae small; each with three sensilla. Labrum small subhemispherical, spinulose; mandibles small, short and stout; apical portion abruptly attenuated and curved medially; surfaces coarsely and densely beset with sharp spinules; with an elongate acute apical tooth. Maxillae reduced; long and narrow; adnate to the head; sparsely spinulose; palp a small short subcylindrical papilla; galea represented by a pair of small short subconical papillae. Labium reduced; mostly concealed; very short and very broad; produced at each corner into a low rounded elevation, which bears a cluster of minute hairs, a few spinules and a single minute discoidal sensillum (= palp). Hypopharynx spinulose. (Material studied: several larvae from British Guiana.)

Sexual larva. Text fig. 2. I have examined three larvae of *cephalotes*, presumably queens and probably fully grown, collected by Dr. N. A. Weber in Trinidad. The largest is 16 mm long, and really enormous; extremely plump, looking as if it were about to burst; more curved ventrally than smaller larvae and hence with the head nearer the anus; no posterior anal lip; head relatively minute; gula inflated into two lobes, which are spinulose.



Text Figure 2.—*Atta cephalotes* (Linnaeus). Sexual larva and two mature worker larvae, ×2.

Tanner (1892, pp. 124-125; quoted by Wheeler, 1907, pp. 682-683; by Wheeler and Bailey, 1920, p. 252; and by Wheeler, 1937, p. 47) described the newly hatched larvae of *cephalotes* as exceedingly minute helpless grubs, both legless and blind. They "are usually placed on top of the nest and are constantly attended by the smallest workers — the nurses — who separate them into divisions according to size. At first it seemed a mystery, how these minute grubs could be fed so systematically, knowing that each individual larva was only one among so many, yet certain it was, that all were equally attended to. Further observations showed that nature had provided most efficiently for them to ask for food when they required it. This the larvae do by pouting their lips; at this notification of their requirement the first nurse who happens to be passing stops and feeds them. The nurses are continually moving about among them with pieces of fungus in their mouths ready for a call for food. The nurses feed the minute larvae by merely brushing the fungus across their lips showing that the spores alone are sufficient for its food at that period of its life. But it is not so when the larvae have increased so much in size, that the pout can be seen without a glass, for then the whole piece after having been manipulated by the nurse's mandibles into a ball, in the same manner as the leaves are served, when they are first brought into the nest, is placed in its throat and if that is not sufficient the pout continues when the next one and even the next passing proceeds with the feeding, till the pout is withdrawn, showing that it is satisfied. No further notice is then taken of it by the feeders, until it again asks for a meal by pouting later on in the day."

Weber (1945): "A larva on its back was watched feeding on a bromatium. The workers in such cases rotate such a mass between their mandibles, then place it on the mouthparts of the pouting larvae. A larva was lying askew on its back feeding. It had a bromatium between its mandibles which went in and out with a somewhat piston-like motion and laterally, the labium being coördinated with these motions. Eating, as in the adults, seemed to be a process of attrition and lapping up of expressed juices. The larva handled the mass easily. Another larva had such a mass on one side of the mouth, the mouthparts working in and out without affecting the bromatium, when a media worker came up and regurgitated to it, working its own hypopharynx and palpi to the corner of the mouth opposite to that of the bromatium. It acted thus for 15-30 seconds when it passed on. The larva worked its mandibles for a moment later, then became quiet" (p. 76). "By April 30 the ants had moved nearly all of the brood (consisting of tiny pupae, larvae and eggs) to the bottom of the nest under the garden except one large pupa, one large larva and one much smaller larva. The garden continued to flourish. The situation was on May 1 as above when the ants were moved to a new nest. The next day the garden appeared much as before with the queen on top towards the center and the large larva and pupa in separate open cells attended by many ants. It was clear for some days that [the] large larva and pupa had been getting much more attention than the remainder of the brood, either from more workers or from workers more times" (p. 77). "A part of one fungus garden of a large, mature colony was collected April 17

and placed in an observation nest. With the garden were huge sexual larvae. . . . By April 20 the ants had removed much exhausted substrate and several sexual larvae which had shrivelled as a result of the ants lapping the cut and damaged integument. One intact sexual larva remained. The others had been too thoroughly defended when the nest was opened and had been cut by the mandibles of the workers. . . . The larva pupated May 1 or 2 (pp. 78-79). "The larvae and pupae are often swathed in mycelium" (p. 84).

