A Comparative Study of the Myrmicine Sting Apparatus (Hymenoptera, Formicidae)

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ABSTRACT

The morphology of the skeletal portions of the sting apparatus is described and compared in 63 genera of myrmicine ants in order to evaluate its taxonomic potential in this difficult subfamily. The survey covers about half of the myrmicine genera, and all but 3 small tribes (Ochetomyrmecini, Melissotarsini, Stegomyrmicini). Interspecific variation in the apparatus is described in a third of the genera examined. In addition, the sting apparatus of the primitive ponerine ant, *Amblyopone pallipes* is described for comparison with the primitive myrmicines; and the sting associated glands (poison gland, Dufour's gland) are illustrated for single species of *Amblyopone, Basiceros, Monomorium, Aphaenogaster, Crematogaster,* and *Zacryptocerus.*

The sting apparatus is found to be a complex structure that is quite variable at the subfamily level and more conservative at lower levels. These properties make it potentially useful in characterizing genera and tribes.

Genera within the Attini, Cephalotini, Dacetini, Basicerotini, Tetramoriini, Myrmicini, Pheidolini, and Emery's (1922) Solenopsidini are still considered closely related. The last 3 tribes, however, may need redefining because of suggested inclusions. Ettershank's (1966) genus group arrangement is questioned in part. The following pairs of genera continue to be closely associated: *Leptothorax* and *Macromischa, Promeranoplus* and *Prodicroaspis, Adelomyrmex* and *Lachnomyrmex. Stereomyrmex, Cataulacus, Crematogaster, Myrmicaria, Ocymyrmex,* and *Cardiocondyla* retain their unique character, but affinities are indicated. The constitution of the Pheidologetini, Leptothoracini, Meranoplini, and Myrmecinini is questioned. Many of the genera traditionally assigned to these tribes probably belong to other tribes or genus groups.

A phylogeny based on the sting apparatus is proposed for most of the genera studied, and 4 grades of reduction in the evolution of the sting apparatus are outlined. An attempt is made to show how myrmicine ecology has affected sting morphology, and in turn, how the loss of the stinging function may have affected other aspects of myrmicine morphology and biology.

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INTRODUCTION

Since the Oligocene, the subfamily Myrmicinae has radiated into the largest, most important group of ants. Some genera, particularly *Crematogaster, Pheidole,* and *Tetramorium,* are radiating and spreading, and replacing dolichoderine genera in their advance (Brown, 1973). As is generally the case with rapidly evolving groups, the internal classification of the subfamily is confused. Except for the Attini, Cephalotini, Dacetini, and Basicerotini there are no clearcut assemblages of genera. Emery (1914, 1915, 1922) attempted to place all myrmicines into tribes. Wheeler (1922) added new genera to Emery's classification and made some modifications. But in the final analysis, Wheeler was unable to write a key that separated the Pheidolini, Myrmecinini, Solenopsidini, Leptothoracini, and Tetramoriini. He had to key them out genus by genus. Of the remaining 15 tribes, 4 are the obvious ones listed above, and 9 are monotypic. So the family was essentially split into 1 tribe with many genera, and a large number of tribes with only 1 genus each. This is a typical «hollow curve» distribution, which, as Mayr (1969: 236) points out, is unsatisfactory for information retrieval. It also illustrates the fact that the relationships among genera were largely unknown. All workers on the Myrmicinae have bemoaned the inadequacy of that classification, beginning with Emery himself (1922: 7).

Today, the reclassification of the Myrmicinae proceeds slowly through the efforts of only a few people. Brown and Kempf have published many taxonomic papers on the myrmicines. Together they revised the Basicerotini (Brown and Kempf, 1960). In addition, Brown has produced scattered generic synonymies (1953a, c; 1971), and major revisions of the Dacetini (1948, 1949a, 1950b, c; 1952a, b, 1953b, d; 1954b, 1958, 1959, 1962, 1964, 1969), and Basicerotini (1949b, 1974). The late Father Kempf added major revisions of the Cephalotini (1951, 1958, 1973b), *Leptothorax* (1959), *Cyphomyrmex* (1964, 1965), *Mycocepurus* (1963), *Irogera* (1961), *Hylomyrma* (1973a) and *Oxyepoecus* (1974). Buren (1958, 1972) has published regional revisions of *Crematogaster* and some species of *Solenopsis.* Bolton (1974, 1976) revised *Cataulacus,* and has begun a revision of the Tetramoriini. Ettershank (1966) revised Emery's Solenopsidini and Pheidologetini, making use of mouthpart and malpighian tubule characters (previously little used in the Myrmicinae). In so doing, he eliminiated the inadequate tribal classification and reorganized the genera into smaller, less formally defined genus groups. In that paper, Ettershank makes it clear that new character systems must be tapped in order to improve the classification of the Myrmicinae. To that purpose Wheeler and Wheeler have been describing the larvae of ants, but the myrmicine larvae are as difficult to sort into tribes as the adults (G. C. and J. Wheeler, 1960).

With that prospect I began the present study. Systematic investigations of the sting apparatus, or its homologue the ovipositor, have shown that this structure can be used successfully to make phylogenetic inferences. Oeser (1961) exposed the remarkable amount of variation in the female genitalia of 20 hymenopteran families and very nicely outlined the evolution of the aculeate sting apparatus. Robertson (1968) used evidence primarily from the glandular elements of the venom apparatus to produce a skeleton phylogeny, of the Hymenoptera. Her small sample and small number of characters make her phylogeny questionable, but her study does portend the importance of the venom glands in hymenopteran systematics. Within the Formicidae, Foerster (1912) was the first to show the intergeneric variation in the sclerites of the sting apparatus. His descriptions were supplemented by Callahan *et al.* (1959), Hazeltine (1967), Hermann and Blum (1966, 1967a, b; 1968), Hermann (1968a, b; 1969a, b) and Hermann *et al.* (1970). Hermann (1969b) studied sting and furcular structure in the Ponerinae, Dorylinae, and Cerapachyinae. His work confirms that these groups are closely related, yet represent distinct lines. Brown (1975) does not agree that the Cerapachyinae should rank as a separate subfamily; but nevertheless, he believes that they are a distinct tribe within the Ponerinae. Hermann (1969b) also reinforces the concept that the New and Old World dorylines are distinct groups of legionary ants. However, in contrast to some (Brown, 1954a, 1975; Gotwald and Kupiec, 1975), he argues that they are monophyletic. Whatever the interpretation of his results, his data demand attention in future classifications.

With these examples for encouragement, I chose to explore the taxonomic potential of the skeletal parts of the sting apparatus. With the help of W. L. Brown, Jr., an attempt was made to select free-living representatives of primitive and derived genera within each of Emery's 19 tribes of the «Eumyrmicinae». Shortage of time and material limited the number of species studied within each genus. Presented here are descriptions of 96 species, representing 63 genera and 18 of Emery's tribes (updated, see Table 5). This covers roughly half of the myrmicine genera. In 21 genera, 2 or more species are described. Of the 41 genera in which 1 species is described, 13 are represented by 1 specimen. Several castes were examined where possible; and the sting associated poison gland and Dufour's gland are illstrated for species where live material was available.

The sting of *Amblyopone pallipes* is described first as a paradigm of a primitive formicid sting apparatus with which to compare the primitive Myrmicinae. *Amblyopone* is a primitive genus of the Ponerinae, which Brown (1954a) believes to be the subfamily ancestral to the myrmicines. (Brown suggests more specifically that although the Amblyoponini is the most primitive tribe, the tribe Ectatommini is more likely the stem group of the Myrmicinae). A thorough study of the origin of the Myrmicinae must be deferred until later, but where possible, comparisons are made between *A. pallipes,* primitive myrmicines, and Hermann and Blum's (1966) description of *Paraponera clavata* (Ectatommini).

A second reason for examining the myrmicine sting apparatus is to set a morphological foundation for future studies on the ecology, behavior, and evolution of the subfamily. The limits of behavior and ecology are set by the morphology of the organism. Ethological and comparative ecological studies may be deficient without an understanding of the underlying morphology, phylogeny, and convergence within the taxon examined. Furthermore, comparative morphological studies can more readily scan a large number of species than can ethological and ecological studies. Consequently, they are more likely to show phylogenetic trends, produce evolutionary hypotheses, and point to specific organisms with which to test those hypotheses. Since the sting apparatus is so intimately involved in the chemical communication of ants, it is hoped that a systematic study of this structure will guide behaviorists and chemical ecologists along phylogenetic lines in future studies.

METHODS

Most of the ants dissected were preserved in ethanol, but occasionally it was necessary to examine dried material. These latter specimens were relaxed in Barber's fluid for at least 24 hours prior to dissection.

The sting apparatus of each ant was removed from the gaster under ethanol and the musculature of some of the larger apparatuses was examined at that time. All others were cleared of muscles in hot lactophenol. Most apparatuses were placed in cold lactophenol, heated to near boiling (80°C), then allowed to cool slowly on the hot plate. Smaller ones were removed from the plate and cooled quickly; larger or more obstinate ones received repeated treatment. After clearing, the sting apparatuses were dissected into components (see below), transferred to 70% ethanol, washed 3 times, then mounted on slides in either glycerin jelly or Canada balsam. For a glycerin jelly mount, a droplet of hot jelly (60°C) was spread on a warmed slide to the diameter of the coverglass, and using fine forceps, the specimen was transferred from the 70% ethanol to the center of this circle. With minuten nadeln the alcohol was mixed into the jelly and the specimen positioned as the jelly cooled and hardened. After it was thoroughly cooled, a coverglass was coated on one side with a thin layer of hot jelly and inverted on the preparation. If the layer of jelly between the specimen and the coverslip was thin enough, the preparation could be examined under 1000x oil immersion. These mounts have the following 3 advantages: any orientation of structures can be achieved simply (especially important for the sting); there is no distortion by flattenning; and specimens can be quickly remounted and repositioned by reheating the slide and removing the coverslip. This last advantage is especially important when only one sting apparatus was available for a species. The disadvantages are that generally oil immersion cannot be used, and the mounts are not permanent. Specimens to be mounted in Canada balsam were placed in two changes of 95% ethanol, each for 15 minutes, then into equal parts of 95% ethanol and clove oil overnight. By morning the alcohol had evaporated and the specimens were ready to be mounted in balsam.

The following dissections were made for the different mounting media. An asterisk indicates which dissections were used when only one specimen was available.

1. Glycerin jelly

   a. Whole mount, lateral view.
   b. Quadrate plates and anal plate removed and mounted in anterior view; remaining sclerites mounted as a unit in dorsal view.
   * c. Sting and furcula, lateral and ventral views.

2. Balsam

   * a. With sting and furcula removed, the anal arc was cut to one side of the anal plate and all other structures divided in half by a midsagittal cut. The two halves were mounted in side view.
   b. Spiracular plates removed and mounted separately in posterior view.
   c. Gonostyli removed and mounted separately in dorsal view.

Preparations were viewed with a Wild M-20 phase-contact microscope. All drawings were made using a grid eyepiece and grid-backed tracing paper.

Gland dissections were made on live chilled ants in Ringer's solution. Drawings were made using the double grid system, with a Wild M5 dissection microscope.

All illustrations, unless otherwise stated, are lateral views of the right side. The scale lines are always in millimeters.

Voucher specimens of nearly all species (either the dissected specimen or one from the same collection) have been placed in the Cornell Insect Collection, Comstock Hall, Cornell University, Ithaca, New York 14853. Each pin bears the lot number 1054 and the label «voucher specimen, Kugler study, 1976». Other specimens are located in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138. They bear the label, «Voucher specimen, Kugler study, 1976». These species are indicated here by the initials MCZ.

Characteristics of the sting apparatus lending themselves to tabular compilation are found in Appendix A. Those requiring additional qualification are marked with an asterisk and are discussed in the text. Character states separated by a comma indicate that both characters can be found in that species. Figures listed in the key to Appendix A are meant to be representative examples, and not a complete listing of figures showing a specific character.

The text is used primarily to describe peculiarities of shape or sclerotization that cannot be given in the table or figures. It is also used to point out important characteristics of the figures, similarities between species, and variability within species or genera. By itself, the text is only supplementary, and the figures and Appendix A must be consulted for a full description. The anal plate is generally not mentioned in the text because it is usually too poorly sclerotized to have a definite, describable shape; the shape that can be discerned is characteristic for only a few genera. The number of stings used to make the descriptions in the text is given after each «species examined». Descriptions (including Appendix A) are the same for different species and castes within the same genus, unless otherwise stated.

For a few polyphenic species the allometric variation in size of the sting apparatus could be described. The slope of the allometric equation (a) was calculated from the best fit of the line $\log y = \log b + a \log x$, where x = pronotal width (excluding spines), y = either sting length (excluding dorsal flange and onterolateral processes) or quadrate plate length, b = the y-intercept.

The «special remarks» included with some descriptions are to focus the reader's attention on striking features of sting apparatus morphology that may have behavioral or ecological signicance.

List of Abbreviations

AA	anal arc
AP	anal plate
FA	fulcral arm
FU	furcula
GO	gonostylus
IV	intervalvifer articulation
LA	lancet
OP	oblong plate
PI	postincision
QP	quadrate plate
R1	first ramus (from TP to LA)
R2	second ramus (from OP to sting)
SB	sting base
SBLB	sting bulb
SP	spiracular plate
SS	sting shaft
TP	triangular plate
VC	valve chamber

RESULTS

(Part I)

GENERAL DESCRIPTION AND HOMOLOGY OF THE STING APPARATUS

The basic structure of the sting apparatus in the Myrmicinae is described below. Each component is described with a discussion of its homology. Wherever possible, the nomenclature follows that of Hermann and Blum (1966), Callahan *et al.* (1959) and Oeser (1961). Equivalent names used by other authors are given in Table 1. The morphological terms are underlined as they are introduced, and abbreviations appear in parentheses. The names and definitions of sensory structures follow Snodgrass (1935: 514-525).

The sting apparatus of aculeate Hymenoptera is derived from the ovipositor, which in turn is composed of the highly modified abdominal segments 8-11. It is invaginated into a sting chamber formed by the 7th abdominal tergum and sternum (Fig. 1).

The spiracular plates (SP, Figs. 1, 2) are paired remnants of the 8th abdominal tergum. In the Myrmicinae they are joined mesad by a narrow membranous or sclerotized band, the medial connection (Figs. 1, 2, 9). They bear the last pair of abdominal spiracles. In most myrmicines the spiracular plates are approximately quadrangular, but in some, the posterodorsal corner is reduced and the shape is essentially triangular (Fig. 148). An anterior apodeme (Figs. 2, 9) of variable size and shape is set off from the rest of the plate by a line continuous with the anterior edge of the medial connection. This line marks the attachment of the 7th-8th intersegmental membrane. A posterodorsal lobe (Fig. 2) is present in some species and is set off from the rest of the plate by a diagonal line that marks the edge of the muscle originating on this lobe. Some species have a dorsal notch (Figs. 2, 35) between the dorsal edge of the plate and the medial connection. This is a membranous area that allows flexion between the plate and the connection. The posteroventral corner often bears a small tubercle projecting ventrad for muscle attachment (Fig. 9).

Beneath the spiracular plates are the bilaterally paired quadrate plates (QP, Figs. 1, 3). These are the hemitergites of the 9th abdominal segment. They are connected medially by a narrow sclerotized band, the anal arc (AA). A vertical midplate line (Figs. 1, 3, 18) runs the length of each plate and divides it into an anterior apodeme (Snodgrass, 1935) and a posterior body. Lateral and medial lobes project from either side of the dorsal end of the apodeme (Figs. 3, 18). In slide preparations of the lateral view, these are often flattened into the same plane of the rest of the plate. The apodeme and its lobes are the attachment sites for 3 large muscles (see Table 2, muscles 17a, 17b, 18). A heavy anterior ridge bears the force of muscle 17a and b. Generally the posteroventral area of the body overlaps the oblong plate laterally, but in some species, this corner is reduced in width (Figs. 131, 148) and/ or the posterior edge is emarginate (Fig. 188) to allow the quadrate plate to fit above the oblong plate without overlapping it.

The anal arc supports a small median sclerite, the anal plate (AP, Figs. 1, 3), on its posterior edge. This is a vestige of either the 10th tergum or the fused 10th and 11th terga (Snodgrass, 1935). It usually bears anal sensilla on its posterior edge, or on both the dorsal surface and posterior edge. Often there are a few very short chaetiform sensilla in the membrane lateral to the plate.

The triangular plates (TP, Figs. 1, 12) are heavily sclerotized paired structures that lie in an indentation of the lateral surface of the oblong plates. The dorsoapical process articulates with the ventral end of the anterior ridge of the quadrate plate. This is the tergovalvifer articulation. The ventroapical process articulates with the oblong plate at the intervalvifer articulation (IV). These apical processses are very wide in the transverse dimension. In some species, mounting the triangular plate in lateral view causes the apical processes to twist and expose dorsal or posterior surfaces. When this happens, the apical processes appear unnaturally wide in side view. In some species (*e.g.*, Fig. 12) a medial tubercle is present on the ventroapical process ,and a dorsal tubercle is found on the dorsoapical process. The dorsal tubercle marks the insertion of muscle 14 (see Table 2), but its absence does not necessarily mean the muscle is absent. The body of the triangular plate lies below the apical processes and is very narrow transversely. Its base is fused to a long flexible ramus from the ipsilateral lancet.

The triangular plates are often considered part of the 8th sternum (Matsuda, 1957, 1958) or the 8th gonocoxae (Michener, 1956; Sharov, 1966; Smith, 1970), but the studies of Gustafson (1950) and Scudder (1961) indicate that they may be homologous with either the 9th sternum or the fused 9th sternum and 9th gonocoxae.

The first rami and lancets (LA, Figs. 1, 12) are derivatives of the gonapophyses of segment 8. A groove runs the length of ramus and lancet. On each lancet, most aculeates have 1 or 2 dorsally projecting lobes, each with a flexible connection to a valve. These are one-way valves. As each lancet is thrust caudad, the valve extends into the lumen of the venom canal and pushes venom ahead of it. On the back stroke the valve collapses against the side of the venom canal as the opposite lancet makes its thrust stroke (Janet, 1898). In the Myrmicinae the posterior pair of valves are greatly reduced or absent. The point at which the anterior valve joins the lancet groove is here arbitrarily called the anterior end of the lancet. Above the lancet groove is a dorsal lamina (Fig. 12). It rapidly attenuates in heigth anterior to the valves, and its distal end may bear a dorsal ridge. Below the groove is a ventral lamina. It is membranous anterior to the valves and continues along the edge of the ramus as the ligulate membrane. Callahan *et al.* (1959) say that the ligulate membrane is a hollow cylinder, but on the lancet it is laterally compressed to form the dorsal and ventral laminae. Unless otherwise stated in the text, the ventral lamina has a ventral ridge along the entire edge of the lancet. The terminal ends of the lancets sometimes have a row of barbs on their lateral surfaces. In most myrmicines, the lancets at rest extend to the end of the sting and not beyond. Exceptions are noted in the appropriate descriptions.

The paired oblong plates (OP, Figs. 1, 10) are usually considered homologous with the 9th gonocoxae. In most myrmicines each plate is divided into 2 arms by a deep membranous incision, the postincision (PI). Another membranous area, the preincision, is not always well defined, and separates the oblong plate from the flexible ramus 2 (see below). The part of the oblong plate dorsal to the postincision and posterior to the intervalvifer articulation (see above) is the posterior arm (Figs. 1, 10). The part bounded by the 2 incisions, and an imaginary line connecting their extreme ends, is the ventral arm (Fig. 10). Each posterior arm has a dorsal ridge that is deflected dorsomesad from the remaining portion, the body of the arm (Fig. 10). The posterior arm may be straight or curved mesad. In most species, the ends of the posterior arms are widely separated but connected by membrane. In some species the end of the dorsal ridge projects mesad beyond the end of the body as the posterior apodeme (Fig. 32), and may reach to the midline. The dorsal ridge may also have a subterminal tubercle pointing dorsad (Fig. 10). The dorsal ridge continues anterior to the posterior arm, and its proximal end is usually produced dorsal for the insertion of muscle 17a to form the anterior apodeme (Figs. 1, 10).

The ventral arm generally has a heavily sclerotized posterior margin, the fulcral arm (FA, Figs. 1, 10), that articulates ventrally with an articular process of the sting (fulcral articulation) and dorsally with the posterior arm. The fulcral arm is «vertical» if its long axis is perpendicular to the dorsal ridge of the oblong plate (Figs. 1, 10) or nearly so; otherwise, it is «oblique» (Figs. 133, 140).

On the oblong plate of most myrmicines are 4 patches of sensilla (Fig. 10). The cluster of sensilla chaetica just anterior to the intervalvifer articulation are the intervalvifer sensilla. The peg-like sensilla midway along the length of the 2nd rami are the ramal sensilla. They project into the grooves in the first rami and presumably sense movement between the first and second rami. The fulcral articulation is flanked by the anterior and posterior fulcral sensilla. Callahan *et al.* (1959) call these «sensory pegs». My own observations could not confirm the existence of pegs. In any case, these sensilla presumably sense movement at the fulcral articulation.

Articulating with the posterior extremity of each oblong plate is a gonostylus (GO, Figs. 1, 4). Some authors (*e.g.*, Scudder, 1961) regard these as secondary buds from the oblong plates. The evidence for this comes from orthopteroid insects. In Hymenoptera, however, the presence of muscles from the oblong plates inserting on the bases of the gonostyli (Smith, 1969), indicates that the gonostyli may be homologous with the styli of the gonocoxae in Thysanura. Each gonostylus is a hollow sac whose lumen is part of the hemocoel. It may be 1-or 2-segmented, and its dorsal, lateral and ventral surfaces are generally sclerotized and bear sensilla. In most Myrmicinae the dorsal surface of the gonostylus bears a chaeta that is generally thicker, blunter, longer, and more terminally positioned than other chaetae on the gonostylus. This is the dorsoterminal chaeta (Fig. 11). In some species, the seta nearest the dorsoterminal chaeta is thicker and longer than other setae on the gonostylus, and is called the companion seta (Fig. 11). In addition to these two sensilla, with few exceptions, the gonostylus of myrmicines have both setae and chaetae, but not campaniform sensilla. Sensilla basiconica are present in some genera. The medial surfaces of the gonostyli are membranous and covered with microtrichiae. The function of the gonostyli has been clearly established for only one aculeate, the sphecid wasp *Philanthus triangulum*. In this insect, they are highly modified and used for locating a precise point on its prey's body to insert the sting (Rathmayer, 1962). In other aculeates they have a less obviously specialized form, and are generally assumed to form a protective sheath for the sting. This is problably part of the truth, but it fails to explain the presence of sensilla on the outer surfaces of the gonostylus, and their variety.

The second rami (R2) and the sting (Figs. 1, 5, 6) are the modified gonapophyses of the 9th abdominal segment. The sting is the cylindrical median sclerite formed by the fusion of the dorsal edges of the gonapophyses; the second rami are the paired structures that lead to it from the anterior apodeme of the oblong plates. The lancets plus the sting make up the aculeus. The central cavity formed by the lancets and the sting is the venom canal. For the purposes of this study, the sting is divided into 3 parts (Fig. 5), based on functional morphology. The boundaries are somewhat arbitrarily defined by internal structures seen in lateral view. The narrow distal portion (with a piercing function in more primitive ants) is the sting shaft (SS). Anterior to the sting shaft is the valve chamber (VC). It is a dilation of the venom canal in which the lancet valves operate. The boundary between the valve chamber and the sting shaft is the point at which the inner and outer dorsal walls of the sting shaft meet (Fig. 5). This point is arbitrary in species where the inner and outer walls do not meet at the caudal end of the valve chamber (Fig. 210) .Between the two walls is the hemocoel. In some species the terminal end of the hemocoel is enlarged (Fig. 83). If the hemocoel is enlarged and then laterally compressed, a dorsal flange is created (Figs. 63, 91, 138, 190). In other species, the hemocoel is partially or entirely reduced distad (Fig. 118). Anterior to the valve chamber, the sting bulb (SBLB, Fig. 5) houses the ends of the venom duct and Dufour's gland and their closing mechanisms. The boundary between the valve chamber and sting bulb is the point at which the internal apophysis (Fig. 5), which is actually a continuation of the inner dorsal wall, seems to join the outer dorsal wall. In some species the apophysis is long and heavily sclerotized and appears to extend the dorsum of the valve chamber anteriad (Figs. 109, 138). For these species the above definition is unrealistic, and the anterior end of the valve chamber is taken as the end of the apophysis. This apophysis is part of the closing mechanism of the venom duct (Janet, 1898). The definition of the sting bulb here differs from that used by Callahan *et al.* (1959), Hermann and Blum (1966), Snodgrass (1935) and Foerster (1912). For these authors the sting bulb (or Kolben) included the valve chamber.

The dorsal half of the anterior surface of the sting is the sting base (SB, Figs. 5, 13, 14). It generally has a transverse basal ridge internally along its margin, and anterolateral processes or corners at its lateral extremities. The sting base does not include the articular processes on the ventral half of the sting, or the basal notches, which arch anterodorsally from the articular processes. If the anterolateral processes of the sting base project ventrad, interrupting the otherwise smooth curve of the basal notch, the notch is said to be «closed» (Fig. 30). If the arch is uninterrupted to the anterior end of the sting, it is «open» (Figs. 13, 33). The second rami are fused to the sting between bases of the articular processes (Fig. 6).

The sting shaft and valve chamber have campaniform sensilla on their outer surfaces (Janet, 1898; Smith, 1970), and the articular processes usually have sensilla on their lateral surfaces. For additional information on the structure of the aculeus, see Janet (1898), Callahan *et al.* (1959), Hermann and Blum (1966), and Smith (1970).[1]

The furcula (FU, Figs. 1, 5, 7, 13, 14) is primitively an inverted Y-shaped sclerite perched above the sting base (hereafter the fact that it is «inverted» will be assumed). It is apparently derived from the fused bases of the gonapophyses (Smith, 1970; Hermann and Blum, 1967b: 1289). Its lateral arms are movably attached to the anterolateral processes; the dorsal arm floats freely in the hemocoel.

In referring to the dimensions of the sting and furcula, the terms wide, narrow, and width refer to the transverse dimension; long, short and length refer to the longitudinal dimension; and high, low, deep, height, and depth refer to the vertical dimension. In reference to other parts of the sting

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[1] See Hermann and Douglas (1976), Ann. Entomol. Soc. Amer. 69: 681-686, for more recent terminology of sting apparatus sensory structures.

apparatus, which are basically 2-dimensional, the length is the particular structure's longest dimension, and the shorter dimension is its width.

The membrane of the 9th abdominal annulus attaches to the posterior edge of the lateral arms of the furcula and to the whole perimeter of the end of the sting bulb (Fig. 1). From the sting base the membrane expands posterodorsad and covers the area between the ventral edges of the 9th abdominal segment and the bases of the gonostyli. It also expands anterodorsad, connecting the whole lengths of the second rami to each other. With the quadrate plates, the oblong plates, and the membranes between them, this completes the annulus of the 9th abdominal segment.

There are many descriptions of the musculature of the sting apparatus and its function. Most pertinent to this study are those of Foerster (1912), Snodgrass (1956), Callahan *et al.* (1959), and Hermann and Blum (1966, 1967a, b). The most thorough and lucid account is given by Snodgrass. He lists 22 sets of muscles associated with the sting apparatus of the honeybee. The most important are listed in Table 2, together with their origins, insertions and actions. The numbering system of Snodgrass (1956) is used. According to Snodgrass, the action of the sting apparatus in the honeybee is performed by three different mechanisms. 1) The sting apparatus is forced out of its chamber by hemolymph pressure produced by compression of the gaster. 2) The aculeus is deflected downward by the contraction of muscles 19a and 19b. 3) Alternate contractions of muscles 17 and 18 extend and retract the lancets. The lancets of either side work alternately. Their sharp points and knifelike edges pierce and cut. In the honeybee, the barbed lancets become anchored in the tissue and aid the penetration of the sting (Snodgrass, 1956; Hermann, 1971). Muscles 19a and 19b also increase maneuverability of the aculeus. By their independent or combined action on the furcula, they can make the sting pitch, roll, and yaw in probing for a suitable sting site (Hermann and Blum, 1967b).

The muscles in Table 2 are present in all of the groups of aculeates discussed by the papers cited above. But there are some other muscles that are not present in all groups. Foerster (1912) described a «transverse muscle» that originates and inserts on the dorsal ridges of the oblong plates of opposite sides. It was present in all myrmicines, dolichoderines, and formicines he studied, but was not present in *Odontomachus* (Ponerinae). Hermann and Blum (1966, 1967b), however, reported its presence in another ponerine, *Paraponera clavata,* and also in the ecitonine, *Eciton hamatum.* Its function is unknown. Foerster also described an «oblique muscle» that originates on the dorsal end of the quadrate plate and inserts on the posterior end of the oblong plate. According to Foerster, it acts in combination with muscle 18, and is present in *Myrmica, Aphaenogaster, Pheidole, Odontomachus,* the Dolichoderinae, and Formicinae. Hermann and Blum (1966) did not mention it in *Paraponera,* nor did Snodgrass (1956) for *Apis.* In *Eciton* (Hermann and Blum, 1967b) it may be fused with muscle 18.

It is possible that the sting musculature has some taxonomic potential, but its relatively slight variation among widely separated groups of aculeate Hymenoptera, as reported in the studies mentioned above, indicates that mainly degenerative variation might be expected among ants. Musculature was not studied extensively in the present work.

TABLE 1

Partial horismology of the sting apparatus. The most commonly used German, French, and English synonyms of the terms used in this paper are listed. Obvious cognates have been eliminated. References cited are not necessarily the first to use the terms. For a more comprehensive horismology, and for the original sources of terms, see Oeser (1961).

Nomenclature Used Here	Synonyms	References
Spiracular plate	8th hemitergite plaque stigmatifère Stigmenplatten	Michener (1956) Janet (1898) Zander (1911)
Quadrate plate	9th hemitergite écaille anale plaque carré Afterplatte	Michener (1956) Lacaze-Duthiers (1849) Janet (1898) Dalla Torre and Kieffer (1910)
Anal arc	anal bar arc chitineaux Chitinbogen der Quadratischen Platte	Callahan *et al.* (1959) Janet (1898) Foerster (1912)
Anal plate	dorsalen Proctigersclerit	Oeser (1961)
Oblong plate	second gonocoxa second valvifer arceau ventral écaille latérale Scheidenplatte	Scudder (1957) Snodgrass (1933) Janet (1898) Lacaze-Duthiers (1849) Dalla Torre and Kieffer (1910)
Dorsal ridge	dorsale Verdickungsleiste	Oeser (1961)
Ventral arm	rostrale Chitinzunge	Oeser (1961)
	Lamina falcata	Oeser (1961)
Fulcral arm	Pars articularis	Oeser (1961)
Intervalvifer sensilla	Sinneshärchen des Intervalviferengelenkes	Oeser (1961)
Gonostyli	gonoplacs third valculae valves du fourreau Stachelscheiden	Scudder (1957) Snodgrass (1933) Lacaze-Duthiers (1849) Foerster (1912)

Nomenclature Used Here	Synonyms	References
Triangulos plate	first valvifer	Snodgrass (1933)
	gonangulum	Scudder (1957)
	crosse	Janet (1898)
	Stiletträger	Dalla Torre and Kieffer (1910)
	Winkel	Kraepelin (1873)
Lancet	first gonapophysis	Scudder (1957)
	first valvula	Snodgrass (1933)
	stylet	Lacaze-Duthiers (1849)
	Stechborste	Kraepelin (1873)
Valves of lancet	lamelles	Janet (1898)
	pistons des stylets	Janet (1898)
	Hemmplättchen	Oeser (1961)
	elastischen Platten	Foerster (1912)
Groove of lancet	rainure de coulissage	Janet (1898)
Ramus 1	arc latéral du stylet	Janet (1898)
	Stechborstenbogen	Foerster (1912)
Sting	second gonapophysis	Scudder (1957)
	second valvulae	Snodgrass (1933)
	sting shaft	Hermann and Blum (1966)
	stylet	Snodgrass (1956)
	gorgeret	Lacaze-Duthiers (1849)
	Schienenrinne	Kraepelin (1873)
	Stachelrinne	Sollman (1863)
Articular processes	Horner der Schienenrinne	Foerster (1912)
Internal apophysis	apophyse	Janet (1898)
Furcula	fourchette	Janet (1898)
	Gabelbein	Foerster (1912)
Aculeus	sting	Snodgrass (1956)
	aiguillon	Janet (1898)
	Stachel in engeren Sinn	Foerster (1912)
Sting apparatus	Stachel	Foerster (1912)
	Stachelapparat	Oeser (1961)

TABLE 2

Major muscle of the sting apparatus; their origin, insertion and action. Foerster (1912), Snodgrass (1956), Hermann and Blum (1966), (1967b), personal observation. Paired muscles may act independently, 1) or together, 2).

MUSCLE			ORIGIN	INSERTION	ACTION
Snod-grass	Foer-ster	Hermann & Blum			
17	a	1	anterodorsal corner of QP; medial and lateral surfaces, lobes	anterior apodeme of OP	Move QP and dorsoapical process of TP anteroventrad. TP pivots about intervalvifer articulation and ramus 1 moves ventrad, *protruding* lancet.
17b	b	1	dorsal end of QP; medial surface, medial lobe	dorsal ridge of OP posterior arm	
18	c	2	medial surface of ventral half of QP apodeme	lateral surface, caudal end of OP	Pulls QP and dorsoapical process of TP caudad, retracting lancets.
19a	f	3	medial surface, distal end of OP posterior arm	dorsal and lateral arms of FU	1) Moves sting laterad. 2) Raise SB, depress SS.
19b	f	4	medial surface of OP proximal to 19a.	dorsal arm of furcula	1) Rotates sting about longitudinal axis. 2) Raise SB, depress SS.
20	g	12	ramus 2	articular process of sting	Antagonistic to 19. Elevates sting shaft.
14	d		posterodorsal lobe of SP	dorsoapical process of TP	May aid retraction of lancet.

RESULTS

(Part II)

DESCRIPTION OF SPECIES

SUBFAMILY PONERINAE

Tribe Amblyoponini

Amblyopone (Figs. 1-8)
Species examined: *A. pallipes* 2 ♀, 2 ☿.

Spiracular plate. (Figs. 1, 2) Unlike Myrmicinae, medial connection broad and completely sclerotized. Spiracle small relative to size of plate, located toward the posteroventral corner of the plate.

Quadrate plate. (Figs. 1, 3) Body and apodeme very wide. Ventral ridge submarginal.

Oblong plate. (Fig. 1) Postincision (PI) extends over dorsal edge of fulcral arm (FA) and continues to dorsal ridge just anterior to intervalvifer sensilla. Dorsal ridge weaker at this point; may be point of flexion between anterior portion of plate and posterior arm. On each side of PI, ridges extend form dorsal ridge to dorsal edge of FA. Anterior apodeme large, subacute, heavily sclerotized. Preincision so large that only long slender FA remains of ventral arm. FA well defined, widest dorsad, tapering evenly to narrow base; most heavily sclerotized on posterior margin.

Gonostylus. (Figs. 1, 4) Two segments distinct, well sclerotized. Sensilla on dorsal and lateral surfaces, clustered near articulation of segments; no terminal sensilla. Most are trichodea, chaetica, basiconica; distinction not always clear. Remaining sensilla possibly coeloconica or campaniformia, probably the latter.

My observations on live ants reveal that when the sting is extended from the gastric apex, the distal end of the proximal gonostylar segment is depressed and pushes against the dorsum of the sting shaft. The distal segment rests on the dorsum of the shaft, and serves as a groove in which the latter slides. Only the very tip of the distal segment ever shows externally, while the entire length of the sting shaft may be produced. So the gonostylus (GO) does not locate the sting site, but it may help steady the sting.

Triangular plate. (Fig. 1) Apical processes not marked extensions from body. Base petiolate; junction with ramus 1 (R1) narrow and perpendicular.

Lancet. (Fig. 1) Long, slender, needlelike; gently arched, and very heavily sclerotized. Barbs small, of equal size. Dorsal lamina low, membranous for most of length; higher terminad, and lightly sclerotized. Ligulate membrane thick (cross section), retains ventral ridge. Valves equal in size.

Sting. (Figs. 1, 5, 6) Long, slender, curved, tapering evenly from sting base (SB) to apex. SS more heavily sclerotized than any other in this study. Venom canal (VC) very low; very long compared to sting bulb (SBLB). SB narrow, but well arched; basal ridge very large. SB in side view obliquely truncate. Note also size and shape of associated poison gland and Dufour's gland (Fig. 8) relative to size of sting. Articular processes reach nearly to SB, do not project ventrad.

Furcula. (Figs. 1, 5, 7) Not typical Y-shape of aculeate Hymenoptera. Dorsal arm expanded anterolaterad as winglike flanges. Lateral arms strongly curved ventromesad around SB.

Special remarks: Note especially the strong slender sting-much longer relative to the size of the ant than in any myrmicine examined (Appendix A, column 41).

Discussion:

Based on an admittedly small sample number of species, the sting apparatus of the primitive Ponerinae differs from that of the primitive Myrmicinae in the following ways: SP with broadly sclerotized medial connection, deeply incised posterior notch; OP with extremely long PI, large preincision, long club-shaped FA, narrow dorsal ridge; GO with 2 heavily sclerotized articulating segments, greater variety of sensilla; TP stalked with abrupt attachment to ramus greater variety of sensilla; TP stalked with abrupt attachment to ramus 1; LA needlelike, valves of equal size; sting with SS much longer than VC, and VC much longer than SBLB; SBLB narrow, FU winged. The sting of a related amblyoponine, *Onychomyrmex,* is illustrated by Hermann (1969b), and is very similar to that of *A. pallipes.*

Tribe Ectatommini

Paraponera clavata
Not examined; see description by Hermann and Blum (1966).

