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THE ANT LARVAE OF THE SUBFAMILY MYRMICINAE[1]

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ABSTRACT

This article serves as the introduction and the conclusion to the authors' studies on the larvae of the Myrmicinae which have appeared in 17 articles in 7 periodicals during the past quarter-century, and which have treated of 202 species in 73 genera, representing 18 of the 21 tribes. The larvae of the Myrmicinae are so heterogeneous that no characterization can be given for the subfamily as a whole. As with their respective adults, larvae of some genera have retained a rather unspecialized structure and others are among the most specialized ant larvae, while the majority fall between these two extremes. Beyond this, there is little concordance between adult taxonomy and larval "taxonomy." Six of the tribes were inadequately represented in the material available, six could be characterized with some degree of satisfaction, and six could not be characterized at all. Despite some discordances at the generic level, the genus was found to be the most suitable unit for classifying ant larvae. Body shape (especially profile) was found the safest character for separating genera, with mandible shape second, and anchor-tipped hairs third. The profiles of myrmicine larvae were generalized into 22 types, and mandible shapes into 30 types, all of which are described and illustrated. A key to some 55 genera is based on larval profile, mandible shape, anchor-tipped hairs, and certain minor characters. The hypothetical larva of the hypothetical ancestor of the subfamily is described; the larva of *Pogonomyrmex* approximates this description most closely. The most specialized larvae are those of the Attini (fungus-growers) and the Crematogastrini.

Epigraph No. 1—"Au contraire, la classification des *Myrmicinae* présente des difficultés presque insurmontables. En dehors des tribus bien caractérisées . . . il y a beaucoup de genres qui offrent des caractères peu marqués et des ressemblances multiples . . La classification suivie dans le présent ouvrage . . . est, je le sais, loin de me satisfaire. Cela tient surtout à l'insuffisance de nos connaissances sur nombre de genres. Mais, dans un travail d'ensemble comme celui-ci, on ne peut pas attendre que les explorations des voyageurs et les études des naturalistes aient éclairci les points en litige; il faut classer tant bien que mal toute chose et se contenter de ce qui est possible actuellement." C. Emery, "Genera Insectorum," 1921.

Epigraph No. 2—"The Myrmicinae are a large and very heterogeneous assemblage of genera . . . In the future the Myrmicinae will probably be resolved into several subfamilies." W. M. Wheeler, "The Social Insects," 1928.

Epigraph No. 3—"It is difficult to speak in general terms about the Subfamily Myrmicinae, for no other group of ants shows so much variation in morphology and habits. Some of the genera have retained a rather primitive structure (Myrmica, Manica); others are among our most highly evolved ants (Strumigenys, Cryptocerus, etc.). The majority of the genera fall between these extremes in the amount of structural differentiation which they show." W. S. Creighton, "The Ants of North America," 1950.

The subfamily Myrmicinae is the largest of the nine subfamilies of Formicidae, comprising somewhat more than half of the total genera—180 out of 350. We have studied the larvae of 202 species in 73 of these genera. The 73 genera, however, represent 18 of the 21 tribes usually recognized for the subfamily. The three tribes (Metaponini, Ocymyrmicini, and Stereomyrmicini) that are not represented in our collections have one genus each, and the three added together have only about 20 species.

We list here the genera whose larvae we have studied, and give references to our various papers dealing with the respective tribes or with genera included therein.

Myrmicini (1952a, 1959a, 1959b): *Hylomyrma, Manica, Myrmica, Paramyrmica, Pogonomyrmex.*
Pheidolini (1953a, 1956, 1959b): *Aphaenogaster, Ischnomyrmex, Messor, Novomessor, Pheidole, Stenamma, Veromessor.*
Melissotarsini (1953b): *Rhopalomastix.*
Metaponini (1953b, from literature only; no specimens studied).
Myrmicariini (1953b): *Myrmicaria.*
Cardiocondylini (1953b): *Cardiocondyla.*
Crematogastrini (1952b, 1959b): *Crematogaster.*
Solenopsidini (1935, 1955a, 1959b): *Allomerus, Anergates, Anergatides, Huberia, Liomyrmex, Megalomyrmex, Monomorium, Solenopsis, Tranopelta, Vollenhovia, Xenomyrmex.*
Pheidologetini (1953c, 1959b): *Carebara, Erebomyrma, Lophomyrmex, Oligomyrmex, Paedalgus, Pheidologeton, Trigonogaster.*
Myrmecinini (1954a, 1959b): *Dacryon, Dilobocondyla, Myrmecina, Podomyrma, Pristomyrmex.*
Meranoplini (1954b): *Meranoplus.*
Leptothoracini (1955b, 1957, 1959b): *Apsychomyrmex, Dacetinops, Harpagoxenus, Leptothorax, Macromischa, Macromischoides, Rogeria.*
Tetramoriini (1954b, 1959b): *Tetramorium, Xiphomyrmex.*
Ochetomyrmicini (1954b): *Wasmannia.*
Cataulacini (1954c): *Cataulacus.*
Cephalotini (1954c): *Cephalotes, Paracryptocerus, Procryptocerus, Zacryptocerus.*
Basicerotini (1954d, 1959b): *Aspididris, Basiceros, Rhopalothrix.*
Dacetini (1954d, 1959b): *Alistruma, Clarkistruma, Daceton, Epopostruma, Mesostruma, Orectognathus, Smithistruma, Strumigenys.*
Attini (1948, 1959b): *Acromyrmex, Apterostigma, Atta, Cyphomyrmex, Myrmicocrypta, Sericomyrmex, Trachymyrmex.*

[1]Accepted for publication June 10, 1959.

Our studies on the subfamily Myrmicinae have been published in 17 separate articles, scattered in seven periodicals, appearing over a period of 25 years. Several entomologists have expressed regret that the studies have not been combined into a monograph. We regret this too, but no foundation has been willing to publish so long a treatise with so many illustrations and without economic or popular appeal, and no journal has been willing to accept it on the installment plan. The exigency of finance, then, has forced us to publish the body of the "monograph" piecemeal. This present article can be regarded as the introduction and conclusion.

LITERATURE ON THE SUBFAMILY

Adlerz 1886:—Wool-hairs ("ullhåren = anchor-tipped hairs) characterize the Myrmicinae (p. 51). Formicine larvae have larger heads than myrmicine larvae (p. 52). Most of the Myrmicinae have stout, more or less cylindrical larvae, which are capable of noticeable movement only at the anterior end of the body (p. 52). Internal anatomy (pp. 59–64). In a formal characterization of the subfamily (p. 258):—"Wool-hairs of the larvae with a double-hooked tip (sometimes, however, single-hooked wool-hairs are found alongside the double-hooked, as for example in *Leptothorax* and *Tomognathus* [= *Harpagoxenus*] which likewise show all intermediate stages between these two types of wool-hairs; such transitional forms are to be found also in *Myrmica* larvae, which at times show wool-hairs with aculeate or short-branched hooks). Larvae stout, movement slight."

Athias-Henriot 1947:—"Les *Myrmicinés* sont intermédiaires [entre les *Camponotinés* et les *Dolichodérinés*]. On y rencontre des types primitifs se rapprochant des premiers (Aphaenogaster) et des types évolués, simples, les reliants aux seconds (Crematogaster)" (p. 253). "Cette sous-famille comprend des larves relativement primitives et des larves très spécialisées. Elle apparaît comme peu homogène, considérée de ce point de vue: larves assez inférieures—(1) *Aphaenogaster*, (2) *Messor*, (3) *Pheidole;* larves évoluées—(4) *Crematogaster*, (5) *Monomorium*. L'ordre évolutif des larves de cette sous-famille concorde avec celui des adultes ♂ et ☿ correspondants. Mais les Formicinés, plus spécialisés comme ☿, ont au contraire des larves plus archaïques" (p. 268). Internal anatomy, pp. 259 and 263.