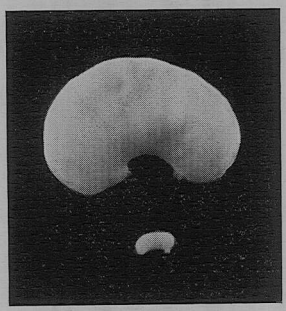
Weber (1946, p. 164): "Then the ant walked over to a shining larva which was longer and bulkier than the nursemaid. The mouthparts of the larva were somewhat extruded. The ant placed the bromatium on these mouthparts, the larva lying on its back, and the larva commenced to feed. The mouthparts went in and out with a piston-like motion. Within two or three minutes the bromatium had been eaten but the larva maintained the working of its mouthparts. . . . Eggs, larvae and pupae were all clean and shining . . . and all free from mycelia."

According to Wheeler (1907, pp. 681-682), Tanner was the first to study Attini "in artificial nests and to prove that not only the adult ants but also the larvae feed on the fungus hyphae. . . . 'It is the fungus they eat, and with small portions of it the workers feed the larvae.' "

Wheeler (1937, pp. 48-49): "The eggs, larvae, and pupae of *cephalotes,* roughly classified by the workers according to size, are kept in the most flourishing portion of the gardens. Tanner's statement concerning the feeding of the young larvae with spores is incorrect, of course, because these fruiting bodies are not produced by the fungus. He also failed to notice that the workers also often feed one another and their larvae with regurgitated food. The workers roll masses of bromatia between their mandibles before placing them in the mouths of the pouting larvae. Dr. Weber noticed that one larva, which was lying on its back, on receiving the pellet of bromatia, worked its mandibles in and out with a piston-like movement while at the same time moving its labrum up and down. Eating, as in the adult, is a process of attrition and a lapping up of the juices exuding from the crushed bromatia. On another occasion, a worker minima was seen to be rotating a mass of bromatia between its mandibles and fore tarsi. It then walked over to a plump larva whose mouthparts were extruded ('pouting'), as it rested on its back, and placed the pellet over its mouth. The larva ate with the piston-like movement of its mandibles and after consuming the pellet within two or three minutes, worked its mouthparts a moment longer before becoming quiet. A third larva had at the side of its mouth a mass of food which it seemed to be unable to masticate, though it worked its mandibles and labrum. A worker media came up and regurgitated to it assiduously, directing its tongue and palpi to the corner of the larva's mouth opposite to the bromatial pellet. The regurgitation continued for thirty seconds, after which the worker passed on. In another *cephalotes* colony the workers for several days kept a worker and a soldier larva, which were much larger than the remainder of the brood, in the same or in separate cells of the garden and gave them special care. They unquestionably received more attention than the small larvae, either

from more workers or from more frequent feeding by the same workers. The more conspicuous 'pouting' of these larger larvae, which is perhaps accompanied, as it is in the larvae of the social wasps, by the emission of some trophallactic secretion, probably tends to attract more of the passing workers and may thus account for the more frequent feeding. . . . On April 17, 1935, Dr. Weber installed in an observation nest a portion of a large *cephalotes* colony that was rearing its huge sexual larvae. The workers had defended these larvae too well when the nest was exposed, swarming over them and holding on to the larvae with their mandibles, so that the integument of nearly all was cut in many places. By April 21 only one was left, the rest shriveling up as the result of the workers' lapping up their juices through the cuts in their integument. This larva was fed with bromatia in the same manner as the worker larvae and similarly rested on its back."

A. columbica Guérin.—Text fig. 3. Similar to *A. cephalotes*. (Material studied: several larvae from Panama Canal Zone.)



Text Figure 3.—*Atta columbica* Guérin. Sexual larva and mature worker larva, ×2.

A. insularis texana (Buckley).—Similar to *A. cephalotes*. (Material studied: several damaged larvae from Texas.)

A. sexdens (Linnaeus).—Similar to *A. cephalotes*. (Material studied: several specimens collected by Dr. N. A. Weber in Venezuela.)