This species combines characters found in *Amblyopone pallipes* and the primitive Myrmicinae. Characters found in *A. pallipes* are PI extending to dorsal ridge, FU winged. Characters found in the primitive Myrmicinae are loss of medial connection of SP, wide-based FA, reduced distal segment of GO, shorter and less curved SS and LA, reduction of second valve of LA. Further comparisons must await a reexamination of *P. clavata* in light of the findings presented here.

SUBFAMILY MYRMICINAE

Myrmica genus group

core genera

Myrmica (Figs. 9-14)
Species examined: *M. emeryana* 3 ☿.[1] See also Foerster (1912: 358) *M. rubra* ☿ description.

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[1] These specimens were determined by Dr. André Francoeur who compared them with Forel's types. He wishes me to caution the reader that the present concept of *Myrmica emeryana* «... does not fit the types and the descriptions presently available... in the literature are completely misleading...» My specimens bear the voucher number 04964 in his collection.

Spiracular plate. (Fig. 9) Large, ovoid, anterior apodeme subtriangular. Body extends a short way into medial connection. Spiracle small, near center of plate.

Quadrate plate. Body and apodeme both much narrower than in *Amblyopone pallipes,* but also more reduced than typical Myrmicini (*e.g., Huberia striata,* Fig. 27). Anterodorsal corner with narrow, digitate, well sclerotized process.

Oblong plate. (Fig. 10) Not as divided by preincision and postincision as that of *A. pallipes.* Dorsal ridge quite wide the entire length of posterior arm. Posterior arms do not meet at midline. Anterior apodeme transversely wide, spatulate. Ventral arm short, wide; FA narrow, slightly and evenly tapering from base, vertical.

Gonostylus. (Fig. 11) Sclerites well defined, but not as heavily sclerotized as those of *A. pallipes.* Only sensilla chaetica and trichodea present. Proximal segment tapered from base.

Triangular plate. (Fig. 12) Less elongate than that of *A. pallipes,* ventroapical process more prominent. Base curves ventrad to join first ramus broadly.

Lancet. (Fig. 12) Swordlike; straighter, less sclerotized than that of *A. pallipes.* Single valve relatively larger than that of *A. pallipes,* but still not very well developed. Groove and ventral ridge convergent.

Sting. (Figs. 13, 14) Very different from that of *A. pallipes* (Figs. 5, 6). SS only slightly longer than SBLB plus VC, slightly upcurved, moderately well sclerotized. VC slightly shorter than SBLB; lateral profile distinctly different in height from SS and SBLB, but with gradual transitions. SB moderately arched and in lateral view obliquely truncate. Basal notch short but well arched. Articular processes much shorter than in *A. pallipes* and directed somewhat ventrad. SBLB relatively wider than in either *A. pallipes* or *Paraponera clavata,* but not extremely so; sides straight and gently convergent.

Furcula. (Figs. 13, 14) Y-shaped; lateral arms widely splayed, their extremities wrapped caudad around anterolateral corners of SB.

Manica (Figs. 15-17)
Species examined: *M. bradleyi* 2 ☿. See also Foerster's (1912: 352-358) description of *M. rubida* sting apparatus, including musculature and function.

Spiracular plate. Shape and size of body of plate basically the same as that of *Myrmica emeryana* (Fig. 9), but body does not extend into medial connection. Instead, a V-shaped dorsal notch cuts deeply into dorsal edge. Anterior apodeme wide for more of its length than in *M. emeryana,* and forms anterior edge of posterior notch.

Quadrate plate. Apodeme and body very wide like those of *Amblyopone pallipes* (Fig. 3), also similar in shape and sclerotization.

Oblong plate. (Fig. 15) Posterior arm similar to that of *M. emeryana* (Fig. 10), but secondary and dorsal ridges not very distinct from each other in caudal half. Insertion of muscle 17a, just anterior to IV, tuberculate. Anterior apodeme short, wide and broadly rounded in lateral view, transversely wide with lateral prominence. Ventral arm short and wide as in *M. emeryana,* but FA (Fig. 15) has large pear-shaped base and long, narrow, ill-defined dorsal extention. Posterior edge of base less heavily sclerotized than anterior edge.

Gonostylus. Much like that of *M. emeryana* (Fig. 11) in shape, sclerotization and setation, but segmental boundaries somewhat less distinct, and on distal segment, a row of small setae close gap behind companion seta.

Triangular plate. Quite different from that of *M. emeryana* (Fig. 12). Body narrower, apical processes shorter and more bluntly rounded, apical end not ridged.

Lancet. (Fig. 16) Basically the same shape as that of *M. emeryana*, but caudad, the groove runs closer to the ventral edge for a greater distance. Although the barbs are reduced and probably functionless, they are as large as, or larger than those of any other myrmicines examined, with the exception of *Pogonomyrmex badius*, and possibly *Solenopsis geminata* and *Liomyrmex* cf. *aurianus*.

Sting. (Fig. 17) SS evenly tapered its whole length. Outer dorsal wall thicker than that of *M. emeryana*. VC, though moderately high, has lateral profile less distinct than that of *M. emeryana*. SBLB dorsum slightly concave anteriad. Basal notch very short because of the prominent anterolateral processes. Articular processes very stout. In ventral view SBLB very similar to that of *M. emeryana* but with thicker walls. All indications are that it is a stronger stinging instrument than that of *M. emeryana*.

Furcula. (Fig. 17) Much like that of *M. emeryana*, but lateral extremities that articulate with SB more robust.

Ephebomyrmex (Figs. 18-22)
Species examined: *E. imberbiculus* 2 ☿; *E. naegeli* 1 ☿.

Spiracular plate. *E. naegeli* much like that of *Manica bradleyi*. SP of *E. imberbiculus* subtriangular, apex caudad due to V-shaped posterior edge that smoothly joins ventral and dorsal edges; dorsal ridge very wide. Anterior apodeme long, rectangular in both species.

Quadrate plate. (Fig. 18) Body wider ventrad and extends well below ventral end of anterior ridge as in *Amblyopone pallipes* (Fig. 1). Large medial and lateral lobes present. In most slide preparations, lateral lobe is folded ventrad against the apodeme and appears to be an enlarged anterodorsal corner, as shown in Fig. 18.

Oblong plate. (Figs. 19, 20) Dorsal ridge of posterior arm narrow anteriad but wide caudad. Subterminal tubercle long, gently rounded. Body of arm uniformly narrow, rounded apically. Anterior apodeme short, narrow, and acute in side view, but transversely rather wide and spatullate. Ventral arm of both species very short and wide. FA of *E. imberbiculus* (Fig. 19) triangular; only base triangular in *E. naegeli*, dorsal half rod like (Fig. 20). In both species, FA well defined, vertical.

Triangular plate. Similar to that of *Amblyopone pallipes* (Fig. 1). Body longer and more slender than in *Myrmica emeryana* (Fig. 12), ventroapical process not projecting abruptly from body, and no apical ridge.

Gonostylus. (Fig. 21) Long, narrow; slight uniform taper. *E. imberbiculus* gives evidence of 2 segments (Fig. 21); *E. naegeli* does not. No obvious companion seta in either species, but in *E. naegeli* seta nearest dorsoterminal chaeta slightly longer than nearby setae.

Lancet. Similar to that of *M. bradleyi* (Fig. 16), but longer, less strongly tapered.

Sting. (Fig. 22) SS similar to that of *M. bradleyi*, gently concave, uniformly tapering; outer dorsal wall very thick. VC and SBLB low, their dorsum almost a smooth convex arc. VC as long as SBLB. SB well arched; obliquely truncate. Basal notch low, articular processes not directed ventrad.

In ventral view (see *Pogonomyrmex badius,* Fig. 26, and Hermann and Blum, 1967a) SBLB narrow; sides straight, not convergent.

Furcula. (Fig. 22) Y-shaped; lateral arms not as divergent as those of *M. bradleyi* and *Myrmica emeryana,* dorsal arm somewhat longer.

Hylomyrma
Species examined: *H. versuta* 2 ☿.

Spiracular plate. Like that of *Ephebomyrmex (naegeli, imberbiculus).*

Oblong plate. Similar to OP of *Ephebomyrmex,* but body of posterior arm more truncate apically. FA as in *E. imberbiculus* (Fig. 19), but shorter.

Gonostylus. Like that of *E. naegeli,* but shorter and with more definite companion seta.

Triangular plate and Lancet. Like those of *Ephebomyrmex spp.*

Sting. As in *Ephebomyrmex* (Fig. 22), but SS less concave, nearly straight.

Furcula. Like that of *Ephebomyrmex* (Fig. 22).

Pogonomyrmex (Figs. 23-26)
Species examined: *P. badius* 1 ☿. See also Hermann and Blum (1967a).

Spiracular plate. Similar to that of *Myrmica emeryana* (Fig. 9) in body and dorsal apodeme, but anterior edge is straighter, and body does not extend into medial connection.

Quadrate plate. Shape and size of apodeme and body similar to that of *Manica bradleyi.* Anterodorsal corner as in *Ephebomyrmex spp.* (Fig. 18) and *Hylomyrma versuta;* lobes narrower, but still large.

Oblong plate. (Fig. 23) Posterior arm very much like that of *Ephebomyrmex,* but body ends subterminally. Posterior apodeme does not extend to midline. Anterior apodeme as in *Myrmica* (Fig. 10) long, slender and acute in side view, broadly spatulate transversely. FA with wide, flat base; uniformly tapered; dorsal half gradually curved anteriad (Fig. 23).

Gonostylus. (Fig. 24) Long, slender, evenly tapered to narrow apex. Caudalmost chaeta not terminal, does not have typical dorsoterminal chaeta shape.

Triangular plate. Relatively longer and narrower than in other species of the *Myrmica* group examined, apical processes are rather short and blunt for the size of the plate.

Lancet. (Fig. 25) Long, slender, well sclerotized. Dorsal ridge well developed on the posterior half; ventral ridge widens near end and bears a row of very large barbs. Barbs larger than in *Amblyopone pallipes,* but fewer and more closely spaced. Second valve small but moderately well sclerotized.

Sting. (Fig. 26) Three parts of sting well differentiated; similar to sting of *M. emeryana* (Fig. 13), but dorsal profile of SBLB and VC even more distinct. SS long, heavily sclerotized, straight; hemocoel lower than that of *M. emeryana.* SBLB most similar to those of *Ephebomyrmex spp.* (Fig. 22), but with longer anterolateral processes and more oblique SB. Ventral view of sting like that of *Ephebomyrmex.*

Furcula. Most similar to that of *Ephebomyrmex* (Fig. 22) and *Hylomyrma,* but with wider lateral extremities.

Special remarks: The very large barbs on the end of the lancet are probably secondarily enlarged. They increase the likelihood of sting autotomy, which seems to be an adaptation for defense against vertebrates (Hermann, 1971). For *Pogonomyrmex*, seed-raiding by rodents may be the raison d'etre for sting autotomy (W. L. Brown, personal communication).

Myrmica genus group

peripheral genera

Huberia (Figs. 27, 28)
Species examined: *H. striata* 2 ☿.

Spiracular plate. Body ovoid, much like that of *Myrmica emeryana* (Fig. 9), but no medial extension visible in the one, slightly distorted preparation available. Anterior apodeme wide for most of SP length, anterior edge saddle-shaped.

Quadrate plate. (Fig. 27) Shaped much like that of *Manica bradleyi,* but body narrower. Anterodorsal corner with moderate-sized lateral lobe.

Oblong plate. (Fig. 28) Posterior arm similar in shape to that of *M. emeryana* (Fig. 10) and *M. bradleyi,* but narrower and dorsal ridge greatly reduced. Anterior apodeme long and digitate like that of *M. emeryana.* Ventral arm and FA most like those of *M. bradleyi* (Fig. 15). FA spindle-shaped, vertical (Fig. 28); narrow ridge extends far anteriad from dorsal end.

Gonostylus. Shape, sclerotization, and setation similar to that of *M. bradleyi,* but without companion seta.

Triangular plate. Shape much like that of *M. emeryana* (Fig. 12), but apical ridge indistinct.

Lancet. Much like that of *M. bradleyi* (Fig. 16).

Sting. Shape very similar to that of *M. emeryana* (Figs. 13, 14), but more slender. SS lower along its whole length and narrower at its base; VC lower. Also very similar to that of *Podomyrma abdominalis* (Figs. 33, 34).

Furcula. Y-shaped; ends of lateral arms do not curve caudad. In the one specimen available, the upper end of the dorsal arm is broken off, so I cannot tell if it is longer than the lateral arms. It is clearly compressed laterally and spatulate in side view (wider than lateral arms).

Stereomyrmex (Figs. 29-31)
Species examined: *S. horni* 1 ☿ (MCZ).

Spiracular plate. Most like *Pogonomyrmex badius,* but less sclerotized.

Quadrate plate. Except for anterodorsal corner, most like that of *Ephebomyrmex (naegeli, imperbiculus)* (Fig. 18) and *Hylomyrma versuta.* Anterodorsal corner short, acute. Similar also to *Vollenhovia* and *Liomyrmex.*

Oblong plate. Posterior arm slender, uniform in width, apex body rounded. Anterior apodeme wide and broadly rounded, similar to that of *Manica bradleyi* in lateral view, but appears to be transversely narrow (only lateral view preparations available). Good preparation of ventral arm and FA unavailable.

Gonostylus. (Fig. 29) Narrow, uniformly tapering as in *P. badius* (Fig. 24). Dense patch of long setae, unique to this species, on lateral surface. Dorsoterminal chaeta subterminal.

Triangular plate. Similar to that of *Ephebomyrmex*, but shorter, more strongly tapered.

Lancet. Good preparations not available.

Sting. (Figs. 30, 31) SS like that of *Ephebomyrmex* (Fig. 22), but VC and SBLB more developed. VC relatively shorter and higher than SBLB, longer than VC. SB feebly arched, in side view, very low and oblique. In ventral view, there is a marked change in width from base of SS to VC, but VC and SBLB not greatly widened; SBLB sides convergent.

Furcula. (Figs. 30, 31) Y-shaped; lateral arm widely spread, about as long as dorsal arm.

Podomyrma (Figs. 32-34)
Species examined: *P. abdominalis* 1 ☿.

Spiracular plate. Triangular anterior apodeme as in *Myrmica emeryana* (Fig. 9), but located more dorsad, forms anterior edge of dorsal notch as in *Manica bradleyi, Leptothorax spp.*, and *Vollenhovia* cf. *pedestris*. Body subsquare; spiracle central, moderately large.

Quadrate plate. Apodeme somewhat reduced, but plate as a whole quite wide. Anterior and dorsal edges nearly straight. Anterodorsal corner square, no process. Ventral ridge heavy with prominent tubercle on medial surface which must at times strike OP at IV articulation. Additional ventral ridge runs along ventral end of midplate line. Anal arc with anterior knob-like projection on mid-dorsal line. The last 3 characters are unique to this species.

Anal plate. Differs from Myrmicini described above in the following ways: circular in shape (rather than subtriangular); very long setae on posterior half of dorsal surface. Most similar in shape and setation to that of *Daceton armigerum*.

Oblong plate. (Fig. 32) Body of posterior arm widest just caudad of articulation with FA. Long posterior apodemes may meet at midline, but have no dorsal view preparations to prove it. Anterior apodeme long, narrow, cylindrical. Insertion of muscle 17a just anterior to IV tuberculate. FA irregularly sclerotized; basically ovoid base with long, narrow, diffuse dorsal extention. OP most similar to those of *Leptothorax spp.* and *Macromischa* (Fig. 52). Somewhat less similar to OP of *D. armigerum* (Fig. 36), but all differ in shape of FA.

Gonostylus. Very much like that of *Pogonomyrmex badius* (Fig. 24), but dorsoterminal chaeta present (though short and slender); s. basiconica scattered along lateral surface in irregular row. S. basiconica and similar shape also seen in *Leptothorax pergandei* and *D. armigerum*.

Triangular plate. Much as in *M. emeryana* (Fig. 12), including distinct apical ridge.

Lancet. Most like that of *Vollenhovia* cf. *pedestris* (Fig. 24). Similar also to that of *Manica bradleyi* (Fig. 16) and *Huberia striata*, but dorsal lamina much wider than ventral lamina.

Sting. (Figs. 33, 34) Much like that of *H. striata*, but differs in the following ways: SS shorter, SBLB dorsum flat anteriad, basal ridge smaller.

Furcula. (Figs. 33, 34) Very much like its presumed shape in *H. striata*. Similar also to FU of *Liomyrmex* cf. *aurianus* (Figs. 69, 70), but lateral arms do not curve as strongly caudad.

Discussion:

The *Myrmica* genus group is a heterogeneous assemblage of genera. As seen through the sting apparatus, it is not well enough defined to be characterized as a tribe; and although it is heterogeneous, I do not feel it wise at this time to dissect it into smaller genus groups, because my small sample may not be representative. Most genera display a mosaic of primitive and derived characters. I have placed in the *Myrmica* core group those that have the highest concentration of primitive characters. In my opinion, no one genus represents the basal stock of the group or the subfamily.

Characters of the *Myrmica* core group: Spiracular plate (SP) with wide anterior apodeme; posterodorsal lobe present, but small; posterodorsal corner well developed; ridge of medial connection completely reduced. Quadrate plate (QP) with well developed body and apodeme (body emarginate in *Myrmica emeryana*). Anal plate (AP) subtriangular; anal sensilla are marginal setae. Oblong plate (OP) with small subterminal tubercle on posterior arm; ventral arm widest terminad, fulcral arm (FA) not angular. Ventroapical process of triangular plate (TP) wide with broadly rounded end. Lancet (LA) sword-shaped, dorsal and ventral laminae high; 2 valves present; anterior valve not especially reduced or enlarged; barbs present (except in *M. emeryana*), usually multiple. Sting well sclerotized, acute, piercing; sting shaft (SS) upturned, hemocoel well developed, no dorsal flange, campaniform sensilla to tip of SS; internal apophysis well developed but not contributing to dorsum of valve chamber (VC); sting base (SB) moderately arched; anterolateral lobes present; basal notch not strongly arched; sting bulb (SBLB) narrow to only moderately wide. Furcula (FU) free; dorsal arm not longer than lateral arms.

Within the *Myrmica* core group itself there seem to be 2 separate lines. *Ephebomyrmex (imberbiculus, naegeli)* and *Hylomyrma versuta* represent a branch more primitive in SP, QP, TP, and sting morphology. *Manica bradleyi* and *Myrmica emeryana* are more closely related to each other than to *Ephebomyrmex* and *Hylomyrma,* and have more advanced characters. They are linked by similar shape, sclerotization and setation of the GO, LA without a dorsal ridge, and a medial tubercle on the TP. In addition, the shape of the sting is quite different from that of *Ephebomyrmex* and *Hylomyrma. M. bradleyi* may be the more primitive of the three because of the very wide OP, 2 valves and 3 barbs on the lancets, more robust sting and FU.

Pogonomyrmex badius shares most characters with *Ephebomyrmex* and *Hylomyrma.* Note the unique anterodorsal corner of QP; shape of secondary ridge and subterminal tubercle of OP posterior arms; dorsal ridge of AL; shape of FU; similar shapes of FA and GO. The profile of the sting, however, is more clearly differentiated into 3 regions, like that of *Manica* and *Myrmica*. I believe that the SBLB and VC enlargement are convergent with those of *Manica* and

Myrmica; the other characters listed above and other characteristics of the sting indicate its closest affinities are with *Ephebomyrmex* and *Hylomyrma.* The *Myrmica* core group agrees with Emery's (1922) Myrmicini (Table 5), and the grouping of *Ephebomyrmex, Hylomyrma,* and *Pogonomyrmex* is also supported by Kempf (1973a).

Of the peripheral genera of the *Myrmica* genus group, *Huberia striata* is the most closely related to the core genera. Characteristics of the GO, LA and sting link it to *Myrmica emeryana* and *Manica bradleyi,* especially the former because of the large dorsal tubercle on TP, single LA valve, and similar SS and SBLB shape.

Stereomyrmex horni and *Podomyrma abdominalis* have many characters that differ from the *Myrmica* core group, but they can be connected to this genus group more easily than to others. For *S. horni,* the GO shape and setation are probably more similar to that of *P. badius* than any other genus. The sting has a SS like that of *Ephebomyrmex* and VC and SBLB most like that of *P. badius. Stereomyrmex* is traditionally placed in its own tribe. *Podomyrma abdominalis* is very different from all other species in this study. Nearly every sclerite has unique characters. Furthermore, its apparent affinities are with 4 divergent genus groups. Similarities in the SP, OP and GO link *Podomyrma* to the *Leptothorax* group, characteristics of the SP, OP, LA and FU link it to the *Vollenhovia* group, and similarities in the AP, OP and GO link it to *Daceton.* Nevertheless, I place *P. abdominalis* in the *Myrmica* group for now because the sting and FU have their greatest affinity to *H. striata,* the TP has a heavy apical ridge as in *M. emeryana,* and the GO shape and setation are much like *P. badius.* It seems likely that *Podomyrma* arose from the *Myrmica* core group at the same time as *Leptothorax, Daceton* and *Vollenhovia,* but diverged independently. The *Podomyrma* sting apparatus has little in common with those of other members of Emery's Myrmecinini: *Pristomyrmex* (Figs. 218-222), *Acanthomyrmex* (Fig. 157), *Lordomyrma* (Figs. 128-129) and *Atopomyrmex* (Figs. 215-217). See also the *Pristomyrmex* discussion.

Tribe Dacetini

Daceton (Figs. 35-38)
Species examined: *D. armigerum* 2 ☿.

Spiracular plate. (Fig. 35) Rectangular, slightly wider dorsad than ventrad. Spiracle in center of plate. Dorsal notch wide, V-shaped.

Quadrate plate. Anterior ridge wide, well sclerotized ventrad but absent dorsad. Dorsal edge convex; anterodorsal corner broadly rounded, not prominent or abruptly protruding from anterior edge. Apodeme reduced in width.

Anal plate. Large, densely covered with setae. The few s. basiconica and tiny s. chaetica are not marginal.

Oblong plate. (Fig. 36) Dorsal ridge wide and shaped like those of *Manica bradleyi* and *Myrmica emeryana.* Body of posterior arm subtriangular, much as in *Vollenhovia* (Fig. 72) and *Podomyrma abdominalis* (Fig. 32).

ventral arm short but high, FA shaped much as in *Ephebomyrmex* (Fig. 19), *P. abdominalis,* and the *Leptothorax* group (Fig. 52).

Gonostylus. Long, slender, evenly tapered, well sclerotized. Long, slender setae densely and uniformly cover distal two-thirds; very small s. chaetica are scattered between setae, mostly at anterior end of patch. Similar also to that of *P. abdominalis,* but without hint of 2 segments, and s. basiconica are few and very small.

Triangular plate. Body very slender, abruptly narrowed below apical process, and very much like that of *Macromischa sallei,* but ventroapical process long and narrow.

Lancet. Long, slender, straight; all but low dorsal lamina heavily sclerotized. Unique to this species are 6-8 campaniform sensilla on terminal quarter. Distal pair of valves almost as large and well sclerotized as proximal pair.

Sting. (Figs. 37, 38) Very long and slender. SS long, straight, evenly tapered to acute tip. VC and SBLB most like those of *Ephebomyrmex;* long, low, and narrow; their dorsum a smooth convex arc. SB with a thin lip extending from dorsal edge anterolateral processes very long. SBLB narrow in ventral view, sides abruptly convergent anteriad.

Furcula. (Figs. 37, 38) Y-shaped.

Special remarks: The sting is very long relative to the size of the individual (Appendix A, column 41).

Orectognathus (Figs. 39-40)
Species examined: *O. sarasini* 1 ☿.

Spiracular plate. Rectangular, spiracle in center of plate. Similar to those of *Daceton armigerum* (Fig. 35) and *Neostruma metopia.*

Quadrate plate. Dorsal edge flat; anterodorsal corner narrow, prominent. Similar to that of *Basiceros singularis* (Fig. 44). Rest of plate poorly preserved.

Oblong plate. Quite similar to that of *B. singularis* (Fig. 45), but posterior apodeme shorter and acute, FA better defined and rod-like as in *Tetramorium* (Fig. 59).

Gonostylus. Like that of *B. singularis* (Fig. 46) only shorter.

Triangular plate. Apical processes prominent, body evenly tapered to base.

Lancet. Much like that of *Leptothorax* (Fig. 54).

Sting. (Figs. 39, 40) SS much like that of *Leptothorax pergandei* but shorter. VC very low; at its anterior end the inner and outer dorsal walls are separated by a large transverse ridge. SBLB also low, narrow; in ventral view, sides only slightly convergent, anterolateral corners prominent.

Furcula. (Figs. 39, 40) Slender, Y-shaped.

Neostruma (Figs. 41-42)
Species examined: *N. metopia* 1 ☿.

Spiracular plate. Rectangular, spiracle in center of plate; similar to *Daceton armigerum* (Fig. 35) and *Orectognathus sarasini.*

Quadrate plate. Similar to that of *Eurhopalothrix speciosa* but anterodorsal corner more abruptly produced. As far as I can tell also similar to *O. sarasini.*

Oblong plate. Most like that of *E. speciosa;* body and dorsal ridge of posterior arm narrow; anterior apodeme digitate; ventral arm short and wide. FA different; with short bulbous base and long, narrow, well defined dorsal part.

Gonostylus. Shaped like that of *Basiceros singularis* (Fig. 46) but shorter, sensilla in evenly spaced row as in *O. sarasini* and some GO of *B. singularis.*

Triangular plate. Similar to that of *E. speciosa* but body longer. Medial tubercle long and hammate.

Lancet. Like that of *O. sarasini* and *E. speciosa.*

Sting. (Figs. 41, 42) SS more tapered in proximal half, as in *O. sarasini* (Fig. 39). Profile of VC and SBLB distinct from base of SS. Inner dorsal wall of VC only grazing outer dorsal wall. SBLB convex, slightly concave anteriad. SB very narrow and truncate in ventral view.

Furcula. (Figs. 41, 42) T-shaped, lateral arms very short, not extending over side of SBLB; dorsal arm wide in side view.

Discussion:

See Basicerotini discussion.

Tribe Basicerotini

Basiceros (Figs. 43-49)
Species examined: *B. singularis* 3 ☿ (MCZ).

Spiracular plate. (Fig. 43) Much like that of *Myrmica emeryana* (Fig. 9) in shape and sclerotization of body and apodeme.

Quadrate plate. (Fig. 44) Dorsal and anterior edges straight; anterodorsal corner prominent, digitate; narrow lateral lobe present. Plate gradually reduced ventrad, especially apodeme.

Oblong plate. (Fig. 45) Body and dorsal apodeme of posterior arm narrow; posterior apodeme bulbous. Ventral arm short, wide; FA well sclerotized, but poorly outlined.

Gonostylus. (Fig. 46) Long, slender, well sclerotized, smoothly tapered to fine point. Few short sensilla evenly spaced along distal half of lateral surface on some GO (Fig. 46); in others (often on same sting apparatus) sensilla more clumped because middle 2 setae are closer together.

Triangular plate. Unmodified except for long narrow dorsal tubercle arising abruptly from plate, much as in *Myrmica emeryana* (Fig. 12).

Lancet. Much as in *Vollenhovia* cf. *pedestris* (Fig. 74). Dorsal lamina weaker than in *Orectognathus sarasini* or *Leptothorax* (Fig. 54).

Sting. (Figs. 47, 48) Long, slender, slightly curved ventrad. SS evenly tapered; VC and SBLB low, not abruptly arising from base of SS. SB low, deeply notched. Note also size and shape of associated glands (Fig. 49).

Furcula. (Figs. 47, 48) T-shaped, extremities of lateral arms extend over sides of SBLB only slightly, if at all.

Eurhopalothrix (Figs. 50-51)
Species examined: *E. speciosa* 2 ☿.

Spiracular plate. Body short, sub-rectangular; anterior apodeme rectangular. Spiracle near the reduced posterodorsal corner.

Quadrate plate. Similar to that of *Basiceros singularis* (Fig. 44), but anterodorsal corner more tapered, body of plate narrower, and dorsal edge gently convex.

Oblong plate. Much like that of *B. singularis* (Fig. 45) but dorsal ridge of posterior arm wider caudad, and posterior apodeme not as prominent or bulbous.

Gonostylus. Shape and sclerotization much like that of *B. singularis* and *Orectognathus sarasini,* but sensilla not evenly spaced; anterior setae clumped.

Triangular plate. Ventroapical process long and narrow; body short, rapidly tapered.

Lancet. Like that of *O. sarasini,* but longer.

Sting. (Figs. 50, 51) Similar to that of *B. singularis,* but differs in the following ways: sting straight, SBLB dorsum more convex, anterolateral processes fused mesad.

Furcula. (Figs. 50, 51) T-shaped, with extremities of lateral arms clearly dipping ventrad over sides of SBLB.

Octostruma

Species examined: *O. balzani* 2 ☿.

Spiracular plate. Body sub-rectangular, narrowest dorsad; apodeme very large, hemispherical; spiracle nearest posterodorsal corner. Most similar to *Eurhopalothrix speciosa* and *Basiceros singularis* (Fig. 43).

Quadrate plate. Shape and sclerotization of body and apodeme most similar to those of *Neostruma metopia* but anterodorsal corner more abruptly produced.

Oblong plate. Quite similar to that of *E. speciosa,* but dorsal ridge wider caudad.

Gonostylus. Shape and sclerotization as in *B. singularis* (Fig. 46) and other dacetines examined. Sensilla clumped as in *E. speciosa.*

Triangular plate. Similar to those of *N. metopia* and *E. speciosa.*

Lancet. Most like that of *N. metopia;* shorter than in *E. speciosa.*

Sting. Differs from that of *B. singularis* (Figs. 47, 48) only in having a more convex SBLB dorsum (like that of *N. metopia,* Fig. 41) and fused anterolateral processes (like *E. speciosa,* Figs. 50, 51).

Furcula. Lateral arm like those of *E. speciosa* (Figs. 50, 51), dorsal arm as in *N. metopia* (Fig. 41).

Discussion of Dacetini and Basicerotini:

The sting apparatus of *Daceton armigerum* is very different from that of the other dacetines and basicerotines examined here. It is far more primitive, and is related to the *Myrmica* group because of the following characters: SP with dorsal notch; OP with wide dorsal ridge, and short, abrupt subterminal tubercle; FA triangular (cf. *Epheboryrmex*); AP large, well defined, with 3 types of sensilla; GO with many long setae (cf. *Pogonomyrmex badius*); LA with numerous barbs and campaniform sensilla; sting hemocoel well developed, VC and SB height not reduced; FU Y-shaped, lateral arms long.

Of the remaining genera, the representatives of the Basicerotini are the most similar with respect to the sting apparatus. *Basiceros singularis, Eurhopalothrix speciosa,* and *Octostruma balzani* share the following characters: SP with sub-rectangular body, wide apodeme, spiracle near posterodorsal corner; similar FA shape; SS long, evenly tapered from VC to tip; VC and SBLB not well differentiated in profile; SB with wide flat anterolateral processes; FU T-shaped. In addition, *E. speciosa* and *O. balzani* share the following characters: more similar QP shape, GO with clumped sensilla, SB truncate in ventral view; FU with lateral arms extending over sides of SBLB. *B. singularis* is probably more primitive than the other 2 species because of the dorsal tubercle of the TP, wider QP body, lightly sclerotized lamina of LA and emarginate SB.

The sting apparatuses of *Orectognathus sarasini* and *Neostruma metopia* do not easily align with either *D. armigerum* or with the Basicerotini. *O. sarasini* has SP, SB, and FU shapes most like those of *D. armigerum,* but QP, AP and OP are more like the basicerotines. *N. metopia* is a higher dacetine, but the SB and FU resemble those of advanced basicerotines. According to Brown (1949b, 1959), the Dacetini and Basicerotini are clearly distinct tribes, with some advanced species converging in external morphology. The same thing may be happening with the sting apparatus in these 2 tribes, but it is hard to tell at present. My samples are too few to separate convergence from genuine relatedness. The Wheelers (1954c) show that the larvae of the Dacetini and Basicerotini are distinct on the basis of the body shape, hairs, mandibles, and maxillae. They note also that 3 groups of dacetine larvae are equally distinct: Dacetiti, Orectognathiti, and Epopostrumiti. The *Eurhopalothrix* larvae are closest to those of *Orectognathus* (G. C. and J. Wheeler, 1973).

If as Brown suggests, *Daceton* gave rise to all the higher Dacetini, this tribe originated at the base of the Myrmicinae because of the very primitive sting apparatus of *D. armigerum*. If the Basicerotini had different roots, they probably originated from similar stock. Whether they originated with the dacetines, with the related *Leptothorax* group (see below), or independently from the *Myrmica* core group is unclear from the sting morphology.

Leptothorax genus group

Leptothorax (Figs. 52-56)
Species examined: *L. longispinosus* 10 ☿; *L. pergandei* 2 ☿. See also Foerster (1912: 359, Fig. 3), *L. acervorum* ☿, including musculature.

Spiracular plate. Body rectangular, but nearly square in *L. longispinosus*. Spiracle at midlength, and slightly caudad of center. Dorsal notch wide, V-shaped, poorly defined. SP of *L. pergandei* much like that of *Daceton armigerum,* but dorsal notch narrower.

Quadrate plate. In *L. pergandei,* QP most like that of *Huberia striata* (Fig. 27) and *Megalomyrmex,* but dorsal edge gently convex. In *L. longispinosus* dorsal edge concave, anterodorsal corner long and spine-like, directed anterodorsad. No medial or lateral lobes in either species, but *L. longispinosus* with short lateral ridge near dorsal end.

Oblong plate. (Fig. 52) Most similiar to those of *Daceton armigerum* (Fig. 36) and *Podomyrma abdominalis* (Fig. 32). Body of posterior arm also like that of *Vollenhovia* (Fig. 72) and *Tetramorium* (Fig. 59) FA similar to that of *Ephebomyrmex imberbiculus* (Fig. 19).

Gonostylus. (Fig. 53) Long, slender, evenly tapered, not noticeably dorsoventrally compressed. Most similar in shape and setation to that of *Calyptomyrmex sp.* 1, but 2-segmented. Similar also to that of *Liomyrmex* cf. *aurianus* and *E. imberbiculus* (Fig. 21), but with fewer distal setae and an obvious companion seta. In *L. pergandei,* basal segment with more than twice as many sensilla as in *L. longispinosus,* including 1-2 basiconic sensilla toward distal end.

Triangular plate. In *L. longispinosus* both apical processes reduced to rounded corners, body moderately narrow, curved. In *L. pergandei* only dorsoapical corner reduced, body and ventroapical process both long and narrow, straight; resembles TP of *S. geminata.*

Lancet. (Fig. 54) Long, slender; tip symmetrical, very acute. Dorsal ridge present on caudal half. Most similar in shape and sclerotization to that of *Calyptomyrmex sp.* 1 but anterior valve smaller. Also similar to LA of *Vollenhovia* cf. *pedestris,* but longer, narrower.

Sting. (Figs. 55, 56) Figures show sting of *L. longispinosus.* In *L. pergandei,* dorsal profile of SBLB and VC is a single smooth curve, rather than undulate. In both species sting curves ventrad, SS short, VC and SBLB long (about half sting length), low narrow. SB unarched, narrowly truncate in ventral view. Basal notch long, low. *Leptothorax pergandei* sting resembles that of *Orectognathus sarasini* (Fig. 39), except for SB. Similar to that of the Tetramoriini (Figs. 63, 64) except for lack of SS flange and longer VC. Also resembles sting of *Vollenhovia* and *Liomyrmex* cf. *aurianus* (Figs. 69, 70) but SS shorter, VC and SBLB lower, narrower.

Furcula. (Figs. 55, 56) T-shaped; most like that of Tetramoriini (Figs. 63, 64). Similar also to that of *Solenopsis geminata* (Figs. 83, 84); but lateral arms shorter ,do not whap around SB.

Macromischa

Species examined: *M. sallei* 4 ☿.

Spiracular plate. Like that of *Leptothorax pergandei.*

Quadrate plate. As in *L. pergandei.*

Anal plate. Plate larger, but setation as in *Leptothorax.*

Oblong plate. Very much like that of *L. pergandei* but body of posterior arm does not expand ventrad behind articulation with FA.

Gonostylus. Very much like that of *L. pergandei,* but distal segment shorter and with only 1 or no sensilla in addition to dorsoterminal chaeta and companion seta. Not all GO have basiconic sensilla.

Triangular plate. Body like that of *L. pergandei* but ventroapical process shorter and wider.

Lancet. Like that of *Leptothorax.*

Sting. Much like that of *L. longispinosus* (Figs. 55, 56) but VC much longer, and dorsum of SS base flat as in *L. pergandei.*

Furcula. Similar to that of *L. longispinosus,* but dorsal arm wider in side view.

Discussion:

The *Leptothorax* genus group displays the following mosaic of primitive and advanced characters: Anal setae marginal; QP with prominent posterior and anterior apodemes, body of posterior arm broad, insertion of muscle 17a tuberculate, ventral ridge wide and extending to IV; FA broad, triangular, its anterior edge most heavily ridged; GO long, slender, evenly tapered, 2 segments present, but not sharply outlined, companion seta present, few additional sensilla on distal segment, not dorsoventrally compressed; LA long, slender, symmetrical, apex acute, dorsal ridge present, valves not reduced or enlarged; campaniform sensilla on SS reach nearly to tip; VC and SBLB long, low, narrow; SB not arched, truncate in ventral view; FU with very short lateral arms and much longer, spatulate dorsal arm.