Bernard 1951:—"Larves à tête petite, omnivores ou spécialisées; hypocéphales, bien segmentées; poils variés, souvent crochus" (p. 1041). "Larves primitivement mobiles, capables de manger des morceaux d'insectes ou de graines placés sur ou près d'elles par les ouvrières (*Pheidole, Novomessor*, . . .), secondairement obèses, peu segmentées, comme pour *Paedalgus*. Les cas de polymorphisme larvaire, déjà cités chez *Allomerus*, ne semblent pas rares et sont à rechercher. Nymphes nues. Les ouvrières peuvent généralement dégorger le contenu du jabot, soit entre elles, soit aux larves et commensaux" (p. 1059).

Bischoff 1927, p. 384:—Many Myrmicinae feed their larvae with the contents of the crop—therefore with liquid food.

Brun 1924, p. 25:—"Die Fütterung wird nun bei den höhern Ameisen . . . gewöhnlich in der Weise vorgenommen, dass die fütternde Arbeiterin einen Tropfen Nahrungsflüssigkeit aus ihrem Kropfe ausbricht und denselben auf den Mund der Larve fallen lässt. Seltener werden grösseren Larven auch mit Speichel durchtränkte Stücke erbeuteter Insekten, oder—bei den Körnersammlern—entsprechend aufgeweichte Körner direkt zum Frasse vorgelegt."

Eidmann 1943:—German Myrmicinae hibernate with larvae.

Emery (1899, p. 8) thought that the larvae of the Myrmicinae lacked antennae.

Emery 1921–1922, p. 4:—"Larves pourvues, au moins dans le jeune âge, de poils d'accrochage en crochet, branchus ou d'autres formes."

Forel 1928:—"Larvae very mobile, without tubercles, but much less independent than those of the *Ponerinae*. The ☿ disgorge food to them" (Vol. I, p. 134). (= 1921, p. 139:—"Les larves sont fort mobiles, sans tubercules, mais bien moins indépendantes que chez les *Ponerinae* et les ☿ leur dégorgent la nourriture.") "The larvae of the *Ponerinae* and some *Myrmicinae* feed on prey, whole or in fragments, which the ☿ supply to them without cramming. As we have seen, they are sufficiently mobile and independent to eat alone" (Vol. I, p. 516). (= 1922, p. 136:—"Les larves des *Ponerinae* et de quelques *Myrmicinae* se nourrissent des proies entières ou découpées que leur donnent les ☿ sans les emboquer; elles sont assez mobiles et indépendantes pour manger seules, avons nous vu.") "The larvae of the granivorous *Myrmicinae* are fed by their workers with fragments of seeds" (Vol. I, p. 517). (= 1922, p. 136:—"Les larves des *Myrmicinae* granivores sont nourries par leurs ouvrières avec des parcelles de graines.") "The larvae of some *Myrmicinae* . . . are directly fed by their ☿, which disgorge to them the contents of their crops" (Vol. I, p. 517). (= 1922, p. 136:—"Les larves de quelques *Myrmicinae* . . . sont nourries directement par leurs ☿, qui leur dégorgent le contenu de leur jabot.")

Gantes 1949, pp. 88–89:—"Chez les deux familles, *Formicidés* et *Myrmicidés*, nous voyons une évolution nette. Cependant l'évolution est plus poussée chez la dernière sous-famille, avec des larves très évoluées comme *Crematogaster* . . . Chez les *Myrmicidés* on part de stades très primitifs, comme *Aphaenogaster* où les larves sont très agiles, pour arriver aux larves très évoluées comme *Crematogaster* dont la forme se rapproche de celle des sexués de *Tapinoma*. Ces larves sont immobiles, ont des mandibules minuscules.

Entre les deux nous avons tous les intermédiaires . . . Nous remarquons que dans cette famille toutes les espèces ont à peu près la même forme de mandibule à trois dents, sauf chez *Crematogaster*. Presque toutes ces larves mangent des boulettes de nourriture que les fourmis ont déposées sur leur ventre, qui sert en quelque sorte de table: j'ai observé ceci chez *Monomorium*. Je n'ai pu voir ce qui se passait pour *Messor*."

Haskins 1939, p. 37:—"The young have changed from the long-necked, athletic types of cylindrically tapered organisms to rather squat, thick-set, helpless grubs, completely dependent upon their nurses for sustenance and care."

Kellogg 1905, p. 541:—"The character and amount of the food given the larvae is carefully controlled by the workers."

Stärcke 1948, pp. 26 and 28:—"Among the *Myrmicinae* four types of larvae can be distinguished. 1°. The ordinary hookform with the head bent perpendicularly to the body or even a little further, the thoracal segments ranged fanlike, the abdomen next without any special demarcation, straight, and only the extremity a little swollen, with some whitish spots of urate cells shining through. Usually the head is for one third sunk into the prothorax. With the fullgrown larva, the head grows still more into the prothoracical segment, until more than half its volume is situated there; but even with the youngest larva the superior headganglion lies already half in the prothorax—that is to say not in reality, but when seen in profile. 2°. The caudal extremity more swollen. The duct of the labial glands broader and its epithelium composed of taller cylindrical cells. *Vide* the fullgrown larvae of *Messor* and *Tetramorium*. 3°. Plump cylindrical swollen body with the head like a small nodule placed upon it on the ventral side, or the first two segments are also extended forward with the head. *Vide* larvae of *Leptothorax* and newly emerged *Myrmica*-larvae. 4°. Body still more swollen, of a short oval or nearly globous shape, with a small head projecting on the ventral side. Some species hypognath. *Vide* soldier larvae of *Pheidole, Solenopsis, Crematogaster*."

Wheeler 1900a, p. 27:—"The worker ants can control the production of individuals like themselves and of individuals like their queen. It is further maintained that these differences are effected by the quantity and quality of the food administered to the larvae at a certain period of their development; but here our knowledge ends. These data have been accumulated from the study of the specialized Myrmicine and Formicine ants of Europe and North America."

Wheeler 1900b, p. 62:—The larvae are "covered with hairs instead of bristly tubercles."

Wheeler 1922, p. 125:—"Larva thick-bodied, orthocephalic, without exudatory papillae around the mouth. The body is, as a rule, abundantly covered with chitinous hairs of very different kinds; dorsal oncochaetae often present."

Wheeler 1937, p. 38:—The harvesting Myrmicinae and the Attini place food within reach of the larval mouth parts, but many Myrmicinae regurgitate liquid food from the nurse's crop to the larvae

HETEROGENEITY

Like their adults, the larvae of the Myrmicinae are a heterogeneous assemblage. Paraphrasing Creighton:—It is difficult to speak about them in general terms, for no other subfamily shows such variation in morphology; some of the genera (like their adults) have retained a rather unspecialized[2] structure; others (like their adults) are among our most highly specialized ant larvae; the majority of the genera (again like their adults) fall between these extremes in the amount of structural differentiation which they show.

Beyond this, however, there is little concordance between the taxonomy of the adults and that of their larvae. We began with the hope (born of a limited sampling of genera) that we might be able to construct a generalized diagram for each subfamily of the Formicidae. But that faded rapidly for the Myrmicinae. Then we hoped that we might be able to get tribal diagrams. That hope was considerably dimmed but not extinguished. Of the 18 tribes in our collection six are not adequately represented and hence do not merit characterization. Six can be characterized with at least some degree of satisfaction: Myrmicini, Crematogastrini, Cataulacini, Cephalotini, Basicerotini and Attini. The remaining six tribes (as adults) are "very unsatisfactorily defined" (W. M. Wheeler 1922, p. 659). We say the same about their larvae:—

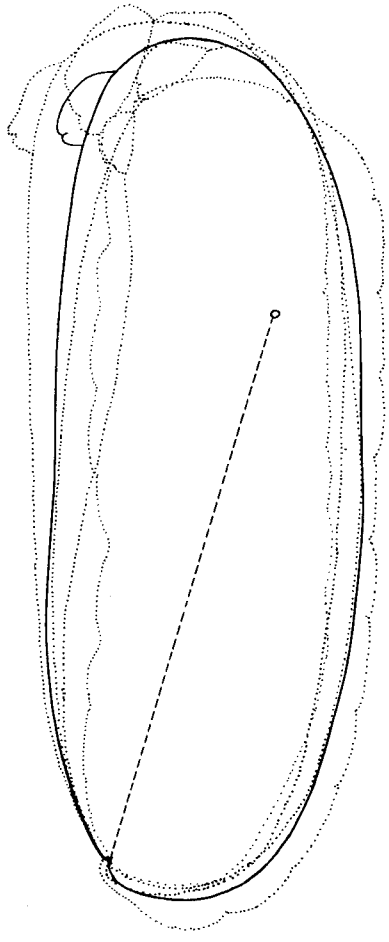
I. The larvae of the Pheidolini fall into two distinct groups: (1) *Pheidole* and *Ischnomyrmex*; (2) *Stenamma, Aphaenogaster, Messor, Novomessor,* and *Veromessor*. We might even go so far as to suggest that the latter group be transferred to the Myrmicini.