Huber, 1905 (translation 1907): "Somewhere about fourteen to sixteen days after the female *Atta* has established her subterranean dwelling, the first larvae can be clearly seen lying among the eggs which by this time amount to over 100. The fungus garden is now from 1 to 1.5 cm in diameter. The number of larvae increases daily and their rapid growth is especially striking, some attaining within a week a length of fully 2 mm. A month or so after the beginning of the imprisonment the first pupae are to be seen" (p. 358). "Eggs and larvae require to be diligently licked, placed in clusters, or spread out separately, put in contact with the fungus or separated from it and later on laid in the hollow center of the fungus garden, or certain individuals of the brood removed from it" (p. 360). "We therefore find a proportion of 9 eggs devoured to every 10 laid. The foregoing especially unfavorable proportion is doubtless to be attributed to the fact that the larvae required from the

beginning to be fed with the eggs. . . . When the egg has been laid, the mother ant tests it for some seconds by a process of tasting, and then turns to one of the larvae, which she caresses with her antennae until it begins to move its mandibles. The egg is then thrust between its mouth parts with considerable force. These continue to work back and forth upon the egg, which either stands perpendicular to the larva, or, as is more frequent, lies along its ventral side. In the latter case the mother-ant often presses the egg with her foot against the larva. If it is still very young, the egg is generally after a time taken away and given to another larva. A good-sized larva is, however, capable of devouring an egg in from three to five minutes, so that nothing but the leathery skin remains, which is later removed by the mother-ant. At any rate, I have clearly observed that a larva whose mouthparts were in vigorous action upon an empty egg-skin had this residue licked away by the mother-insect, and that then the movement of the larva ceased. It is no doubt due to the rapidity with which the larvae devour the eggs that one so very rarely comes upon them in the actual process of eating them, but I have clearly established the fact that feeding of larvae with eggs is a very frequent occurrence. Thus, for example, I have noted in a forenoon the process of egg laying to take place four times and the feeding of larvae with eggs an equal number, and in the afternoon during two hours eight cases of egg-laying and four of feeding these to the larvae. I am of the opinion that up to the time of the appearance of the workers eggs form the exclusive food of both the mother-ant and her brood. I have never detected a case of the *Atta* female supplying the larvae with either the mycelial threads or the kohlrabi of the fungus (*Rosites*). . . . In regard to the feeding of the brood by a solitary maternal ant, Janet and Forel, as I understand it, have advanced the opinion that the larvae are fed with a nutritive liquid derived from the eggs devoured by her and which she secretes in the communal stomach (jobot). In respect to *Atta*, at least, this is not the case. The eggs are here directly fed to the larvae. Comparative investigations must determine whether or not this method of feeding takes place with other ants. It is at least noteworthy that in the case of *Atta* the larvae are not later on fed by the workers with their stomach contents, but directly with the kohlrabi growth of the fungus" (pp. 361-363). "The larvae, the number of which rapidly increases, are still fed with eggs [after the first workers emerge]. It is of interest to observe how in this task the workers gradually relieve the mother-ant of the larger share. It often happens that the mother-ant places an egg in the regular way against the mandibles of the larva, but it is frequently seen that it is not satisfactorily arranged or is simply deposited in the nest; in the latter case the workers pick it up and give it to the larva. The workers also stroke the larvae with their antennae in the same manner as the mother-ant, so as to cause them to move their mandibles when the egg is given to them. I have generally been able to observe the same egg being given to several larvae by the workers, who slowly squeeze it with their mouthparts" (pp. 363-364). "In consequence of this steady enlargement of the fungus garden the larvae (and the eggs as well) are gradually removed from the domain of the mother-ant. It is not surprising that at first the larvae continue to be fed with eggs, since at this

period the quantity of kohlrabi is small, being barely sufficient for the adult workers. Nevertheless, I once noticed a small worker offering a half-eaten kohlrabi to a larva, and finally mashing it up in a very practical way in front of its mouth. In this way a beginning is doubtless made in the further feeding of the larvae with kohlrabi, which comes to be the general thing as soon as the necessary supply is obtainable" (p. 366).

"*Summary.*— . . . The larvae are at first fed with eggs by the mother ant, and during the transitional period by the young workers" (p. 367).

Huber, 1905 (translation 1907): Photographs of numerous larvae in fungus gardens (Pl. II, fig. 12 and Pl. IV, fig. 22); the feeding of a larva (Pl. IV, fig. 20).

Weber (1946): "Larvae and pupae were naked and glistening" (p. 167). "Smooth and glistening larvae and pupae" (p. 168). "A minima worker was seen to give a bromatium to a larva lying obliquely on its dorsal surface, *i.e.,* turned partly on one side. The larva grasped it readily with the mouthparts" (p. 168).