This characterization contains similarities with members of the *Myrmica* genus group, *Vollenhovia* group, Dacetini, and Basicerotini. The straight SS, low truncate SB, and the T-shaped FU make the *Leptothorax* group more advanced than the *Myrmica* group. But the more primitive nature of the OP, fulcral arm, and the low, narrow VC and SBLB separates *Leptothorax* and *Macromischa* from the *Vollenhovia* group, and allies them to the Dacetini, Basicerotini, and Tetramoriini. In addition, SP and OP structure is much like that of *Daceton armigerum*. Whether the *Leptothorax* group originated from a common ancestor with *Daceton* or whether it arose separately from the *Myrmica* core group cannot be determined from this study. See also Tetramoriini discussion.

Tribe Tetramoriini

Tetramorium (Figs. 57-66)
Species examined: *T. grassii* 4 ☿; *T. caespitum* 2 ☿; *T. pacificum* 2 ☿; *T.* cf. *insolens* group 2 ☿ (MCZ); *T. spinosum* (formerly in *Xiphomyrmex;* B. Bolton in prep.) 5 ☿; *T. tenuicrine* (formerly in *Xiphomyrmex,* B. Bolton; in prep.) 2 ☿. See also Foerster (1912: 358, Fig. 2) *T. caespitum* ☿, including musclature.

Spiracular plate. (Fig. 57) Body sub-restangular, dorsal end narrower than ventral end, much as in SP of *Solenopsis geminata* (Fig. 78), *Chelaner sp.* 1, *Megalomyrmex,* and *Calyptomyrmex sp.* 1. Apodeme varies in size, but large and semilunar in all species examined. Strong ridges present on dorsal and ventral edges of SP in some species; all degrees of reduction seen.

Quadrate plate. (Fig. 58) Apodeme large, its posterior margin very convex; body reduced in width, but with well defined, often ridged posterior edge. Anterior edge straight, or nearly so; dorsal edge convex, with narrow lateral lobe. Anterodorsal corner long and hamate in most (shorter in *T. grassii* and *T. tenuicrine*). In *T. grassii* body narrower than figured; wider than figured in *T.* cf. *insolens.* QP similar to that of *S. geminata* except for size of medial and lateral lobes, also similar to that of *Vollenhovia,* but apodeme slightly narrower ventrad.

Anal plate. Very poorly sclerotized, its presence usually indicated only by presence of anal setae.

Oblong plate. (Fig. 59) Dorsal ridge of posterior arm very wide but acute at tip; weakly sclerotized, nearly perpendicular to body (in preparations, often flattened into same plane as body, either dorsad above it as shown in Fig. 59 or ventrad onto body). Subterminal tubercle broadly rounded. Body of arm wide, varying from broadly lunate (Fig. 59) to sub-rectangular (*T. pacificum*). Body of posterior arm always widest just caudad of articulation with FA. Same trait also seen in *Leptothorax, Daceton armigerum, Vollenhovia* and *Podomyrma abdominalis*. Ventral ridge always present but varies from a heavy ridge running from IV to tip of posterior arm (*T. caespitum*), to a lightly sclerotized region only around articulation with FA (*T.* cf. *insolens*). This ridge also present in *Leptothorax* group. In most species, anterior apodeme has wide base and tapers evenly to a subacute apex when viewed from the side. Seen from above, the apodeme is actually transversely spatulate. In these species a diffuse sclerotized ridge extends from the base of the anterior apodeme toward the PI (Fig. 58). In *T. pacificum* and *T. tenuicrine* the apodeme is more digitate, cylindrical when viewed from above, and no ridge extends from its base. Ventral arm short; FA long, straight, well defined, rod-like.

Gonostylus. (Figs. 60, 61) Very short, wide, blunt, with microtrichiae covering anteroventral quarter; notch on terminal end. There is much variation among species, in setation segmentation (Appendix A) and notch size and shape. Sensilla may be greatly reduced in number and size (*T. tenuicrine, T. spinosum*). Terminal notch is manifest on lateral surface in *T. caespitum* (Fig. 60), but only a pocket in end of GO in all others (*e.g.*, Fig. 61). It is hardly visible in *T. spinosum*. Shape and setation could be derived by shortening of *Ephebomyrmex imberbiculus* type of GO (Fig. 21).

Triangular plate. Varies considerably in shape between species, but basically with body and ventroapical process short and wide. TP of some species (*T.* cf. *insolens, T. spinosum, T. tenuicrine*) bear a strong resemblance to that of *Vollenhovia* cf. *pedestris*.

Lancet. (Fig. 62) *T. grassii* much like that of *Leptothorax* (Fig. 54) and *Macromischa sallei*. In all others, top of LA spinelike due to a more sudden convergence of groove and ventral ridge, and reduction of dorsal lamina (Fig. 62).

Sting. (Figs. 63-66) The most primitive sting is that of *T. grassii* (Figs. 63, 64) and it bears a strong resemblance to that of the *Leptothorax* genus group (Figs. 55, 56), particularly *L. pergandei*. SS straight, evenly tapered to acute apex. A large laterally compressed pyriform flange arises subterminally as an outpocketing of the hemocoel and outerdorsal wall. VC and SBLB low and narrow; their dorsum evenly convey; SBLB dorsum slightly concave anteriad. Sting naturally curved ventrad at level of VC. Basal notch low. Articular processes not strongly directed ventrad. SB in ventral view truncate.

Other *Tetramorium spp.* examined here very similar to *T. grassii* in shape of anterior half of sting, but vary in morphology of end of SS. In those species, hemocoel not reduced toward apex, and on each side of flange is a flat lobe that has its broadest surface caudad (Figs. 65, 66). Shape of lobe varies among these species; median flange pennant-shaped in *T. pacificum* (Fig. 65), *T. caespitum,* and *T.* cf. *insolens*. Neck wider in these species, and finger-like extensions of hemocoel project into flange. Median flange spatulate in *T. spinosum* and *T. tenuicrine,* and more constricted basad, as in *T. grassii.*

Furcula. (Figs. 63, 64) T-shaped as in *Leptothorax* genus group (Figs. 55, 56). Extremities of lateral arms do not extend over sides of SBLB.

Special remarks: See *Triglyphothrix.*

Triglyphothrix
Species examined: *T. lanuginosa* 2 ☿.

Spiracular plate. As in *Tetramorium spp.* (Fig. 57).

Quadrate plate. As in *Tetramorium spp.* (Fig. 58). Anterodorsal corner short.

Oblong plate. As in *Tetramorium* (Fig. 59). Body of posterior arm the narrower, sub-rectangular type. Ventral ridge complete from IV to tip of arm. Anterior apodeme with wide base, and sclerotized ridge extending to PI.

Gonostylus. Most like that of *Tetramorium caespitum* (Fig. 60), but with fewer sensilla on each segment, and terminal notch wider.

Triangular plate. Like those of *Tetramorium spp.*, particularly *T.* cf. *insolens*, *T. spinosum*, and *T. tenuicrine*.

Lancet. Apex spine-like as in all *Tetramorium* except *T. grassii* (Fig. 62).

Sting. Like those of *T. pacificum*, *T. caespitum*, and *T.* cf. *insolens*. Flange pennant-shaped; and flanked by lateral lobes (Figs. 65, 66).

Furcula. Like those of *Tetramorium spp.* (Figs. 63, 64).

Special remarks: Unlike all other ants in this study, the aculeus in these genera has a well developed dorsal flange, but nevertheless retains piercing ability. For that reason the end of the sting shaft and lancets have a unique morphology, for which there may be unique behavioral correlates.

Discussion:

Tetramorium and *Triglyphothrix* cannot be distinguished on the basis of the sting apparatus. Together these 2 genera are distinct enough to represent a separate tribe. The characters that distinguish them are: SP with large lunate apodeme; QP with large apodeme and body reduced in width, but with distinct posterior edge; unique shape of OP, including a very deep PI; GO short, wide, blunt, with no companion seta; SS with prominent stalked flange.

The ancestor to the Tetramoriini probably originated nearest the *Leptothorax* group because of similarities in shape of the sting, FU and LA. The shape of the OP posterior arm also links this tribe to *Vollenhovia, Daceton armigerum,* and *Podemyrma abdominalis.* The unique GO results from a reduction in length rather than in setation and segmentation as in the *Leptothorax* group, *Vollenhovia* group, Dacetini, and Basicerotini; but it could very well have an origin close to these other groups. Bolton (1976: 289) also believes that the Tetramoriini are closely related to the Leptothoracini and Myrmicini.

Vollenhovia genus group

Liomyrmex (Figs. 67-70)
Species examined: *L.* cf. *aurianus* (Nangagete, Flores) 2 ☿ (MCZ).

Spiracular plate. Shape including anterior apodeme nearly square. Anterior apodeme no more heavily sclerotized than body.

Quadrate plate. Well developed; ventral end of body much wider than dorsal end; dorsal edge convex. Anterodorsal corner short and acute. Lateral lobe present, not enlarged.

Oblong plate. (Fig. 67) Dorsal ridge narrow anteriad and gradually wider caudad; caudal end broadly rounded and may project slightly beyond body. Body of posterior arm narrow anteriad, gradually narrowed caudad. Anterior apodeme short, broadly rounded, with arched lateral ridge along its dorsal edge. FA poorly defined dorsad; slightly inclined caudad.

Gonostylus. Long, gently and evenly tapered; no sharp transition between segments either in taper or sclerotization. Distal segment about one-third length of proximal segment. Sensilla of proximal segment short, mostly chaetiform; arranged in 2 rows along ventrolateral edge. Entire lateral surface of distal segment covered with long slender setae, all ventral to dorsoterminal chaeta, most distad of it. GO resembles that of *Ephebomyrmex imberbiculus* (Fig. 21).

Triangular plate. (Fig. 68) Short, thick-bodied, ventroapical process wide in lateral view.

Lancet. Long, straight; dorsal lamina wider than ventral lamina. Groove closely parallels ventral ridge for nearly half of LA length, but remains distinct to apex. Groove upturned at end. Barbs reduced, but slightly larger than in most myrmicines except *Pogonomyrmex badius* and *Daceton armigerum*.

Sting. (Figs. 69, 70) SS heavily sclerotized; long, straight, narrower than deep. VC though large, not markedly distinct in profile from base of SS. SBLB dorsum gently convex caudad, but slightly concave anteriad. Sting shown in Fig. 69 probably slightly flexed ventrad due to heating in lactophenol (see *Vollenhovia*). SB profile subacute, slightly arched in anterior view. Basal notch like that of *Myrmica emeryana*, wide but not greatly arched. In ventral view, SBLB not greatly widened; its sides slightly convex and convergent. Sting quite similar to that of *Stereomyrmex horni* (Fig. 30), but SS straight and SBLB longer. Also resembles sting of *Myrmica emeryana* (Fig. 13) and *Huberia striata*.

Furcula. (Figs. 69, 70) Y-shaped, with lateral arms slender and curved at their ends. Well developed dorsal arm is expanded longitudinally.

Special remarks: The sting of *Liomyrmex* is quite long for a myrmicine ant (Appendix A, column 41).

Vollenhovia (Figs. 71-77)
Species examined: *V. sp.* 1 (Lafoa-Canala, New Caledonia) 5 ♀ (MCZ); *V.* cf. *pedestris* (Wolasi, Celebes) 2 ☿ (MCZ).

Spiracular plate. (Fig. 71) Sub-rectangular, about twice as long dorsoventrally as anteroposteriorly. Anterior apodeme narrow in *V.* cf. *pedestris*, but in *V. sp.* 1 (Fig. 71) an abrupt hornlike projection arises midlength. Spiracle in center of plate. Dorsal notch deep and wide in *V.* cf. *pedestris*, small in species 1. Medial connection nearly complete.

Quadrate plate. In *V. sp.* 1 much like that of *Solenopsis geminata* (Fig. 78), but body about twice as wide. In *V.* cf. *pedestris*, apodeme narrower; anterodorsal corner shorter and like that of *Liomyrmex* cf. *aurianus*.

Oblong plate. (Fig. 72) Poor preparations from species 1. In species 2, dorsal ridge of posterior arm widest midlength, acute terminad, weakly sclerotized (often folded against body in preparations, as in *Tetramorium spp.*). Body of posterior arm very narrow above FA, widest midlength; truncate terminad. Anterior apodeme very short as in *L.* cf. *aurianus* (Fig. 67), but without crescent-shaped ridge; anterior corner of OP sclerotized below anterior apodeme and dorsal ridge. FA similar to that of *L.* cf. *aurianus* but more uniformly sclerotized, less angular, vertical. Ventral arm short, wide.

Gonostylus. (Fig. 73) Basal segment wide and triangular in lateral view; with patch of sensilla terminad on ventral edge. Distal segment narrow, cylindrical; dorsoterminal chaeta at about midlength; setae on ventrolateral edge.

Triangular plate. Short and wide in side view, similar to that of *L.* cf. *aurianus,* but exact shape varies among species.

Lancet. (Fig. 74) Long, straight, and slender. Similar to that of *L.* cf. *aurianus* in shape, but groove and ventral ridge merge subterminally.

Sting. (Figs. 75, 76, 77) Much like that of *L.* cf. *aurianus* (Figs. 69, 70) especially in species 2, where SB is less arched. SBLB dorsum not concave anteriad in either species. Sting tends to flex at level of VC when heated too long in lactophenol. Flexed specimens look more like Fig. 69 of *L.* cf. *aurianus*. An unflexed specimen of species 1 is shown in Fig. 75 for comparison.

Furcula. (Fig. 77) Y-shaped in *V.* cf. *pedestris;* dorsal arm a little shorter than lateral arms. FU of *V. sp.* 1 more T-shaped, and lateral arms wrap around sides of narrow SB. Neither with wide dorsal arm as in *L.* cf. *aurianus.*

Discussion:

Liomyrmex cf. *aurianus* and the *Vollenhovia spp.* differ in some rather striking ways, particularly in shape and setation of the gonostylus, shape of the dorsal ridge and body of the posterior arm of the QP, and shape of the SBLB dorsum. Nevertheless, I feel the following similarities link those representatives of the 3 genera: SP rectangular; QP with large convex apodeme; PI reduced; FA angular; GO with 2 segments indicated by sclerotization; TP short, wide; LA straight, with dorsal lamina wider than ventral lamina, groove and ventral ridge parallel for substantial distance; SS straight; VC large, but not abruptly rising above base of SS; SB shallowly arched, truncate in ventral view, with small anterolateral processes in *L.* cf. *aurianus* and *Vollenhovia sp.* 2. For further similarities see comparisons with the *Myrmica* genus group (Table 3) and the *Solenopsis* genus group (Table 4). The important characters that link and separate the *Vollenhovia* and *Myrmica* genus groups are given in Table 3. I believe the differences are sufficient to separate the 2 groups. The similar characters tend to be plesiomorphic, or characters that link *Liomyrmex* cf. *aurianus* to *Stereomyrmex* and *Podomyrma,* peripheral genera in the *Myrmica* group. See also the *Podomyrma* discussion. *Liomyrmex* is probably more primitive than *Vollenhovia* with respect to the sting apparatus, and it has more ties to the *Ephebomyrmex* branch of the *Myrmica* group than to the *Myrmica, Manica* branch.

TABLE 3

Comparison of sting apparatus characters in *Vollenhovia* and *Myrmica* genus groups. More important characters are asterisked.

Similarities

*1. SP with posterodorsal lobe.
2. QP shape, especially in *Liomyrmex*, similar to that of *Stereomyrmex horni.*
3. Dorsal ridge of OP wide and rounded caudad, with low rounded subterminal tubercle in *Liomyrmex, Ephebomyrmex* and *Pogonomyrmex.*
*4. GO 2-segmented.
*5. Shape and setation of GO similar in *Liomyrmex* and *E. imberbiculus.*
6. LA with 2 pair of valves.
7. Valves of LA neither reduced nor enlarged.
8. Shape of VC and SBLB of *Liomyrmex* quite similar to those of *Stereomyrmex.*
9. Shape of FU of *Vollenhovia* group similar to that of *Stereomyrmex.*

Differences

*1. SP in *Myrmica* group more oval or round, in *Vollenhovia* group rectangular or square.
2. PI missing, or nearly so, in *Vollenhovia* group; present in *Myrmica* group.
3. Dorsal ridge of OP narrower in *Vollenhovia* group.
*4. FA shape quite different.
*5. In *Vollenhovia* group. LA straight, dorsal lamina higher than ventral, groove parallels ventral ridge for half of LA. *Myrmica* group differs in all respects.
6. Hemocoel of SS not as large in *Vollenhovia* group as in most of *Myrmica* group (except *Stereomyrmex* and *Podomyrma*).
*7. SS straight in *Vollenhovia* group, curved dorsad in *Myrmica* group.
8. VC larger in *Vollenhovia* group.

Solenopsis genus group
core genera

Solenopsis (Figs. 78-84)
Species examined: *S. geminata* 4 ♀. See also Foerster (1912: 359, Fig. 4) *S. fugax* ♀, including musculature.

Spiracular plate. (Fig. 78) Body sub-rectangular, dorsal end narrower; intermediate in width between those of *Liomyrmex* cf. *aurianus* and *Vollenhovia* (Fig. 71). Anterior apodeme large, triangular.

Quadrate plate. (Fig. 79) Similar to those of the *Vollenhovia spp.* Body reduced to narrow band, but plate as a whole quite wide. Dorsal edge convex, with moderately large medial and lateral lobes. Anterodorsal corner prominent, hamate in lateral view.

Oblong plate. (Fig. 80) Dorsal ridge on posterior arm very wide as in *Myrmica* group, but body narrower. Long, spinelike posterior apodemes meet at midline. Anterior apodeme short, wide, apex broadly rounded; with lateral projection. Insertion of muscle 17a, just anterior to IV, tuberculate. FA well defined, slightly bent midlength; basal half only slightly wider than dorsal half; narrow ridge extends anteriad along PI.

Gonostylus. (Fig. 81) Triangular in dorsal view, very slender and dorsoventrally compressed in side view. Anterior sensillar patch on ventrolateral surface, terminal sensilla on dorsolateral surface.

Triangular plate. (Fig. 82) Body slender, apical processes prominent.

Lancet. Similar to that of *Vollenhovia* cf. *pedestris* (Fig. 74), but longer, more slender. Dorsal lamina at widest point about twice as wide as ventral lamina. Groove closely parallels ventral ridge for about two-thirds of LA, but remains distinct to very end. Barbs about same size as in *L.* cf. *aurianus*.

Sting. (Figs. 83, 84) SS long, straight, deeper than wide. VC deeper than that of *L.* cf. *aurianus* (Fig. 69) and *Vollenhovia* (Fig. 75) and very distinct from base of SS in profile. As in *Liomyrmex* cf. *aurianus* (Fig. 69) SBLB dorsum convex caudad but concave anteriad. SB profile subacute. Basal notch a low arch. Articular processes directed slightly ventrad. In ventral view (Fig. 84) SBLB not very wide: sides slightly convex, strongly convergent; SB narrow, truncate. In *S. fugax* ventral view, SBLB does not strongly taper anteriad (Foerster, 1912: 359).

Furcula. (Figs. 83, 84) Intermediate between T- and Y-shaped. Lateral arms perpendicular to dorsal arm mesad, but lateral extremities curve ventrad and caudad. Dorsal arm subequal to lateral arms in length, laterally flattened; spatulate in side view.

Oxyepoecus (Figs. 85-88)
Species examined: *O. rastratus* 4 ☿.

Spiracular plate. Body subtriangular due to reduced posterodorsal corner; anterior apodeme narrow except for abrupt horn-like projection as in *Vollenhovia sp.* 1 (Fig. 71) from ventral end. Medial connection nearly complete.

Quadrate plate. (Fig. 85) Body not as reduced as in *Solenopsis germinata* and the *Vollenhovia spp.;* apodeme narrower. Dorsal edge nearly flat, with small lateral lobe and wider medial lobe. Anterodorsal corner prominent as in *S. geminata* and *Vollenhovia sp.* 1.

Oblong plate. (Fig. 86) Dorsal ridge of posterior arm narrower than in *S. geminata,* uniform in width; subterminal tubercle low, not prominent. Body narrow, uniform in width, truncate terminad. Posterior arms do not meet at midline. Anterior apodeme cylindrical, digitate, longer than in *Vollenhovia* (Fig. 72), but similar to that of *Chelaner sp.* 1 (Fig. 89). Ventral arm and FA like that of *S. geminata* (Fig. 80) and *Rogeria inermis* but PI does not penetrate as deeply.

Gonostylus. Like that of *Solenopsis* (Fig. 81).

Triangular plate. Similar to that of *Solenopsis* in size and shape, body slightly wider in side view.

Lancet. Similar to that of *Liomyrmex* cf. *aurianus* (Fig. 69); also much like that of *S. geminata* but not as long and slender.

Sting. (Figs. 87, 88) SS like that of *Solenopsis,* but shorter. VC deep and well defined in profile as in *Solenopsis,* but shorter. SBLB dorsum convex throughout; SB short and vertical in side view. In ventral view, SBLB moderately wide; sides only slightly convex and gently convergent. SB wide and truncate in this view; anterolateral processes reduced to low rounded corners.

Furcula. (Figs. 87, 88) Similar to FU of *Solenopsis* (Figs. 83, 84), but lateral arms longer. Similar to that of *Liomyrmex* (Figs. 69, 70)), except for shape of dorsal arm.

Chelaner (Figs. 89-90)
Species examined: *C. sp.* 1 (New Caledonia) 5 ☿ (MCZ).

Spiracular plate. Body sub-rectangular, similar in proportions, shape and in position of spiracle to that of *Solenopsis geminata*, but apodeme semilunar rather than triangular.

Quadrate plate. Most similar in shape to that of *Oxyepoecus rastratus*, but dorsal edge convex, and lateral lobe larger than medial lobe; both lobes narrower than in *S. geminata*.

Oblong plate. (Fig. 89) Posterior arm very much like that of *O. rastratus* (Fig. 86), but end of dorsal ridge slightly more drawn out making a short posterior apodeme. Insertion of muscle 17a tuberculate. Anterior apodeme like that of *O. rastratus*. Ventral arm and FA much as in *S. geminata* (Fig. 80) but basal half of FA distinctly wider than upper half (Fig. 89).

Gonostylus. Like those of *Solenopsis* (Fig. 81) and *Oxyepoecus*.

Triangular plate. As in *Solenopsis* (Fig. 82), *Chelaner*, *Rogeria inermis*, and *Megalomyrmex* (?) *sp.* 1.

Lancet. Like that of *Oxyepoecus*.

Sting. (Fig. 90) SS like that of *Solenopsis*. VC well developed and distinct, but not as long as in *Solenopsis*, nor as high as in *O. rastratus*. SBLB and SB very much like that of *O. rastratus* both in profile and ventral view.

Furcula. (Fig. 90) Like that of *O. rastratus*, but dorsal arm narrower in lateral view.

Rogeria *(in part)* (Fig. 91)
Species examined: *R. inermis* 2 ☿.

Spiracular plate. Ventral half of plate much like that of the *Vollenhovia spp.* (Fig. 71), without apodemal prominence. Dorsal half has smoothly curved rather than angular posterior edge (but not as reduced as in *Oxypoecus rastratus*), and anterior apodeme is gently dilated near dorsal end.

Quadrate plate. Similar in shape to that of *Chelaner sp.* 1 and *O. rastratus* (Fig. 85) but body extends more ventrad, below IV. Dorsal edge convex, medial and lateral lobes of moderate size, anterodorsal corner prominent and hamate.

Oblong plate. Posterior arm and anterior apodeme most like those of *O. rastratus*. Ventral arm and FA similar to those of *Solenopsis geminata* (Fig. 80), but FA not angular. Similar to OP of *O. rastratus* (Fig. 86), but postincision penetrates deeper.

Gonostylus. Shape not well preserved in any preparations, but seems to be wider in dorsal view than lateral view, and evenly tapered caudad from a rather wide base. Sensilla present on posterior half of ventral surface; most at midlength, some at tip, and a few connect the two patches. Dorsoterminal chaeta and companion seta on dorsal surface at very end of sclerotized portion of GO. Shape and setation seem to be similar to those of *Monomorium (Holcomyrmex) scabriceps* (Fig. 93) and «*Rogeria*» *spp.* 1 and 2 (*stigmatica* group).

Triangular plate. Similar to that of *Solenopsis* (Fig. 82) *Chelaner*, *Monomorium minimum*, and *Megalomyrmex* (?) *sp.* 1.

Lancet. Like that of *O. rastratus* and *Chelaner sp.* 1, but dorsal lamina slightly higher.

Sting. (Fig. 91) SS not as deep as that of *Solenopsis*, *Oxyepoecus*, and *Chelaner;* only slightly higher than wide. Terminal end looks swollen in profile due to low dorsal flange. Absence of enlarged hemocoel at this point possibly a result of lateral compression of outer dorsal wall to produce flange. VC and SBLB almost identical to those of *Oxyepoecus* (Figs. 87, 88) in both lateral and ventral views.

Furcula. (Fig. 90) Like that of *Chelaner sp.* 1 (Figs. 87, 88).

Solenopsis genus group
peripheral genera

«Rogeria» (*stigmatica* group). (Fig. 92).
Species examined: *R. sp.* 1, (Solomon Islands) 2 ☿ (MCZ); *R. sp.* 2 (Fiji) 2 ☿ (MCZ). These may be the same species.

Spiracular plate. Posterior portion of body greatly reduced, so that the remainder is nearly circular. Spiracle very large, occupies entire upper half of body. Enlarged spiracles also found in *Crematogaster*, *Cyphoidris spinosus*, *Myrmicaria* (Fig. 170), *Trigonogaster recurvispinosa*, *Cephalotes atratus*, and *Ocymyrmex* cf. *arnoldi*, but they do not rival those of *«Rogeria» spp.* 1 and 2. Shape of SP also differs.

Quadrate plate. Apodeme narrow, triangular (widest dorsad) like that of *Veromessor andrei;* but body very wide, convex behind. Anterodorsal corner rounded, not prominent, medial and lateral lobes reduced to prominent lateral and medial spines on apex.

Oblong plate. Dorsal ridge and body of posterior arm long, narrow, uniform in width, much like those of *Acanthomyrmex* cf. *notabilis* and *Aphaenogaster;* arms gradually curve mesad and meet at midline. Anterior apodeme short, acute to subacute. Ventral arm not clearly seen; looks similar to that of *Rogeria inermis* but FA seems oblique.

Gonostylus. Similar in shape and setation to those of *Rogeria inermis* and *Monomorium scabriceps* (Fig. 93).

Triangular plate. Body moderately wide, sub-rectangular; narrow stalk leading to ramus at right angle to body. Ventroapical process long, slender, acute. TP much like that of *Myrmecina graminicola* (Fig. 237).

Lancet. Weakly sclerotized; shape like that of *Pheidole sp.* 2 (Fig. 152). Similar also to that of *Megalomyrmex* (?) *sp.* 1, but narrower.

Sting. (Fig. 92) SS blunt, weakly sclerotized. Dorsal profile of sting nearly flat, except at anterior end. SB profile gently convex, inclined anteriad. SBLB and basal notch wide. This SBLB and SB profile similar to that of *Pheidole morrisi*, *Pheidole sp.* 3 minors, *Atopomyrmex mocquerysi* (Fig. 216), *Zacryptocerus* (Fig. 200), and *Cephalotes atratus* (Fig. 190). In ventral view, sting like that of *Acanthomyrmex* cf. *notabilis.*

Furcula. (Fig. 92) Broad U-shaped arch, nearly uniform in diameter. Like that of *Pheidole* and *Promeranoplus* groups.

Monomorium (Holcomyrmex) (Figs. 93-95)
Species examined: *M. scabriceps* 1 major ☿, 3 media ☿, 9 minor ☿.

Spiracular plate. Much like that of *Vollenhovia* cf. *pedestris.* Rectangular in minors; more nearly square in majors.

Quadrate plate. Dorsal edge straight or concave, anterodorsal corner short and subacute, quite thick transversely, but without definite medial or lateral lobes. Body divided into dorsal and ventral sclerites by a membranous area much like that in *Myrmica emeryana,* but deeper and wider. Apodeme reduced and would be smaller in area than body if body were not excavated.

Oblong plate. Posterior arm and anterior apodeme most similar to those of *Monomorium minimum.* Also similar to those of *Oxyepoecus rastratus* (Fig. 86), but body of posterior arm narrower distad. Ventral arm short and wide; FA much like that of *O. rastratus* ventrad, but reduced in width and ill-defined dorsad, and not reaching to posterior arm.

Gonostylus. (Fig. 93) Dorsoventrally flattened; in dorsal view widest near base, rapidly tapering to acute apex. Dorsoterminal chaeta and companion seta on dorsal surface of distal end; all other sensilla on ventral surface and clustered into 2 groups. As worker size increases, more sensilla are added to each group; in majors (Fig. 93) the gap between the two groups becomes less distinct. GO may be similar to that of *Rogeria inermis.*

Triangular plate. Similar to that of *Solenopsis* (Fig. 82), but body wider.

Lancet. Long and slender with a very acute apex. Dorsal lamina low; at widest point it equals height of ventral lamina. Groove and ventral ridge subparallel, and distinct to very end. Moderately well sclerotized in majors, more lightly sclerotized in minors.

Sting. (Figs. 94, 95) SS acute, deeper than wide; not heavily sclerotized in minors, but seems quite strong in majors. VC very reduced in all dimesions. SBLB large, its dorsum very convex. SB profile straight, slightly oblique. Basal notch situate. Sting length increases with worker size, but it is negatively allometric to pronotal width (slope of allometric regression line: 0.57, $n = 10$). Ratio of SBLB width to sting length seems to decrease with increased sting length (from shortest to longest sting: 0.28, 0.875, 0.27, 0.26, 0.25, 0.27, 0.26, 0.25, 0.23). That is, major workers have relatively longer, narrower stings.

Furcula. (Figs. 94, 95) Lateral arms meet in very broad angle. Dorsal arm reduced to low rounded tubercle.

Monomorium (Monomorium) (Figs. 96-100)
Species examined: *M. minimum* 4 ☿.

Spiracular plate. (Fig. 96) Posterodorsal corner greatly reduced to broad convex arc; spiracle near posterodorsal edge. Anterior and ventral edges straight, and form an acute angle. Prominent anteroventral corner does not articulate with TP.

Quadrate plate. Well developed. Similar to that of *Solenopsis geminata* (Fig. 79), but with body about twice as wide, its posterior edge more convex; and anterodorsal corner slightly longer with narrower lobes.

Oblong plate. Anterior apodeme and posterior arm similar to that of *Monomorium scabriceps* and *Oxyepoecus rastratus.* Ridge of posterior arm moderately wide, but acute distad; body narrow, evenly tapered caudad. Anterior apodeme long, digitate, cylindrical; apex curves laterad. Ventral arm short, FA with short oval base and longer, narrower dorsal part, similar to FA of *Chelaner sp.* 1 (Fig. 89) and *Vollenhovia* cf. *pedestris* (Fig. 72), but somewhat more oblique.

Gonostylus. (Fig. 97) Dorsoventrally compressed, very short and blunt; sensilla relatively very large. This shape and setation would probably result if GO of *Solenopsis* (Fig. 81) *Oxyepoecus, Chelaner,* or *Megalomyrmex* (?) *sp.* 1 (Fig. 102) were greatly reduced in length, and their sensilla remained their original size.

Triangular plate. Similar to that of *Solenopsis* (Fig. 82), *Chelaner, Rogeria inermis,* and *Megalomyrmex* (?) *sp.* 1.

Lancet. (Fig. 98) Weakly sclerotized, subacute, spatulate. Groove and ventral lamina closely parallel for most of LA length. Groove ends subterminad.

Sting. (Fig. 99) Shape and sclerotization very similar to that of *Megalomyrmex* (?) *sp.* 1, but SBLB longer and distal end of SS hemocoel not enlarged. Note also size of associated poison and Dufour's glands relative to sting length (Fig. 100).

Furcula. (Fig. 99) Slender, arc shaped, lateral extremities not enlarged or curved caudad.

Undetermined genus (cf. **Monomorium** or **Megalomyrmex**) (Figs. 101-104).[1]

Species examined: *Megalomyrmex* (?) *sp.* 1 (Kerala State, India) 1 ☿ (MCZ).

Spiracular plate. Sub-rectangular, like body of SP of *Solenopsis geminata* (Fig. 78); similar also to SP of *Megalomyrmex* near *incisus* and *M. modestus,* but with even narrower anterior apodeme.

Quadrate plate. Similar to that of *Megalomyrmex spp.* Moderately wide apodeme and body. Dorsal edge straight; dorsal half of anterior edge gently curved anteriad and meeting dorsal edge in broad subacute anterodorsal corner. No medial or lateral lobes.

Oblong plate. (Fig. 101) Posterior arm and anterior apodeme similar to those of *Chelaner sp.* 1. Length of posterior apodeme not clear from preparations at hand, may be longer than that of *Chelaner sp.* 1. Ventral arm (Fig. 101) narrow; FA short, not even half the length of posterior edge, narrow, lightly sclerotized, oblique.

Gonostylus. (Fig. 102) In dorsal view, similar to GO of *Solenopsis* (Fig. 81), *Chelaner,* and *Oxyepoecus* except for shape of base. Proximal sensilla on ventrolateral surface. Dorsoterminal chaeta and companion seta on dorsal surface.

Triangular plate. Body slender, tapering. Apical processes prominent, slender in side view. Similar to those of *Solenopsis, Chelaner,* and *Rogeria inermis.*

Lancet. Weakly sclerotized. Similar in shape to LA of *Rogeria inermis;* tip slightly spatulate near apex, but not as acutely pointed. Similar to *Monomorium minimum,* but tip more acute and groove extends to very end.

Sting. (Figs. 103, 104) Very similar to sting of *Chelaner sp.* 1 (Fig. 90), but SS much shorter and not as heavily sclerotized. In ventral view, VC wider than in *Chelaner,* but width of SBLB about the same. No anterolateral processes, but definite corners. Basal ridge weak laterad, absent mesad.

Furcula. (Figs. 103, 104) Y-shaped with low dorsal arm. Slender, lateral extremities only slightly enlarged.

Megalomyrmex (Figs. 105-111)

Species examined: *M.* near *incisus* (Heredia, Costa Rica) 2 ☿ (MCZ); *M. modestus* 1 ☿.

Spiracular plate. Shape of body like that of *Solenopsis geminata* (Fig. 78), but posterodorsal corner slightly reduced and spiracle closer to posterodorsal edge. Anterior apodeme not as wide as in *Chelaner* or *Solenopsis.*

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[1] Could be either genus from external morphology, but palpi (3,2) and malpighian tubules (5) are typical of *Megalomyrmex.*

Quadrate plate. Shape and size of body and apodeme much as in *Megalomyrmex* (?) *sp.* 1, but anterodorsal corner of *M.* near *incisus* projects more abruptly from anterior edge. No medial or lateral lobes. Apodeme shape also similar to that of *Huberia striata* (Fig. 27).

Oblong plate. (Figs. 105, 106) Posterior arm similar to those of *Chelaner sp.* 1 and *Rogeria inermis.* Subterminal tubercle low and inconspicuous. Anterior apodeme very narrow in side view, wider transversely. Ventral arm of *M.* near *incisus* (Fig. 105) short, wide; FA with bulbous base and long narrow dorsal part as in *Chelaner sp.* 1 (Fig. 89) and *Monomorium minimum;* but FA not angled, and dorsal part more clearly defined. FA of *M. modestus* (Fig. 106) wider and less well defined.

Gonostylus. Like that of *Solenopsis* (Fig. 81), *Chelaner,* and *Oxyepoecus* in shape and setation.

Triangular plate. Unmodified; most similar to those of *Chelaner* and *Rogeria inermis.*

Lancet. (Figs. 107, 108) In *M.* near *incisus* moderately wide with bulb-like terminal end. Groove closely parallels weak ventral ridge for most of length of LA. In *M. modestus* LA wider subterminally, but subacute and not spatulate terminally. Groove ends farther subterminad.

Sting. (Figs. 109, 110, 111) SS long and very narrow. Ridges on which lancets glide end near base of SS; sides of SS beyond that point low and very lightly sclerotized. Shape of end of SS differs between the two species (see Figs. 109, 110). VC very low but clearly present. SBLB dorsum very convex; SB only slightly arched in *M. modestus,* and seems unarched in *M.* near *incisus.* In ventral view (Fig. 111), SBLB not greatly expanded; sides convex, convergent anteriad; anterolateral processes long.

Furcula. (Figs. 109, 111) Y-shaped. In *M.* near *incisus* dorsal arm spatulate, only slightly longer than lateral arms. In *M. modestus* dorsal arm longer and more slender.

Special remarks: The aculeus in this genus seems particularly specialized for holding a large droplet of fluid between the two large spatulate lancets and the weak, flexible sting shaft. I have seen museum specimens holding dried droplets in that manner. It would be interesting to know 1) if this is an adaptation for defense, if so 2) is its use similar to that of *Crematogaster* and *Monomorium* (see conclusions), and 3) does this genus draw trails with its aculeus, as do most myrmicines, or has it evolved a different method as has *Crematogaster.*

Calyptomyrmex (Figs. 112-115)
Species examined: *C. sp.* 1 (New Caledonia, Chapeau Gendarme) 2 ☿ (MCZ).

Spiracular plate. Body sub-rectangular, shaped much like that of *Solenopsis geminata* (Fig. 78), *Chelaner sp.* 1, and *Megalomyrmex* (?) *sp.* 1. Apodeme much like that of *S. geminata* but ventral edge inclined dorsad.

Quadrate plate. Nearly identical to that of *Monomorium minimum,* but more heavily sclerotized.

Oblong plate. (Fig. 112) Dorsal ridge and anetrior apodeme very similar to those of *Liomyrmex* cf. *aurianus* (Fig. 67). Body of posterior arm narrower anteriad and truncate caudad, more like that of *Oxyepoecus rastratus* (Fig. 86). Ventral arm similar to those of *Chelaner sp.* 1, (Fig. 89) and *Rogeria inermis;* FA with well defined spindle-shaped basal half, and dorsal half broadly and diffusely sclerotized (Fig. 112).