II. The larvae of the Solenopsidini may be divided into six groups: (1) *Vollenhovia*; (2) *Monomorium* (except *antarcticum*), *Solenopsis, Anergates* and *Megalomyrmex*; (3) *Monomorium antarcticum*; (4) *Allomerus*; (5) *Liomyrmex*; (6) *Xenomyrmex*.

III. The larvae of the Pheidologetini may be grouped into the subtribes recognized in the Genera Insectorum: (1) *Trigonogaster* and (probably) *Lophomyrmex* (subtribe Lophomyrmicini); (2) *Pheidologeton, Oligomyrmex, Erebomyrma, Carebara* and *Paedalgus* (subtribe Pheidologetini).

[2] "*Specialized*. Adapted to a special, limited way of life. The opposite of this word is *unspecialized*, not *primitive*. *Unspecialized* and *specialized* concern animals' relation to the environment. *Primitive* and *derivative* concern animals' phylogenetic relation to each other. An unspecialized animal can be derivative, and a specialized one can be primitive. To use these words properly is not an affectation. It is necessary to clear thinking." (Darlington 1957, p. 25.)

IV. The larvae of the Myrmicinini fall into two groups: (1) *Podomyrma* and *Dilobocondyla*; (2) *Myrmecina* and *Pristomyrmex*.



TEXT FIGURE 1.—Illustration of method of arriving at generalized body profiles. The dashed line is the 8-cm. "base line" (first abdominal spiracle to anus). The dotted lines are the profiles for the genera *Cephalotes*, *Crematogaster*, *Paracryptocerus* and *Xenomyrmex*. The solid line is the "averaged" generalized crematogastriform profile.

V. The larvae of the Leptothoracini must be divided into five groups: (1) *Macromishoides*; (2) *Apsychomyrmex*; (3) *Rogeria*; (4) *Leptothorax* (subgenera *Myrafant* and *Dichothorax*) and *Macromischa*; (5) *Harpagoxenus* and *Leptothorax* (subgenera *Leptothorax* and *Nesomyrmex*). Emery (1922, pp. 244 and 266) was puzzled by the adults of this tribe: "J'ai rattaché, comme 'genera incertae sedis', à la tribu des Leptothoracini *Rogeria* et un certain nombre de petits genres (*Lachnomyrmex*, *Apsychomyrmex* et *Adelomyrmex*) qui ont la massue des antennes de deux articles." "Je classe les quatre genres suivants [*Rogeria*, *Apsychomyrmex*, *Adelomyrmex*, *Lachnomyrmex*] dans la tribu des Leptothoracini, non sans de forts doutes, attendu que les ♂ et même les ailes de ♀ me sont inconnus. Les genres *Rogeria*, *Apsychomyrmex* et *Adelomyrmex* me semblent constituer un groupe naturel et se rattacher, par *Rogeria*, à *Leptothorax* et à *Macromischa*."

VI. The sixth tribe, Tetramoriini, is inadequately represented in our collection, but the larva of *Tetramorium* (the largest genus) shows rather close affinity to the unspecialized Myrmicini.

In contrast to the tribes on Wheeler's list stands the tribe Dacetini—an easily defined and specialized group (as adults) showing an extreme reduction in the number of antennal segments, while the head shape, head hairs and mandibles could be characterized as bizarre. But their larvae are a heterogeneous group and, besides that, they are all quite ordinary and far less specialized than the larvae of many other genera.

In addition to these tribal troubles there are a few discordances at the generic level. The differences between *Novomessor manni* and the other species of that genus are of generic magnitude. *Monomorium antarcticum* is generically distinct from all our other species of *Monomorium*. *Leptothorax* is divisible into two generic groups: subgenera *Dichothorax* and *Myrafant* vs. subgenera *Leptothorax* and *Nesomyrmex*. The differences between *Acromyrmex lundi* and the other two species studied (*octospinosus* and *emilii*) are of generic magnitude. *Sericomyrmex amabilis* is generically distinct from *S. wheeleri*; Weber (1958, p. 54) has recently transferred *wheeleri* to *Trachymyrmex*, but that merely enhances the discordance.

Then there are differences of the opposite sort: *Smithistruma* is generically indistinguishable from *Strumigenys*; *Macromischa* from *Leptothorax* (subgenera *Dichothorax* and *Myrafant*).

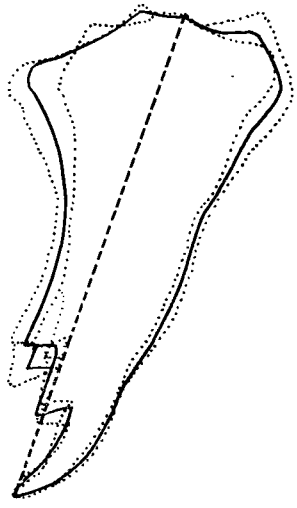
Nevertheless we have come to regard the genus as the basic unit in the classification of myrmicine ant larvae. With few exceptions, the genus (based on adults) is easily defined in terms of larval characters and is readily distinguishable from related genera. Our key is therefore a key to genera.

Our opinions on specific differences must be based on insufficient data; 39 of our 73 genera are represented by only a single species, while only 10 are represented by more than half a dozen species (*Aphaenogaster* 11, *Crematogaster* 10, *Leptothorax* 13, *Monomorium* 8, *Myrmica* 8, *Paracryptocerus* 7, *Pheidole* 10, *Smithistruma* 8, *Solenopsis* 10, *Strumigenys* 12). The species of a genus usually differ in characters which are both variable and quantitative and even these differences are slight compared with generic differences.

CHARACTERS

What characters are to be relied upon as indicators of kinship among ant larvae? What characters are tribal? Generic? Specific? Which characters are phylogenetic and which caeno-

gentic? Is there any evidence of convergence? What characters are specialized? Unspecialized? Primitive? Derived? Body shape is variable in life, especially in active larvae. Hence it might vary according to nutritional state or the technique of preservation. Is body shape therefore unreliable? Mandibles are hard structures and their shape is probably not altered by activity or preservation. Are mandibles therefore useful taxonomically? What about other mouth parts? Hairs? A myrmecologist may hold certain views about the taxonomy of adults and accordingly may tend to view as phylogenetic such larval traits as support his preconceived notions and as caenogenetic those that contravene. Are there any checks and balances for his prejudices? How does one detect convergence?



TEXT FIGURE 2.—Illustration of method of arriving at generalized mandible shapes. The dashed line is the 6-cm. "base line" (anterior condyle to apex). The dotted lines are the outlines for the genera *Ischnomyrmex* and *Pheidole*. The solid line is the "averaged" generalized pheidoliform mandible shape.

We have found these questions extremely difficult to answer. And we have not answered them to our satisfaction. But answers are expected from a study of this sort. Therefore we have endeavored to reach tentative—very tentative—conclusions.

We certainly do not claim that the taxonomy of ants should be based on the relationships among their larvae, but we can at least hope that in puzzling cases our findings might prove ancillary to a solution.

Body shape is the character which is most nearly constant throughout the genus. It is also the character which most closely correlates larval taxonomy with adult taxonomy: those genera which have usually been regarded as unspecialized all have similar larval shapes (which are likewise unspecialized), while the most highly specialized tribes have the most highly specialized larvae and a high degree of concordance. Therefore we have chosen body shape as the basic character for classifying the larvae of the Myrmicinae.