Wheeler, 1907, pp. 698-699: "As soon as the larvae appear they are fed directly with eggs thrust into their mouths by their mother. Huber concludes that this is their normal diet till the first workers hatch. . . . [Then these] feed the larvae with their mothers' eggs. . . . [Later] the 'kohlrabi' has become so abundant that it can be fed to the larvae."

Wheeler and Bailey (1920, p. 252) give in translation a part of the passages from Huber (pp. 361-362) that I have quoted above.

Wheeler (1928, p. 203 and 1933, p. 9): Colony-founding queens feed their eggs to larvae.

Wheeler, 1937, p. 49: "Larval feeding in an *A. sexdens* colony kept under observation in British Guiana was found to be precisely the same as in *cephalotes.*"

A. sexdens rubropilosa Forel.—Autori (1942) gives the life cycle as follows: egg 22 days, larva 22 days, pupa 10 days.

A. sexdens vollenweideri Forel.—Bruch (1917) has published photographs of queen larvae (Fig. 3 on p. 160 and Pl. I, c).

DISCUSSION

The larvae of the tribe Attini constitute a well defined and homogenous group which is sharply distinguished from typical myrmicine larvae (such as *Megalomyrmex,* illustrated in Text fig. 1) by the position of the head and of the anus; the shape of the body; the indistinct segmentation; the arrangement of the spiracles; the scarcity of hairs and their restricted distribution; the genal lobes; the reduced mouth parts; the spinules on the mandibles; and the reduced number of mandibular teeth. None of these characters is alone distinctive, but as a group they define the Attini very well.

The larvae of the tribe may be separated into two groups: (1) *Myrmicocrypta* and *Apterostigma*. These agree in having the maxillae and labium fully exposed; the mandibles not curved; and the absence of genal lobes. (2) *Cyphomyrmex, Sericomyrmex, Trachymyrmex, Acromyrmex* and *Atta*. These have the maxillae and labium mostly concealed; the apical portion of the mandibles curved medially; and genal lobes. This grouping confirms in general Emery's opinions on adult taxonomy (as expressed in the *Genera Insectorum*): *Cyphomyrmex, Trachymyrmex, Acromyrmex* and *Atta* represent the main stem of the Attini; *Mycocepurus, Myrmicocrypta* and *Apterostigma* are another line, perhaps more primitive; *Sericomyrmex* is an aberrant genus. The last item is not confirmed in larval taxonomy, for *Sericomyrmex* resembles closely the genera of my second group; it does, however, differ from all other attine larvae in having two apical teeth on the mandibles. Wheeler (1910, p. 320) thought adult *Apterostigma* "very aberrant, resembling in form certain Myrmicines of the subgenera *Aphaenogaster* and *Ischnomyrmex*." The larva of *Apterostigma* is certainly aberrant in the extreme reduction of the mouth parts and in the lack (or extreme scarcity) of spinules on the mandibles, but it does not even remotely resemble the typically myrmicine larvae of Aphaenogaster and Ischnomyrmex.

Within the groups (referred to in the preceding paragraph) larval taxonomy does not correlate closely with adult taxonomy. Genera, to be sure, are easily differentiated, but some congeneric species show differences of generic magnitude,[1] while others differ only in trival characters[2] or not at all.[3]

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1 *Sericomyrmyrmex amabilis* versus *S. wheeleri; Acromyrmyrmex lundi* versus *A. octospinosus.*

2 *Apterostigma collare angulatum* versus *A. tramitis; Cyphomyrmex rimosus* versus *C. strigatus.*

3 *Myrmicocrypta urichi* and *M. spinosa; Apterostigma collare angulatum* and *mayri; Cyphomyrmex strigatus* and *olitor; Trachymyrmex septentrionalis obscurior* and *jamaicensis; Atta cephalotes, colombica, insularis texana* and *sexdens.*

* Bibliography of the larvae of the Attini.

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EXPLANATION OF PLATES

PLATE I.—*Myrmicocrypta urichi* Weber, Figs. 1-8.—1, head in anterior view, ×78; 2, mature larva (1.7 mm) in side view, ×25; 3, very young larva (0.7 mm) in side view, ×25; 4, body hair, ×427; 5, labrum in posterior view, ×427; 6, right maxilla in anterior view, ×427; 7, right mandible in anterior view, ×427; 8, labium in anterior view, ×427.