Gonostylus. (Fig. 113) Most like that of *Leptothorax longispinosus* (Fig. 53), but single segmented. Also similar to that of *Liomyrmex* cf. *aurianus,* but with distal setae fewer, finer, more confined to ventral surface, and with companion seta present. Less similar to *Solenopsis* type of GO (Fig. 81); not dorsoventrally compressed; dorsiterminal chaeta and seta not isolated.

Triangular plate. Much like that of *L.* cf. *aurianus* (Fig. 68) but ventroapical processes prominent, more slender.

Lancet. Long slender; tip symmetrically acute; dorsal ridge present on caudad half. Most similar to that of *Leptothorax* (Fig. 54), but anterior valve smaller. Similar also to that of *Vollenhovia* (Fig. 74), but narrower and with dorsal ridge. Barb very small.

Sting. (Figs. 114, 115) SS long, slender, slightly curved dorsad; distal half almost as wide as high. VC intermediate in shape and size between those of *Vollenhovia* (Fig. 75) and *Oxyepoecus rastratus* (Fig. 87). SBLB and SB as in *Vollenhovia* cf. *pedestris*. In ventral view (Fig. 115) sides of SBLB more convergent than in *O. rastratus* (Fig. 88), *Chelaner sp.* 1 and *Rogeria inermis;* more similar to that of *V.* cf. *pedestris* (Fig. 77).

Furcula. (Figs. 114, 115) Like that of *Chelaner sp.* 1 (Figs. 89, 90) and *Rogeria inermis* (Fig. 91).

Wasmannia (Figs. 116-119)

Species examined: *W. auropunctata* 2 ☿; *W. sp.* 2 (Heredia, Costa Rica) 2 ☿ (MCZ).

Spiracular plate. Sub-rectangular in *W. sp.* 2 and very similar in shape and proportions to bodies of *Solenopsis peminata* (Fig. 78), *Chelaner sp.* 1, *Megalomyrmex* (?) *sp.* 1, *Megalomyrmex spp.* and *Calyptomyrmex sp.* 1. SP of *W. auropunctata* is more trapezoidal; posterior edge shorter than anterior edge. Medial connection completed only by very fine ridge in *W. auropunctata;* only slightly separated in *W. sp.* 2.

Quadrate plate. Most similar to QP of *Vollenhovia sp.* 1. Also similar to that of *Calyptomyrmex sp.* 1, but body narrower and anterodorsal corner not quite as long. Appears to have moderate-sized medial lobe and no lateral lobe.

Oblong plate. (Fig. 116) Posterior arm very narrow, especially body which is much like that of *Oxyepoecus rastratus* (Fig. 86) in shape. Dorsal ridge does not extend beyond body, but nevertheless is drawn out and very nearly meets opposite dorsal ridge at midline, much as in *S. geminata*. Anterior apodeme also similar to that of *S. geminata* (Fig. 80). Ventral arm short and wide as in *S. geminata, Chelaner sp.* 1, *Rogeria inermis, Megalomyrmex spp.* and *Calyptomyrmex sp.* 1 (Fig. 112); but FA shape very different, more comparable to that of *Manica bradleyi* (Fig. 15), *Huberia striata* (Fig. 28), and *Lordomyrma caledonica* and *L. tortuosa.*

Gonostylus. (Fig. 117) Most similar in shape, setation and sclerotization to that of *Huberia striata,* especially in *W. auropunctata* which lacks a distinct gap between terminal and proximal sensilla. *W. sp.* 2 also similar to *Calyptomyrmex sp.* 1, but shorter, without fine distal setae. It is also not very different from GO of *Solenopsis* (Fig. 81) and related genera, including *Monomorium scabriceps* (Fig. 93).

Triangular plate. Unmodified; similar to that of *Calyptomyrmex sp.* 1.

Lancet. Similar to that of *Calyptomyrmex sp.* 1, but even narrower and more needle-like. Barb very small, only barely visible at 1000X.

Sting. (Figs. 118, 119) Very similar to that of *Calyptomyrmex sp.* 1, but SS wider than deep, and SBLB less convex anteriad.

Furcula. (Figs. 118, 119) Like those of *Calyptomyrmex sp.* 1 (Figs. 114, 115), *Chelaner sp.* 1 (Fig. 90), and *Rogeria inermis* (Fig. 91).

Discussion:

From this comparison of the sting apparatus (see Table 4), *Liomyrmex* and *Vollenhovia* seem properly separated by Ettershank (1966) from the other genera described above. Although there are many similarities, I believe the differences are important, and reflect a divergence of the *Solenopsis* group (my combination) from the more primitive condition seen in *Liomyrmex* cf. *aurianus* and *Vollenhovia* cf. *pedestris* and *sp.* 1.

Within the *Solenopsis* core group, the sting apparatuses of *Oxyepoecus rastratus* and *Chelaner sp.* 1 are most similar in nearly all sclerites, especially the sting and GO. They differ in length of SS, width of dorsal arm of FU, and shape of FA and SP. *Rogeria inermis* seems closely related to these two, especially because of the shape of the sting and OP, but the GO shape differs strikingly. The sting apparatus of *Solenopsis geminata* is also similar to that of *Oxyepoecus, Chelaner,* and *Rogeria inermis,* but the anterior end of the SBLB is concave, and the SB is narrow and not arched. Foerster (1912) does not describe the sting of *Solenopsis fugax* in lateral view, but its ventral SB shape is wide like those of *Chelaner* and

TABLE 4

Comparison of the sting apparatus characters of the *Vollenhovia* and *Solenopsis* genus groups.

Similarities

1. SP rectangular; shape similar in *Liomyrmex* cf. *aurianus, Chelaner sp.* 1, and in *Vollenhovia spp., Rogeria inermis, Monomorium* (?) *sp.* 1, and *Megalomyrmex spp.*
2. QP well developed, apodeme wide, shape similar in *Vollenhovia* and *Solenopsis.*
3. FA shape similar in *Vollenhovia, Chelaner sp.* 1, and *Monomorium minimum,* others not greatly different.
4. GO sensilla bimodal (except in *Wasmannia auropunctata*).
5. LA shape similar (except in *M. minimum* and *Megalomyrmex*).
6. SS deeper than wide (except in *Wasmannia spp.*).
7. Similar range of variation in SB shape; *S. geminata* similar to *Vollenhovia sp.* 2, SB of *Vollenhovia sp.* 1 much like that of *Calyptomyrmex sp.* 1 and *Wasmannia spp.*

Differences

1. *Vollenhovia* group with dorsal notch and posterodorsal lobe on SP, *Solenopsis* group lacking both (except in *Monomorium scabriceps* and *Wasmannia spp.*).
2. Shape of OP, especially posterior arm, anterior apodeme, and PI different.
3. GO of *Vollenhovia* group 2-segmented, not dorsoventrally flattened, no companion seta; in *Solenopsis* group 1-segmented, flattened, with companion seta.
4. Body of TP narrower in *Solenopsis* group.

5. LA with 2 valves in *Vollenhovia* group, first valve not enlarged; 1 enlarged valve in *Solenopsis* group (not enlarged in *M. scabriceps* and *Megalomyrmex spp.*).
6. Hemocoel of SS better developed but without terminal enlargement in *Vollenhovia* group; in *Solenopsis* group hemocoel generally more reduced (except in *M. scabriceps*), and with slight terminal enlargement (except in *R. inermis* and *M. minimum*).
7. *Vollenhovia* group with camponiform sensilla to tip of SS; only in basal half in *Solenopsis* group.
8. VC larger in *Solenopsis* group (except in *Megalomyrmex spp.* and *M. scabriceps*).
9. SBLB generally more convex in *Solenopsis* group.

Oxyepoecus. Of the peripheral genera, *Monomorium minimum* and *Megalomyrmex* (?) *sp.* 1 are the most similar; particularly in the shape of the sting. *Megalomyrmex* (?) *sp.* 1 has a less derived GO and LA structure, and may in turn be related to *Chelaner sp.* 1 because of similarity in shape of the GO, OP and sting. The SP and QP look similar to those of the definite *Megalomyrmex* species, but other sclerites have little similarity. *Monomorium scabriceps* does not seem more closely related to *M. minimum* than to any other species. There is a marked difference in shape of SP, QP, GO, FA, and sting; and the highly reduced dorsal arm of the FU is about their only special similarity. Arnold (1915: 200, 211) mentions that *Monomorium albopilosum* and *Monomorium tchelichofi* (both subgenus *Xeromyrmex* in Emery, 1922) sting freely. It may be that most of the genus is like *M. scabriceps* in sting morphology and *M. minimum* is an aberrant reduced form. The GO of *M. scabriceps* is more similar to that of *R. inermis*. *Megalomyrmex* also stands alone because of the unique shape of its sting and lancets. It may be most closely related to *S. geminata* because of the very weakly arched SB and the shape of the FU.

The sting apparatuses of «*Rogeria*» *spp.* 1 and 2 (*stigmatica* group) in some ways look like an intermediate stage in reduction between that of *Aphaenogaster/Messor* and *Pheidole*, particularly in LA, SBLB, and FU shape, but other characters are quite different: spines on anterodorsal corner of QP; shape of OP ventral arm; TP shape; SP spiracle size. Either these species arose in the *Pheidole* group and developed some unique characters, or originated in some other group and converged. I suspect the latter occurred. In external morphology, «*Rogeria*» (*stigmatica* group) is very much like the New World *Rogeria*. If the *stigmatica* group of species belongs in *Rogeria*, their sting apparatus has been highly modified so that it now shows little similarity (except for GO) with at least one New World species, *Rogeria inermis*.

Calyptomyrmex sp. 1, *Wasmannia auropunctata*, and *W. sp.* 2 differ from the *Vollenhovia* group in many of the same ways that the rest of the *Solenopsis* group does, but they are on a distinct branch (or branches) within the group because that is where their closest similarity lies, and because I believe it is premature at this time to name a separate group for them. The unique FA of the *Wasmannia spp.* separates them from *Calyptomyrmex sp.* 1, the *Solenopsis*, *Leptothorax*, and *Vollenhovia* groups, and the Tetramoriini, but links them more closely to *Manica bradleyi*, *Huberia striata*, *Lordomyrma tortuosa* and *L. caledonica*. This genus probably split off the ancestral myrmicine stock before the rest of the *Solenopsis* group, and near the divergence of the *Promeranoplus* group.

Wheeler and Wheeler (1960) divide the larvae of Emery's Solenopsidini into 6 groups: 1) *Vollenhovia;* 2) *Monomorium* except *antarcticum*, *Solenopsis*, *Anergates*, and *Megalomyrmex;* 3) *Monomorium antarcticum* (= *Chelaner*, Ettershank, 1966); 4) *Allomerus;* 5) *Liomyrmex;* and 6) *Xeromyrmex*. This differs from affinities seen in the sting apparatus. Ettershank (1966) organizes these yet another way. He synonymizes *Holcomyrmex* with *Monomorium*, and puts *Chelaner* and *Monomorium* in the same genus group. *Solenopsis* and *Oxyepoecus* are placed in a separate group, and *Megalomyrmex* in yet another (accompanied by *Tranopelta* — see description below). Kempf (1974) in revising *Oxyepoecus* says that that genus «... bears a great resemblance with *Solenopsis*...», but «... the male sex makes the placement of *Oxyepoecus* in the '*Solenopsis* Genus Group' (Ettershank 1966: 134) somewhat doubtful, in as much as the existing similarities rather point towards *Megalomyrmex* (and *Nothidris*)...».

The only certainty in all of this is that the generic relationships are still unresolved (except that *Vollenhovia* and *Liomyrmex* seem to be separate from other «solenopsidine» genera). These descriptions of the sting apparatus do not resolve the dilemma; but may help in the future as more are described.

Promeranoplus genus group

Promeranoplus (Figs. 120-127)
Species examined: *P. rouxi* 2 ☿ (MCZ); *P. sp.* 2 (New Caledonia) 2 ♀, 2 ☿ (MCZ).

Spiracular plate. (Fig. 120) Large, rectangular; spiracle in ventral half of plate.

Quadrate plate. (Fig. 121) Well developed with long, digitate anterodorsal corner. In *P. rouxi* apodeme gradually reduced in width dorsad and anterodorsal corner projects anterodorsad.

Anal plate. Very poorly sclerotized.

Oblong plate. (Fig. 122) Most similar to those of *Manica bradleyi* (Fig. 15), and *Huberia striata* (Fig. 28), especially in low anterior apodeme with crescent-shaped ridge, and FA shape. FA of *P. rouxi* slightly wider.

Gonostylus. (Fig. 123) Segments weakly sclerotized but distinctly outlined; separated by oblique membranous band. In *P. sp.* 2 distal segment wider proximad, more strongly tapered, end not truncate. Single seta on distal segment larger in *P. sp.* 2. GO bears some resemblance to that of *Vollenhovia*

(Fig. 72), except for oblique intersegmental membrane. Both types probably derived from GO like that of *Myrmica emeryana* (Fig. 11), *M. bradleyi*, and *H. striata*. GO of *P. sp.* 2 especially resembles that of *H. striata*, but distal segment longer and with reduced setation.

Triangular plate. Body short, wide; much like that of *Liomyrmex* cf. *aurianus* (Fig. 68). Lateral surface bears U-shaped ridge connecting rather short apical processes.

Lancet. (Fig. 124) Groove widens caudad, its heavily sclerotized ventral edge merges with ventral ridge of LA; rest of groove gradually blends into dorsal lamina. LA in profile evenly tapered in distal half.

Sting. (Figs. 125, 126, 127) SS straight, wedge-shaped in both directions, in *P. sp.* 2 sides abruptly reduced in height near distal end. VC profile not distinct from base of SS; dorsal profile of sting nearly flat in *P. sp.* 2. SBLB short and high; height greater than in more primitive myrmicines due to greater arch of SB rather than expansion of basal notch. Internal ridge of SB attenuates mesad. Although the SS is highly midified, VC and SBLB bear resemblance to those of *M. bradleyi*, in both views.

Furcula. (Figs. 125, 127) U-shaped; lateral extremities slightly enlarged, curved caudad; much as in *M. emeryana* and *M. bradleyi* (Fig. 17).

Special remarks: The interesting characteristics of the aculeus of these species are the unique coneiform shape of the sting and the weak but acute lancets. The sting shaft is also somewhat shortened relative to the size of the ant (Appendix A, column 41).

Prodicroaspis

Species examined: *P. sarasini* 2 ☿ (MCZ).

Spiracular plate. Like that of *Promeranoplus rouxi* (Fig. 120).

Quadrate plate. Much like that of *Promeranoplus sp.* 2, but anterodorsal corner shorter.

Oblong plate. Shape and sclerotization of all parts like that of *P. sp.* 2 (Fig. 122).

Gonostylus. Like that of *P. rouxi.*

Triangular plate. Similar to that of *P. rouxi* and *P. sp.* 2.

Lancet. Like that of *P. rouxi.*

Sting. Dorsal profile like that of *P. rouxi* (Fig. 125), but anterior end of SBLB flat instead of convex; more like that of *P. sp.* 2. Apex of SS intermediate in shape between that of *P. rouxi* and *P. sp.* 2 (Figs. 125, 126). SB shorter, basal notch wider than in both *Promeranoplus* species, but ventral view of sting similar (Fig. 127).

Furcula. V-shaped; less sclerotized mesad.

Special remarks: See *Promeranoplus.*

Lordomyrma (Figs. 128-129)

Species examined: *L. caledonica* 3 ☿; *L. tortuosa* (*L. tortuosa* was originally placed in *Rogeria*, but it is generally considered to belong to *Lordomyrma*, see Brown, 1953: 4) 1 ☿ (MCZ).

Spiracular plate. Much like that of *Promeranoplus* (*sp.* 2, *rouxi*) (Fig. 120).

Quadrate plate. Shape of apodeme and anterodorsal corner in *L. caledonica* most like that of *P. rouxi*, but in *L. tortuosa* more like that of *P. sp.* 2. (Fig. 121).

Oblong plate. Much like that of *Promeranoplus*, but posterior apodeme shorter; anterior apodeme narrower, digitate without crescent ridge; FA more like that of *Wasmannia sp.* 2 (Fig. 116).

Gonostylus. Like that of *P. sp.* 2.

Triangular plate. Body narrower than in *Promeranoplus;* lateral ridge more broadly U-shaped in *L. tortuosa*, absent in *L. caledonica*. Medial tubercle of *L. caledonica* long, hamate.

Lancet. In *L. caledonica*, more primitive than that of *Promeranoplus;* same cuneiform shape, but groove remains strong, closely parallel to ventral ridge, but distinct do apex. In *L. tortuosa*, LA reduced as in *Promeranoplus*, but end drawn out into weakly sclerotized filamentous point.

Sting. (Figs. 128, 129) In *L. tortuosa*, dorsal profile like that of *P. rouxi* (Fig. 125); apex of SS even more reduced than in *P. sp.* 2; SB and basal notch as in *Prodicroaspis sarasini*. Sting of *L. caledonica* (Figs. 128, 129) differs markedly; not cuneiform in ventral view; SS shorter, its sides flattened dorsoventrally into a terminal spatulate structure; SBLB longer, its dorsal profile flatter; SB vertical in profile.

Furcula. (Fig. 128) Like those of *P. rouxi* and *P. sarasini*, but lateral extremities not as strongly curved caudad.

Special remarks: See *Promeranoplus*.

Discussion:

The comparative morphology of the sting apparatus supports the belief (based on external morphology) *Promeranoplus*, *Prodicroaspis*, and *Lordomyrma* are all very similar, possibly congeneric. Definition of generic boundaries awaits a revision of this group that includes the many new species awaiting description in museum collections today (W. L. Brown, personal communication).

The species examined here share the following sting apparatus characters: SP rectangular, with well developed posterodorsal lobe, anterior apodeme reduced to narrow ridge; AP highly reduced; OP with postincision not penetrating body of plate; FA distinct, wide midlength with narrow base; GO shape (as described for *Promeranoplus*), TP with distinct medial tubercle; LA shaped similar (as described for *Promeranoplus*), with 2 valves (second highly reduced); sting cuneiform (less so in *L. caledonica*), hemocoel of SS highly reduced, SB strongly arched; FU without dorsal arm. Although the sting of *L. caledonica* is somewhat aberrant for the group, it is not so different that it outweighs similarities in the rest of the apparatus.

The sting, lancets, and often the QP are highly modified in the *Promeranoplus* genus group, but other parts of the sting apparatus retain primitive characters that link this group to *Manica bradleyi* and *Huberia striata* of the *Myrmica* genus group: posterodorsal lobe on SP; dorsal ridge of OP wide, shape of anterior apodeme in *P. rouxi* and *P. sarasini*, FA shape in *L. caledonica* and *L. tortuosa;* GO shape and sclerotization; TP with medial tubercle, with dorsal tubercle in *P. rouxi* and *P. sarasini;* LA with 2 valves; sting shape similar in *P. rouxi* (Fig. 125) and *M. bradleyi* (Fig. 17).

Some characters, such as the posterodorsal lobe of the SP and shape of OP and GO are similar to those of the *Vollenhovia* genus group. Also the FA of the 2 *Lordomyrma* species closely resembles that of *Wasmannia sp.* 2. I believe these are primitive characters shared by virtue of a common ancestry in the *Myrmica* group, rather than shared derived characters.

Pheidole genus group
core genera

Messor (Figs. 130-139)
Species examined: *M. aciculata* 1 ♀ (MCZ); *M. sp.* 1 (Sanaá, Yemen) 2 major ☿, 5 media ☿, 6 minor ☿. See also Foerster (1912: 361-362, Fig. 7) description of *M. structor* ☿, including musculature.

Spiracular plate. (Fig. 130) Suboval, with anteroventral corner somewhat prolonged. Ventral edge angular in *M. aciculata;* smoothly curved in *M. sp.* 1.

Quadrate plate. (Fig. 131) Subtriangular in *M. aciculata* due to reduction in ventral width of body. Body of *M. sp.* 1 not reduced. Anterior and dorsal edges of apodeme in both species straight; form acute angle. Narrow lateral lobe present. The shape of this corner varies within individuals, and is not determined by caste.

Anal plate. Very poorly sclerotized, its presence indicated primarily by sensilla.

Oblong plate. (Figs. 132, 133) Dorsal ridge and body of posterior arm narrow, uniform in width. Anterior apodeme very long and slender; wider transversely than in profile, but not spatulate. Ventral arm long and narrow; in *M. sp.* 1 subparallel to posterior arm, with rounded end; in *M. aciculata* tapered and truncate (Fig. 133). FA weak, narrow; has no distinct point of articulation with posterior arm.

Gonostylus. (Figs. 134, 135) In ventral view, long, slender, unevenly tapered (Fig. 134). In dorsal view (see *Aphaenogaster,* Fig. 141), sides subparallel, base abruptly expanded laterad. If dorsal and ventral faces flattened into same plane (Fig. 135), GO appears subtriangular. Proximal third of GO less sclerotized than distal two-thirds. Sensilla in general restricted to distal two-thirds.

Triangular plate. (Fig. 136) Long, slender, with abruptly prominent, long, slender ventroapical process. Body evenly tapered in *M. sp.* 1, much longer and only slightly tapered in *M. aciculata.* Dorsal and medial tubercles not prominent in either species, difficult to see; dorsal tubercle somewhat larger in *M. sp.* 1 majors.

Lancet. (Fig. 137) Very lightly sclerotized. Groove ends subterminad as ventral ridge widens and curves dorsad to form acute apex.

Sting. (Figs. 138, 139) SS very low, narrow; its hemocoel very reduced for most of length, and laterally compressed caudad to form low rounded dorsal flange. Sides of SS reduced in height caudad. VC well developed, markedly rising above base of SS. SBLB long, its dorsal profile gently convex. Profile of SB straight, vertical in *M. sp.* 1, inclined slightly caudad in *M. aciculata.* Articular processes wide, directed somewhat ventrad. Basal ridge mesad. Basal notch low, long; rounded anterolateral process low, only slightly closes notch. In ventral view, VC narrow, but SBLB very wide with convex sides. The ratio of SBLB width to sting length remains the same in all castes of *M. sp.* 1. The sting length increases with size of worker, but is negatively allometric when compared with pronotal width (slope of allometric regression line: 0.72, n = 7).

Furcula. (Figs. 138, 139) Broadly U-shaped. Not weaker or narrower mesad; lateral extremities only weakly curved caudad.

Special remarks: See *Aphaenogaster*.

Aphaenogaster (Figs. 140-144)

Species examined: *A. rudis* 4 ☿; *A. phalangium* 6 ☿. See also Foerster (1912: 361-363, Fig. 6) description of *A. subterranea* ☿ and *A. gibbosa* ☿, including musculature.

Spiracular plate. Much like that of *Messor* (Fig. 130), particularly *M. sp.* 1.

Quadrate plate. Much like that of *M. aciculata* (Fig. 131), but apodeme wider in *A. phalangium*, and body even more reduced ventrad (shapes unclear in *A. rudis* preparations). Anterodorsal process long, acute in *A. rudis*, very short in *A. phalangium;* with lateral lobes in both species.

Anal plate. Very lightly sclerotized and detected only by presence of setae.

Oblong plate. (Fig. 140) Much like that of *Messor sp.* 1 (Fig. 132), but body of posterior arm narrower in *A. phalangium,* and FA articulates with posterior arm.

Gonostylus. (Fig. 141) Shape and setation most like that of *M. aciculata* (Fig. 134), but with companion seta. *A. rudis* has 1-2 additional terminal setae. Shape and setation also similar to some members of the *Solenopsis* genus group (Fig. 81), but not as dorsoventrally flattened.

Triangular plate. Much like that of *Messor sp.* 1.

Lancet. Same as in *Messor*.

Sting. (Figs. 142, 143) Very similar to that of *Messor* (Figs. 138, 139), but dorsal lobe higher at expense of sides of SS; SBLB shorter and narrower, its sides not as convex. SB slightly inclined caudad. Note also size of poison gland reservoir and Dufour's gland (Fig. 144).

Furcula. Like that of *Messor* (Figs. 138, 139). In *A. subterranea,* FU retains a small dorsal arm (Foerster, 1912: 361).

Special remarks: The sting apparatuses of *Messor* and *Aphaenogaster* are interesting in several respects — all possibly related to chemical defense (see conclusions). The aculeus has a low flange and weak lancets. The sting base is very enlarged, possibly to accommodate the enlarged poison gland reservoir and Dufour's gland, particularly the latter. In *Aphaenogaster longiceps* the Dufour's gland is actually «... 1-1/4 times as long as the venom reservoir and twice the diameter» (Robertson, 1968). In *Aphaenogaster* and *Messor* the paired sclerites of the sting apparatus (except the gonostyli) have spread apart (from parallel to nearly perpendicular to the midline) and the apparatus is flattened against the end of the gaster.

Chemical defense has never been conclusively demonstrated in *Messor* or *Aphaenogaster.* W. L. Brown has seen an *Aphaenogaster rudis* individual flex its gaster under and aim it at an approaching bethylid wasp. The wasp suddenly retreated without having touched the ant (personal communication). Brown believes that the ant actually sprayed a defensive substance, but diffusion of a volatile component of the venom could also be the mechanism.

Chemical defense has been documented for some *Zacryptocerus* species (Coyle, 1966), which have very similar sting apparatus characteristics (see conclusions).

Veromessor
Species examined: *V. andrei* 3 ☿.

Spiracular plate. Similar to that of *Messor sp.* 1, but dorsal end of body reduced to membrane, making plate shorter and dorsal notch wider, shallower. Spiracle in dorsal half of plate. Plate large relative to size of other sclerites.

Quadrate plate. Anterior and dorsal edges of apodeme nearly straight, and form slightly acute angle as in *Messor* (Fig. 131). Anterodorsal corner narrowly rounded, not prominent, and without medial and lateral lobes. Apodeme much wider dorsad than in *Messor*. Width of body abruptly cut in half at about midlength.

Oblong plate. Dorsal half of plate similar to that of *Messor* (Fig. 132), but posterior arm shorter, body wider and ending abruptly before end of dorsal ridge. Ventral arm and FA like those of *Aphaenogaster rudis* (Fig. 140) and *Acanthomyrmex* cf. *notabilis*.

Gonostylus. Similar to that of *Messor sp.* 1 (Fig. 135), but shorter and with broader base. Also similar in shape and setation to that of the Cephalotini (Figs. 192, 199) particularly *Procryptocerus scabriusculus*.

Triangular plate. As in *Acanthomyrmex* cf. *notabilis;* body short, wide, with thickened apical margin, dorsal and medial tubercles much reduced.

Lancet. Much like that of *Messor* (Fig. 137) and *Aphaenogaster*, but more weakly sclerotized, ventral ridge ends subterminad, and terminal point shorter. Probably in intermediate stage of reduction between *Messor* type and *Pheidole* type (Fig. 152) .

Sting. Very similar to that of *A.* cf. *notabilis* (Fig. 157), but SS evenly tapered to fine point in side view (no flange), sides of SBLB in ventral view more convex as in *Messor* (Fig. 139).

Furcula. Arched, but membranous except for lateral extremities articulating with anterolateral processes of SB.

Special remarks: This sting apparatus is quite reduced in size relative to the size of the ant, and quite wide relative to its length (Appendix A, column 41; G. C. and J. Wheeler, 1965, Fig. 3). According to the Wheelers (1965) *Veromessor lobognathus* bites tenaciously, but cannot sting (although it does exert the sting and make stinging motions with its gaster).

Stenamma (Figs. 145-147)
Species examined: *S. diecki* 1 ☿; *S.* near *manni* 1 ☿ (MCZ).

Spiracular plate. In *S.* near *manni*, body of plate ovoid, only slightly longer than broad. Anteroventral corner not prolonged. Dorsal end of plate reduced as in *Veromessor andrei*. Specimens of *S. diecki* not well preserved.

Quadrate plate. In *S.* near *manni* similar to that of *V. andrei* in shape of body and apodeme, but anterodorsal corner drawn out into a long pollicate process shaped much like that of *Promeranoplus spp.* (Fig. 121). No lateral or medial lobes present. *S. diecki* similar, but body not abruptly reduced. Lateral lobe present on apodeme.

Oblong plate. Dorsal ridge wide, posterior apodeme short, acute. Body of posterior arm narrow (especially in *S. diecki*), truncate. Anterior apodeme long, slender. Ventral arm of *S. diecki* tapered as in *Aphaenogaster rudis* (Fig. 140), but end more rounded. In *S.* near *manni,* ventral arm club-shaped, widest distad. FA of both species narrowly fusiform and curved along edge of arm, not articulating with posterior arm. These OP are composites of shapes found in other species of the *Pheidole* group. They also resemble OP of *Monomorium (Holcomyrmex) scabriceps.*

Gonostylus. Much like that of *Aphaenogaster phalangium* (Fig. 141) in shape and setation. In some indiduals of *S. diecki,* a single seta fills gap in setal pattern.

Triangular plate. Body of TP long, moderately wide, sides slightly curved, nearly parallel. Apical processes short. Similar to TP of *Leptothorax longispinosus.*

Lancet. (Fig. 145) Weak, narrow, ribbon-like; apex tapered, narrowly rounded (end more blunt in *S. diecki*). Groove and ventral ridge closely parallel, both end subterminad. Similar to LA of *Acanthomyrmex* cf. *notabilis* and *V. andrei.*

Sting. (Figs. 146, 147) SS weak, long, slender, blunt. SBLB long, convex. SB inclined caudad in *S.* near *manni,* but in *S. diecki,* more vertical like that of *Messor* (Fig. 138), and with more prominent anterolateral processes. SB profile in *S. diecki* much like those of *Cyphoidris spinosus* (Fig. 161) and *Lachnomyrmex* cf. *scrobiculatus* (Fig. 163). Basal ridge very wide in both *Stenamma* species; similar to those of *Procryptocerus scabriusculus* (Figs. 196, 197), and *Myrmicaria* (Figs. 175, 176). SBLB quite wide in ventral view ,not as wide as in *Messor* (Fig. 138), but wider than in *L.* cf. *scrobiculatus* (Fig. 164).

Furcula. (Figs. 146, 147) Broadly U-shaped, with uniform diameter and sclerotization.

Pheidole (Figs. 148-156)

Species examined: *Ph. morrisi,* 2 major ☿, 10 minor ☿; *Ph. sp.* 1 (*biconstricta* group, Heredia, Costa Rica) 3 minor ☿ (MCZ); *Ph. sp.* 2 (*christopherseni* group, Heredia, Costa Rica) 4 minor ☿ (MCZ); *Ph. sp.* 3 (Boraceia, Brazil) 4 major ☿, 4 minor ☿ (MCZ). See also Foerster (1912: 362-363, Figs. 8 and 9) description of *Ph. pallidula* major and minor ☿, including musculature.

Spiracular plate. (Fig. 148) Triangular due to reduction of posterodorsal corner of plate. Posteroventral corner tuberculate, closely associated with basal end of OP (may articulate with TP). Tubercle short, truncate in *Ph. sp.* 3 majors; long, spine-like in all other individuals examined.

Quadrate plate. (Fig. 148) Those of *Ph. morrisi* majors not well preserved in slide preparations. Apodeme of *Ph. sp.* 1 sub-rectangular, in all others subtriangular with long, spine-like anterodorsal corner (Fig. 148). Majors of *Ph. sp.* 3 and minors of *Ph. sp.* 1 with lateral lobe. Body always gradually in width ventrad, much as in *Messor aciculata* (Fig. 131).

Oblong plate. (Figs. 148, 149) Posterior arm short, dorsal ridge widens caudad. Anterior apodeme moderately long, digitate. Ventral and posterior arms separate in *Ph. sp.* 3 (Fig. 148) and *Ph. morrisi;* FA restricted to distal end. Other species have ventral and posterior arms fused; FA even weaker, horizontal (Fig. 149) QP lenght dimorphic among workers of *Ph. sp.* 3, but does not increase in size at same rate as pronotal width (slope of allometric regression line; 0.85, n = 7).

Gonostylus. (Figs. 150, 151) Shape and setation in *Ph. sp.* 3, *Ph. morrisi*, and *Ph. sp.* 1 like that of *Veromessor andrei* and *Messor sp.* 1 (Fig. 135). GO of *Ph. sp.* 2 very reduced (Fig. 151), but note cluster of long setae around dorsoterminal chaeta, a pattern seen in other *Pheidole spp.* and *Aphaenogaster rudis.*

Triangular plate. (Fig. 148) Body short, slender. Ventroapical process long, narrow.

Lancet. (Fig. 152) Very lightly sclerotized, narrow, blunt. Groove and ventral ridge merge in caudal half, widen at apex.

Sting. (Figs. 153-156) In majors of *Ph. sp.* 3, very much like that of *Messor sp.* 1 (Figs. 138, 139), but without dorsal flange of SS, and SB profile slightly inclined anteriad. Minors of *Ph. sp.* 3 and majors of *Ph. morrisi* also similar, but with much lower VC and slightly lower SB; in profile much like sting of «*Rogeria*» *stigmatica* group (Fig. 92), but dorsum smoothly convex to SB. Minors of other species with even lower VC, and SB narrower in ventral view (Figs. 153, 154). In *Ph. spp.* 1 and 2, anterior end of SBLB pinched in both directions (Figs. 155, 156). The same is true of *Pheidole pallidula* (Foerster, 1912, Fig. 9). Sting length in *Ph. sp.* 3 workers is diphenic and negatively allometric to pronotal width (slope of allometric regression line: 0.68, $n = 5$). SB wider relative to sting length in soldiers of *Ph. sp.* 3 majors 0.35, 0.33; minor 0.27).

Furcula. (Figs. 153-156) In *Ph. sp.* 3 and *Ph. morrisi* majors, a broad, free arch like that of other species in *Pheidole* group. In minor workers, lower (depending on arch of SB), closely appressed to SB, dorsoventrally flattened, less sclerotized mesad than laterad.

Special remarks: The sting apparatus in this genus is very reduced relative to the size of the ant (Appendix A, column 41). Moreover, it is polyphenic in shape and size. The sting shaft is relatively shorter in the soldiers (though larger in absolute size), and the sting bulb is wider relative to sting length. *Pheidole fallax* soldiers have hypertrophied poison gland reservoirs; the minors do not (Law *et al.*, 1965).

Also of interest is the striking difference in gonostylar shape between some species which may be useful in defining species groups.

Discussion:

The characters considered primitive, and used to separate the *Pheidole* core group from other groups, are essentially those of *Messor* and *Aphaenogaster*. Note especially SP without posterodorsal lobe; ventral arm of OP tapered caudad; FA inclined; GO frequently with several terminal setae in addition to dorsoterminal chaeta; LA weak, uniform in height; groove closely parallels ventral ridge, dorsal lamina equal to or higher than ventral lamina; SS slender in both directions, with dorsal flange; SBLB long, wide; SB well arched, basal ridge low, reduced mesad (except *Stenamma*), FU broadly arched, no dorsal arm.

The *Pheidole* group's closest relatives are probably found in a common ancestor with the *Promeranoplus* group. The 2 groups differ in many important ways, but are similar in the following ways: AP very reduced; TP with medial and dorsal tubercles in more primitive members; SS hemocoel very reduced; SBLB long in *Lordomyrma caledonica* and *Pheidole* group, anterior end truncate in profile; SB well arched, with reduced basal ridge; FU strongly arched, dorsal arm lost, or nearly so. GO shape and setal pattern are more similar to those of genera in the *Solenopsis* group.

Within the *Pheidole* core group, *Aphaenogaster* and *Messor* are clearly the most closely related. *Veromessor andrei* is quite similar, but more reduced. Although the sting apparatus of some *Pheidole* species is highly reduced, its primitive condition, seen in the soldiers of some species, clearly links this genus to *Messor* and *Aphaenogaster,* unless some *Messor* or *Aphaenogaster* species have a well developed ridge. In other respects, *Stenamma* is very much like other members of the *Pheidole* core group. It may be on a separate, closely related line; but I am including it with the *Pheidole* core group because it is quite similar, and because it is traditionally placed here (Emery, 1922; Wheeler, 1922). At present, I do not know how important the differences are.

Pheidole genus group
peripheral genera

On the basis of sting apparatus morphology, the following 8 genera cannot yet be placed in any other group described above. They do seem to be closer to the *Pheidole* and *Promeranoplus* groups than to the *Myrmica, Vollenhovia, Solenopsis, Leptothorax* groups, or the Tetramoriini. As the variation in these groups becomes better known our concept of the genus group boundaries may expand, and absorb some of these errant genera. Some may remain distinct.

Acanthomyrmex (Fig. 157)

Species examined: *A.* cf. ***notabilis*** 4 minor ☿ (MCZ).

Spiracular plate. Similar to that of *Messor aciculata,* but shorter, with much wider anterior apodeme, posteroventral corner with short, broadly rounded prominence. The latter probably does not articulate with TP.

Quadrate plate. Apodeme wide, dorsal edge slightly concave, anterior edge gently convex. Anterodorsal corner narrowly rounded in some, with short acute process in others. Body narrow, with broad V-shaped emargination midlength on posterior edge; very lightly sclerotized.

Oblong plate. Posterior arm long, very narrow. Anterior apodeme reduced to subacute corner. Ventral arm and FA like those of *Aphaenogaster* (Fig. 140).

Gonostylus. Similar to that of *A. phalangium* in shape, but narrower, with all terminal sensilla lost. Much like that of *Megalomyrmex* (?) *sp.* 1 (Fig. 102), but without terminal sensilla.

Triangular plate. Body short and wide, weakly sclerotized. Apical margin more heavily sclerotized; ventroapical process prominent, but shorter than in *Messor* (Fig. 136).

Lancet. Short, slender, ribbon-like, very lightly sclerotized, end narrowly rounded. Groove very closely parallels ventral ridge. Additional details not clearly seen.