The next most useful character is mandible shape. There are more kinds of mandible shapes than body shapes. Mandible shape shows more intrageneric, intraspecific, and intranidal variation.

Third in utility is the presence or absence of anchor-tipped hairs on the dorsum. If they are present at all they characterize the whole genus (with two exceptions, *Novomessor* and *Monomorium*). Incidentally, anchor-tipped hairs are found only in the subfamily Myrmicinae, occurring in 24 of the 73 genera in our collection.

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.

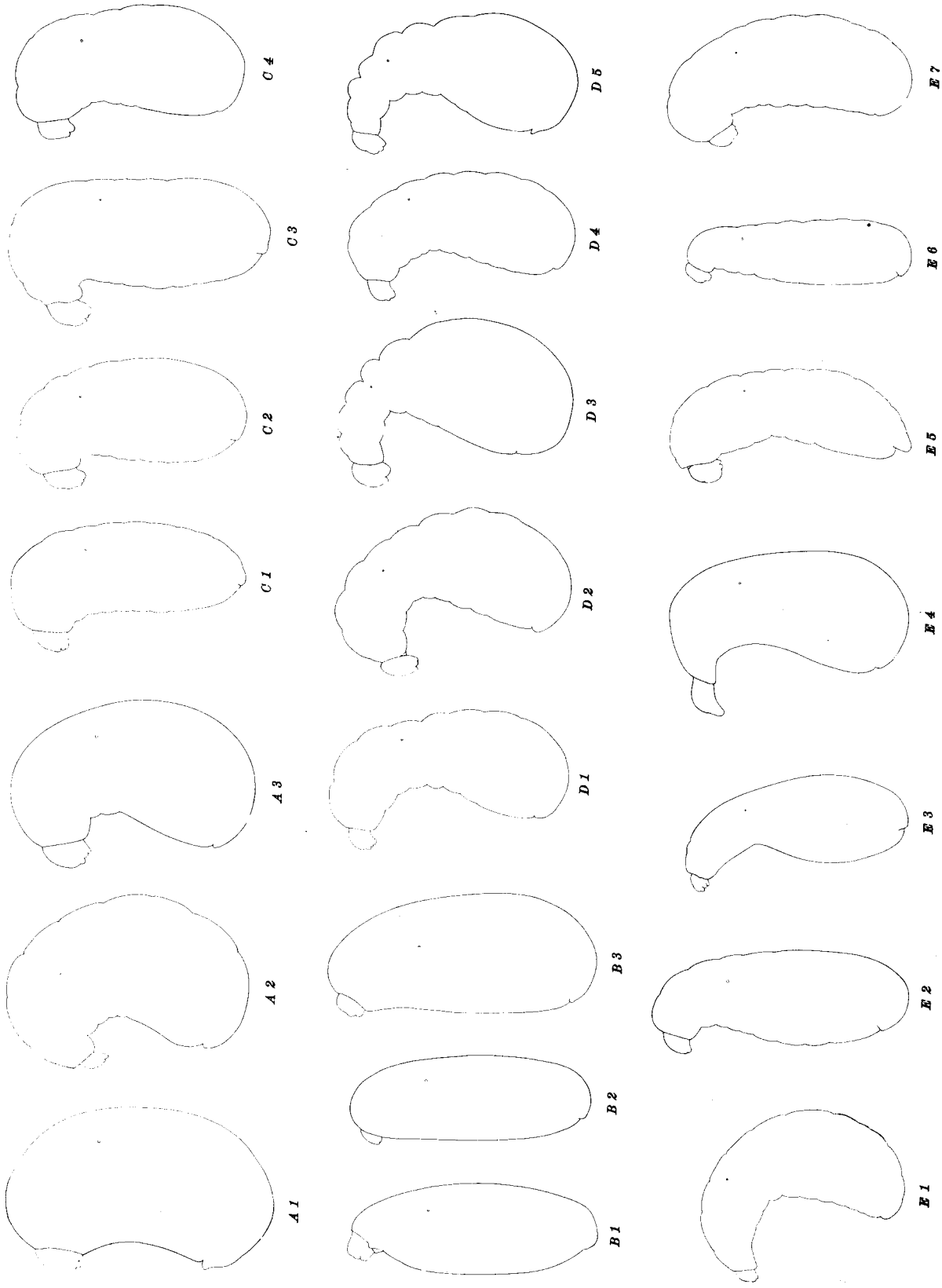
BODY SHAPE

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. To facilitate comparison of profiles we decided that all drawings would have to be of the same size. This, however, presented a problem in all larvae which have a flexible thorax, for these have been preserved with the thorax curved to different extents and extended to different lengths. Hence it was necessary to select a standard measurement to be the same for all profiles. We chose the distance (on the drawing) from the anus to the first abdominal spiracle, for two reasons: (1) the abdomen is relatively inflexible and scarcely extensible; (2) these are two easily located points (in contrast, for example, to the posterior end, which would have to be designated arbitrarily on a curve).

Our actual procedure was this:—(1) We pulled from our files the original drawings for our published figures of mature larvae in side view (profile). (2) The drawings were sorted according to similarity of profile. (Actually several groups included only one drawing each.) (3) Each

EXPLANATION OF PLATE

PLATE 1.—Generalized body profiles. *Group A*—1, attiform; 2, myrmicariform; 3, strumigenyform. *Group B*—1, cataulaciform; 2, crematogastriform; 3, macromischiform. *Group C*—1, allomeriform; 2, cardiocondyliform; 3, pheidoliform; 4, solenopsidiform. *Group D*—1, aphaenogastriform; 2, aspididriform; 3, epopostrumiform; 4, myrmiciform; 5, orectognathiform. *Group E*—1, dacetiform; 2, dilobocondyliform; 3, liomyrmeciform; 4, pristomyrmeciform; 5, rhopalomasticiform; 6, trigonogastriform; 7, vollenhoviform.


A 1
A 2
A 3
B 1
B 2
B 3
C 1
C 2
C 3
C 4
D 1
D 2
D 3
D 4
D 5
E 1
E 2
E 3
E 4
E 5
E 6
E 7

group was treated as follows: (a) One drawing was placed on a Vertical Sketchmaster (manufactured by Harrison C. Ryker, Inc., Oakland, California) and the instrument was adjusted until the distance (on the image) from anus to first abdominal spiracle measured 8 cm. (not a significant figure; merely convenient). (b) The image of the profile and first abdominal spiracle were traced on paper. (If a "group" included only one drawing, that "group" was finished at this point.) (c) The first drawing was removed and replaced by the second; the instrument was adjusted until the images of anus and first abdominal spiracle were superimposed on corresponding parts of the outline of the first drawing; then the image of the second profile was traced on the same paper. (d) All other drawings in that group were processed in the same manner as the second. An actual example of such a collection of profiles is shown by the dotted outlines in text fig. 1; the dashed line joining anus and first abdominal spiracle (8 cm. long on the original) is the base-line for all profiles in this group. (e) The generalized profile for the group was obtained by a sort of averaging of all individual profiles. This step is illustrated by the solid profile in text fig. 1.

When the above procedures had been completed for all groups, we found ourselves with a collection of 22 generalized profiles for the subfamily (plate I and appendix A). The next step was obvious—naming the profiles. Descriptive terms were out of the question; no one word could characterize meaningfully such shapes. They could have been designated arbitrarily by letters or numerals, but such designations would have no intrinsic meaning. So we combined the name of a representative genus in each group with the root of the Latin word *forma* to make an English adjective for each generalized profile. (We deeply regret the excessive length and resounding cacophony of some of these adjectives.)

Next, a simultaneous comparison of the 22 generalized profiles showed that they could be arranged in five groups on the basis of more superficial resemblances. We have not, however, attempted generalized diagrams of the second order and we have not named these larger groups.