Apterostigma collare angulatum Weber, Figs. 9-17.—9, head in anterior view, ×50; 10, mature larva in ventral view, ×17; 11, mature larva in side view, ×17; 12, young larva in side view, ×26; 13, labium in anterior view, ×123; 14. left maxilla in anterior view, ×123; 15, body hair, ×77; 16, labrum in posterior view, ×123; 17, left mandible in anterior view, × 307.

Apterostigma tramitis Weber, Fig. 18, left mandible in anterior view, ×297.

PLATE II.—*Cyphomyrmex rimosus* Spinola, Figs. 1-6.—1, head in anterior view, ×100; 2, mature larva in side view, ×27; 3, young larva in side view, ×53; 4, right maxilla in anterior view, ×185; 5, body hair, ×185; 6, right mandible in anterior view, ×267.

Cyphomyrmex strigatus Mayr, Figs. 7 and 8.—7, right mandible in anterior view, ×413; 8, young larva in side view, ×47.

Sericomyrmex wheeleri Weber, Figs. 9-13.—9, head in anterior view, ×60; 10, larva in side view, ×29; 11, right mandible in anterior view, ×185; 12, left maxilla in anterior view, ×103; 13, body hair ×185.

Trachymyrmex septentrionalis obscurior Wheeler, Figs. 14-19.—14, head in anterior view, ×55; 15, larva in side view, ×13; 16, larva in ventral view, ×13; 17, right maxilla in anterior view, ×96; 18, body hair, ×92; 19, left mandible in anterior view, ×92.

PLATE III.—*Acromyrmex lundi* Guérin, Figs. 1-6.—1, head in anterior view, ×56; 2, larva in side view, ×7; 3, larva in ventral view, ×7; 4, head hairs, ×183; 5, body hair, ×183; 6, mandible in anterior view, ×92.

Acromyrmex octospinosus (Reich), Figs. 7-9.—7, head in anterior view, ×58; 8, mandible in anterior view, ×92; 9, five body hairs, ×183.

Atta cephalotes (Linnaeus), Figs. 10-16.—10, head in anterior view, ×45; 11, larva in side view, ×10; 12, larva in ventral view, ×10; 13, left maxilla in anterior view, ×78; 14, body hair, ×78; 15, mandible in anterior view, ×107; 16, spinules on hypopharynx, ×78.