Sting. (Fig. 157) Much like that of *Messor* (Figs. 138, 139), but VC and SBLB lower, their dorsal profile gently and evenly convex; anterolateral processes do not project anteriad, and not seen in ventral view, nor are SBLB sides as convex.

Furcula. (Fig. 157) Like those of *Aphaenogaster* and *Messor* (Figs. 138, 139), but less arched.

Special remarks: This sting apparatus is quite reduced in size relative to the size of the ant (Appendix A, column 41).

Discussion:

Acanthomyrmex is normally placed near *Pristomyrmex* (Figs. 218-222) and *Myrmecina* (Figs. 237-239) in the tribe *Myrmecinini*. There is no evidence for that relationship in the sting apparatus, which looks more like a somewhat reduced *Messor*-type. However, because of similarities in external morphology of *Acanthomyrmex* and *Pristomyrmex*, I remove *A.* cf. *notabilis* from the *Pheidole* core group and acknowledge the possibility of convergence. See also *Pristomyrmex* discussion.

Cyphoidris (Figs. 158-161)
Species examined: *C. spinosus* (Duque de Bragança Falls, Angola) 1 ☿; (Dundo, Angola) 3 ☿.

Spiracular plate. Ovoid, with gently concave anterior edge. Spiracle moderately large, near center of plate. Most like SP of *Rogeria inermis* and *Vollenhovia sp.* 2.

Quadrate plate. (Fig. 158) Like that of *Crematogaster atkinsoni*, *C. cerasi*, and *C. ashmeadi*. Lateral lobe reduced to weak ridge.

Oblong plate. (Fig. 159) Posterior arm and anterior apodeme much like those of *Crematogaster* (Fig. 180) but without large posterior apodeme. Ventral arm FA much like those in *Lachnomyrmex* cf. *scrobiculatus*.

Gonostylus. In Duque de Bragança Falls specimen, like that of *Vollenhovia* (Fig. 73) in shape and setation; segments not as clearly outlined. GO of Dundo specimen seem 1-segmented, narrower.

Triangular plate. Body long, slender; ventroapical process long, but wide; dorsoapical process very low.

Lancet. (Fig. 160) Like that of *C. atkinsoni* (Fig. 182) but end notched.

Sting. (Fig. 161) Much like that of *L.* cf. *scrobiculatus* (Figs. 163, 164), but with distinct basal ridge, narrower VC, and apex of SS more clearly forked. SBLB of Dundo specimen (Fig. 161) looks more like that of *Messor* (Fig. 138) and *Aphaenogaster*, because of shorter, more broadly rounded anterolateral processes. SB resembles that of *Stenamma diecki*.

Furcula. (Fig. 161) Arched as in *L.* cf. *scrobiculatus*, but dorsal arm not present.

Special remarks: The sting shaft and lancets are long and very slender, almost filamentous.

Discussion:

See *Lachnomyrmex* discussion.

Lachnomyrmex (Figs. 162-164)
Species examined: *L.* cf. *scrobiculatus* 1 ♀, 1 ☿ (MCZ).

Spiracular plate. None available.

Quadrate plate. Similar to *Cyphoidris spinosus* (Fig. 158) and some *Crematogaster,* but narrower ventrad.

Oblong plate. Much like that of *C. spinosus* (Fig. 159), but posterior arm very narrow and with prominent posterior apodeme.

Gonostylus. (Fig. 162) Much like those of *C. spinosus, Vollenhovia* (Fig. 73) and *Meranoplus,* but uniformly sclerotized. May also be related to GO of *Adelomyrmex,* but basal half is larger.

Triangular plate. Much like that of *C. spinosus,* but ventroapical process narrower.

Lancet. Long, very narrow, weak, distal end tapers slightly to subacute apex. Groove and ventral ridge very closely parallel for most of LA length, end subterminad. Similar to that of *Meranoplus,* but end symmetrical and less acute.

Sting. (Figs. 163, 164) SS very long, slender, hemocoel highly reduced, end slightly forked as seen in ventral view. VC and SBLB very well developed, distinct in profile. SBLB dorsal profile gently convex. SB vertical in profile, with prominent anterolateral processes, and very weak basal ridge.

Furcula. (Figs. 163, 164) U-shaped; lateral arms do not curve caudad like those of *Crematogaster* (Fig. 183) and *Trigonogaster recurvispinosa* (Fig. 186); dorsal arm reduced to small tubercle.

Special remarks: See *Cyphoidris.*

Discussion:

Cyphoidris spinosus and *Lachnomyrmex* cf. *scrobiculatus* are closely related. They have a primitive GO almost identical to that of *Vollenhovia,* and similar to that of the *Promeranoplus* group, but the sting is more derived and more similar to that of *Meranoplus, Aphaenogaster,* and *Messor*. The LA is likewise derived and much like that of *Crematogaster* and *Meranoplus*. These observations suggest that *Cyphoidris* and *Lachnomyrmex* arose with the *Pheidole* group from a common ancestor near the *Vollenhovia* and *Promeranoplus* groups. Emery (1922) and Wheeler (1922) placed *Lachnomyrmex* in the *Leptothoracini,* and Brown (1950a) said that *Lachnomyrmex* seems closely related to *Rogeria* because of similar thoracic structure, eyes, sculpture, and pilosity, but I find no particular support for that hypothesis in the sting apparatus.

Adelomyrmex (Figs. 165-169)
Species examined: *A.* near *tristani* (Chiapas, Mexico) 4 ☿ (MCZ); *A. sp.* 2 (San Luis Potosí, Mexico) 2 ☿ (MCZ).

Spiracular plate. Anterior and ventral edges of body straight, nearly perpendicular; posterior and dorsal edges merged into broad curve. Similar to that of *Cyphoidris spinosus,* but body narrower, and spiracle smaller, closer to posterodorsal edge. In *Adelomyrmex sp.* 2, anterior apodeme absent on dorsal half of plate.

Quadrate plate. In *A.* near *tristani* most like that of *C. spinosus* (Fig. 158) and some *Crematogaster,* but with prominent medial and lateral lobes. In *A. sp.* 2, much like that of *Myrmicaria spp.* (Fig. 171), and *Lachnomyrmex* cf. *scrobiculatus.*

Oblong plate. (Fig. 165) Posterior arm moderately wide; widest just behind articulation with FA. This shape also seen in *Vollenhovia* (Fig. 72). Posterior apodemes do not meet at midline. Ventral arm short, wide; FA vertical, poorly defined. OP seems similar to that of *C. spinosus,* differing primarily in height of FA and presence of posterior apodeme.

Gonostylus. (Fig. 166) Very slender in both directions, base somewhat larger. Similar to GO of *C. spinosus* Dundo specimen in shape, segmentation, and setation, but seems narrower.

Triangular plate. Body long, slender, evenly tapered basad; ventroapical process prominent, narrow. Most similar in shape to that of *Messor sp.* 1 (Fig. 136), *C. spinosus, L.* cf. *scrobiculatus* and *Myrmicaria spp.*

Lancet. (Fig. 167) Long (project far beyond end of sting even when retracted), weak, end upturned. Groove and ventral ridge closely parallel proximad, but groove curves dorsal near distal end. Spatula formed by both dorsal and ventral laminae.

Sting. (Figs. 168, 169) SS short, weak, blunt, hemocoel undetectable except at base. SS may be broken in my preparations (look broken off in specimens of *A.* near *tristani,* but not in the others). VC larger in *A. sp.* 2; its profile distinct from base of SS. SBLB long; lateral profile like that of *L.* cf. *scrobiculatus* (Fig. 163) and *C. spinosus* Dundo specimen (Fig. 161), but basal notch smaller. Anterior half of SBLB similar to that of *Myrmicaria* (Figs. 175, 176), but basal ridge lower.

Furcula. (Figs. 168, 169) Intermediate between U- and Y-shaped; lateral arms arched, dorsal arm short, especially in *A.* near *tristani.*

Discussion:

Adelomyrmex seems related to *Cyphoidris spinosus* and *Lachnomyrmex* cf. *scrobiculatus* because of similarities in all sclerites with one or the other of these genera. Usually the differences seem to be due to the greater degree of reduction in *Adelomyrmex.* The major differences are the shorter FA and the short SS. The latter may be broken in all of my specimens. The long weak stings of *L.* cf. *scrobiculatus* and *C. spinosus* break easily and without obvious signs of breakage; the same could be happening in *Adelomyrmex.*

Adelomyrmex may also be related, but more distantly, to *Myrmicaria,* primarily because of similarities in the QP, TP, and anterior half of the SBLB.

See also *Lachnomyrmex* discussion.

Myrmicaria (Figs. 170-176)
Species examined: *M. eumenoides* 4 ☿; *M. carinata* 2 ☿; *M. arachnoides* (var. *luteiventris* (?) 3 ☿ (MCZ).

Spiracular plate. (Fig. 170) Bodies of *M. arachnoides* and *M. eumenoides* sub-rectangular, that of *M. carinata* nearly square; shape similar to that of *Messor aciculata*. Spiracle slightly enlarged, near posterodorsal corner. In *M. eumenoides*, anterior apodeme absent on dorsal half of plate.

Quadrate plate. (Fig. 171) Long, narrow; apodeme and body greatly reduced in width. Anterodorsal corner short, wide, broadly rounded. Shape similar to that of *Adelomyrmex sp.* 2 and *Lachnomyrmex* cf. *scrobiculatus*, but norrower, without lateral and medial lobes.

Oblong plate. (Fig. 172) Dorsal ridge narrow. body of posterior arm very wide. Body widest midlength as in *Adelomyrmex*. Anterior apodeme short, wide, rounded, indented form anterior end of plate. Ventral arm short, wide, with reduced FA like that of *Adelomyrmex*.

Gonostylus. (Fig. 173) Very elongate, lightly sclerotized. In dorsal view, evenly tapered from narrow base. In *M. carinata* and *M. arachnoides* sensilla less numerous, mostly clustered in distal half with a few stragglers proximad. No sensilla distal to dorsoterminal chaeta.

Triangular plate. Body very long, slender, evenly tapered basad. Ventroapical process prominent, narrow. Dorsal tubercle greatly reduced. Similar in shape to that of *Adelomyrmex* and *Messor sp.* 1 (Fig. 136).

Lancet. (Fig. 174) Weak, very long (extends well beyond end of SS when retracted), gradually wider caudad. As in *Promeranoplus* (Fig. 124), ventral edge of groove widens caudad and merges into dorsal lamina.

Sting. (Figs. 175, 176) SS with very reduced hemocoel, sides reduced in height caudad; similar construction seen in *Promeranoplus* group (Figs. 125, 126). VC completely reduced, its space usurped by long SBLB. SBLB dorsum thick, well sclerotized, well developed basal ridge. Anterior half of SBLB much like that of *Adelomyrmex sp.* 1 (Figs. 168, 169).

Furcula. (Figs. 175, 176) Y-shaped, with lateral arms strongly curved caudad.

Special remarks: The highly weakened and flexible sting shaft and the large spatulate lancets are remarkably similar to those of *Megalomyrmex* (see *Megalomyrmex* special remarks).

Discussion:

Myrmicaria has been placed in its own monotypic tribe by both Emery (1922) and Wheeler (1922). Its unusual sting apparatus does not change this classification, but does suggest that the *Promeranoplus* group and *Adelomyrmex* are related to it. An origin near the *Promeranoplus* group is possible because of similar LA structure, reduced hemocoel and sides of SS, and shape of anterior end of SBLB. But major differences in FU and OP shape indicate that *Myrmicaria* does not belong in this group. *Myrmicaria* may have closer affinities to *Adelomyrmex*, because of similarities in QP, OP, TP, and SBLB shape. But the differences in LA, GO, SS, and VC are so great that a very close relationship is doubtful.

Meranoplus (Figs. 177-178)
Species examined: *M. sp.* 1 (*oceanicus* group, Brindabella Ridge, Australia) 2 ☿ (MCZ); *M. sp.* 2 (*mars* group, Stuart Highway near Darwin, Australia) 2 ☿ (MCZ).

Spiracular plate. Body long, oval. Anterior apodeme absent on dorsal half of plate. Plate similar to that of *Messor sp.* 1.

Quadrate plate. In *Meranoplus sp.* 2 apodeme and body very wide, dorsal and anterior edges straight, meet at right angles no anterodorsal prominence. In *M. sp.* 1, apodeme reduced in width dorsad, anterodorsal drawn out as in *Lordomyrma caledonica* and *Promeranoplus rouxi*, but not as long and narrow.

Oblong plate. Posterior arm long; dorsal ridge narrow; body moderately wide, truncate behind. Anterior apodeme long, digitate in *M. sp.* 2; in *M. sp.* 1, short, wide, with crescent-shaped ridge as in *Liomyrmex* cf. *aurianus* (Fig. 67), *Manica bradleyi*, and *Promeranoplus* (Fig. 122). Ventral arm short, wide; FA long, narrow, with short, slightly wider base in *M. sp.* 1. Ventral arm of *M. sp.* 2 similar to that of *Solenopsis geminata* (Fig. 80) Ventral arm of *M. sp.* 1 similar to those of *Chelaner sp.* 1 (Fig. 89) and *Monomorium minimum.*

Gonostylus. In *M. sp.* 2 size and shape of segments most like those of *Vollenhovia* (Fig. 73) and *Cyphoidris spinosus*, but intersegmental membrane oblique as in *Promeranoplus* (Fig. 123). Basal segment setation similar to both of these genera, but more dense; distal setation as in *Vollenhovia sp.* 1 (Fig. 73), but with more and longer setae in a row along ventroapical surface and dorsoterminal chaeta longer. In *M. sp.* 1 segments fused on lateral surface (not on dorsal surface), but setal pattern remains similar to that of *M. sp.* 2; shape much like that of *Lachnomyrmex* cf. *scrobiculatus* (Fig. 162).

Triangular plate. Apical end wide, with U-shaped lateral ridge, as in *Promeranoplus* group; body abruptly narrows midlength. Ventroapical process short, wide.

Lancet. Long, slender, weak. Groove closely parallels ventral ridge, ends subterminad. Apex tapered asymmetrically. Much like LA of *Messor* (Fig. 137) and *Aphaenogaster,* only narrower.

Sting. (Figs. 177, 178) SE lightly sclerotized toward end; dorsal flange produced in same way as that of *Aphaenogaster, Messor* (Fig. 138), and *Crematogaster* (Fig. 183). As in *Promeranoplus* group, height of sting decreases near tip. SBLB similar to that of *Cyphoidris spinosus,* but with lower SB. In ventral view SBLB also similar to that of *Messor* (Fig. 139) but not as wide. Notice also distinct VC in this view.

Furcula. (Figs. 177, 178) Ventral arms form broad arch. Short dorsal arm wider transversely than longitudinally.

Special remarks: The dorsal flange on the sting shaft, and the spatulate lancets are similar to those of *Crematogaster,* and may be used in similar fashion (see conclusions and *Crematogaster* special remarks).

Discussion:

Emery (1922) and Wheeler (1922) placed *Meranoplus* in the same with *Promeranoplus* and *Prodicroaspis.* The GO, anterior apodeme of the QP, and possibly the end of the SS do link it to these genera; but the SP, OP ventral arm, FU, SBLB and VC are all distinctly different. *Calyptomyrmex* was later added to the Meranoplini, but its sting apparatus is also much more primitive in nature than that of *Meranoplus*. Instead, *Meranoplus* seems most closely related to *Cyphoidris* and *Lachnomyrmex,* because of similarities in the GO, SBLB, and LA. There are also similarities with *Crematogaster,* but that genus is more derived.

Crematogaster (Figs. 179-185)
Species examined: *C. minutissima* 2 ☿; *C. atkinsoni* 4 ☿; *C. cerasi* 3 ☿; *C. ashmeadi* 3 ☿. See also Foerster (1912: 359-360) *C. sordidula* ☿ description, including musculature.

Spiracular plate. (Fig. 179) Square in *C. cerasi* and *C. atkinsoni; rectangular* in *C. minutissima* and *C. ashmeadi* where body seems to have expanded anteriad (Fig. 179). Spirarle large, about 1/6 to 1/4 area of body. Large spiracles also seen in the *«Rogeria» stigmatica* group, *Cyphoidris, Ocymyrmex, Myrmicaria* (Fig. 170), *Trigonogaster* and *Cephalotes,* but plate shapes are different.

Quadrate plate. Not distinctive in *C. minutissima.* Anterior edge straight, dorsal edge gently convex, anterodorsal corner short, wide, subacute. In other 3 species anterodorsal corner more drawn out, much like that of *Pheidole sp.* 3 (Fig. 148), *Messor sp.* 1, *Lordomyrma tortuosa,* and *Cyphoidris spinosus* (Fig. 158). No lateral or medial lobes.

Oblong plate. (Fig. 180) Dorsal ridge bends mesad at right angle, does not meet opposite OP at midline. Body of posterior arm uniform in width, weakly sclerotized. Ventral arm and FA most like those of *Messor aciculata* (Fig. 133), *Aphaenogaster* (Fig. 140) and *Veromessor andrei.*

Gonostylus. (Fig. 181) Dorsal surface narrow, evenly tapered caudad. In some individuals an area of weaker sclerotization can be seen just caudad of proximal patch of sensilla. Most individuals have an additional seta also located in this gap.

Triangular plate. Body moderately wide in dorsal half, petiolate below. Apicoventral process long and slender. Dorsal and medial tubercles quite distinct, similar in size and shape to those in *Promeranoplus* group.

Lancet. (Fig. 182) Long, weak, spatulate, with apex bluntly subacute to rounded, depending on species. Groove ends subterminad. Most like that of *Cyphoidris spinosus* (Fig. 160).

Sting. (Figs. 183-184) Good preparations not available for *C. ashmeadi.* In other species, SS long, low, narrow with very reduced hemocoel, as in *Pheidole* core group (Figs. 138, 146) and *Meranoplus* (Fig. 177); flange also formed in same way, but unlike Tetramoriini (Figs. 63, 65). Flange orientation varies, angled more dorsad in *C. minutissima.* SBLB moderately long, and wide. SB only slightly arched. VC reduced in *C. minutissima;* shape of sting more as in *Meranoplus sp.* 1 (Fig. 177). Ventral view in all species much like that of *Meranoplus sp.* 1 (Fig. 178). In *Crematogaster sordidula,* SB evidently as wide as that of *Aphaenogaster spp.* (Foerster, 1912: 360). Note size of poison gland reservoir and especially Dufour's gland of *C. minutissima* (Fig. 185).

Furcula. (Figs. 183, 184) Unlike SB, FU strongly arched. Dorsal arm reduced to small tubercle. Foerster (1912: 360) says that no dorsal arm is present in *C. sordidula.* FU shape most like that of *Meranoplus* (Figs. 177, 178).

Special remarks: The spatulate dorsal flange and the spatulate lancets hold a droplet of fluid on the end of the aculeus when these ants are disturbed. The fluid is a repellent and an irritant to other ants. The dorsal attachment of the postpetiole to the gaster allows the ant to place the droplet far forward over its allotrunk for defense, but prevents the ant from laying trails with its aculeus. Instead, trail pheromone is produced in the hind legs and deposited by the hind tarsi (Leuthold, 1968a, b).

Discussion:

Although the sting apparatus of *Crematogaster* is very distinct from all others described, it has similarities with other members of the *Pheidole* genus group. The ventral arm and FA of the OP are similar to those of *Messor aciculata*. The LA is most similar to that of *Cyphoidris spinosus*, and the highly derived and specialized sting and FU morphology looks as though it could be just slightly more reduced than the *Meranoplus*-type. For these reasons it looks as though *Crematogaster* diverged early from the same ancestral group that produced *Cyphoidris* and *Meranoplus*.

Trigonogaster (Figs. 186-187)

Species examined: *T. recurvispinosus* 1 ☿ (MCZ).

Spiracular plate. Ventral edge straight, anterior and posterior edges convex, strongly converge dorsad. Spiracle in center of plate, moderately large, about 1/10 area of body (see *Crematogaster*).

Quadrate plate. Very much like that of *Crematogaster minutissima;* similar also to that of *Adelomyrmer sp.* 2.

Oblong plate. Posterior arm like that of *Crematogaster* (Fig. 180). Ventral arm long, uniform in width to broadly rounded apex, most like that of *Cyphoidris spinosus* (Fig. 159). FA long, slender well defined, fusiform.

Gonostylus. Preparation not good enough to describe in detail. Short, wide, with broadly rounded apex; long setae on lateral surface, some distad of dorsoterminal chaeta.

Triangular plate. Body moderately slender, ventroapical process wide, but prominent. Large, blunt tubercle arises from medial surface, just below dorsoapical process.

Lancet. Very long, slender, weak. Groove and ventral ridge very closely parallel for most of length, end slightly subterminad. Dorsal lamina does not appear to enlarge caudad, but specimen is twisted and I cannot be sure of exact shape. If not spatulate, LA similar to those of *Stenamma* (Fig. 145) and *Lachnomyrmex* cf. *scrobiculatus*. If spatulate, more like those of *Crematogaster* (Fig. 182) and *Cyphoidris spinosus* (Fig. 160).

Sting. (Figs. 186, 187) Whole sting very weakly sclerotized. SS very long and slender as in *C. spinosus* and *L.* cf. *scrobiculatus* (Fig. 163). VC and SBLB more as in *C. minutissima,* but SBLB lower and narrower.

Furcula. (Figs. 186, 187) Most like that of *Crematogastor* (Figs. 183, 184). Short, weak dorsal arm seems to be present.

Special remarks: The aculeus is very long relative to the size of the ant (Appendix A, column 41) and very slender and weak.

Discussion:

Emery (1922) and Wheeler (1922) included *Trigonogaster* with the *Pheidologetini* and the *Solenopsidini,* respectively. I think Ettershank (1966) was correct in separating it from both of these groups of genera. Sting apparatus morphology indicates that *Trigonogaster* is related to *Cyphoidris, Lachnomyrmex* and *Crematogaster,* possibly closest to the latter. Whether it is an independent branch, or an offshoot of the *Crematogaster* line is unclear.

Tribe Cephalotini

Cephalotes (Figs. 188-191)
Species examined: *C. atratus* 2 major ☿, 2 minor ☿.

Spiracular plate. Dorsal half of body reduced to membrane. Body short, ovoid; spiracle large (about 1/7 body area) near dorsal edge. Dorsal notch distinct, V-shaped. Medial connection wide, heavily sclerotized.

Quadrate plate. (Fig. 188) Apodeme subtriangular with long pollicate anterodorsal corner, no lateral or medial lobes. Body wide, emarginate in majors.

Anal plate. About 3 times wider than long, moderately well sclerotized, densely covered with sensilla; not fused to AA.

Oblong plate. (Fig. 189) Posterior arm turns sharply mesad at point where body rapidly narrows; does not meet dorsal ridge of opposite side. Ventral arm largely membranous; FA slightly inclined.

Gonostylus. Similar to that of *Eucryptocerus opacus* (Fig. 192), but dorsal surface wider basad (more than twice height of lateral surface), and sensilla cover whole lateral surface. Chaetae, s. basiconica, and largest setae located anteriad. No obvious companion seta.

Triangular plate. Much like that of *E. opacus* (Fig. 193), but with lateral welt on body much reduced or absent.

Lancet. Much like that of *E. opacus* (Fig. 194), but with shorter, more acutely tapered apex.

Sting. (Figs. 190, 191) SS well sclerotized basad, lightly sclerotized distad, sides reduced at apex. Low dorsal flange much like that of *Acanthomyrmex* cf. *notabilis* (Fig. 157), and *Messor* (Fig. 138). SS hemocoel highly reduced. VC indistinguishable from SS. SBLB long, basal notch wide. Note also unique articular process shape and well developed basal ridge. In ventral view SBLB very wide, VC narrow.

Furcula. (Figs. 190, 191) Shallowly arched, bar-shaped, narrower mesad and at extremities. In some individuals, membranous mesad.

Eucryptocerus (Figs. 192-194)
Species examined: *E. opacus* 1 ☿.

Spiracular plate. Distorted in my preparations, but appear to be similar to that of *C. atratus.*

Quadrate plate. Like those of *C. atratus* minor workers (Fig. 188).

Anal plate. As in *C. atratus.*

Oblong plate. Dorsal half like that of *C. atratus.* Ventral arm lost in preparation.

Gonostylus. (Fig. 192) Dorsal surface subtriangular; lateral surface narrower, less tapered. Apex broadly rounded. Setae present distal to dorsoterminal chaeta; no obvious companion seta. Shape and setation similar to that of *Pheidole morrisi* (Fig. 150).

Triangular plate. (Fig. 193) Body short, wide, with heavy apical and basal ridges, and mid-lateral welt. Dorsoapical process reduced.

Lancet. (Fig. 194) Note extremely reduced valve, and low dorsal lamina. Groove and ventral ridge not closely parallel.

Sting. Much like that of *C. atratus*, but SS sides not reduced at apex; articular processes less prominent, not ridged behind.

Furcula. Shallow arch with small dorsal tubercle. Narrowest mesad, gradually wider laterad.

Procryptocerus (Figs. 195-197)
Species examined: *P. scabriusculus* 1 ☿ (MCZ).

Spiracular plate. Much like that of *Zacryptocerus haemorrhoidalis* (Fig. 198), but with more triangular anterior apodeme and without posteroventral tubercle. Similar also to those of other *Zacryptocerus spp.* and *Cataulacus tardus*. Dorsal notch wide, shallow.

Quadrate plate. Much like that of *Z. haemorrhoidalis* (Fig. 198), but apodeme and body narrower, and anterior edge of plate a smooth arc, rather than angular.

Anal plate. Like those of *Cephalotes atratus, Eucryptocerus opacus,* and *Zacryptocerus,* but not as extremely short and wide.

Oblong plate. Much like that of *C. atratus* (Fig. 189), but posterior arm shorter, without subterminal tubercle and FA more strongly inclined; even more like OP of *Zacryptocerus*. Ventral arm and FA much like those of *Aphaenogaster rudis* (Fig. 140) and *Veromessor andrei*.

Gonostylus. Very similar to that of *Zacryptocerus minutus* (Fig. 199) but broader, and without dorsoterminal chaeta. Sensilla basiconica in short row dorsad; stout chaetae anteriad. Similar also to GO of *V. andrei*.

Triangular plate. (Fig. 195) Body long, narrow. Ventroapical process long, abruptly prominent. Dorsoapical process low. Shape most similar to that of *C. tardus*.

Lancet. Like those of *C. atratus, E. opacus* (Fig. 194) and *Z. haemorrhoidalis*.

Sting. (Figs. 196, 197) Similar to that of *C. atratus,* but without dorsal flange on SS and with SBLB more square in ventral view.

Furcula.(Figs. 196, 197) Bar-shaped; compressed longitudinally; appressed to SB.

Zacryptocerus (Figs. 198-201)
Species examined: *Z. haemorrhoidalis* 2 ☿; *Z. multispinosus biguttatus* 3 ☿; *Z. minutus* 3 ☿.

Spiracular plate. (Fig. 198) Not well preserved in *Z. minutus*. Body short, ovoid as in *Cephalotes atratus,* but anterior apodeme wider, more irregular in shape, spiracle not as large. Apodeme shape varies among species.

Quadrate plate. (Fig. 198) Anterodorsal corner with long, pollicate process and narrow lateral lobe. Rest of apodeme subtriangular. Body uniformly wide. SP fits under anterodorsal process as in *Trachymyrmex* (Fig. 212) and *Cataulacus tardus,* but overlaps QP more.

Anal plate. Short and very wide; covered with sensilla, like those of *C. atratus* and *Eucryptocerus opacus*.

Oblong plate. Basically like that of *C. atratus* (Fig. 189), but posterior arm narrower, more evenly tapered caudad; anterior apodeme longer in *Z. minutus*, shorter in *Z. haemorrhoidalis;* FA more inclined as in *Procryptocerus scabriusculus*, *Aphaenogaster rudis* (Fig. 140), and *Veromessor andrei*.

Gonostylus. (Fig. 199) Most like that of *E. opacus*, but wider basad, as in *C. atratus* and *P. scabriusculus*. Shape and setation also similar to that of *Veromessor andrei*, except for presence of s. basiconica.

Triangular plate. Quite variable in shape, depending on species, similar to either *C. atratus* or *E. opacus*. All with prominent dorsoapical processes.

Lancet. Most similar to those of *C. atratus* and *P. scabriusculus;* also similar to LA of *E. opacus*, but end more blunt. In *Z. minutus* and *Z. m. biguttatus*, end of LA truncate.

Sting. (Fig. 200) Quite similar to that of *C. atratus* (Fig. 190), but SBLB lower, SB more rounded in profile, and basal ridge reduced mesad. In *Z. minutus* SBLB not as wide, sides straighter and more convergent in ventral view, SB more narrowly rounded. Note disproportionately large Dufour's gland in *Z. m. biguttatus* (Fig. 201) as compared with that of *Amblyopone pallipes* (Fig. 8) and *Basiceros singularis* (Fig. 49).

Furcula. (Fig. 200) Slightly arched, bar-shaped. In some species, narrower mesad. Varies in length within species.

Special remarks: See *Aphaenogaster*.

Discussion:

The Cephalotini are quite homogeneous in sting morphology. The sting apparatus of the tribe can be defined by the following characters: SP with wide, complete medial connection; AP wider than long, with many dorsal sensilla; OP with long, well defined, angular FA; GO short, wide, with basiconic sensilla, and without gap in sensillar pattern; sting with SS weak, VC reduced, SBLB long, wide, low; SB only weakly arched, primitively with dsitinct basal ridge.

Within the Cephalotini, *Eucryptocerus opacus* and *Cephalotes atratus* are the most similar species examined, and the *Zacryptocerus* sting apparatus is probably only a more reduced form. *Procryptocerus scabriusculus* differs from these in TP, AP and SBLB shape (lateral and ventral views), and in lack of the SS dorsal flange. In other respects, particularly in SP, QP, and OP shape, the sting apparatus is much like that of *Zacryptocerus*.

This tribe possibly had its origins close to the base of the *Pheidole* group. The most important similar characters are: SP with dorsal notch and complete, or nearly complete, medial connection; AP with dorsal setae; SBLB long, wide; SB with wide basal ridge in *Stenamma* and Cephalotini; GO shape and setation similar in some advanced species of *Pheidole* group *(Veromessor andrei, Pheidole* *morrisi)* and the Cephalotini. Dense GO setation is probably a primitive character rather than convergent in the *Pheidole* group and cephalotines. The lower SBLB seen in the more derived species of both groups is probably a parallel development.

Tribe Cataulacini

Cataulacus (Figs. 202-204)
Species examined: *C. tardus* 2 ☿.

Spiracular plate. Body ovoid, with distinct but shallow dorsal notch. Spiracle near dorsal edge of plate. Anterior apodeme triangular. Shape most similar to that of *Procryptocerus scabriusculus* and some *Zacryptocerus*.

Quadrate plate. Much like that of *Trachymyrmex* (Fig. 212), but body emarginate on posterior edge. SP fits under long anterodorsal process, much as in *Trachymyrmex*, but overlaps QP more. Also similar to, but narrower than, that of *P. scabriusculus*.

Anal plate. Similar to that of *Trachymyrmex* (note Appendix A).

Oblong plate. (Fig. 202) Ventral arm and body of posterior arm very weakly sclerotized, almost indistinguishable from membrane connecting them. FA extremely narrow and short.

Gonostylus. Shape and setal pattern much as in *Cephalotes atratus* and *Eucryptocerus opacus* (Fig. 192). Setae cover almost entire lateral and ventral surfaces as in *C. atratus*. But no s. basiconica or dorsoterminal chaeta present.

Triangular plate. Very much like that of *P. scabriusculus* (Fig. 195).

Lancet. Dorsal lamina lost. Groove and ventral ridge gradually converge to form long, slender, spinelike LA. Moderately well sclerotized, but probably not able to pierce thin cuticle. Shape similar to that of *Trachymyrmex* (Fig. 212), but latter is weaker, lack ventral ridge, and has dorsal lamina.

Sting. (Figs. 203, 204) Much like that of the Cephalotini, particularly the SS of *P. scabriusculus* (Figs. 196, 197), and the SBLB of some *Zacryptocerus spp.* Sting also bears some resemblance to that of *Trachymyrmex* (Figs. 213, 214), particularly *T. turrifex*, in shape of SS low, wide SBLB and wide basal notch. But *Trachymyrmex* has internal ridge in VC area, and differs in shape of articular processes. A 3-pronged structure is visible inside SBLB of *C. tardus* that may be an extension of internal apophysis, and seems to surround and support end of poison duct. *Atopomyrmex mocquerysi* has a similar 2-pronged structure (Figs. 216, 217).

Furcula. (Figs. 203, 204) Bar-shaped; longitudinally compressed; widest mesad.

Discussion:

On the basis of similar external morphology, earlier workers placed *Cataulacus* and the cephalotines in the same tribe or section. But since Emery (1922) there has been unanimous agreement that the similarities in external morphology are convergent, and result from similar arboreal, twig-nesting life ways (see historical review by Bolton, 1974: 9). Wheeler and Wheeler (1954a) concluded that the larvae are also convergent in body shape and pilosity. This seems reasonable because other obviously unrelated twig-nesting larvae have the same shape.

The sting apparatus of *Cataulacus tardus* is most similar to those of the cephalotines and attines. But *C. tardus* is distinct from both tribes because of unique features of the GO, OP, and sting, and unique combinations of other characters (*e.q.*, complete medial connection of SP, but very reduced AP). Furthermore, some similarities between the 3 tribes are most likely convergent or parallel: the interlocking SP and QP, the low SBLB, the fused, bar-shaped FU and possibly the wide SBLB. These are characters *C. tardus* shares with the advanced members of the Cephalotini and Attini (except wide SBLB, which is present in primitive cephalotines). These characters are convergent, assuming the 3 tribes had separate origins. It is not clear from the present study whether that assumption is correct. Because *C. tardus* and the primitive cephalotines share distinctive shapes of the SP, GO and articular processes of the sting, along with a wide SBLB, I think it is possible that they originated from the same ancestral group. That group may be the *Pheidole* group for reasons outlined in the Cephalotini discussion.

Tribe Attini

Cyphomyrmex (Figs. 205-207)
Species examined: *C. salvini* 1 ☿.

Spiracular plate. Very much like that of *Trachymyrmex seminole* (Fig. 212), but without tubercle on posteroventral corner.

Quadrate plate. Apodeme wide, anterior edge only slightly concave, dorsal edge gently convex; anterodorsal corner pollicate, directed anteriad. Body wide dorsad; narrow, very weakly sclerotized ventrad.

Oblong plate. Similar to that of *Trachymyrmex*, (Fig. 212), particularly *T. turrifex*. Ventral arm wider than posterior arm, and almost as long, end truncate. Anterior apodeme lower. FA a wide vertical bar on very end of ventral arm, a fine ridge trails from it along PI; similar to that of *Atta cephalotes*, but also with a thin sub-rectangular lobe attached to its caudal edge.

Gonostylus. (Fig. 205) Dorsoventrally flattened. Dorsal surface narrowly subtriangular; ventral surface narrower. Sensilla along lateral surface.

Triangular plate. Body short, evenly tapered basad. Ventroapical process moderately long.

Lancet. Short, acute, well sclerotized. With short, but distinct dorsal ridge at apex. Probably piercing.

Sting. (Figs. 206, 207) SS wide, blunt, but well sclerotized, with distinct hemocoel. SBLB long, but not very wide. Basal ridge of SB reduced mesad.

Furcula. (Figs. 206, 207) Dorsoventrally compressed, widest mesad. Tightly appressed to SB.

Apterostigma (Figs. 208-209)
Species examined: *A. collare* 2 ☿.

Spiracular plate. Like that of *Cyphomyrmex salvini* and *Trachymyrmex seminole* (Fig. 212), but anterior edge of body gently convex, rather than angular.

Quadrate plate. Apodeme narrow, reduced in width ventrad; anterodorsal corner long pollicate, directed anterodorsad. Body wide ventrad, reduced dorsad. No anal arc.

Oblong plate. Similar to that of *Atta cephalotes* (Fig. 211), but FA curved, spindle-shaped. Anterior apodeme digitate.

Gonostylus. No dorsal view available, but lateral view shape similar to that of *C. salvini* (Fig. 205). Setation differs; no gap in sensilla, no obvious dorsoterminal chaeta for same reasons as in *T. seminole* (see below). No obvious companion seta.

Triangular plate. Much as in *C. salvini.*

Lancet. Like that of *Trachymyrmex* (Fig. 212).

Sting. (Figs. 208, 209) SS slender and evenly tapered in both directions about as wide as high. Note also wide SBLB, short basal notch, well developed basal ridge, and anterolateral processes. Anterolateral processes may actually be fused remnants of FU (see FU description following).

Furcula. (Figs. 208, 209) In one individual, rod-shaped; ends larger, fused to «anterolateral processes» of SB, but separate from SB mesad. In the other, free mesal portion lost except for small dentate medial projections from the elongate «anterolateral processes». It may be that «anterolateral processes» themselves are remnants of FU. Ancestors of this species may have had large, dorsoventrally compressed FU with tendency for medial reduction, as in *Trachymyrmex* (Figs. 213, 214).

Mycetophylax (Fig. 210)
Species examined: *M. emeryi* 2 ☿.

Spiracular plate. Similar to that of *Apterostigma collare,* but without enlarged anterior apodeme, ventral and anterior edges merged into smooth curve, spiracle in center of plate.

Quadrate plate. Apodeme reduced to very narrow band, anterodorsal corner without projection. Body wide dorsad, gradually reduced ventrad.

Anal plate. Very nearly membranous. No sensilla in one individual; with only very short marginal chaetae in the other.

Oblong plate. Similar to that of *Pheidole morrisi* minor workers (Fig. 149) in all respects except for shorter anterior apodeme. This similarity is no doubt convergent due to deduction of sting apparatus in both genera.

Gonostylus. Very short, dorsoventrally compressed. Dorsal surface about as wide as long. Ventral surface about half as wide. Sensilla few, short, lacated in distal half of lateral surface. Long terminal seta present on some GO; not an obvious companion seta.