After the profiles were classified, the next question was: which profile is unspecialized? On a priori grounds one might answer: that of the larva of the least specialized adults. But this answer presupposed accordance of larval taxonomy with adult taxonomy, which was what we were trying to prove (=test). And so we got to reasoning in a circle. We finally broke out of the circle by the following arguments: (1) A certain larval profile is found in more genera than is any other profile; most of these genera have unspecialized adults. (2) This certain profile resembles rather closely the unspecialized profiles in the two next largest subfamilies (Formicinae and Ponerinae), i.e., taxa large enough to show a wide range of specialization. (3) Among larvae exhibiting this profile no character shows an extreme deviation from an average for all known ant larvae. (4) Among larvae exhibiting this profile no character shows adaptation to any limited function or habit. (5) Among larvae having this profile the majority of characters are only moderately developed in contrast to the extremes of the same characters in the subfamily.

Employing the above reasoning, we have concluded that the least specialized profile is myrmiciform. Very similar (and only a little more specialized) is the aphaenogastriform profile. The most specialized profiles are the attiform and the crematogastriform.

The only clear instance of convergence is found in the crematogastriform profile. Larvae with this profile have an elongate, straight, subcylindrical body and the hairs are mostly minute to short. Both of these characters are apparently adaptations to life in plant cavities, particularly tubular cavities of small bore. A long larva parked parallel and close to the wall would be less of a traffic hazard than a shorter larva parked obliquely or crosswise. These two characters occur (as far as we know) only in ants that inhabit plant cavities: *Cataulacus*, *Crematogaster*, *Leptothorax*, *Paracryptocerus* and *Xenomyrmex* among the Myrmicinae; *Azteca* in the Dolichoderinae; *Camponotus* in the Formicinae; and all four genera of the subfamily Pseudomyrmecinae. *Leptothorax* is somewhat stouter than the others; perhaps it is only in the early stages of adaptation.

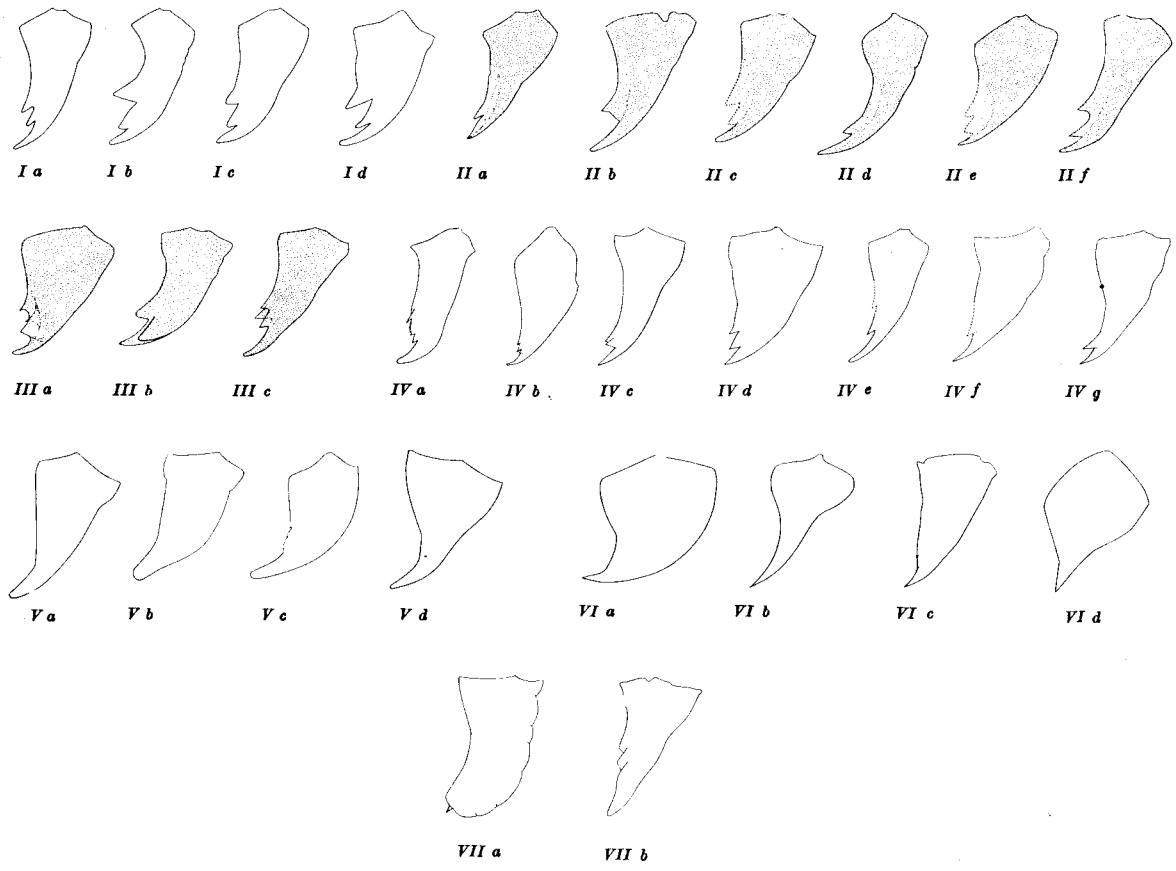
MANDIBLE SHAPE

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 text fig. 2.) The results of our generalizations are shown in text figure 3 and appendix B.

By the same reasoning we have concluded that the least specialized mandible shape is aphaenogastriform, while the specialized shapes are those which lack medial teeth—anergatidiform, anergatiform, attiform, cephalotiform, crematogastriform, messoriform and myrmicocryptiform.

HYPOTHETICAL ANCESTRAL LARVA

The hypothetical larva of the hypothetical ancestor of the subfamily Myrmicinae might be synthesized from the following generalized description. Profile myrmiciform. Body hairs short, moderately abundant and uniformly distributed, of two types: (1) simple and (2) denticulate. Integument of ventral surface of thorax and first two abdominal somites spinulose. Spiracles small, the mesothoracic slightly larger than the others. Nine distinct somites. Leg, wing, and gonopod vestiges present. Cranium transversely subelliptical in anterior view. Antennae small, each with three sensilla, each of which bears a



TEXT FIGURE 3.—Generalized mandible shapes. *Group I*—a, aphaenogastriform; b, basicerotiform; c, podomyrmiform; d, pogonomyrmeciform. *Group II*—a, dilobocondyliform; b, huberiform; c, leptothoraciform; d, liomyrmeciform; e, paracryptoceriform; f, vollenhoviform. *Group III*—a, carebariform; b, lophomyrmeciform; c, pheidoliform. *Group IV*—a, apsychomyrmeciform; b, cataulaciform; c, macromischoidiform; d, pheidologetiniform; e, pristomyrmeciform; f, tranopeltiform; g, wasmanniform. *Group V*—a, allomeriform; b, anergatiform; c, cephalotiform; d, messoriform. *Group VI*—a, attiform; b, crematogastriform; c, meranopliform; d, myrmicocryptiform. *Group VII*—a, anergatidiform; b, dacetiform.

spinule. Head hairs few (less than 40), moderately long, denticulate. Labrum bilobed; posterior surface sparsely spinulose. Mandibles aphaenogastriform, with spinules on the anterior surface. Maxillae with the apex spinulose; palp paxilliform, with five sensilla; galea digitiform, with two apical sensilla. Labium with spinules on the anterior surface; each palp a short paxilla bearing five sensilla; opening of the sericteries a short transverse slit. Hypopharynx spinulose.

No larvae are known which fit this description. *Pogonomyrmex* is the closest approximation. It deviates with respect to the mandibles (which are pogonomyrmeciform and without spinules on the anterior surface) and the galeae (which are paxilliform).

SPECIALIZED LARVAE

The most specialized larvae of the subfamily Myrmicinae are those of the tribes Crematogastrini and Attini. The Crematogastrini exhibit the following specializations: profile crematogastriform; mesothoracic spiracle much the largest, the remainder small and diminishing progressively toward the posterior end; body hairs sparse, mostly minute to short; head with the dorsal and dorsolateral regions thin and depressed; mouth parts very small and without spinules; from each gena a sclerotized band passes out of the head and enters the prothorax; head hairs very few and very short; palps and galeae represented by clusters of agglomerated sensilla.

The Attini: profile attiform; body almost naked; body hairs short, simple and mostly confined to the ventral surface; mandibles attiform or myrmicocryptiform, usually beset with numerous coarse acute spinules; other mouth parts abundantly provided with spinules.