PLATE I

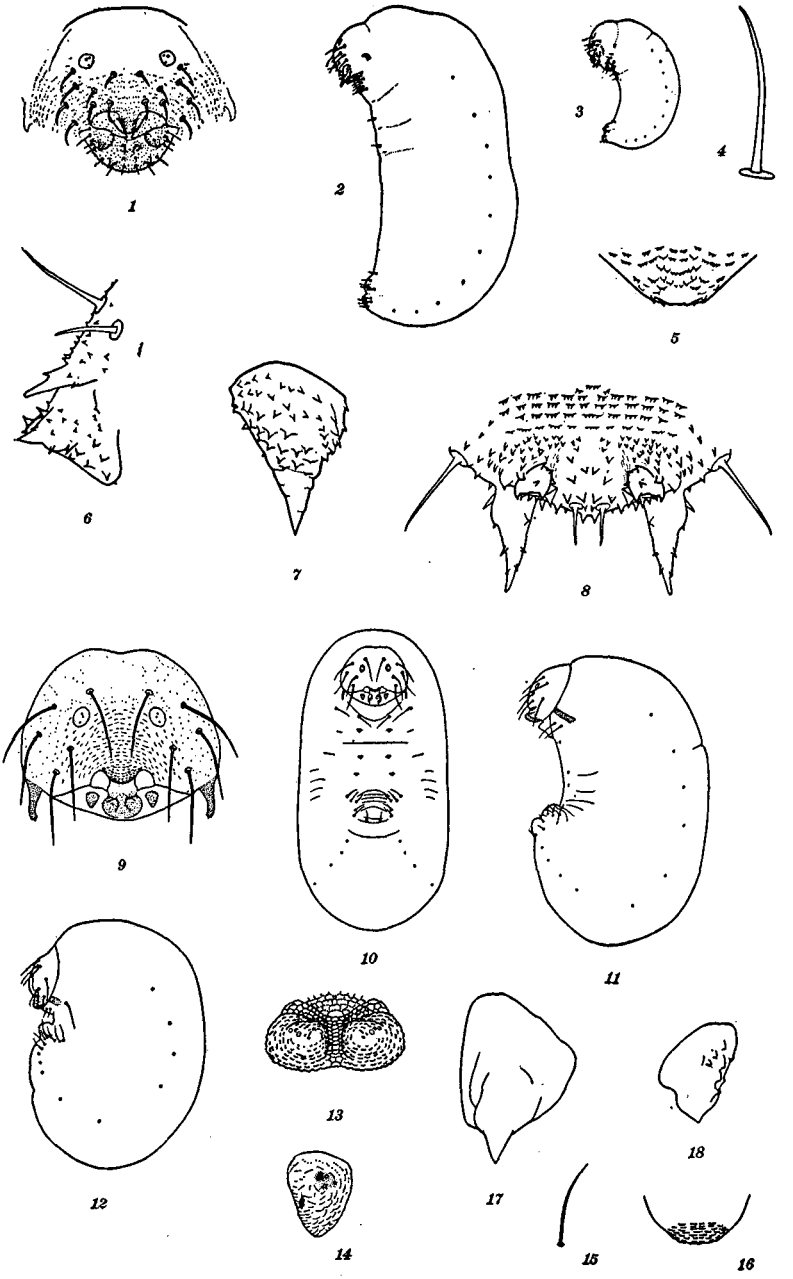

PLATE II

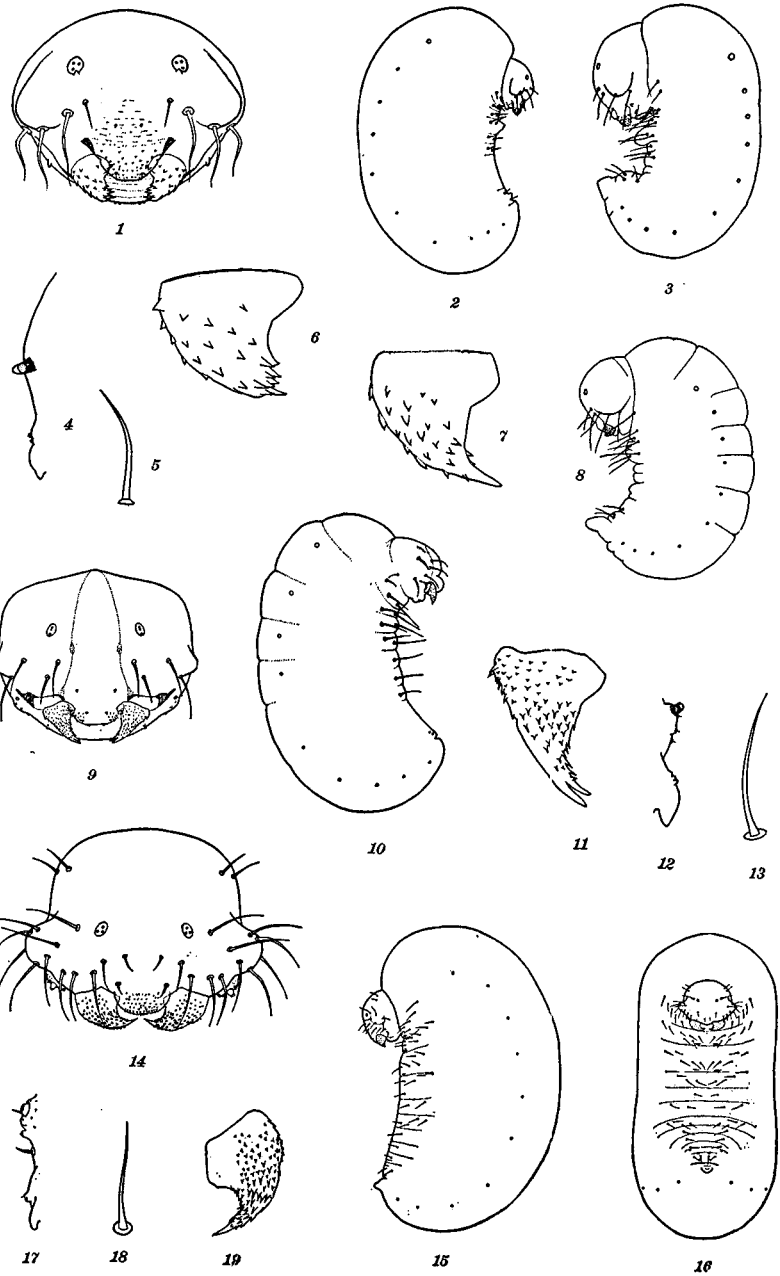

PLATE III