Triangular plate. Like that of *C. salvini* and *A. collare.*

Lancet. Like that of *Atta cephalotes* and *Trachymyrmex intermedius.*

Sting. (Fig. 210) In ventral view, much like that of *C. salvini,* but basal ridge not reduced mesad. SS low, but wide, with distinct hemocoel. VC not well defined internally, but nevertheless present. SBLB low, wide; SB only weakly arched.

Furcula. Looks weakly arched and bar-shaped from anterior view; mesal portion compressed longitudinally, when seen from below.

Atta (Fig. 211)
Species examined: *A. cephalotes* 2 minor ♀. See also Hermann, *et al.* (1970) description of *A. texana,* and Foerster (1912: 360, Fig. 5) description of *A. colombica,* including musculature.

Spiracular plate. Most similar to that of *Apterostigma collare.* Anterior edge flat, with apodeme reduced to very low, uniformly wide ridge. Ventral, posterior, and dorsal edges merged into a smooth curve.

Quadrate plate. Intermediate in shape between those of *Cyphomyrmex salvini* and *Trachymyrmex seminole* (Fig. 212). Anterior edge strongly concave and plate reduced in width as in *T. seminole,* but anterodorsal process not as long and apodeme distinguishable from body. Lower half of body strongly reduced in width.

Oblong plate. (Fig. 211) Greatest resemblance to that of *A. collare* in length and shapes of posterior and ventral arms.

Gonostylus. Very much like that of *T. seminole* (Fig. 212).

Triangular plate. Body slender evenly tapered, ventroapical process long, wide, blunt, abruptly jutting from body. Dorsoapical process low, rounded.

Lancet. Very weak, evenly tapered to subacute apex. Dorsal and ventral laminae equal in height. Groove and ventral ridge end subterminad.

Sting. Similar to that of *T. seminole* (Figs. 213, 214) but internal ridge above VC area lower and basal ridge of SB larger.

Furcula. Much like that of *T. seminole* (Figs. 213, 214) but wider and not reduced in width mesad. In *Atta texana* (Hermann, *et al.*, 1970, Fig. 2G) and *Atta colombica* (Foerster, 1912, Fig. 5), FU apparently reduced mesad; membranous in the latter.

Special remarks: See *Trachymyrmex.*

Trachymyrmex (Figs. 212-214)
Species examined: *T. seminole* 3 ☿; *T. turrifex* 2 ☿; *T. intermedius* 1 ☿.

Spiracular plate. (Fig. 212). Similar to that of *Cyphomyrmex,* but with short dentate posteroventral process in *T. seminole* and a long, broadly truncate process in *T. intermedius.* Both possibly articulate with TP. Ventral edge in *T. turrifex* smoothly convex rather than angular.

Quadrate plate. (Fig. 212) Anterior edge extremely concave, anterodorsal process extremely long. Posterior edge of SP fits into this arc, just overlapping it. Similar interlocking of QP and SP seen in *Zacryptocerus* (Fig. 198) and *Cataulacus tardus.* QP very narrow in both species, especially in *T. seminole* and *T. intermedius* where apodeme and body are indistinguishable.

Oblong plate. (Fig. 212) In *T. seminole* ventral arm long, wider than posterior arm; PI deeply incised; anterior apodeme very low; no definite FA, end of arm diffusely and lightly sclerotized. OP of *T. turrifex* and *T. intermedius* very similar, but ventral arm shorter, only slightly tapered, broadly truncate.

Gonostylus. (Fig. 212) Dorsoventrally flattened. Dorsal surface wide at base, subtriangular; ventral surface narrower, more strongly tapered in distal half. No obvious dorsoterminal chaeta; in all 3 species, distalmost chaeta no larger or blunter than other chaetae on GO, and not always terminal. No obvious companion seta.

Triangular plate. (Fig. 212) Large relative to size of OP and other sting parts; very large in *T. intermedius.* In *T. turrifex,* body wider dorsad and more rapidly tapered ventrad than in *T. seminole* and *T. intermedius.* Ventroapical process prominent; wide in *T. intermedius,* narrow in others.

Lancet. (Fig. 212) Weak, evenly tapered to fine acute apex. Ventral lamina higher than dorsal lamina, neither with ridge. Groove extends to tip of LA.

Sting. (Figs. 213, 214) SS weak, slender in both directions. Large internal ridge separates inner and outer dorsal walls of SS in region where VC would normally be. SB weakly arched. Basal notch long, low. SBLB quite wide in ventral view.

Furcula. (Figs. 213, 214) In *T. seminole* and *T. intermedius* long, dorsoventrally compressed, tightly appressed to SB as in *Atta cephalotes*. In *T. turrifex* reduced to 2 small sclerites appressed to anterolateral corners of SBLB, as in *Atta colombica* and possibly *Apterostigma collare* (Fig. 209).

Special remarks: The sting apparatus is quite reduced in size (Appendix A, column 41), with the paired sclerites widely spread (compare Figs. 2A and 2B with Fig. 2C in Hermann *et al.* 1970), and the whole apparatus is flattened against the rear of the gaster.

Discussion:

Although the attines are considered a distinct tribe, their sting apparatus cannot be characterized as easily as the other tribes described above. There is much variation within my sample of species. The constant characters are few and not particularly distinctive: body of SP similar in shape; anterodorsal corner of QP usually elongated; GO short, dorsoventrally compressed, dorsal surface wider than combined lateral and ventral surfaces, sensilla along lateral edge; LA with both laminae present, ventral lamina usually wider; SS without dorsal flange, hemocoel distinct in anterior half; FU bar-shaped, appressed to SB.

Within the tribe, *Apterostigma collare, Atta cephalotes,* and the *Trachymyrmex spp.* are more closely related because of greater similarities in QP, GO, LA, sting and FU. *Cyphomyrmex salvini* may be closer to the ancestral stock. It is similar to, but more primitive than, the 3 genera above in QP, OP, LA and sting shape. Its SP is like that of *Apterostigma* and *Trachymyrmex;* its GO is more reduced. *Mycetophylax emeryi* is the most dissimilar of the species examined, due to greater reductions in SP, QP, OP and GO. But the sting retains some *Cyphomyrmex*-like characters (ventral view shape, VC). It may be derived from *Cyphomyrmex,* or its ancestor; but it is probably on a branch separate from *Apterostigma, Atta,* and *Trachymyrmex.*

I have only begun to tap the variation in this tribe, so these phylogenetic speculations should only be regarded as suggestions. For the same reason, I hesitate to speculate on the origins of the tribe. Emery (1895) suggested that the attines originated near *Wasmannia,* and Forel (1902) thought that the Decetini were the ancestral group. So far the sting apparatus does not resolve the debate. There are some similarities with *Cataulacus,* but these are in advanced attine species and may well be convergent.

Unplaced Genera

The following genera cannot be included with any of the foregoing groups at present, on the basis of the sting apparatus.

Atopomyrmex (Figs. 215-217)
Species examined: *A. mocquerysi* 2 ☿.

Spiracular plate. Anterior apodeme reduced; body instead continues dorsad to make complete medial connection. Plate triangular, no dorsal edge.

Quadrate plate. Relatively small, about half the size of SP, but body and apodeme wide. Anterodorsal projection low, wide, broadly rounded. Body with small V-shaped emargination midlength in posterior edge.

Anal plate. Very short, wide, well sclerotized as in Cephalotini but without anal setae. Unlike all other ants examined, AP indistinguishably fused with AA, except for mesal third.

Oblong plate. Dorsal ridge of posterior arm long, moderately wide, uniform in width. Body of arm only half as long. Anterior apodeme low, digitate. Ventral arm long (extends beyond body of posterior arm), narrow, distal half gently tapered, narrowly rounded. FA strongly inclined anteriad, with short bulbous base and narrow dorsal extention that gets wider and more diffuse.

Gonostylus. Dorsal surface broadly subtriangular, lateral and ventral surface wide, with broadly rounded apex. Shape most similar to that of *Procryptocerus scapriusculus;* similar also to that of other Cephalotini (Fig. 199) and *Cataulacus tardus* but wider basad. Setation much as in *C. tardus,* but with short chaetae anteroventrad, fine setae and microtrichiae posteroventrad, and 2 dorsoterminal chaetae of equal size and shape. Apparently has companion chaeta instead of companion seta.

Triangular plate. Shape unique. Body very long, slender (narrower than dorsoapical process), gently tapered ventrad. Dorsoapical process large, prominent. Ventroapical process long, slender, projects perpendicular to body and dorsoapical process.

Lancet. (Fig. 215) Long, weak, end tapered to flagellate apex. Ventral lamina wider than dorsal lamina for most of LA, but reduced and lost caudad. Groove widens slightly near apex, its ventral edge attenuates.

Sting. (Figs. 216, 217) SS very weak, slender, evenly tapered to fine apex. Hemocoel reduced, but visible except at tip. Internal apophysis well sclerotized, seems to connect to 2 large ventrolaterally projecting prongs. Prongs similar to those of *C. tardus.* SB well arched, SB basal ridge reduced mesad, mesal area of anterior SBLB also weakly sclerotized, almost membranous. SBLB very wide, as in *Messor.* Basal notch rimmed with distinct ridge.

Furcula. Not present.

Special remarks: Most interesting is the lack of a furcula and the medial membranization of the sting bulb.

Discussion:

Emery (1922) and Wheeler (1922) placed *Atopomyrmex* in the tribe Myrmecinini along with *Podomyrma, Lordomyrma, Myrmecina,* *Pristomyrmex,* and *Acanthomyrmex.* On the basis of the sting apparatus, I place none of these very close together (see also *Pristomyrmex* discussion). The GO and the unique structure inside the SBLB suggest a relationship with *Cataulacus tardus.* The AP and GO morphology indicate an affinity to the Cephalotini. But nearly all sclerites have unique properties that make *A. macquerysi* difficult to assign to any group.

Pristomyrmex (Figs. 218-222)
Species examined: *P. brevispinosus* (Wolasi, Celebes) 2 ☿; (Balampesoang, S. Celebes) 2 ☿.

Spiracular plate. (Fig. 218) Body ovoid, almost twice as long as wide. Apodeme especially wide dorsad. Spiracle in center of plate.

Quadrate plate. (Fig. 219) Apodeme trapezoidal (narrower ventrad), body rectangular. Anterodorsal corner digitate to hamate; distinct lateral lobe present, possibly medial lobe also.

Oblong plate. Posterior arm wide, long; dorsal ridge narrow; body uniform in width, truncate. Anterior apodeme long, digitate. Ventral arm long, narrower than posterior arm, tapered to subacute apex. OP most similar to that of *Cyphoidris spinosus* (Fig. 159); also similar to that of *Crematogaster minutissima* (Fig. 180) and *Aphaenogaster rudis* (Fig. 140), but dorsal edge of ventral arm slightly convex rather than concave, and posterior apodeme spinate.

Gonostylus. (Fig. 220) Narrow in both directions. Shallow notch between 2 groups of sensilla. Distal setae very long and marginal as in *Meranoplus spp.*

Triangular plate. Body short, strongly tapered basad. Ventroapical process long, narrow.

Lancet. Very slender, weak; gradually tapers to fine point. Dorsal and ventral laminae equal in height except near apex where ventral lamina is lost. Groove extends to end of LA.

Sting. (Figs. 221, 222) SS very long, slender, hemocoel highly reduced, flattened dorsal wall continues far beyond end of sides (and lancets). Outer dorsal wall of SS secondarily thickened near junction with VC; original condition may be like that of *Messor* (Fig. 138) or that of *Oxyepoecus rastratus* (Fig. 87). VC deep, short as in *Messor* (Fig. 138), *Aphaenogaster, C. spinosus* (Fig. 161) and *O. rastratus* (Fig. 87). SBLB short as in *O. rastratus,* but junction of SBLB dorsum with SB angular in side view, more as in *Messor,* and related species including *C. spinosus.*

Furcula. (Fig. 221) Y-shaped; dorsal arm laterally compressed, wide longitudinally.

Special remarks: The sting shaft is quite long (Appendix A, column 41), but even so has a long flexible extension of the dorsal wall that almost doubles its length. The lancets, in contrast, are short and not spatulate. The filamentous sting appendage is often seen extending from the gaster of *Pristomyrmex spp.* museum specimens. It is not known if the sting can be completely pulled into the sting chamber.

Discussion:

The sting apparatus seems to have its closest affinities with 3 sets of genera: *Messor/Aphaenogaster* (sting, OP), *Cyphoidris spin-*

osus (sting, OP), and *Oxyepoecus rastratus/Rogeria inermis* (sting). The SBLB is probably most like that of the *Pheidole* group, but the FU has a well developed dorsal arm as in the *Solenopsis* group. At present I am unable to sort out true relatedness from convergence.

In the present classification, *Pristomyrmex* is placed in the Myrmecinini along with *Podomyrma* (Figs. 32-34), *Acanthomyrmex* (Fig. 157), *Myrmecina* (Figs. 237-239), *Lordomyrma* (Figs. 128, 129) and *Atopomyrmex* (Figs. 215-217). Sting apparatus morphology does not support the unity of the Myrmecinini. Wheeler and Wheeler (1954b) examined the myrmecinine larvae, and also concluded that it is «... a heterogeneous lot. In fact, each of the five genera studied might as well be in a different tribe. To be sure, *Myrmecina* and *Pristomyrmex* both have the head extremely elongate-a most unusual and bizarre character, but they have little else in common».

Proatta (Figs. 223-224)
Species examined: *P. butteli* 1 ☿ (MCZ).

Spiracular plate. Ovoid, dorsal notch shallow, wide. Anterior apodeme very narrow. Spiracle in dorsal half of plate.

Quadrate plate. Apodeme wide, posterior edge strongly convex, with large medial and lateral lobes. Anterodorsal corner prominent, subacute. Body narrow, uniform in width. QP shape similar to that of *Tetramorium* (Fig. 58).

Oblong plate. Posterior arm partially obscured in my preparations. Dorsal ridge heavily sclerotized, but body weak, very narrow. Ventral arm, FA and anterior apodeme similar to those *Tetramorium spp.* that have dorsal ridge wider in anterior corner (Fig. 59). Anterior end of dorsal ridge (and possibly posterior arm) like that of *Cardiocondyla elegans*.

Gonostylus. Very short, weakly sclerotized, but clearly 2-segmented in sclerotization and setal pattern. Exact shape unclear. Appears to be wide at base, uniformly tapering to narrow apex. Dorsoterminal chaeta and companion seta isolated from rest of sensilla.

Triangular plate. Body and ventroapical process wide. Both shaped much as in some *Vollenhovia* and *Tetramorium*.

Lancet. Like that of *Tetramorium pacificum* (Fig. 62), but shorter. Also like that of *C. elegans*, but more heavily sclerotized, and with rudimentary barb.

Sting. (Figs. 223, 224) End of SS enlarged like that of *Rogeria inermis* (Fig. 91). Outer dorsal wall thickened above VC as in higher Attini (Fig. 213), *Cardiocondyla* (Fig. 226), *Oligomyrmex* (Fig. 233), and *Tranopelta* (Fig. 230).

Furcula. (Figs. 223, 224) Y-shaped; dorsal arm short.

Discussion:

Emery (1922) placed *Proatta* in a separate subtribe within the Attini. There is no support for this relationship in sting apparatus morphology. The internal ridge of the sting is the only similarity, and that character is probably convergent, since a variety of unrelated, but reduced stings have it. Wheeler (1922) liberated *Proatta* from the attines, but was unable to put it in any other tribe. Its closest relatives may be the Tetramoriini or *Cardiocondyla,* because of similarities in the QP, OP, TP, and LA shapes. Note however, that sting morphology and external morphology do not particularly support such relationship.

Cardiocondyla (Figs. 225-227)
Species examined: *C. elegans* 1 ☿.

Spiracular plate. No good preparation.

Quadrate plate. Body and apodeme both wide. Anterior and dorsal edges straight; meet perpendicularly.

Anal plate. Weakly sclerotized, about a third as long as wide, with numerous setae.

Oblong plate. (Fig. 225) Note anterior thickening of dorsal ridge, which is most like that of *Proatta butteli.* This character is also suggestive of OP sclerotization in *Vollenhovia* (Fig. 72) and some *Tetramorium* (Fig. 59).

Gonostylus. Much like that of *Tetramorium caespitum* (Fig. 60), but without terminal notch. Distinctly 2-segmented in sclerotization and setation. Many long setae on both segments.

Triangular plate. Body short, slender, but ventroapical process long, wide, rectangular. Dorsoapical process very low, bluntly rounded. Similar to TP of *Triglyphothrix,* but body narrower.

Lancet. Like that of *T. pacificum* (Fig. 62) but shorter, without rudimentary barb, less heavily ridged. Also similar to that of *P. butteli.*

Sting. (Figs. 226, 227) SS very short, high, but laterally compressed. Hemocoel very large, due to large internal ridge above VC. SBLB short, very convex. SB only shallowly arched.

Furcula. Lost in preparation.

Special remarks: The knife-like sting shaft of this species is unique in its extreme development.

Discussion:

Cardiocondyla was placed in its own monotypic tribe by both Emery (1922) and Wheeler (1922). Sting apparatus morphology suggests relationships with *Proatta butteli* and the Tetramoriini. The GO and LA are very much like those of some *Tetramorium spp.* The QP, OP, TP and sting could also be derived from the *Tetramorium* type of sting apparatus by reductions in length and sclerotization. The LA and part of the OP are also like those of *P. butteli.* See also *Proatta butteli* discussion.

Tranopelta (Figs. 228-231)
Species examined: *T. gilva* 2 ☿.

Spiracular plate. (Fig. 228) Roughly fusiform with obliquely truncate ventral end. Posteroventral corner tuberculate; in one preparation, closely associated with basal end of QP and dorsoapical process of TP.

Quadrate plate. Apodeme narrow, uniform in width; anterior edge straight, dorsal edge slightly concave; anterodorsal corner short, pollicate. Body narrow dorsad, abruptly ends about midlength of apodeme. QP very much like that of *Stenamma* near *manni* and *Veromessor andrei*.

Oblong plate. (Fig. 229) Anterior apodeme very long, narrow, as in *Messor* (Fig. 132), *Aphaenogaster*, *Veromessor*, some *Pheidole* species (Fig. 149). Ventral arm most similar to those of *Acanthomyrmex* cf. *notabilis*, *Veromessor andrei*, and *Stenamma diecki*.

Gonostylus. Very short, wide in both directions, broadly rounded apically. Few short setae scattered over distal half of dorsal surface; in some preparations uniformly distributed, in others bimodally. Dorsoterminal chaeta and companion seta at very end of GO; much larger than other sensilla.

Triangular plate. Body long, narrow, uniformly tapered basad, ventroapical process also long, narrow, tapered. Dorsoapical process prominent, subacute.

Lancet. Short, weak, evenly tapered to subacute apex. Ventral ridge and groove distinct, convergent to very end. Dorsal lamina very low.

Sting. (Figs. 230, 231). SS short, stout, weak, blunt. Hemocoel of SS large, due to large internal expansion of outer dorsal wall. SBLB long; SB well arched, with weak basal ridge.

Furcula. (Figs. 230, 231) Y-shaped, but with very small dorsal arm. Extremities of lateral arms enlarged in transverse dimension.

Discussion:

I find it difficult to align the sting apparatus of *Tranopalta gilva* with that of any genera generally considered related. These are the genera I have placed in the *Solenopsis* and *Vollenhovia* groups, plus *Trigonogaster*, *Pheidologeton*, and *Oligomyrmex*. The QP, OP and SBLB shapes suggest an affinity with the *Pheidole* group, but differences in the SS and FU (particularly the SS hemocoel) prevents me from firmly associating *T. gilva* with the *Pheidole* group.

Oligomyrmex (Figs. 232-234)
Species examined: *O. corniger (sodalis?)* 2 major ☿, 8 minor ☿.

Spiracular plate. Subtriangular due to merging of posterior and dorsal edges into nearly straight line. Similar SP to that of *Pheidole sp.* 3 (Fig. 148), but without posteroventral tubercle.

Quadrate plate. Poorly preserved in all specimens. Apodeme and body both seem wide. Anterior edge straight, dorsal edge convex, with prominent lateral lobe. Anterodorsal corner with short subacute process. QP length is diphenic between majors and minors, but it is negatively allometric compared to pronotal width (slope of allometric regression line: 0.77, $n = 6$).

Oblong plate. Dorsal ridge and anterior apodeme like that of *Tranopelta gilva* (Fig. 229) and *Pheidole morrisi* (Fig. 149). Ventral and posterior arms fused as in *P. morrisi*, but much wider dorsoventrad. Similar also to *Mycetophylax emeryi* and *Pheidologeton* cf. *diversus*. FA a diffuse horizontal ridge in minor workers; in majors with bulbous base and ill-defined dorsal extention along posterior edge, much as in *P. diversus*.

Gonostylus. Like that of *M. aciculata* (Fig. 134), but shorter, and with companion seta.

Triangular plate. (Fig. 232) Construction of body unusual. Either body greatly reduced and replaced by dorsal end of ramus, or ramus broadly overlaps body of plate laterally. Both apical processes long.

Lancet. Short, but well sclerotized, acute. Dorsal ridge present at apex. Lamina equally developed. Symmetrically acute apex and dorsal ridge similar in appearance to that of *Leptothorax* (Fig. 54).

Sting. (Figs. 233, 234) Note stout SS with well developed hemocoel, large internal tubercle in VC area and well developed basal ridge. Sting length is diphenic between the 2 castes, but is negatively allometric relative to pronotal width (slope of allometric regression line: 0.33, n = 6). The SBLB is relatively wider in major workers (SBLB width/sting length, smallest to largest workers: 0.20, 0.19, 0.19, 0.26, 0.32).

Furcula. (Figs. 233, 234) Concave posterior surface fits tightly over end of SBLB.

Discussion:

See *Pheidologeton* discussion.

Pheidologeton (Figs. 235-236)
Species examined: *P.* cf. *diversus* (North Celebes) 2 minor ☿ (MCZ).

Spiracular plate. Shape similar to that of *Oligomyrmex corniger* but longer, less triangular, with long digitate posteroventral tubercle that may articulate with TP. Medial connection completed by dorsal extension of body (as in *Atopomyrmex mocquerysi*) rather than by extension of anterior apodeme.

Quadrate plate. Most similar to that of some Attini, particularly *Apterostigma*. Anterior and dorsal edges very concave; anterodorsal process long, pollicate, directed anterodorsad. SP fits into anterior edge as in higher Attini. Apodeme narrow, uniformly more sclerotized than body. Body about twice as wide as apodeme.

Oblong plate. Similar to that of *O. corniger* majors, but with shorter anterior apodeme.

Gonostylus. Very short; basal half wide, tapers rapidly to subacute apex. Sensilla few; depending upon absence or presence of a single seta, there may or may not be a gap in setal pattern. Seta nearest dorsoterminal chaeta longer than others; may be companion seta.

Triangular plate. Like that of *O. corniger* (Fig. 232), but with more slender body.

Lancet. Short, weak, evenly tapered to subacute tip. Groove extends to end of LA, does not closely parallel ventral ridge. Dorsal lamina slightly higher than ventral lamina.

Sting. (Figs. 235, 236) SS extremely short, weak. SBLB slender, very long. SS hemocoel very reduced. Outer dorsal wall without large internal tubercle above VC area. SB very low; truncate in ventral view.

Furcula. (Figs. 235, 236) Bar-shaped; adnate to SBLB. Lateral extremities wrap around sides of SBLB.

Special remarks: The sting shaft is very reduced relative to the size of the individual (at least in minor workers — see Appendix A, column 41).

Discussion:

Emery (1922), Wheeler (1922), and Ettershank (1966) all associate *Pheidologeton* and *Oligomyrmex*. The shapes of The SP, OP, and TP are similar in the two species I have examined (TP shape is unique), but the LA and stings are very different. *O. corniger* probably retains the ability to sting, while *P.* cf. *diversus* has lost it. It is possible that the differences in their sting apparatuses are due to the reduction of the *P.* cf. *diversus* sting and LA following the loss of stinging function, but at present, that scenario requires too much imagined reshaping of the *O. corniger* sting to be comfortable. In the future a convincing intermediate may be found.

These two genera have been placed either with *Trigonogaster* in a separate tribe (Emery, 1922), or with the Solenopsidini Wheeler, 1922). The sting apparatus morphology offers no support for these classifications, nor does it rule them out.

Myrmecina (Figs. 237-239)
Species examined: *M. graminicola* 2 ☿.

Spiracular plate. (Fig. 237) No definite dorsal edge; posterior edge continues dorsad, gradually becoming membranous. Posteroventral tubercle very enlarged; whether or not it articulates with TP is unclear in my preparations. Medial connection nearly complete.

Quadrate plate. (Fig. 237) Narrow, every elongate. Similar to that of *Cataulacus tardus*, but with much shorter anterodorsal process. Roughly similar to that of *Atta cephalotes* and *Trachymyrmex seminole* (Fig. 212), but dorsal edge and anterodorsal process different.

Oblong plate. (Fig. 237) Small, weakly sclerotized, with almost nonexistent FA, and fused dorsal and ventral arms; most similar to that of some *Pheidole* minor workers (Fig. 149), and *Mycetophylax emeryi*. Anterior apodeme low, denticulate.

Gonostylus. Short; dorsal surface narrowly triangular; lateral surface narrow. Sensilla on lateral surface. Several long setae accompany dorsoterminal chaeta, but other proximal setae just as long. No obvious companion seta.

Triangular plate. (Fig. 237) Body short, wide; basal stalk nearly perpendicular to body. Apical processes long, slender.

Lancet. Slender, weak, end truncate. Groove and ventral ridge very closely parallel, possibly fused distad. Dorsal lamina with row of very fine, widely spaced denticles along its dorsal edge. Denticles directed caudad.

Sting. (Figs. 238, 239) SS very weak; hemocoel almost completely lost. SBLB long, wide. Basal ridge reduced mesad.

Furcula. (Figs. 238, 239) Dorsoventrally flattened, tightly appressed to SBLB, as in the Attini.

Special remarks: The sting apparatus is very reduced in size relative to the size of the ant (Appendix A, column 41).

Discussion:

Emery (1922) places *Myrmecina* in the tribe and subtribe Myrmecinini along with *Pristomyrmex* and *Acanthomyrmex*. Wheeler (1922) lengthens the list of relatives to include *Atopomyrmex*, *Podomyrma*, and *Lordomyrma*. The sting apparatus of *M. graminicola* betrays no hint of relationship with these genera (see also *Pristomyrmex* discussion). The sting apparatus most resembles that of the advanced Attini, but the similarities are probably convergent due to reduction of the apparatus. The ants are very different in external morphology.

Ocymyrmex (Figs. 240-243)
Species examined: *O.* cf. *arnoldi* (Victoria Falls, Rhodesia) 4 ☿ (MCZ).

Spiracular plate. Similar in shape and size of plate and spiracle to that of *Myrmicaria arachnoides* (Fig. 170), but with nearly complete medial connection and distinct dorsal notch, much as in *Messor aciculata*. Similar also to SP of *Cephalotes atratus*, but plate narrower and medial connection incomplete.

Quadrate plate. Subtriangular shape of apodeme and ventrally emarginate body similar to those in *Veromessor andrei*, but both body and apodeme much wider. Anterodorsal corner square.

Anal plate. Extremely short, wide, weakly sclerotized; but anal setae long. Similar plate seen in Cephalotini, but less sclerotized.

Oblong plate. Dorsal half of plate similar to that of *Myrmicaria* (Fig. 172), but anterior apodeme long and digitate. Ventral arm slender, club shaped; FA comma-shaped; similar to that of *Stenamma* near *manni*.

Gonostylus. (Fig. 240). In dorsal view, evenly tapered from base. Sensilla long, dense; occur distal to dorsoterminal chaeta. Setation dense as in some species in *Pheidole* group (Fig. 151) and Cephalotini (Figs. 192, 199).

Triangular plate. Body long, slender, evenly tapered. Ventroapical process low, rounded.

Lancet. (Fig. 241). Very short, wide, weak. Both dorsal and ventral laminae well developed. Similar to LA of *Adelomyrmex* (Fig. 167), but much shorter.

Sting. (Figs. 242, 243) SS very short, weak, evenly tapered in both directions to fine point. SBLB shape in lateral and ventral views much like that of *Prodicroaspis sarasini*. Basal notch borderline between open and closed.

Furcula. (Figs. 242, 243) V-shaped; arms do not curve strongly caudad.

Special remarks: The sting shaft, and possibly the rest of the apparatus, is smaller relative to the size of the ant than in any other species examined (Appendix A, column 41).

Discussion:

In the classifications of Emery (1922) and Wheeler (1922), *Ocymyrmex* stands alone in its own tribe. So far the sting apparatus supports this unique standing. It seems to have a shortened version of the *Promeranoplus* genus group type of sting. But the SP, AP, LA and GO seem to resemble those in some peripheral genera of the *Pheidole* group. The apparatus as a whole does not look as though it belongs to either genus group at present.

Part I

Table 5 shows Emery's (1922) classification (updated to include new genera) of the myrmicine genera in this study. Table 6 and Fig. 244 illustrate phylogenetic relationships of the same genera as

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TABLE 5

A partial listing of Emery's (1922) classification of the Eumyrmicinae (with spelling corrections and new tribes). Only genera in this study are included.

1. Myrmicini
    - *Pogonomyrmex*
        - Subg. *Pogonomyrmex*
        - Subg. *Ephebomyrmex*
    - *Myrmica*
        - Subg. *Myrmica*
        - Subg. *Manica*
2. Pheidolini
    - *Stenamma*
    - *Aphaenogaster*
    - *Messor*
    - *Pheidole*
3. Stereomyrmecini
    - *Stereomyrmex*
4. Myrmicariini
    - *Myrmicaria*
5. Cardiocondylini
    - *Cardiocondyla*
6. Crematogastrini
    - *Crematogaster*
7. Solenopsidini
    - *Vollenhovia*
    - *Monomorium*
        - Subg. *Chelaner*
        - Subg. *Monomorium*
        - Subg. *Holcomyrmex*
        - Subg. *Oxyepoecus*
    - *Megalomyrmex*
    - *Tranopelta*
    - *Solenopsis*
8. Pheidologetini
    - *Trigonogaster*
    - *Pheidologeton*
    - *Oligomyrmex*
9. Meranoplini
    - *Prodicroaspis*
    - *Calyptomyrmex*
    - *Promeranoplus*
    - *Meranoplus*
10. Myrmecinini
    - *Pristomyrmex*
    - *Acanthomyrmex*
    - *Lordomyrma*
    - *Podomyrma*
    - *Atopomyrmex*
11. Leptothoracini
    - *Leptothorax*
    - *Rogeria*
    - *Adelomyrmex*
    - *Lachnomyrmex*
12. Ocymyrmecini
    - *Ocymyrmex*
13. Tetramoriini
    - *Triglyphothrix*
    - *Tetramorium*
14. Cataulacini
    - *Cataulacus*
15. Cephalotini
    - *Cephalotes*
    - *Eucryptocerus*
    - *Cryptocerus*
        - Subg. *Zacryptocerus*
        - Subg. *Eucryptocerus*
    - *Procryptocerus*
16. Dacetini
    - *Daceton*
    - *Orectognathus*
    - *Neostruma*

17. Basicerotini
  Basiceros
  Octostruma
  Eurhopalothrix
18. Attini
  Proatta
  Apterostigma
  Cyphomyrmex
    Subg. *Cyphomyrmex*
    Subg. *Trachymyrmex*
  Atta

TABLE 6

Generic groups based on apparent affinities of the sting apparatus as viewed in this study.

Myrmica group
  core genera
    Myrmica
    Manica
    Ephebomyrmex
    Hylomyrma
    Pogonomyrmex
  peripheral genera
    Huberia
    Stereomyrmex
    Podomyrma
19. Dacetini
    Daceton
    Orectognathus
    Neostruma
20. Basicerotini
    Basiceros
    Eurhopalothrix
    Octostruma
Leptothorax group
    Leptothorax
    Macromischa
21. Tetramoriini
    Tetramorium
    Triglyphothrix
Vollenhovia group
    Liomyrmex
    Vollenhovia
Solenopsis group
  core genera
    Chelaner
    Oxyepoecus
    Rogeria
    Solenopsis
  peripheral genera
    Holcomyrmex
    Monomorium
    Megalomyrmex
    Calyptomyrmex
    Wasmannia
Promeranoplus group
    Promeranoplus
    Prodicroaspis
    Lordomyrma
Pheidole group
  core genera
    Messor
    Aphaenogaster
    Veromessor
    Stenamma
    Pheidole
  peripheral genera
    Acathomyrmex
    Cyphoidris
    Lachnomyrmex
    Adelomyrmex
    Myrmicaria
    Meranoplus
    Crematogaster
    Trigonogaster
22. Cephalotini
    Cephalotes
    Eucryptocerus
    Procryptocerus
    Zacryptocerus
23. Cataulacini
    Cataulacus
24. Attini
    Cyphomyrmex
    Mycetophylax
    Apterostigma
    Atta
    Trachymyrmex
Unplaced genera
    Atopomyrmex
    Pristomyrmex
    Proatta
    Cardiocondyla
    Tranopelta
    Oligomyrmex
    Pheidologeton
    Myrmecina
    Ocymyrmex

indicated by the sting apparatus (some genera of poorly known affinities are omitted from Fig. 244). See discussions at the end of each tribe, group or genus in the results section for the reasoning behind the branching pattern. Throughout the investigation, external morphology was consulted to check the feasibility of relationships suggested by the sting apparatus comparisons, but final decisions generally rested on the latter. Since the scheme is so largely based on a single character system, it is not meant to replace any preexisting classification, and should only be regarded as an alternate hypothesis.

The following relationships of the existing classification are supported by the sting apparatus morphology:

1) *Ephebomyrmex, Hylomyrma,* and *Pogonomyrmex* are closely related, and in turn, close to *Manica* and *Myrmica*.

2) Dacetini and Basicerotini are distinct from other myrmicines. *Daceton* is very primitive.

3) *Leptothorax* and *Macromischa* are closely related.

4) *Tetramorium* and *Xiphomyrmex* are not distinguishable. *Tetramorium* and *Triglyphothrix* are very closely related.

5) *Vollenhovia* and *Liomyrmex* are probably separate from other «solenopsidine» genera (see Ettershank, 1966).

6) *Chelaner, Oxyepoecus, Solenopsis* are related.

7) *Promeranoplus* and *Prodicroaspis* are closely related.

8) *Aphaenogaster* and *Messor* are closely related; related also to *Veromessor, Pheidole,* and possibly *Stenamma.*

9) *Adelomyrmex* and *Lachnomyrmex* are related.

10) *Cephalotini* and *Cataulacini* are probably distinct tribes.

11) *Crematogaster* is quite distinct from all other genera.

The following changes in the existing classification are suggested by comparisons of the sting apparatus:

1) *Stereomyrmex, Podomyrma,* and *Huberia* may belong to the *Myrmica* genus group.

2) *Basicerotini* and *Dacetini* may be more closely related than previously suggested. They may have originated near *Leptothorax* and *Tetramorium*.

3) *Leptothorax* group and *Tetramoriini* may be closely related.

4) *Triglyphothrix* may not be distinct from *Tetramorium*.

5) *Vollenhovia* and *Liomyrmex* may be related.

6) *Calyptomyrmex* and *Wasmannia* may be related, and in turn related to the *Solenopsis* group.

7) *Rogeria* probably should be included with *Solenopsis* group closest to *Oxyepoecus* and *Chelaner,* less so to *Solenopsis*.

8) The New World *Rogeria* and Old World *Rogeria stigmatica* group may be distinct genera.

9) *Chelaner* and *Oxyepoecus* seem more similar than indicated by Ettershank (1966).

10) *Monomorium (Monomorium)* and *Monomorium (Holcomyrmex)* may be distinct genera although they were placed as subgenera by Emery (1922) and synonymized by Ettershank (1966).

11) *Lordomyrma* is closely related to *Promeranoplus* and *Prodicroaspis.*

12) *Acanthomyrmex, Cyphoidris, Lachnomyrmex, Adelomyrmex, Myrmicaria, Meranoplus, Crematogaster, Trigonogaster,* and *Ocymyrmex* may be peripherally related to the Pheidolini.

13) *Acanthomyrmex* may actually belong to the Pheidolini.

14) *Cyphoidris, Lachnomyrmex,* and *Adelomyrmex* seem to be a closely related unit.

15) *Cataulacus* and the Cephalotini may have had a common origin in the Pheidolini.

16) Present positions of the following genera are questioned, but no strong alternatives are offered: *Atopomyrmex, Pristomyrmex, Proatta, Cardiocondyla, Myrmecina.*

17) The affinities of the Attini remain unknown.

These suggestions are based on a small sample of species in each genus (see introduction). How much weight we can give to the characters used will depend on what further studies tell us of their variability within species and genera.

In my samples, there is usually little variation in the sting apparatus within a species, especially among workers of the same caste. The most variable characters are counts of sensilla on the GO, IV, R2, and FA. These counts often differ slightly between 2 sides of the same sting apparatus. The shape of the TP also seems to vary among individuals, but the apparent variation may sometimes be due to its orientation in the preparation.

There is no obvious variation in shape of sclerites between the workers and the queens of *Promeranoplus sp.* 2 and *Lachnomyrmex scrobiculatus,* even though the apparatus is somewhat larger in the queens. In no other species are both castes described.