APPENDIX A. GENERALIZED BODY PROFILES (PLATE I)

GROUP A

(Short and very stout; dorsal profile very long and C-shaped; ventral profile short; head ventral.)

1. **Attiform.** Short, very stout, plump, bean-shaped; depth greatest at the middle and decreasing slightly and equally toward each end; dorsal profile (occiput to anus) extremely long, C-shaped; ventral profile (anus to gula) relatively short and concave. Head on the ventral surface, often at a considerable distance from the anterior end. Anus ventral, usually at some distance in front of the posterior end; with one or two prominent lips. Genera: *Acromyrmex, Apterostigma, Atta, Cyphomyrmex, Myrmicocrypta, Sericomyrmex, Trachymyrmex.* (=Tribe Attini.)

2. **Myrmicariform.** Short and very stout; diameter greatest at the third abdominal somite; decreasing gradually through the mesothorax, then rapidly to the anterior end; thorax strongly arched ventrally; head on the anterior end but directed posteriorly; dorsal profile long and C-shaped, ventral much shorter; posterior end broadly rounded. Anus posteroventral. Genus: *Myrmicaria.*

3. **Strumigenyform.** Very short and very stout; thorax and first abdominal somite strongly curved ventrally; dorsal profile C-shaped, ventral profile feebly sinuate; diameter of body increasing gradually from the anterior end to abdominal somite 5, then decreasing to the posterior end, which is broadly rounded. Segmentation indistinct. Genera: *Carebara, Erebomyrma, Oligomyrmex, Paedalgus, Pheidologeton, Smithistruma, Strumigenys.*

GROUP B

(Elongate-subelliptical; head applied to the ventral surface near the anterior end.)

1. **Cataulaciform.** Straight, elongate-subelliptical; prothorax forming a very short, stout neck which is inclined ventrally to 45°; segmentation indistinct. Genus: *Cataulacus.*

2. **Crematogastriform.** Straight, elongate-subelliptical; head anteroventral; no neck; segmentation indistinct. Genera: *Cephalotes, Crematogaster, Paracryptocerus, Xenomyrmex.*

3. **Macromischiform.** Plump, chunky, elongate-suboval, nearly straight; posterior end broadly rounded, anterior end narrowly rounded; no neck. Head anteroventral. Segmentation indistinct. Genera: *Leptothorax* (subgenera *Myrafant* and *Dichothorax*), *Macromischa.*

GROUP C

(Short and stout; superficially straight, but with the anterior portion of the thorax curved ventrally, i.e., L-shaped.)

1. **Allomeriform.** Prothorax and mesothorax short, stout, and bent ventrally; rest of body subcylindrical and somewhat stout; anterior end broadly rounded; posterior end narrowly rounded. Anus terminal or subterminal. Segmentation indistinct. Genera: *Allomerus, Wasmannia.*

2. **Cardiocondyliform.** Short and stout; thorax stout and arched ventrally; abdomen straight and a little stouter; posterior end broadly rounded. Genera: *Cardiocondyla, Macromischoides.*

3. **Pheidoliform.** Short, stout, and straight; head ventral, near the anterior end, mounted on a small, short neck formed from the anterior portion of the prothorax; anterior end broadly rounded, formed from the dorsa of prothorax and mesothorax; posterior end narrowly rounded. Anus subterminal. Genus: *Pheidole.*

4. **Solenopsidiform.** Short and stout; head ventral, near the anterior end; prothorax bent ventrally to form a very short, stout neck, or neck lacking; rest of body straight or nearly straight; both ends broadly rounded. Anus ventral or posteroventral. Genera: *Anergates, Megalomyrmex, Monomorium, Solenopsis.*

GROUP D

(Moderately long and moderately stout; whole thorax curved ventrally and separated more or less from the remainder of the body by a change in diameter.)

1. **Aphaenogastriform.** Stout and rather elongate; diameter greatest at the fourth or fifth abdominal somite; slightly constricted at abdominal somite 1; thorax stout and arched or bent ventrally, but not differentiated into a neck; posterior end broadly rounded. Anus ventral. Genera: *Aphaenogaster, Novomessor, Stenamma, Veromessor.*

2. **Aspididriform.** Moderately stout; no neck, but thorax and first two abdominal somites strongly curved ventrally; diameter greatest at abdominal somite 5, decreasing to abdominal somite 1, then increasing slightly to the mesothorax, then decreasing rapidly to less than the diameter of the head; dorsal profile C-shaped, ventral J-shaped. Anus ventral, with a small posterior lip. Genera: *Alistruma, Aspididris.*

3. **Epopostrumiform.** Shaped somewhat like a crookneck squash; thorax and first abdominal somite forming a long and rather slender neck, which is strongly bent ventrally; mesothorax usually constricted; remainder of abdomen stout to very stout; dorsal profile C-shaped, ventral nearly straight. Anus ventral. Genera: *Clarkistruma, Epopostruma, Mesostruma.*

4. **Myrmiciform.** Stout and rather elongate; diameter greatest at the fourth abdominal somite; slightly attenuated anteriorly; thorax stout (when mature) and arched or bent ventrally, but not differentiated into a neck; posterior end broadly rounded. Anus posteroventral. Genera: *Dacryon, Manica, Messor, Myrmica, Paramyrmica, Pogonomyrmex, Tetramorium.*

5. **Orectognathiform.** Abdomen rather stout, diameter greatest at abdominal somites 4 and 5; attenuated anteriorly; thorax rather slender and curved ventrally, forming an indistinct neck; posterior end broadly rounded. Anus ventral, with a small posterior lip. Genus: *Orectognathus*.

GROUP E
(Miscellaneous)

1. **Dacetiform.** Somewhat stout; thorax and first two abdominal somites strongly curved ventrally; diameter greatest at abdominal somites 4 and 5, decreasing gradually to the anterior end and more abruptly to the posterior end, which is round-pointed; dorsal profile C-shaped, ventral J-shaped. Anus ventral. Genus: *Daceton*.

2. **Dilobocondyliform.** Prothorax (or prothorax and mesothorax) inclined or curved ventrally to form a short neck, which is stout but nevertheless attenuated when compared with the abdomen; rest of body straight and paunchy; posterior end narrowly rounded. Anus ventral. Segmentation indistinct. Genera: *Dilobocondyla*, *Leptothorax* (subgenera *Leptothorax* and *Nesomyrmex*), *Podomyrma*.

3. **Liomyrmeciform.** Shaped somewhat like a short-necked gourd; thorax and first abdominal somite forming a rather long, stout neck which is slightly curved ventrally; rest of abdomen swollen; diameter greatest at fifth abdominal somite. Anus terminal. Segmentation indistinct. Genus: *Liomyrmex*.

4. **Pristomyrmeciform.** Stout and rather short; anterior end strongly bent ventrally so that the slender, elongate head is directed ventrally or posteriorly; prothorax narrowed rapidly to the diameter of the head. Genera: *Myrmecina*, *Pristomyrmex*.

5. **Rhopalomasticiform.** Moderately slender, diameter nearly uniform throughout; slightly constricted between the first and second abdominal somites; slightly curved ventrally; dorsal profile evenly convex; ventral profile angulate between the first and second abdominal somites, otherwise nearly straight; anterior end broadly rounded and formed from the dorsal surface of the prothorax. Head protruding from the ventral surface near the anterior end. Anus posterior, with a conspicuous posterior lip. Genus: *Rhopalomastix*.

6. **Trigonogastriform.**. Long, slender, club-shaped, with only the prothorax bent ventrally to form a very short neck; diameter greatest at abdominal somites 5 and 6, diminishing gradually to the anterior end; posterior end broadly rounded. Anus ventral. Genus: *Trigonogaster*.

7. **Vollenhoviform.** Diameter greatest at the third abdominal somite, decreasing only slightly toward either end; thorax stout and curved ventrally to about 90°; abdomen nearly straight; posterior end narrowly rounded. Anus ventral. Genus: *Vollenhovia*.