There are some differences in shape and size between different worker castes of the same species. The absolute size of the sting apparatus is larger in larger workers of *Messor sp.* 1, *Pheidole sp.* 3, *Monomorium scabriceps* and *Oligomyrmex corniger,* but its relative size is smaller in the larger workers (based on measurements of QP, sting length and pronotal width). The ratio of SBLB width/sting length does not vary between *Messor sp.* 1 castes, but is larger in soldiers of *Ph. sp.* 3 and *O. corniger,* and smaller in soldiers of *M. scabriceps.* That is, the sting bulb is relatively wider in *Ph. sp.* 3 majors and *O. corniger* majors, but relatively narrower in *M. scabriceps* majors. Sensilla counts on the GO, IV, and R2 are always larger in the larger workers of polyphenic species. In addition, the major and minor workers of *Pheidole spp.* differ in length of the spine on the SP, the presence of a lateral lobe on the QP, the degree of fusion of posterior and ventral arms of the OP, and in SBLB, SB, and FU shape and degree of FU fusion to SB. The majors of *M. scabriceps* have a more strongly sclerotized sting and lancets, and less obvious bimodal arrangement of sensilla on the GO (because more setae are present), but otherwise vary little in shape. In *O. corniger*, the width of the SBLB is the only difference is shape between majors and minors. In *Messor sp.* 1, I see no obvious shape differences between castes.

In several species, *Pristomyrmex brevispinosus* and *Cyphoidris spinosus*, specimens came from separate collections. No particular difference is seen between the 2 collections of the former genus. But in *C. spinosus*, the SBLB shape and GO segmentation differ slightly.

There is much more variation between species in the same genus. As one would expect from the discussion of intraspecific variation, counts of sensilla nearly always differ between species. Plots of sensilla number made against some measure of body size (*e.g.*, pronotal width) indicate that the number of sensilla in the GO, IV, and R2 are in part a function of body size. Larger species within genera tend to have more sensilla. Most intrageneric variation in shape is confined to the SP (particularly the anterior apodeme), the anterodorsal corner of the QP, the TP, and the anterior apodeme of the OP. Fewer congeneric species vary in shape of the rest of the OP and shape anl degree of segmentation of the GO. Most species of the same genus have the same sting and LA shape. However, in *Tetramorium, Pheidole, Crematogaster,* and *Lordomyrma,* species do differ in these sclerites. In *Tetramorium* the end of the SS varies in presence of accessory lobes; the LA differs in shape of the apex. In *Crematogaster* the dorsal flange is also the main variable character, but the VC height is different in one species. In *Pheidole,* modifications occur in shape of the SBLB and SB, but the same degree of modification can be seen between castes of the same species. In the last three genera the variation, though at first striking, does not affect the important features of the sting and LA. In *Lordomyrma* the differences are more serious because they affect the basic form of the sting and lancets, and probably their function, and the taxonomic value of the sting and LA is therefore more questionable.

Intrageneric variation is remarkable between some species in *Rogeria* and *Monomorium,* and includes major differences in the sting, LA and GO. Such structural divergence usually occurs at the generic level. For that reason, I question whether the species involved are congeneric.

The intergeneric variation of the sting apparatus is often considerable. For that reason, and because there is generally much less variation within genera, I believe that the sting apparatus is useful in characterizing some genera and tribes and in establishing phylogenies. But unrelated genera may show convergent developments due to similar selection pressures in the apparatus. In the remainder of Part I some general trends in sting apparatus evolution are described in order to give future workers an idea of where to expect convergences.

The sting apparatus of the primitive ponerine, *Amblyopone pallipes*, is described in the results to help establish the primitive characters in the Formicidae and Myrmicinae.

The archetype of the Myrmicinae probably had the following sting apparatus description: Spiracular plate (SP) large, about as long as broad; with deep dorsal notch; distinct posterodorsal corner; 1 large, well sclerotized posterodorsal lobe; large, uniformly wide anterior apodeme; complete medial connection (dorsal continuation of apodeme) and small spiracle near center of plate. Quadrate plate (QP) with body and apodeme wide (body especially wide ventrad, and produced below level of tergovalvifer articulation), anterodorsal corner prominent, medial and lateral lobes well developed. Anal plate (AP) well defined, about as long as broad, dorsal surface covered with many setae, fewer s. basiconica. Posterior arm of oblong plate (OP) with wide dorsal ridge that does not extend beyond body but does have subterminal tubercle; body wide, well sclerotized. Ventral arm short, high; fulcral arm (FA) long, straight, vertical, well defined and sclerotized, with wide base. Postincision (PI) deep, nearly reaching intervalvifer articulation (IV). Anterior apodeme of oblong plate long, transversely spatulate. Gonostylus (GO) with 2 well sclerotized, articulating segments; distal segment shorter, narrower; sensilla bimodally distributed, with distinct gap, with many setae, some chaetea, probably some basiconic and companiform sensilla, without dorsoterminal chaeta or companion seta. Body of triangular plate (TP) long, wide; apical processes short, stout; dorsal and medial tubercles distinct. Lancet (LA) long, slender, well sclerotized, upcurved, acute with many small barbs and possibly campaniform sensilla at apex; groove and ventral ridge heavy, wide; dorsal lamina thin, without ridge. Valves 2 per lancet, subequal in size and sclerotization, prominent, but not enlarged. Sting gradually decreases in diameter caudad; no abrupt differentiation of parts in profile or ventral view. Sting shaft (SS) long, gently tapered, upturned, acute, heavily sclerotized, with well developed hemocoel and companiform sensilla present to tip. Valve chamber (VC) well developed, much longer than high, internal apophysis short, weak, covered with campaniform sensilla. Sting bulb (SBLB) subequal in length to VC, and slightly higher. Sting base (SB) moderately well arched, with well developed basal ridge and prominent anterolateral processes. Basal notch short, low, open. Articular processes short, directed anteriad. Furcula (FU) Y-shaped, free; dorsal and lateral arms subequal in length and width.

Arising from such an ancestor I see 4 basic grades of evolution within the Myrmicinae. These grades do not have distinct boundaries; there are always intermediates. Grade 1 is primarily represented by the *Myrmica* core group of genera, and has most of the characters listed for the hypothetical ancestor. Note especially that the sting apparatus is well sclerotized. The sclerites are large, with well developed muscle insertions. The SS is upcurved and has campaniform sensilla present to the very end. The VC, SBLB, and SB are relatively low. The aculeus is heavily sclerotized and able to pierce arthropod cuticle. Grade 2 species are also able to sting.

But the sting apparatus is not so heavily constructed. The width of the QP, SP, and posterior arm of the OP tends to be reduced. The muscle insertions on these and the TP are reduced in size and sclerotization. The GO tends to decrease in length, sclerotization, and setation; its 2 segments tend to fuse. The LA loses its barbs. The sting becomes straight or curved ventrad. Campaniform sensilla drop out, beginning at the distal end of the SS and proceeding anteriad. There is a dichotomy in the grade 2 stings with respect to the VC and SBLB shapes. In some they remain low and slender and the SB and basal notch decrease in height (Dacetini, Basicerotini, *Leptothorax* group, Tetramoriini, some in the *Vollenhovia* group, *Oligomyrmex*). In others the VC, SBLB, and SB or basal notch tend to dilate (some species in the *Vollenhovia* group, *Calyptomyrmex, Wasmannia,* primitive species of the *Solenopsis* group, *Promeranoplus* group, *Tranopelta, Proatta*).

Out of this second group of the grade 2 species the grade 3 type of sting apparatus seems to have evolved. The grade 3 species tend to have an even more enlarged VC and SBLB. The SB and FU are more strongly arched; the dorsal arm of the FU, and the SB basal ridge are reduced or lost; the basal notch is longer. The aculeus is even less strongly sclerotized. It loses its piercing function and with the loss of the FU dorsal arm, its mobility (Hermann and Blum, 1967b). But it usually remains long or may even lengthen (relative to the size of the ant), and the ends of LA and SS tend to become spatulate. Representative of this group are primitive species in the *Pheidole* group, *Acanthomyrmex, Meranoplus, Cyphoidris, Lachnomyrmex, Myrmicaria, Adelomyrmex, Crematogaster* and *Pristomyrmex.*

Finally, in grade 4, the SP, QP, and OP become even thinner and weaker. The 2 arms of the OP tend to fuse. The SP and QP may intermesh in jig-saw puzzle fashion, rather than broadly overlap. The GO gets shorter, wider, and weaker, with fewer sensilla. The TP may remain relatively larger than in more primitive grades. The aculeus becomes weaker, shorter, evenly tapered to its apex. The VC is highly reduced or absent. The SBLB is disproportionately long, often very wide. The SB becomes less arched, and with it the FU becomes roughly bar-shaped. In advanced stages the FU may be partially or completely membranous. Representatives of this grade are the advanced species in the *Pheidole* group, *Cataulacus,* the Cephalotini, advanced Attini, *Pheidologeton, Myrmecina, Atopomyrmex,* and *Rogeria spp.* 1 and 2 (*stigmatica* group). Some grade 4 type apparatuses probably came directly from a grade 2 type apparatus ,others passed through grade 3 (e.g., *Zacryptocerus spp., Pheidole spp.*).

Through the sequence of events outlined above, the shape ot the sting apparatus as a whole is also transformed. In grade 1, the QP, SP, OP, and TP of opposite sides are close to the midline and roughly parallel to the midsagittal plane. Through grades 2 and 3 the anteriormost portions of the sting apparatus (TP, anterior edges of SP and QP) spread farther apart. In some grade 3 and 4 species, (*Messor,* Attini, Cephalotini) the 2 halves of the sting apparatus are almost perpendicular to the sagittal plane, and are flattened against the 7th tergum and sternum.

The trends in reduction described here were also observed by Foerster (1912) in his broader survey of the Formicidae. From his descriptions, the Dorylinae would fall into grade 2 and the Dolichoderinae into grade 4. The highly reduced and modified sting apparatus of the Formicinae would represent an even more advanced grade of evolution.

Part II

What characteristics of the myrmicine radiation could explain the pattern of evolution described above? Dr. W. L. Brown has suggested that the radiation of the Myrmicinae was based on their ability to incorporate vegetable matter into their diet (personal communication). This general adaptation freed them from dependence upon a single source of food (small live arthropods), increased their adaptibility by providing a secondary food source during times of low arthropod abundance, and greatly broadened the range of niches they could exploit. The acquisition of plant-product feeding probably accounts for many of the changes seen in the myrmicine sting apparatus. With decreased dependence on live arthropod food, selection pressures maintaining the aculeus as an offensive weapon would be released or diminished. The first effect of that release may have been to cause the aculeus to shorten, straighten and ultimately become weak and blunt. Foerster (1912) also suggested disuse to account for sting reduction in the Formicidae. A second result was to make the sting apparatus susceptible to other selection pressures that could modify its form and function.

The ramifications of the loss of stinging ability on the biology and morphology of the Myrmicinae, Dolichoderinae, and Formicinae are probably far-reaching. I will discuss here only the more immediate effects as I see them. The primitive myrmicine aculeus probably has 3 functions: trail-laying, personal and colony defense, and subduing of prey. In non-stinging ants we would expect to see compensatory adaptations to take over some or all of these functions.

First of all, reduction or modification of the sting does not prevent the formation of recruitment trails. In the Formicinae and advanced Myrmicinae, trail-laying is common, and «the great majority, perhaps all, of the Dolichoderinae employ trails» (Wilson, 1971: 258). Species of *Monomorium, Tetramorium, Messor, Pheidole, Veromessor, Zacryptocerus* and *Atta* all lay trails from the end of the gaster, presumably through the sting. In other ants the trail pheromone may not be released through the sting. Its source is the tibial glands in *Crematogaster,* the hindgut in the formicines, and Pavan's gland in the dolichoderines (see Wilson, 1971: 257 for references). Although trail-laying behavior is not lost in non-stinging ants, it may be that there is a tendency for the trail pheromone to be produced and applied in alternate ways when the sting shaft is highly reduced (*e.g.*, Dolichoderinae and Formicinae), or highly modified for other functions (*e.g.*, *Crematogaster* — see below).

One can see several compensatory adaptations for defense in non-stinging ants. Biting mandibles are already used to some degree for defense in stinging ants, and with the loss of a potent sting one would expect to see more mandibular specialization for fighting. The falcate mandibles of the obligate dulotic formicine *Polyergus* are a good example of this kind of specialization (although they are used for offense rather than defense). It must be noted that the *Polyergus* mandibles can no longer perform many of the normal mandibular functions, and that this ant is totally dependent upon its slaves for brood and nest care. Probably for that reason other species have evolved specialized castes for mandibular defense. Defensive soldier castes are well developed in *Pheidole* (Creighton and Creighton, 1959; Law *et al.*, 1965; Wilson, 1975). The soldier is larger, has a disproportionately larger head, and shearing or crushing mandibles. In at least some species, the soldier also has a different glandular morphology and chemistry from the minor workers. The soldier is also behaviorally distinct. It is often more aggressive against intruders, but except in time of colony defense appears to do little for the colony. It tends to stay in the nest or within a small radius of it. In *Pheidole dentata* the soldiers do not lay trail pheromones, and in *Pheidole militicida* they do not forage for seeds or husk or crush them in the nest. In an *Atta* colony «the soldiers very rarely cut or carry leaves or other objects. They sometimes go out on trails or cluster around nest entrances, but their primary function is to quard the colony» (Weber, 1972: 16). It is they who rush to the site of a disturbance; the minors often freeze or flee danger. The media workers do most of the leaf-cutting. Whether or not defensive polyethism is present in other polyphenic non-stinging genera has not been examined. It may be present in *Pheidologeton ocellifer,* where the huge soldiers appear to do nothing, but on the other hand the soldiers do not seem pugnacious (Wroughton, 1892).

Defensive polyphenism and polyethism are seen in some stinging ants, *e.g.,* the dorylines *Labidus* and *Eciton* (Shneirla, 1971: 39-40, 267-70). But the sting is probably not potent enough in these species to offer much protection. Hermann and Blum (1967b) say that the sting of *Eciton humatum* is not strong, nor is its effect very painful to humans.

Sting reduction is not the only factor that promotes polyphenism. Large-headed workers of *Pheidole ridicula* are also used to crush seeds (Creighton, 1966). It is not known how widespread this behavior is, but large-headed workers are common among granivorous species (including *Pogonomyrmex spp.,* which have a well developed, powerful sting). Seed crushing is apparently not the function of major workers in at least some of these granivorous species (Brown, personal commnication).

Thus sting reduction and poyphenism are not mutually exclusive, and their presence in any given species is determined by a variety of selection pressures. I would expect a greater frequency of defensive polyphenism in species that have a weak sting.

Chemical defenses also increase in frequency following the loss of a stinging defense. This is clearly exemplified by the Dolichoderinae and Formicinae. The former subfamily produces a stickly substance and a powerful alarm pheromone in its anal glands (Wheeler, 1910: 45-46). The latter group sprays formic acid from an enormously hypertrophied poison gland reservoir, and produces an alarm pheromone in the Dufour's gland (see discussion and references in Wilson, 1971). In the Myrmicinae, chemical defenses are also common, but only the alarm component centered in the mandibular glands has been extensively explored. The morphology of the grade 3 sting seems to be adapted for dispensing defensive allomones. Buren (1958) was the first to note the unique sting morphology of *Crematogaster* and to suggest its function in the well-known defensive posture of this ant. My observations corroborate his hypothesis. The spatulate appendage on the sting shaft, possibly together with the spatulate lancets (Figs. 182, 183) hold a droplet of fluid on the end of the aculeus. This fluid seems to have a repellent effect at a distance on other ants. If the droplet is wiped onto an intruder, the recipient immediatedy commences self-grooming. The fluid seems to become more viscous aftter removal from the sting. *Crematogaster* species repel much larger ants from a honey bait merely by aiming a droplet loaded sting at the intruder. Furthermore, the high mobility of the petiole and the habit of raising the gaster well over tre allotrunk, enables these ants to place a droplet directly into the mouthparts of a larger ant. *Monomorium minimum* is probably not closely related to *Crematogaster* but has an analogous chemical defense. It cannot raise its gaster over its allotrunk; nor does its sting have a spatulate appendage. But its lancets (Fig. 98) are weak and spatulate; and it does point a droplet laden aculeus at an offender. Other ants are repulsed at a distance, and when contacted with the droplet become sticky and begin grooming. *Monomorium* is an aggressive competitor for food. It lays strong recruitment trails and can drive much larger *Pheidole* and *Pogonomyrmex* species from baits by virtue of its chemical defense (or offense) and its greater numbers.

It would be interesting to know if other grade 3 species that have aculeus structures analogous to those of *Crematogaster* and *Monomorium* show analogous behaviors. There are indications that they do. Collingwood (1970: 377) describes how *Meranoplus bicolor* workers (Figs. 177, 178) «... were seen to excrete anally a whitish substance which stiffened into threads when caught, these threads then building up into foam-like material rather as in *Philaenus* (Cicadina»). I have seen dried specimens of *Megalomyrmex foreli* workers in the MCZ collection with a large solidified droplet held between 2 large spatulate lancets and overtopped by the slender sting shaft. The persistence of this amorphous substance may indicate that when fresh it is viscous like that of *Crematogaster* and *Monomorium*. The end of the aculeus of *Myrmicaria* (Figs. 174, 175) is very similar to that of *Megalomyrmex* (Figs. 107, 109) and probably performs in the same way.

The function of the aculeus of *Tetramorium* and *Triglyphothrix* species (Figs. 62, 63, 65, 66) is more in question. These species have a well developed sting flange, but strong piercing lancets. The smaller lateral lobes on the end of the sting in some species must prevent the sting shaft from penetrating the wound made by the lancets and in this manner probably protect the large median flange from breakage. The median flange probably airs some defensive secretion. These ants may have evolved a chemical defense while retaining their ability to sting.

Grade 4 ants have chemical defenses also, but the allomones are not held on the end of the aculeus. *Rogeria stigmatica* (Fig. 92) produces a while vermiform filament from the end of its gaster when disturbed. The filament can be up to 20 mm long, and it twists and turns as it is extruded (Mann, 1919: 342-3; 1921: 451). Coyle (1966) reports defensive behaviors of some *Zacryptocerus* species. *Z. umbraculatus* raises its gaster to the vertical and produces a «clear malodorous fluid». *Z. multispinosus biguttatus* also raises its gaster and covers most of the gastric tergum with a «clear fetid fluid». *Z. multispinus* does not raise its gaster or produce any visible fluid, but acquires an odor similar to that of the other 2 species. *Pheidole fallax* soldiers produce skatole in hypertrophied poison glands; the minors neither have enlarged glands, nor do they produce detectable amounts of skatole (Law, *et al.,* 1965). Skatole has a strong fecal odor to humans, and may be used as a repellant allomone in the *Ph. fallax* soldiers.

As noted for *Ph. fallax,* enlarged glands accompany chemical defenses. Chemical defense is associated with an enlarged poison gland in the Formicinae and with enlarged anal glands in the Dolichoderinae. Compare also the sting associated glands in *Amblyopone pallipes* and *Basiceros singularis* with those of *Aphaenogaster phalangium, Monomorium minimum, Crematogaster minutissima,* and *Zacryptocerus multispinosus biguttatus* (Figs. 8, 49, 100, 144, 185, 201). The last 3 species have chemical defenses. *A. phalangium* may also employ allomones. The enlarged glands, in turn, have an effect on sting apparatus morphology. In grade 3 ants, the SBLB enlarges and the SB and FU arch and/or the basal notch widens to accomodate the large ducts from the poison gland reservoir and Dufour's gland (see Figs. 99, 138, 183, 184). The VC and lancet valves enlarge to pump large quantitites of fluid quickly. In grade 4 ants, where the sting shaft, is probably functionless, or nearly so, the SBLB retains a large meatus to accept the gland ducts, although the height of the SB, SBLB, and VC are greatly reduced (Figs. 200, 203, 213, 238). The gland contents are probably released by compression of the gaster. The Dufour's gland has no musculature, and the poison gland reservoir is surrounded by only a thin layer of muscles. In some grade 4 ants the whole sting apparatus may function as the closing mechanism of the glands, analogously to the formicine apparatus (Foerster, 1912: 368-371). The widening and flattening of the sting apparatus against the rear wall of the sting chamber, as described above, may be necessary to provide more room in the gaster for the enlarged glands.

Alarm pheromones are also an important component of defense (see Wilson and Regnier, 1971; Maschwitz, 1964b; and Ghent, 1961 for the different ways they are used), but their occurrence is not correlated with sting reduction. They are common in stinging Hymenoptera, including primitive ants (*e.g., Myrmecia gulosa*), bees and wasps (Maschwitz, 1964b). Furthermore they are apparently absent in at least some non-stinging myrmicines such as *Myrmecina graminicola* (Maschwitz, 1964a). Maschwitz (1964a, b, 1966) makes a good case for the correlation of alarm pheromones with high socal development and large colony size.

The final function of the primitive myrmicine sting is to subdue active prey. With the loss of a potent stinging ability, one would expect to see new methods of immobilizing prey. Soldier castes may be suitable for this function as well as defense. Soldiers of *Pheidole spp.* are used to carve large prey, and there are indications the *Pheidole titanis* soldiers aid in capturing termites (Creighton and Gregg, 1955). Doryline soldiers also hunt and help shred large prey. Chemical defenses may also have a dual function. The alarm pheromone of the slave raider *Formica subintegra* acts as propaganda substance to disperse defending adults of the slave species during raids. Formicine ants spray their defensive secretion, which includes formic acid, into wounds made by their mandibles. How common these types of behaviors are in the Myrmicinae is unknown. It is unlikely that the viscous defense substances of *Crematogaster, Monomorium,* and possibly other species' defenses are ever used to overcome prey. But, as mentioned above, it is clear that their chemical defenses are used offensively in competition with other ants.

A remarkable foraging behavior, well documented for *Oecophylla longinoda* (Gotwald, 1972), *Labidus praedator* and *Eciton burchelli* (Schneirla, 1971: 85) is «gang pulling». The unfortunate prey is surrounded and pulled in all directions until it succumbs or is torn apart. *O. longinoda* is a formicine and does not have a sting. *L. praedator* and *E. burchelli* have the strongest stings in the Dorylinae. But in *Eciton,* gang pulling is evidently only used to overcome «... scorpions and other large victims given to strong resistence...» (Schneirla, 1971). It is problable that the sting is not strong enough to be effective against such animals.

It is important to note that gang pulling requires cooperation between workers. Many ants of the higher subfamilies engage in group retrieval of prey (Wilson, 1958), but most Ponerinae and all Myrmeciinae do not cooperate in foraging (Wilson, 1971: 36-38; Gotwald, 1972; Hermann, 1973). Legionary ants are probably group predatory in order to capture larger prey and social insects (Wilson, 1958). Interestingly the non-stinging doryline genera, *Anomma* and *Dorylus,* attack victims in far greater numbers than the stinging dorylines (Schneirla, 1971: 29). The increase in group retrieval may be one of the most significant effects of sting reduction on the adaptive radiations of the Myrmicinae, Dolichodernae, and Formicinae. So far, it has received little attention beyond the legionary ants.

In summary, the Myrmicinae probably radiated because of their ability to incorporate vegetable food sources into their diet. Because of decreased dependence upon live prey, the sting shortened, straightened, and in some groups lost its stinging function. The loss of this function probably freed the sting apparatus for the development of defensive polyethism and/or chemical defenses in some genera. These defenses in turn led to morphological adaptations in the sting apparatus and in the external morphology of the ants. Finally, the loss of the ability to sting may have accompanied the evolution of group retrieval of prey in the higher subfamilies of ants.

CONCLUSIONS

The female terminalia have been useful in subdividing the order Hymenoptera. This is so because changes in their morphology reflect adaptive radiations of successive groups. The saw-like ovipositor of the tenthredinids and cephids is used to place eggs inside soft plant tissues. A longer, cylindrical ovipositor evolved in groups that exploited harder plant tissues. These ovipositors, in turn, were preadapted for parasitism. In groups where selection favored a shift in larval diet from relatively unnutritious plant tissue to the protein-rich tissue of other insect larvae encountered in the same stem, the parasitic Hymenoptera radiated. The long, slender, hypodermic-like ovipositor became used for piercing all manner of things: galls, pupae, eggs, and exoskeletons of live insects.

With the evolution of brood care in some parasitic groups, eggs and paralyzed host were placed together in some sort of nest. The female genitalia no longer needed to function as an ovipositor. In the aculeate Hymenoptera, it shortened and became specialized for the injection of a powerful toxin that would quickly subdue prey. The ovipositor became the sting. A special Y-shaped sclerite, the furcula, separated from the base of the sting in response to the need for greater mobility in probing for a sting site (Hermann and Blum, 1967b; Oeser, 1961). The sting was then preadapted for a defensive function. With the evolution of the social Hymenoptera and the greater need for nest defense, this function became more important (see Smith, 1970; Oeser, 1961; Machwitz and Kloft, 1971; and Robertson, 1968 for references and summaries of hymenopteran ovipositor evolution).

It is at this point in the evolution of hymenopteran female terminalia that we meet the primitive Formicidae. Ants in the subfamily Ponerinae use the sting to subdue active arthropod prey and for personal and colony defense. It is probably from the Ponerinae that the Myrmicinae evolved (Brown, 1954a; Eisner, 1957; Hermann, 1969: 132; see also dissenting viewpoint of Robertson, 1968). I believe that the radiation of this very successful group is also reflected in sting apparatus morphology. The remainder of this discussion will 1) summarize phylogeny and classification as indicated by the sting apparatus, and 2) show how the biology of the myrmicines may have affected the sting apparatus, and in turn, how these modifications of sting morphology may account for aspects of myrmicine biology.

KEY TO APPENDIX A

Spiracular plate (SP)

1. Medial connection
  ++ with completely sclerotized ridge (Figs. 2, 148).
  + ridge absent mesad, but present laterad (Fig. 71).
  — ridge completely membranous (Fig. 57).

2. Anterior apodeme width
  ++ some part very wide (Fig. 9).
  + reduced to narrow margin (Fig. 2).

3. Dorsal notch
  + present (Figs. 2, 35).
  — absent (Figs. 9, 43).

4. Posteroventral corner
  + very elongate, closely associated with ventral end of anterior ridge of quadrate plate; possibly articulating with triangular plate (Fig. 148).
  — absent or only a low tubercle, not noticeably associated with quadrate plate; obviously not articulating with TP (Fig. 9).

5. Posterodorsal lobe
  ++ very wide (Figs. 71, 120).
  + narrow (Fig. 9).
  — absent (Fig. 43).

6. Posterodorsal edge
  + distinct corner present, either rounded (Figs. 9, 57) or angular (Fig. 35).
  — posteroventral corner of plate reduced to membrane, and posterior and ventral edges reduced to a single arc or line between the anteroventral corner and posterodorsal corner (Figs. 96, 148).

Quadrate plate (QP)

7. Ventral width
    - \+ ventral width nearly equal to dorsal width (Fig. 44).
    - — ventral width about half of dorsal width, or less (Figs. 3, 18).

8. Apodeme area
    - \+ much larger than body of plate (Fig. 27).
    - = about the same as body (Fig. 44).
    - — much smaller than body (Fig. 3).

9. Posterior edge
    - \+ entire.
    - — emarginate (Fig. 188), or ventral portion abruptly excavated.

Anal plate (AP)

10. Definition
    - ++ whole perimeter well defined.
    - \+ only partially defined, usually lateral edges diffuse; or defined only by presence of sensilla.
    - — whole plate membranous, or nearly so; no edges discernable.

11. Sensillar location
    - md margin and dorsal surface; usually posterior margin and posterior portion of dorsal surface.
    - m margin only.

12. Sensillar types
    - t trichodea present.
    - c chaetica present.
    - b basiconica present.

Oblong plate (OP)

13. Posterior apodeme
    - ++ long (Fig. 32).
    - \+ short (Fig. 45).
    - — absent (Fig. 10).

14. Subterminal tubercle
    - \+ present (Figs. 10, 36).
    - — absent.

15. Ventral ridge of posterior arm
    - ++ wide, well sclerotized (Fig. 59).
    - \+ present, but narrow and not heavily sclerotized.
    - — absent.

16. Postincision (PI)
    - ++ extends far anterior to dorsal end of fulcral arm (Figs. 1, 32).
    - \+ present above dorsal end of fulcral arm, but not far anterior (Figs. 10, 23).
    - — does not extend around dorsal end of FA (Fig. 149).

Gonostylus (GO)

17. Number of segments
    - 1 only one segment indicated by sclerotization (Fig. 24).
    - 1-2 two segments not distinct, but indicated by thinning of cuticle at one point (Fig. 21).
    - 2 two distinct sclerotized segments (Figs. 4, 11).
18. Sensillar pattern
    - 2 bimodal, with distinct gap between 2 groups of sensilla (Figs. 60, 81).
    - 1-2 bimodal, but without distinct gap.
    - 2 unimodal (Fig. 24).
19. Terminal membranous flange
    - ++ long relative to length of gonostylus (Figs. 162, 166).
    - + present, but not remarkably long (Fig. 11).
    - — absent (Fig. 46).
20. Terminal sensilla
    - c dorsoterminal chaeta present (Fig. 21).
    - s companion seta present (Fig. 11).
    - — dorsoterminal chaeta and companion seta absent (Figs. 1, 24).
21. Sensilla basiconica
    - + present (Fig. 192).
    - — absent.

Triangular plate (TP)

22. Shape (width is maximum distance between ends of apical lobes; height is from highest point of dorsoapical process to ventral edge of bend at base of TP).
    - + elongate; length greater than or equal to twice width (Fig. 1).
    - — length less than twice width (Fig. 12).
23. Dorsal tubercle
    - ++ prominent and distinct (Fig. 12).
    - + small and indistinct (Fig. 136).
    - — absent.
24. Medial tubercle
    - + present (Fig. 12).
    - — absent.

Lancet (LA)

25. Number of valves: 1, 2.
26. Size of first valve
    - ++ greatly enlarged (Fig. 98).
    - + moderate size (Fig. 12).
    - — reduced (Fig. 212).
27. Number of barbs.

28. Distal half, strength and shape
    + well sclerotized and acute; probably piercing (Fig. 12).
    weakly sclerotized; probably not piercing.
        d dorsal and ventral edges *diverge* toward end (*i.e.,* subterminad) (Fig. 9j).
        p dorsal and ventral edges *parallel,* or nearly so (Figs. 137, 152).
        c dorsal and ventral edges *converge* toward apex (Fig. 212).

29. Dorsal ridge
    + present (Fig. 25).
    — absent (Fig. 12).

Sting

30. Strength of sting shaft
    + acute, heavily sclerotized; probably piercing (Fig. 13).
    — weakly sclerotized or blunt; probably not piercing (Figs. 99, 109).
31. Hemocoel development in sting shaft
    ++ high, well developed throughout (Figs. 13, 22).
    + low, but visible throughout (Figs. 30, 33).
    — at least part very reduced and not visible (Figs. 92, 118).
32. Apical end of hemocoel (excluding that in dorsal flange)
    + enlarged (Fig. 83).
    — not enlarged (Fig. 99).
33. Dorsal flange
    ++ large, prominent (Figs. 63, 142).
    + low (Figs. 138, 190).
    — absent.
34. Valve chamber
    ++ with its own convexity in profile, very distinct from base of sting shaft (Fig. 83).
    + dorsum indistinct, or nearly so from that of base of sting shaft in profile (Figs. 5, 13).
    — not a distinct section of sting even internally (Fig. 175).
35. Internal apophysis
    ++ long, well sclerotized; probably extends dorsum of valve chamber (Figs. 99, 138).
    + present, but not greatly lengthened and probably not significantly extending length of valve chamber (Figs. 13, 114).
    — absent (Fig. 242).
36. Sting base arch (as seen from anterior view)
    ++ strongly arched (Fig. 37).
    + weakly arched (Figs. 13, 39).
    — no arch, sting base flat (Fig. 63).
37. Basal ridge
    ++ large (Figs. 5, 197).
    + present, but not greatly developed (Fig. 13).
    — absent (Figs. 99, 142).
38. Anterolateral processes
    + present (Fig. 14).
    — absent (Fig. 76).

39. Basal notch
    + open (Fig. 13).
    — closed (Figs. 30, 125).
40. Campaniform sensilla
    ++ on valve chamber and beyond basal half of sting shaft.
    + not extending beyond basal half of sting shaft; often only on valve chamber.
    — absent.
41. Index of sting reduction

$$IR = \frac{LSS \times 100}{PW}$$

LSS = length of sting shaft (excluding dorsal flange).
PW = maximum pronotal width (excluding spines).

Furcula (FU)

42. Dorsal arm
    ++ longer than lateral arms (Figs. 63, 64).
    + present, but equal to or shorter than lateral arms (Figs. 13, 14).
    — absent (Figs. 125, 137).
43. Articulation
    + free; attached to sting base only at lateral extremities (Fig. 14).
    — appressed or fused to sting base (Figs. 153, 154).

Appendix A(1). Table of characters for spiracular, quadrate, anal, and oblong plates and gonostylus. See above for key to symbols.