APPENDIX B. GENERALIZED MANDIBLE SHAPES (TEXT FIGURE 3)

GROUP I
(With three large teeth which are approximately equal and approximately in the same plane.)

a. **Aphaenogastriform.** Narrow; tapering gradually and curving gradually to a long and rather slender apical tooth, which is curved medially; two moderate-sized, subequal medial teeth; without ~~of~~ blade. Genera: *Alistruma*, *Aphaenogaster*, *Aspididris*, *Epopostruma*, *Mesotruma*, *Novomessor* (except *N. manni*), *Smithistruma*, *Stenamma*, *Strumigenys*, *Veromessor*.

b. **Basicerotiform.** Long and narrow, slightly curved medially; apical tooth moderately slender, slightly curved, and round-pointed; with two medial teeth, the proximal much the larger and projecting at approximately right angles to the long axis. Genus: *Basiceros*. (*Rhopalothrix* may have mandibles of this type, but all our specimens are immature.)

c. **Podomyrmiform.** Moderately broad, straight, tapering gradually; the apex forming a moderately stout and nearly straight tooth which is directed medially; two coarse, blunt, medial teeth. Genera: *Cardiocondyla*, *Dacryon*, *Podomyrma*, *Rhopalomastix*.

d. **Pogonomyrmeciform.** Basal half broad; distal half narrow; apical tooth curved medially moderately long, moderately slender, tapering only slightly to a rounded point; two prominent medial teeth, the proximal considerably larger. Genus: *Pogonomyrmex*.

GROUP II
(With a medial blade bearing one or two teeth in the same plane.)

a. **Dilobocondyliform.** Rather narrow; apex forming a sharp tooth which is slightly curved medially; anterior surface with a medial blade bearing a blunt medial tooth; posterior surface with a narrow medial blade. Genus: *Dilobocondyla*.

b. **Huberiform.** Of two parts—a sout, sickle-shaped body and a narrow medial blade; apex forming a long, slender, curved tooth; blade bearing a single, conspicuous, medial tooth. Genus: *Huberia*.

c. **Leptothoraciform.** Moderately narrow; tapering gradually and curving gradually to an apical tooth; anterior surface produced medially into a blade; edge of blade variable, but usually with two subapical teeth. Genera: ~~*Alistruma*~~, *Clarkistruma*, *Hylomyrma*, *Leptothorax*, *Macromischa*, *Manica*, *Megalomyrmex*, *Monomorium*, *Myrmica*, *Orectognathus*, *Paramyrmica*, *Rogeria*, *Solenopsis*, *Tetramorium*.

d. **Liomyrmeciform.** Slender, rather long and strongly curved medially; apex forming a rather long, slender tooth which is curved medially; with a medial blade which bears a rather stout, blunt tooth. Genus: *Liomyrmex*.

e. **Paracryptoceriform.** Short, stout, and trapezium-shaped; apex forming a short tooth which is slightly curved medially; anterior surface produced medially to form a blade which usually bears two short, stout teeth (but may bear only one or none). Genera: *Paracryptocerus, Procryptocerus, Xenomyrmex, Zacryptocerus.*

(*Harpagoxenus* may have mandibles of this sort, but all our specimens are immature.)

f. **Vollenhoviform.** Slender, rather long, and nearly straight; apex forming a moderately long, slender tooth which is slightly curved medially; with a narrow medial blade, from the edge of which arise two conspicuous medial teeth. Genus: *Vollenhovia.* (*Dacetinops* may have mandibles of this type, but our specimen is immature.)

GROUP III

(With two or three subapical teeth, not all in the same plane.)

a. **Carebariform.** Stout; very broad at the base, narrowing rapidly to the apex, which is curved medially as a rather small, slender, round-pointed tooth; a short, narrow medial blade arises from the anterior surface and bears two teeth; one or two medial teeth arise from the posterior surface. Genera: *Carebara, Erebomyrma, Oligomyrmex, Paedalgus.*

b. **Lophomyrmeciform.** Moderately stout, curved medially; apex forming a round-pointed tooth which is curved medially; a large subapical anterior tooth which is directed anteroventrally; a large, blunt medial tooth which is directed posteroventrally. Genera: *Lophomyrmex, Trigonogaster.*

c. **Pheidoliform.** Moderately broad; apex forming a moderately long, slender tooth which is slightly curved medially and posteriorly; medial border with three stout, blunt teeth, two anterior and one posterior. Genera: *Ischnomyrmex, Pheidole.*

GROUP IV

(Subapical teeth small.)

a. **Apsychomyrmeciform.** Long, straight, and narrow, with the sides almost parallel; apical tooth rather stout, sharp-pointed and strongly curved medially; near the base of the apical tooth the medial border bears a series of four or five small, blunt teeth. Genus: *Apsychomyrmex.*

b. **Cataulaciform.** Roughly trapezium-shaped; the apex forming a slender, short, acute tooth which is curved medially; subapical portion of medial border more or less projecting, and bearing two to five minute teeth. Genus: *Cataulacus.*

c. **Macromischoidiform.** Narrowly subtriangular in anterior view, somewhat thin and sinuous in side view; apex forming a slender, acute tooth; with two subapical medial teeth, one anterior, the other posterior. Genus: *Macromischoides.*

d. **Pheidologetiniform.** Subtriangular, short, and stout; apical tooth short, stout, and curved medially; two small medial teeth. Genera: *Myrmicaria, Pheidologeton.*

e. **Pristomyrmeciform.** Long and slender; tapering gradually; moderately curved medially; with a small, acute, medial tooth at the distal third which points toward the apex. Genera: *Myrmecina, Novomessor manni, Pristomyrmex.* (*Xiphomyrmex* may have mandibles of this type, but all our specimens are immature.)

f. **Tranopeltiform.** Moderately broad; middle half bent medially; distal fourth curved medially and forming an acuminate apical tooth; with or without a small tooth on the medial border. Genus: *Tranopelta.*

g. **Wasmanniform.** Slender and moderately long, slightly bent at the middle; apex forming a short, acute tooth which is scarcely larger than the subapical medial tooth. Genus: *Wasmannia.*

GROUP V

(Apex rounded; no medial teeth.)

a. **Allomeriform.** Basal three-fourths triangular, rather narrow and with the medial border straight; the distal fourth strongly bent medially to form a long, stout, blunt, apical tooth. Genus: *Allomerus.*

b. **Anergatiform.** Distal third narrowed and abruptly turned medially; apex rounded. Genus: *Anergates.*

c. **Cephalotiform.** Strongly curved medially; basal half wide; apical half narrowed to form a long, rather stout, round-pointed, apical tooth; middle of medial border erose. Genus: *Cephalotes.*

d. **Messoriform.** Basal three-fourths broadly subtriangular; apical fourth curved medially to form a long and moderately slender apical tooth. Genus: *Messor.*

GROUP VI

(Apex sharp-pointed; no medial teeth.)

a. **Attiform.** Broad, short, stout; apical portion abruptly attenuated and curved medially to form a sharp-pointed apical tooth. Genera: *Acromyrmex, Atta, Cyphomyrmex, Trachymyrmex.*

b. **Crematogastriform.** Basal half inflated and narrowing more or less abruptly to the apical half, which is sharp-pointed and slightly curved medially. Genus: *Crematogaster.*

c. **Meranopliform.** Triangular and moderately broad, apex slightly turned medially and forming a sharp pointed tooth. Genus: *Meranoplus.*

d. **Myrmicocryptiform.** Of two parts, a stout base and a smaller, acute, conical apex. Genera: *Apterostigma, Myrmicocrypta.*

GROUP VII

(Miscellaneous.)

a. **Anergatidiform.** Plump and slightly curved medially; apex paraboloidal and surmounted by a single small tooth. Genus: *Anergatides.*

b. **Dacetiform.** Triangular, straight, and rath-

er narrow in anterior view; curved posteriorly; apex stout, straight, and blunt; medial border with two blunt teeth near the middle. Genus: *Daceton*.

KEY TO THE GENERA OF MATURE WORKER LARVAE OF MYRMICINAE IN OUR COLLECTION[3]

GROUP A

Short and very stout; dorsal profile very long and C-shaped; ventral profile short; head ventral.

1. Body attiform (A1); without anchor-tipped hairs..a
   - a_1 Mandibles attiform (VIa).....b
   - a_2 Mandibles myrmicocryptiform (VId).....e
   - b_1 Body hairs stout, with the tip branched or simple **Acromyrmex**
   - b_2 Body hairs slender, with the tip unbranched.....c
   - c_1 Head hairs numerous (about 100).....**Atta**
   - c_2 Head hairs few (less than 40).....d
   - d_1 Some head hairs above antennal level..... **Trachymyrmex**
   - d_2 Head hairs all below antennal level..**Cyphomyrmex**
   - e_1 Head hairs all below antennal level..**Myrmicocrypta**
   - e_2 Some head hairs above antennal level.**Apterostigma**
2. Body myrmicariform (A2); mandibles pheidologetiniform (IVd); hairs unknown.....**Myrmicaria**
3. Body strumigenyform (A3).....f
   - f_1 Mandibles aphaenogastriform (Ia); anchor-tipped hairs present.....**Smithistruma** and **Strumigenys**
   - f_2 Mandibles pheidologetiniform (IVd); without anchor-tipped hairs.....**Pheidologeton**
   - f_3 Mandibles carebariform (IIIa); without anchor-tipped hairs.....g
   - g_1 Head hairs all simple.....**Carebara**
   - g_2 Head hairs deeply bifid or with the tip bifid..... **Paedalgus**
   - g_3 Head hairs of 4 types: simple, bifid, multifid, denticulate.....**Oligomyrmex**

GROUP B

Elongate-subelliptical; head applied to the ventral surface near the anterior end.

1. Body cataulaciform (B1); mandibles cataulaciform (IVb); without anchor-tipped hairs....**Cataulacus**
2. Body crematogastriform (B2); anchor-tipped hairs present.....a
   - a_1 Mandibles cephalotiform (Vc).....**Cephalotes**
   - a_2 Mandibles crematogastriform (VIb)..**Crematogaster**
   - a_3 Mandibles paracryptoceriform (IIe).....b
   - b_1 Cranium circular in anterior view....**Xenomyrmex**
   - b_2 Cranium transversely subelliptical..**Paracryptocerus**
3. Body macromischiform (B3); mandibles leptothoraciform (IIc); anchor-tipped hairs present.. **Macromischa** and **Leptothorax** (subgenera **Myrafant** and **Dichothorax**)

GROUP C

Short and stout; superficially straight, but with the anterior portion of the thorax curved ventrally, i. e., L-shaped.

1. Body allomeriform (C1); without anchor-tipped hairs.....a
   - a_1 Mandibles allomeriform (Va).....**Allomerus**
   - a_2 Mandibles wasmanniform (IVg).....**Wasmannia**
2. Body cardiocondyliform (C2).....b
   - b_1 Mandibles macromischoidiform (IVc); anchor-tipped hairs present.....**Macromischoides**
   - b_2 Mandibles podomyrmiform (Ic); without anchor-tipped hairs.....**Cardiocondyla**
3. Body pheidoliform (C3); mandibles pheidoliform (IIIc); anchor-tipped hairs present.....**Pheidole**
4. Body solenopsidiform (C4).....c
   - c_1 Mandibles anergatiform (Vb); anchor-tipped hairs present.....**Anergates**
   - c_2 Mandibles leptothoraciform (IIc).....d
   - d_1 Anchor-tipped hairs present..... **Monomorium antarcticum**
   - d_2 Without anchor-tipped hairs.....e
   - e_1 Head hairs minute; ventral and lateral surfaces of abdomen nearly naked.....**Megalomyrmex**
   - e_2 Head hairs moderately long; abdomen moderately hairy.....f
   - f_1 Some head hairs simple.....**Solenopsis**
   - f_2 All head hairs branched..... **Monomorium** (except *antarcticum*(

GROUP D

Moderately long and moderately stout; whole thorax curved ventrally and usually separated (more or less) from the remainder of the body by a change in diameter.

1. Body aphaenogastriform (D1); mandibles aphaenogastriform (Ia); without anchor-tipped hairs.a
   - a_1 Without spinules on the anterior surface of the mandibles.....**Novomessor** (except *manni*)
   - a_2 Spinules present on the anterior surface of the mandibles.....b
   - b_1 Deeply bifid body hairs with the branches rather stout and recurved at the tip.....**Veromessor**
   - b_2 Deeply bifid body hairs with the branches slender and flexuous.....c
   - c_1 Head hairs deeply 2- to 4-branched (usually 2-branched), rarely denticulate.....**Stenamma**
   - c_2 Head hairs simple or with the tip bifid or denticulate **Aphaenogaster**
2. Body aspididriform (D2); without anchor-tipped hairs; mandibles aphaenogastriform (Ia).....d
   - d_1 With unbranched denticulate body hairs..**Aspididris**
   - d_2 Body hairs mostly bifid.....**Alistruma**
3. Body epopostrumiform (D3); without anchor-tipped hairs.....e
   - e_1 Mandibles leptothoraciform (IIc); body hairs stout, scarcely tapering, with blunt tip; of two types—denticulate and deeply bifid...**Clarkistruma**
   - e_2 Mandibles aphaenogastriform (Ia).....f
   - f_1 Head hairs minute and simple.....**Mesostruma**
   - f_2 Head hairs moderately long and denticulate..... **Epopostruma**
4. Body myrmiciform (D4).....g
   - g_1 Mandibles messoriform (Vd); without anchor-tipped hairs.....**Messor**
   - g_2 Mandibles podomyrmiform (Ic); anchor-tipped hairs present.....**Dacryon**
   - g_3 Mandibles pogonomyrmeciform (Id); without anchor-tipped hairs.....**Pogonomyrmex**
   - g_4 Mandibles leptothoraciform (IIc).....h
   - h_1 Anchor-tipped hairs present.....i
   - h_2 Without anchor-tipped hairs.....j
   - i_1 Spinules on maxillae and labrum.....**Tetramorium**
   - i_2 Without spinules on maxillae and labrum..**Myrmica**
   - j_1 Anterior surface of mandibles spinulose.....**Manica**
   - j_2 Mandibles without spinules.....**Paramyrmica**
5. Body orectognathiform (D5); mandibles leptothoraciform (IIc); without anchor-tipped hairs. **Orectognathus**

GROUP E

Miscellaneous

1. Body dacetiform (E1); mandibles dacetiform (VIIb); without anchor-tipped hairs.....**Daceton**
2. Body dilobocondyliform (E2); anchor-tipped hairs present.....a
   - a_1 Mandibles dilobocondyliform (IIa)...**Dilobocondyla**

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[3]The following genera which we have studied are not included in the key because the material we have does not show adequate body profiles, the larvae are immature, the integuments are damaged, or our specimens are semipupae: *Anergatides, Apsychomyrmex, Basiceros, Dacetinops, Erebomyrma, Harpagoxenus, Huberia, Hylomyrma, Ischnomyrmex, Lophomyrmex, Meranoplus, Novomessor manni, Procryptocerus, Rhopalothrix, Rogeria, Sericomyrmex, Tranopelta, Xiphomyrmex, Zacryptocerus.*

a_2 Mandibles leptothoraciform (IIc)..... **Leptothorax** (subgenera **Leptothorax** and **Nesomyrmex**)

a_3 Mandibles podomyrmiform (Ic)..... **Podomyrma**

3. Body liomyrmeciform (E3); mandibles liomyrmeciform (IId); anchor-tipped hairs present.... **Liomyrmex**

4. Body pristomyrmeciform (E4); mandibles pristomyrmeciform (IVe)..... b

b_1 Anchor-tipped hairs present..... **Pristomyrmex**

b_2 Without anchor-tipped hairs..... **Myrmecina**

5. Body rhopalomasticiform (E5); mandibles podomyrmiform (Ic); without anchor-tipped hairs.. **Rhopalomastix**

6. Body trigonogastriform (E6); mandibles lophomyrmeciform (IIIb); without anchor-tipped hairs..... **Trigonogaster**

7. Body vollenhoviform (E7); mandibles vollenhoviform (IIf); without anchor-tipped hairs..... **Vollenhovia**

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