	SP					QP				AP			OP			GO					
SPECIES	1 med con	2 apo wid	3 nch	4 p-v cnr	5 p-d lobe	6 p-d edg	7 v wid	8 apo siz	9 p edg	10 def	11 sen loc	12 sen typ	13 p apo	14 sub tub	15 v rdg	16 PI	17 # seg	18 sen pat	19 trm mem	20 trm sen	21 bas
Ponerinae																					
Amblyopone pallipes............	++*	+	+	-	++	+	+	-	+	++	m	t	-	+	-	++	2	2	-	-	+
Myrmicinae																					
Myrmica genus group																					
core genera																					
Myrmica emeryana...............	+	++	-	-	+	+	+	=	-	+	m	t	-	+	+	+	2	2	+	cs	-
Manica bradleyi................	-	++	+	-	+	+	+	-	+	+	m	t	-	+	+	+	2	2	+	cs	-
Ephebomyrmex imberbiculus......	-	++	+	-	+	+	+	+	+	++	m	t	-	+*	-	+	1-2	2	+	c	-
E. naegeli.....................	-	++	+	-	+	+	+	+	+	?	?	?	-	+*	-	+	1	1-2	+	c*	-
Hylomyrma versuta..............	-	++	+	-	+	+	+	+	+	++	m	t	-	-	-	+	1	1	+	cs	-
Pogonomyrmex badius............	-	++	-	-	+	+	+	-	+	+	m	t	+	-	+	+	1	1	+	*	-
peripheral genera																					
Huberia striata................	-	++	?	-	++	+	+	+	+	+	m	t	-	+	+	++	2	2	+	c	-
Stereomyrmex horni.............	-	++	-	-	+	+	+	+	+	+	m	t	-	-	-	?	1	1	+	c	-
Podomyrma abdominalis..........	-	+	+	-	-?	+	+	=	+	++	md	tb	++	-	++	++	1-2	1-2	+	c*	+
Dacetini																					
Daceton armigerum..............	-	+	+	-	-	+	+	-	+	++	md	tbc	-	+	-	++	1	1	-	-	+*
Orectognathus sarasini.........	+	+	-	-	-	+	?	?	?	+	m	t	+	-	+	++	1	1	-	c	-
Neostruma metopia..............	-	+	-	-	-	+	-	+	+	+	m	t	-	-	-	++	1	1	-	c	-
Basicerotini																					
Basiceros singularis...........	-	++	-	-	-	-	-	=	+	+	m	t	+	+	+	++	1	1,2	-	c	-
Eurhopalothrix speciosa........	-	++	-	-	-	+	-	+	+	+	m	t	+	-	-	+	1	2	-	c	-
Octostruma balzani.............	-	++	-	-	-	+	-	+	+	+	m	t	-	+	+	+	1	1-2	-	c	-
Leptothorax genus group																					
Leptothorax longispinosus......	+	++	+*	-	-	+	+	+	+	+	m	t	++	-	++	++	1-2	1	+	cs	-
L. pergandei...................	+	++	+*	-	-	+	+	+	+	+	m	t	++	-	++	++	1-2	1	+	cs	+
Macromischa sallei.............	+	++	+	-	-	+	+	+	+	+	m	t	++	-	++	++	1-2	2	+	cs	+*
Tetramoriini																					
Tetramorium grassii............	-	++	-	-	-	+	+	+	+	+*	m	t	-	+	++	++	1	1	-	c	-
T. pacificum...................	-	++	-	-	-	+	+	+	+	+*	m	t	-	+	++	++	2	2	-	c	-
T. cf. *insolens* group........	-	++	-	-	-	+	+	+	+	+*	m	t	-	+	++	++	1-2	2	-	c	-
T. caespitum...................	-	++	-	-	-	+	+	+	+	+*	-	-	-	+	++	++	1-2	2	-	c	-
T. spinosum....................	-	++	-	-	-	+	+	+	+	+*	m	t	-	+	++	++	1	1	+	c	-
T. tenuicrine..................	-	++	-	-	-	+	+	+	+	+*	m	t	-	+	++	++	1	1	-	c	-
Triglyphothrix lanuginosa......	-	++	-	-	-	+	+	+	+	-	-	-	-	+	++	++	2	2	-	c	-
Vollenhovia genus group																					
Liomyrmex cf. *aurianus*.......	-	++	-	-	++	+	+	+	+	++	m	t	-	+	-	-	1-2	1-2	+	c	-
Vollenhovia sp. 1..............	+*	++	+	-	++	+	+	+	+	+	md	t	-	-	?	-	2	2	+	c	-
V. cf. *pedestris*.............	+*	+	+	-	+	+	+	+	+	+	md	t	-	-	-	+	2	2	+	c	-

Appendix A(1), continued

SPECIES	SP					QP				AP			OP				GO				
	1 med con	2 apo wid	3 nch	4 p-v cnr	5 p-d lobe	6 p-d edg	7 v wid	8 apo siz	9 p edg	10 def	11 sen loc	12 sen typ	13 p apo	14 sub tub	15 v rdg	16 PI	17 # seg	18 sen pat	19 trm mem	20 trm sen	21 bas
Solenopsis genus group																					
core genera																					
Solenopsis geminata	-	++	-	-	-	+	+	+	+	+	m	t	++	-	-	++	1	2	+	cs	-
Oxyepoecus rastratus	+	++	-	-	-	-	+	+	+	+	m	t	-	+*	-	+	1	2	+	cs	-
Chelaner sp. 1	-	++	-	-	-	+	-	+	+	+	m	t	+*	-	-	++	1	2	+	cs	-
Rogeria inermis	-	+	-	-	-	-*	+	+	+	+	md	t	-	-	-	++	1	1-2	+	cs	-
peripheral genera																					
"Rogeria" spp. 1 and 2	+	+	-	-	-	+	+	-	+	-	-	-	-	-	-	++	1	1	+	c	-
Monomorium (H.) scabriceps	++	+	-	-	+	+	+	=*	-	+	m	t	-	-	-	+	1	2*	+	cs	-
Monomorium (M.) minimum	-	+	-	-	-	-	+	+	+	+	m	t	-	-	-	+	1	2	-	cs	-
Megalomyrmex(?) sp. 1	-	+	-	-	-	+	+	+	+	++	m	t	++*	-	-	++	1	2	+	cs	-
Megalomyrmex near incisus	-	++*	-	-	-	-	+	+	+	++	m	t	-	+*	-	++	1	2	+	cs	-
M. modestus	-	++*	-	-	-	-	+	+	+	++	m	t	-	-	-	++	1	2	+	cs	-
Calyptomyrmex sp. 1	-	++	-	-	-	+	+	+	+	+	m	t	-	+	-	++	1	2	+	cs	-
Wasmannia sp. 2	+*	+	-	-	+	+	+	+	+	+	m	t	-*	-	-	++	1	2	+	cs	-
W. auropunctata	++*	+	-	-	-	+	+	+	+	+	m	t	-*	-	-	++	1	1	+	cs	-
Promeranoplus genus group																					
Promeranoplus rouxi	-	+	-	-	++	+	+	=	+	+	m	t	++	-	+	-	2	2	-	-	-
P. sp. 2	-	+	-	-	++	+	+	+	+	-	-	-	++	+	+	+	2	2	-	-	-
Prodicroaspis sarasini	-	+	-	-	++	+	+	+	+	+	-	-	++	-	+	-	2	2	-	-	-
Lordomyrma caledonica	-	+	-	-	+	+	+	+	+	+	m	t	+	+	+	+	2	2	-	-	-
L. tortuosa	+	++	-	-	+	+	+	+	+	-	-	-	+	-	+	+	2	2	-	-*	-
Pheidole genus group																					
core genera																					
Messor sp. 1 major ϙ	++	+	+	-	-	+	-	-	+	+	md	t	-	+	-	++	1	1	+	cs	-
M. sp. 1 minor ϙ	++	+	+	-	-	+	-	-	+	+	md	t	-	+	-	++	1	1	+	cs	-
M. aciculata	+	+	+	-	-	+	-	-	+	+	md	tb	-	+	-	++	1	2	+	c	-
Aphaenogaster phalangium	+	+	+	-	-	+	-	+	+	+	m	t	++	+	-	++	1-2	2	+	cs	-
A. rudis	+	+	+	-	-	+	-	+	+	+	m	t	-	+	-	++	1-2	2	+	cs	-
Veromessor andrei	+	+	+	-	-	+	-	+	-	+	md	t	+	-	-	++	1	1	+	c	-
Stenamma diecki	+	+	+	-	-	+	+	+	-	+	m	t	+	-	-	+	1	1,2	+	cs	-
S. near manni	+	+	+	-	-	+	-	+	-	+	md	t	+	-	-	++	1	2	+	cs	-
Pheidole morrisi major ϙ	++	+	+	+	-	-	+	+	+	+	md	t	-	+	-	-	1	1	+	c	-
Ph. morrisi minor ϙ	++	+	+	+	-	-	+	+	+	+	md	t	-	+	-	-	1	1	+	c	-
Ph. sp. 1 minor ϙ	+	+	+	+	-	-	+	+	+	+	md	t	-	+?	-	-	1	1	+	c	-
Ph. sp. 2 minor ϙ	++	+	+	+	-	-	+	+	+	+	m	t	-	+?	-	-	1	2	+	c	-
Ph. sp. 3 major ϙ	++	+	+	+*	-	-	+	+	-	+	md	t	-	+	-	+	1	1	+	c	-
Ph. sp. 3 minor ϙ	++	+	+	+*	-	-	+	+	-	+	md	t	-	+	-	+	1	1	+	c	-

Appendix A(1). continued

SPECIES	SP 1 med con	2 apo wid	3 nch	4 p-v cnr	5 p-d lobe	QP 6 p-d edg	7 v wid	8 apo siz	9 p edg	AP 10 def	11 sen loc	12 sen typ	OP 13 p apo	14 sub tub	15 v rdg	GO 16 PI	17 # seg	18 sen pat	19 trm mem	20 trm sen	21 bas
Pheidole group peripheral genera																					
Acanthomyrmex cf. notabilis	-	++	+	-*	-	+	+*	+	-	+	m	t	-	+	-	++	1	1	+	-	-
Cyphoidris spinosus	-	+	-	-	-	+	+	+	+	+	m	t	-	-	-	++	1-2	2	++	c	-
Lachnomyrmex cf. scrobiculatus	?	?	?	?	?	?	+	+	+	+	m	t	++	-	-	++	1	2	++	c	-
Adelomyrmex near tristani	-	+	-	-	-	-	+	-	+	+	m	t	++	-	-	++	1-2	2	++	c	-
A. sp. 2	-	+*	-	-	-	-	+	=	+	+	m	t	++	-	-	++	1-2	2	++	c	-
Myrmicaria arachnoides	-	+	-	-	-	-	+	-	+	+	m	t	++	-	-	+	1	2	-	c	-
M. carinata	-	+	-	-	-	+	+	-	+	+	m	t	++	-	-	+	1	2	-	c	-
M. eumenoides	-	+*	-	-	-	+	-	-	+	+	m	t	++	-	-	+	1	1	-	c	-
Meranoplus sp. 1	-	+*	-	-	-	+	+	=	+	+	m	t	+	-	-	++	1-2	1	+	c	-
Meranoplus sp. 2	-	+*	-	-	-	+	+	=	+	+	md	t	++	+	-	++	2	2	+	c	-
Crematogaster atkinsoni	-	+	-	-	-	+	?	?	?	+	m	t	++	-	-	-	1-2	2	+	c	-
C. ashmeadi	-	+	-	-	-	+	+	=	-	+	m	t	++	-	-	-	1	2	+	c	-
C. cerasi	-	+	-	-	-	+	+	=	-	+	m	t	++	-	-	-	1	2	+	c	-
C. minutissima	-	+	-	-	-	+	+	=	+	+	m	t	++	-	-	-	1	2	+	c	-
Trigonogaster recurvispinosus	+	+	-	-	-	-	+	+	+	+	md	t	++	-	-	-	1	1	?	c	-
Cephalotini																					
Cephalotes atratus major ♀	++	+	+	-	-	+	+	+	-	+	md	tb	++	+	-	+	1	1	+	c	+
C. atratus minor ♀	++	+	+	-	-	+	+	-	+	+	md	tb	++	+	-	+	1	1	+	c	+
Eucryptocerus opacus	++	+	+	-	-	+	?	?	?	+	md	t	++	+	-	+	1	1	+	c	+
Procryptocerus scabriusculus	++	++	+*	+	-	+	+	=?	+	+	md	t	+	-	-	++	1	1	+	-	+
Zacryptocerus haemorrhoidalis	++	++	-	+	-	+	+	+	+	+	md	t	+	+	+	++	1	1	+	c	+
Z. multispinosus biguttatus	++	++	-	-	-	+	?	+	+	+	md	tb	+	+	-	++	1	1	+	c	+
Z. minutus	?	++	?	?	-	?	+	+	+	+	md	t	+	+	-	+	1	1	+	c	+
Cataulacini																					
Cataulacus tardus	++	++	+	-	+	+	+	-	-	-	-	-	++	+	-	++	1	1	+	-	-
Attini																					
Cyphomyrmex salvini	-	++	-	-	-	-	+	+	?	+	-	-	-	+	+	++	1	2	+	c	-
Apterostigma collare	-	++	-	-	-	-	+	-	+	+	md	t	-	-	-	+	1	1,2	+	-*	-
Mycetophylax emeryi	-	+	-	-	-	-	-	-	+	+	m*	*	-	-	-	-	1	1	-	-*	-
Atta cephalotes	-	+	-	-	-	-	-	+	-	+	m	t	+	-	-	+	1	1	+	-*	-
Trachymyrmex turrifex	-	++	-	-	-	-	+	-	+	-	-	-	+	-	-	++	1	1	+	-*	-
T. seminole	-	++	-	+	-	-	+	-	+	-	-	-	+	+	-	++	1	1	+	-*	-
T. intermedius	-	++	-	+	-	-	+	-	+	-	-	-	+	+	+	++	1	1	+	-*	-
Unplaced genera																					
Atopomyrmex mocquerysi	++*	+	-	-	+	-	+	+	-	++	-	-	++	-	-	++	1	1	+	cc*	-
Pristomyrmex brevispinosus	-	++	+	-	-	+	-	+	+	++	m	t	++	-	-	++	1	2	+	-	-
Proatta butteli	+	+	+	-	-	+	+	+	+	+	m	t	?	-	-	-	2	2	+?	cs	-
Cardiocondyla elegans	-	?	?	-	?	?	+	=	+	+	md	t	-	-	-	-	2	2	-	c	-
Tranopelta gilva	++	+	-	+?	-	-	-	+	-	+	md	tb	+	+	-	+	1	1,2	+	cs	-
Oligomyrmex corniger	-?	+	-	-	-	-	+	-	+	+	m	t	++	-	-	-	1	2	+	cs	-
Pheidologeton cf. diversus	+++*	++	-	+	-	-	+	-	+	+	m	t	++	-	-	-	1	1,2	+	cs*	-
Myrmecina graminicola	+	+	-	+	-	-	-	-	+	-	m	t	++	-	-	-	1	2	+	c*	-
Ocymyrmex cf. arnoldi	+	+	+	-	-	-	-	=	-	+	md	t	-	++	+	++	1	1	+	c	-

Appendix A(2). Table of characters for triangular plate, lancet, sting, and furcula. See above for key to symbols.

	TP			LA							STING										FU	
SPECIES	22 shp	23 d tub	24 m tub	25 vlv #	26 # siz	27 # brb	28 sth shp	29 d rdg	30 sth SS	31 hem SS	32 end hem	33 d flng	34 VC	35 int apo	36 SB	37 bas rdg	38 a-1 pcs	39 bas nch	40 cam sen	41 IR	42 d arm	43 art
Ponerinae																						
Amblyopone pallipes	+	-	+	2	-*	8	+	+	+	++	-	-	+	+	++	++	-	+	++	119	++	+
Myrmicinae																						
Myrmica genus group																						
core genera																						
Myrmica emeryana	-	++	+	2	+	0	+	-	+	++	+	-	+	+	+	+	+	+	++	36	+	+
Manica bradleyi	-	-	+	2	+	3	+	-	+	++	-	-	+	+	+	+	+	-	++	42	+	+
Ephebomyrmex imberbiculus	-	-	-	2	+	2	+	?	+	++	-	-	+	+	+	+	+	+	++	41	+	+
E. naegeli	-	-	-	2	+	2	+	+	+	++	-	-	+	+	+	+	+	+	++	44	+	+
Hylomyrma versuta	-	-	-	2	+	2	+	+	+	++	-	-	+	+	+	+	+	+	++	47	+	+
Pogonomyrmex badius	+	+	-	2	+	6	+	+	+	++	+	-	+	+	+	+	+	+	++	44	+	+
peripheral genera																						
Huberia striata	-	++	+	1	-	1	+	-	+	++	+	-	++	+	+	++	+	+	++	41	?	+
Stereomyrmex horni	-	-	-	1	+	2	+	?	+	+	-	-	+	+	+*	+	+	-	++	?	+	+
Podomyrma abdominalis	-	++	-	2	+	1	+	-	+	+	-	-	++	+	+	+	+	+	++	26	+	+
Dacetini																						
Daceton armigerum	-	+	-	2	+*	8,9	+	-	+	++	-	-	+	+	++	+	+	+	++	70	+	+
Orectognathus sarasini	-	-	-	1	+	1	+	+?	+	+	-	-	+	-	+	+	+	+	++	47	+	+
Neostruma metopia	-	-	+	1	+	1	+	-	+	+	-	-	+	+	-	+	-	+	+	56	++	+
Basicerotini																						
Basiceros singularis	-	++	+	1	+	1	+	-	+	+	-	-	+	+	-	+	+	+	++	?	++	+
Eurhopalothrix speciosa	-	-	+	1	+	1	+	+	+	+	-	-	+	+	-	+	-	+	++	64	+	+
Octostruma balzani	-	-	-	1	+	1	+	-	+	+	-	-	+	+	-	+	-	+	++	52	++	+
Leptothorax genus group																						
Leptothorax longispinosus	+	-	-	2	+	0	+	+	+	+	+	-	+	+	-	+	-	+	++	53	++	+
L. pergandei	-	-	+	2	+	0	+	+	+	+	-	-	+	+	-	+	-	+	++	63	++	+
Macromischa sallei	+	-	+	1	+	0	+	+	+	+	+	-	+	+	-	+	-	+	++	60	++	+
Tetramoriini																						
Tetramorium grassii	-	-	-	1	+	1	+	+	+	+	-	++	+	+	-	+	+	+	++	46	++	+
T. pacificum	-	-	-	1	+	1	+	+	+	++	-	++	+	+	-	+	-	+	++	42	++	+
T. cf. insolens group	-	-	-	1	+	1	+	+	+	++	-	++	+	+	-	+	-	+	++	41	++	+
T. caespitum	-	-	-	1	+	1	+	+	+	++	-	++	+	+	-	+	-	+	++	38	++	+
T. spinosum	-	-	-	1	+	1	+	+	+	++	-	++	+	+	-	+	-	+	++	36	++	+
T. tenuicrine	-	-	-	1	+	1	+	+	+	++	-	++	+	+	-	+	-	+	++	49	++	+
Triglyphothrix lanuginosa	-	-	-	1	+	1	+	+	+	++	-	++	+	+	-	+	-	+	++	36	++	+
Vollenhovia genus group																						
Liomyrmex cf. aurianus	-	-	-	2	+	4,3	+	-	+	++	-	-	+	+	+	+	+	+	++	72	+	+
Vollenhovia sp. 1	-	-	-	2	+	1	+	-	+	++	-	-	+	+	-	+	-	+	++	54	+	+
V. cf. pedestris	-	-	-	2	+	1	+	-	+	++	-	-	+	+	+	+	+ -	+	++	56	+	+

V. cf. *pedestris*............... - - - 2 + 1 + - + ++ - - + + + + + - + ++ 56 + +

Appendix A(2), continued

SPECIES	TP			LA									STING							FU		
	22 shp	23 d tub	24 m tub	25 vlv #	26 # siz	27 # brb	28 sth shp	29 d rdg	30 sth SS	31 hem SS	32 end hem	33 d flng	34 VC	35 int apo	36 SB	37 bas rdg	38 a-l pcs	39 bas nch	40 cam sen	41 IR	42 d arm	43 art
Solenopsis genus group																						
core genera																						
Solenopsis geminata...........	-	-	-	1	++	5	+	-	+	+	+	-	++	+	-	+	-	+	+	?	+	+
Oxyepoecus rastratus..........	-	-	+	1	++	2	+	-	+	+	+	-	++	+	+	+	+*	+	+	47	+	+
Chelaner sp. 1................	-	-	+	1	+	3	+	-	+	+	+	-	++	++	+	+	+	+	+	50	+	+
Rogeria inermis...............	-	-	-	1	++	1	+	-	+	+	-*	+*	++	+	+	+	+	+	+	42	+	+
peripheral genera																						
"*Rogeria*" *spp*. 1 and 2........	-	-	-	1	+	0	p	-	-	-	-	-	+	++	++	+	-	+	-	31	-	+
Monomorium (*H.*) *scabriceps*....	-	-	-	1	+	1	+*	-	+	++	+	-	+	+	+	+	+	+	+	?	+*	+
Monomorium (*M.*) *minimum*.......	-	-	-	1	++	0	d	-	-	+	-	-	++	++	+	-	-	+	-	47	-	+
Megalomyrmex(?) *sp*. 1.........	-	-	-	1	++	0	d	-	-	+	+	-	++	++	+*	-	-	+	+	48	+	+
Megalomyrmex near *incisus*.....	-	-	-	1	-	0	d	-	-	+	+	-	+	++?	-	++	+	-	+	45	++	+
M. modestus..................	-	-	+	1	-	0	d	-	-	+	-	-	+	++?	+*	++	+	-	+	50	++	+
Calyptomyrmex sp. 1...........	-	-	+	2	++	1*	+	+	+	+	-	-	++	+	+	+	+	+	+	56	+	+
Wasmannia sp. 2...............	-	-	-	1	++	1*	+	+	+	-	-	-	+	+	+	+	+	+	+	55	+	+
W. auropunctata...............	-	-	-	1	++	1*	+	+	+	-	-	-	+	+	+	+	+	+	+	60	+	+
Promeranoplus genus group																						
Promeranoplus rouxi...........	-	+	+	2	+	0	+	-	+	+	+	-	+	+	++	+*	+	-	++	27	-	+
P. sp. 2......................	-	-	+	2	+	0	+	-	+	+	+	-	+	+	++	-	+	-	++	24	-	+
Prodicroaspis sarasini........	-	+	+	2	+	0	+	-	+	+	+	-	+	+	++	-	+	+	++	28	-	+
Lordomyrma caledonica.........	-	-	+*	2	+	0	+	-	+	+	-	-	+	+	++	-	+	+	++	24	-	+
L. tortuosa...................	-	-	+	2	+	0	c	-	-	+	-	-	+	+	++	-	+	-	++	26	-	+
Pheidole genus group																						
core genera																						
Messor sp. 1 major ♀..........	-	+*	+*	1	++	0	p	-	-	+	-	+	++	++	++	-	+	-	-	18	-	+
M. sp. 1 minor ♀..............	-	+*	+*	1	++	0	p	-	-	+	-	+	++	++	++	-	+	-	-	23	-	+
M. aciculata..................	+	+*	+*	1	++	-	p	-	-	+	-	+	++	++	++	-	+	-	+	13	-	+
Aphaenogaster phalangium......	+	-	+*	1	++	0	p	-	-	+	-	++	++	++	++	-	+	-	+	36	-	+
A. rudis......................	-	-	-	1	++	0	p	-	-	+	-	++	++	++	++	-	+	-	+	?	-	+
Veromessor andrei.............	-	+*	+*	1	+	0	p	-	-	-	-	-	+	+	++	-	+	-	+	15	-	*
Stenamma diecki...............	-	-	-	1	+	0	p	-	-	-	-	-	+	++	++	++	+	+	-	32	-	+
S. near *manni*.................	-	-	-	1	+	0	p	-	-	-	-	-	+	++	++	++	+	+	-	26	-	+
Pheidole morrisi major ♀......	-	-	-	1	-	0	p	-	-	-	-	-	+	++	++	+	-	+	-	19	-	+
Ph. morrisi minor ♀...........	-	-	-	1	-	0	p	-	-	-	-	-	+	++	+	-	-	+	-	24	-	-
Ph. sp. 1 minor ♀.............	-	-	-	1	-	0	p	-	-	-	-	-	+	++	+	-	-	+	-	22	-	-
Ph. sp. 2 minor ♀.............	-	-	-	1	-	0	p	-	-	-	-	-	+	++	+	-	-	+	-	22	-	-
Ph. sp. 3 major ♀.............	-	-	-	1	-	0	p	-	-	-	-	-	++	++	++	+	+	-	-	19	-	+
Ph. sp. 3 minor ♀.............	-	-	-	1	-	0	p	-	-	-	-	-	+	++	+	-	-	+	-	22	-	-

Appendix A(2), continued

SPECIES	TP			LA											STING								FU	
	22 shp	23 d tub	24 m. tub	25 vlv #	26 # siz	27 # brb	28 sth shp	29 d rdg	30 sth SS	31 hem SS	32 end hem	33 d flng	34 VC	35 int apo	36 SB	37 bas rdg	38 a-1 pcs	39 bas nch	40 cam sen	41 IR	42 d arm	43 art
Pheidole group peripheral genera																						
Acanthomyrmex cf. notabilis....	-	-	+	1	+	0	p	-	-	-	-	+	+	++	++	-	+	-	-	18	-	-
Cyphoidris spinosus...........	-	-	+	1	+	0	d	-	-	-	-	-?	++	++	++	+	+	-	+	38	-	+
Lachnomyrmex cf. scrobiculatus.	-	-	-	1	+	0	p	-	-	-	-	-	++	+	++	-	+	-	+	♀48	+*	+
Adelomyrmex near tristani......	+	-	-	1	+	0	d	-	-	-	-	-	+	++	++	+	+	-	+	32	+	+
A. sp. 2......................	-	-	-	1	+	0	d	-	-	-	-	-	+	++	++	+	+	+	+	30	+	+
Myrmicaria arachnoides.........	-	+	-	1	-	0	d	-	-	+	-	-	-	+	++	+	+	-	+	50	+	+
M. carinata..................	-	+	-	1	-	0	d	-	-	+	-	-	-	+	++	+	+	-	+	49	+	+
M. eumenoides................	+	+	-	1	-	0	d	-	-	+	-	-	-	+	++	+	+	-	+	36	+	+
Meranoplus sp. 1..............	-	+	+	1	+	0	p	-	-	+	-	++	+	++	+	+	+	-	+	39	+	+
Meranoplus sp. 2..............	-	+	+	1	+	0	p	-	-	+	-	++	+	++	+	+	+	-	+?	31	+	+
Crematogaster atkinsoni........	-	-	+	1	+	0	d	-	-	+	-	++	++	++	+	-	+	+	-	47	+	+
C. ashmeadi..................	-	-	+	1	+	0	d	-	-	+	-	++	?	?	?	?	?	+	?	61	?	?
C. cerasi....................	-	-	+	1	+	0	d	-	-	+	-	++	++	++	+*	-	+	+	-	57	+	+
C. minutissima...............	-	-	+	1	+	0	d	-	-	+	-	++	+	+	+*	-	+	+	-	65	+	+
Trigonogaster recurvispinosus..	-	-	-	1	-	0	p	-	-	-	-	-	+	+	-	-	-	+	+	68	+	+*
Cephalotini																						
Cephalotes atratus major ♀.....	-	+	+	1	-	0	p	-	-	-	-	+	-	++?	+	+	-	+	-	28	-	+
C. atratus minor ♀...........	-	+	+	1	-	0	p	-	-	-	-	+	-	++?	+	+	-	+	-	25	-	+
Eucryptocerus opacus..........	-	-	-	1	-	0	p	-	-	-	-	+	-	++	+	+	-	+	-	13	+*	+
Procryptocerus scabriusculus...	-	-	-	1	-	0	p	-	-	-	-	-	-	++	-	++	-	+	-	22	-	-
Zacryptocerus haemorrhoidalis..	-	-	-	1	-	0	p	-	-	-	-	+	-	++	+	-	-	+	-	15	-	-
Z. multispinosus biguttatus....	-	-	-	1	-	0	d	-	-	-	-	+	-	++	+	-	-	+	-	11	-	-
Z. minutus...................	-	-	-	1	-	0	p	-	-	-	-	+	-	++	-	-	-	+	-	21	-	-
Cataulacini																						
Cataulacus tardus.............	-	-	+	1	-	0	c	-	-	-	-	-	+	+	-	+	-	+	-	12	-	-
Attini																						
Cyphomyrmex salvini............	-	+*	+	1	+	1	+	+	+?	+	-	-	+	++	-	+	-	+	++	22	-	-
Apterostigma collare..........	-	-	-	1	-	0	c	-	-	-	-	-	-	-	+	+	+?	-	-	27	-	-
Mycetophylax emeryi...........	-	-	-	1	+	0	c	-	-	+	-	-	+	-	+	+	-	+	-	29	-	-
Atta cephalotes...............	-	+	+	1	-	0	c	-	-	-	-	-	-	-	+	+	-	+	-	24	-	-
Trachymyrmex turrifex..........	-	-	+	1	-	0	c	-	-	-	-	-	-	-	+	+	+	+	-	23	-	-
T. seminole..................	-	-	+	1	-	0	c	-	-	-	-	-	-	-	+	+	-	+	-	25	-	-
T. intermedius...............	-	-	-	1	-	0	c	-	-	-	-	-	-	-	+	+	-	+	-	19	-	-
Unplaced genera																						
Atopomyrmex mocquerysi..........	-	-	-	1	-	0	c	-	-	-*	-	-	-	+	+	-	+?	+	-	21	-	*
Pristomyrmex brevispinosus.....	-	+	+	1	++	0	c	-	-	-	-	++	+	+	++	+	-	+	+	44	+	+
Proatta butteli...............	-	-	+	1	+	1	+	+	+	++	+	-	+	+	++	+	-	+	++	34	+	+
Cardiocondyla elegans..........	-	-	-	1	+	0	+?	+	+?	++	-	-	+	+	-	+	+	-	++	29	?	?
Tranopelta gilva..............	-	+	+	1	-	0	c	-	+	++	-	-	-	-	++	++*	-	+	-	25	+	+
Oligomyrmex corniger..........	*	-	-	1	+	0	+	+	+	++	-	-	+	-	-	+	-	+	++	?	-	-
Pheidologeton cf. diversus.....	*	-	-	1	-	0	c	-	-	+	-	-	+	++	-	+	-	+	-	15	-	-
Myrmecina graminicola..........	-	-	-	1	-	0	c	-	-	-	-	-	+	++	-	-*	-	+	-	15	-	-
Ocymyrmex cf. arnoldi..........	-	-	-	1	+	0	d	-	-	+	-	-	+	-	++	-	+	-*	-	10	-	+

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APPENDIX B

Illustrations

Unless otherwise stated, the lateral view of the right side is shown. The scale is in millimeters in all cases.

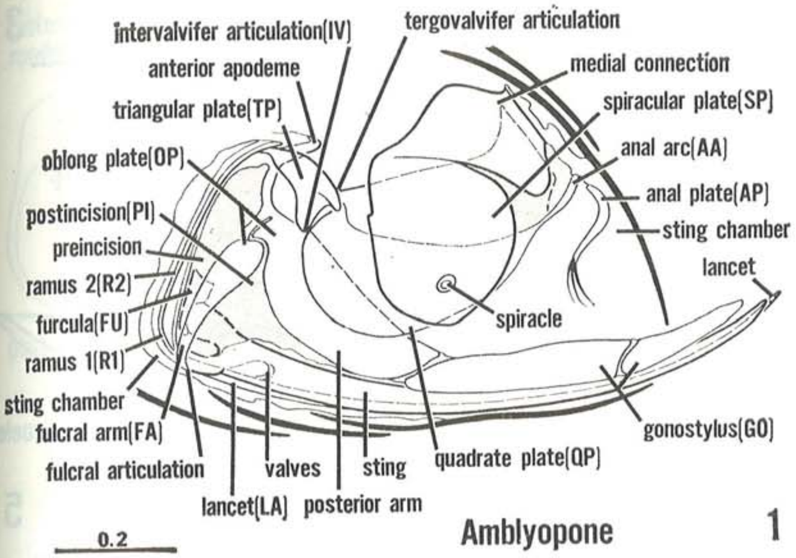
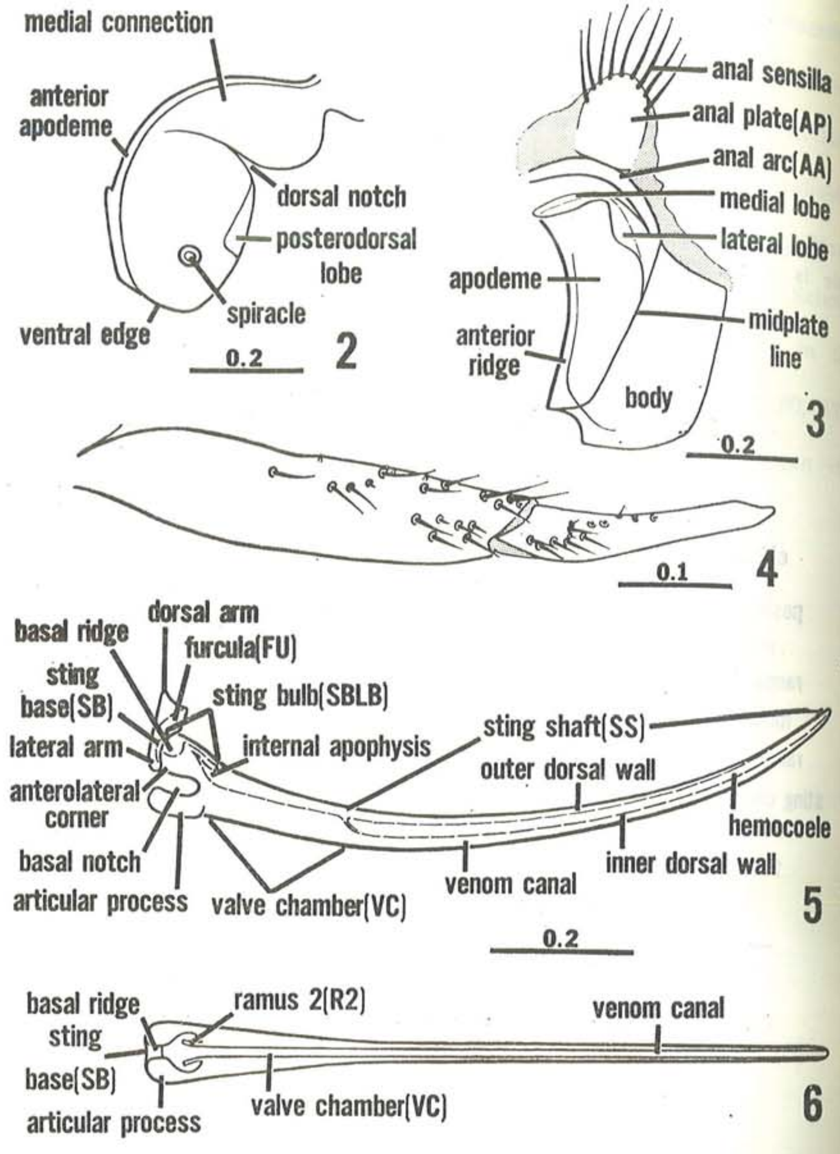
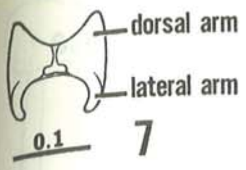


Fig. 1. *Amblyopone pallipes,* sting apparatus sclerites in sting chamber.



Amblyopone

Figs. 2-6. *Amblyopone pallipes* (continued); 2. spiracular plate, flattened to show lateral and posterior surfaces; 3. quadrate plate, posterior view of anal arc and anal plate; 4. gonostylus; 5. sting and furcula; 6. sting, ventral view.



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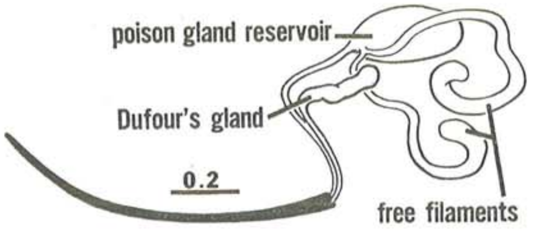

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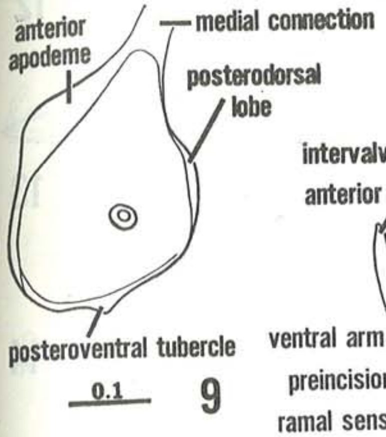
Myrmica



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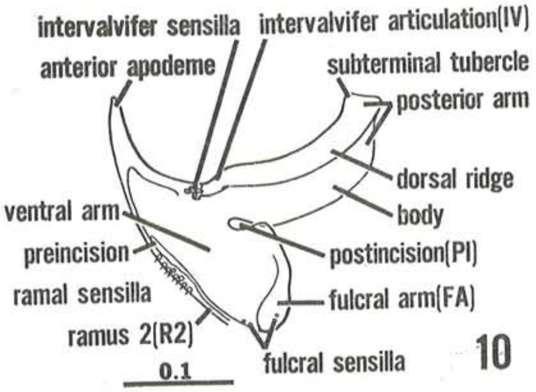

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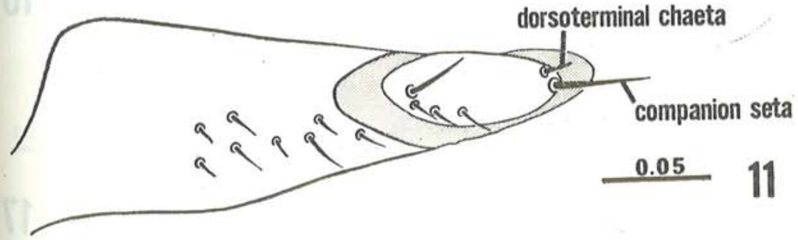

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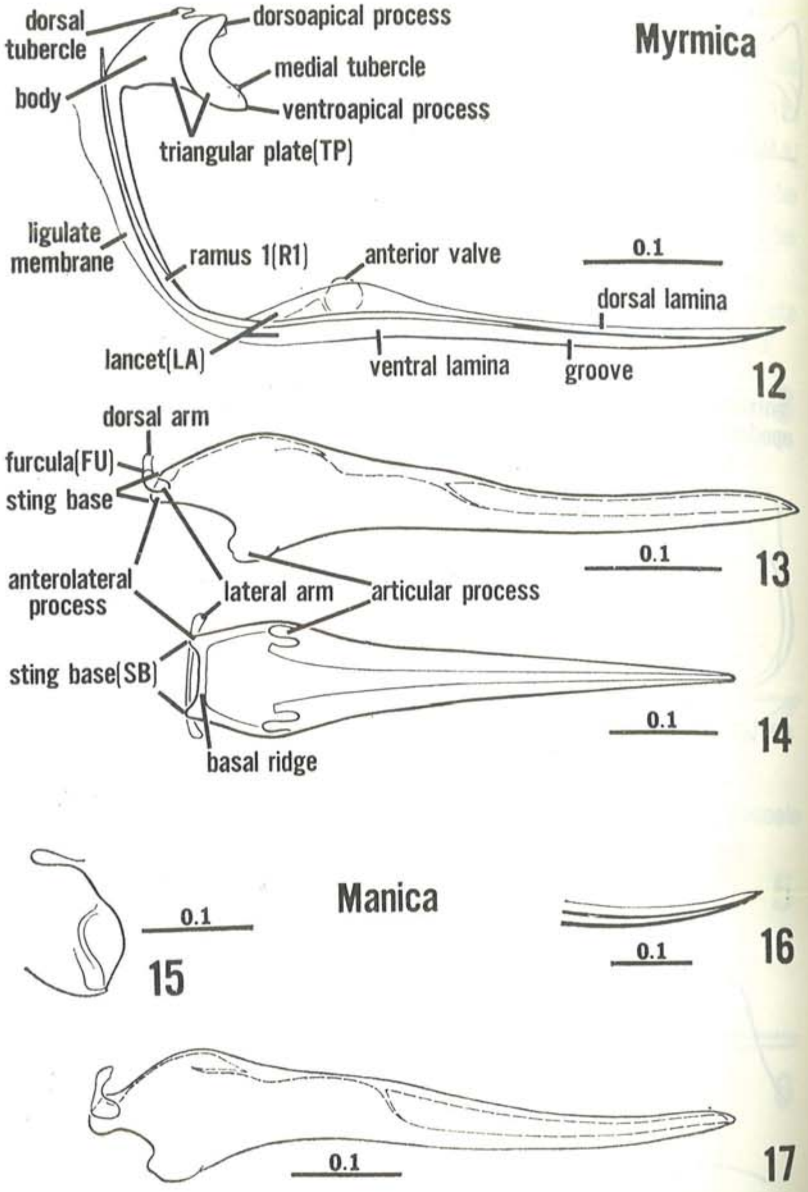
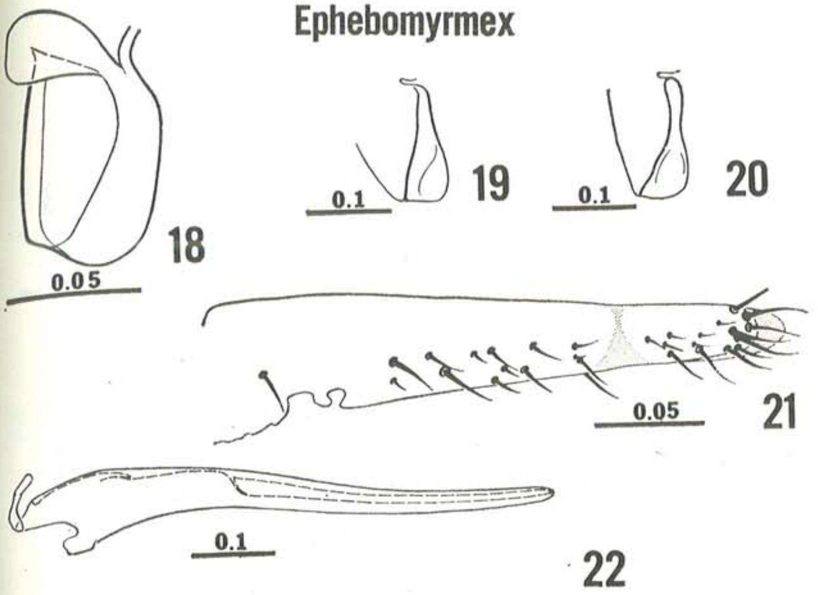
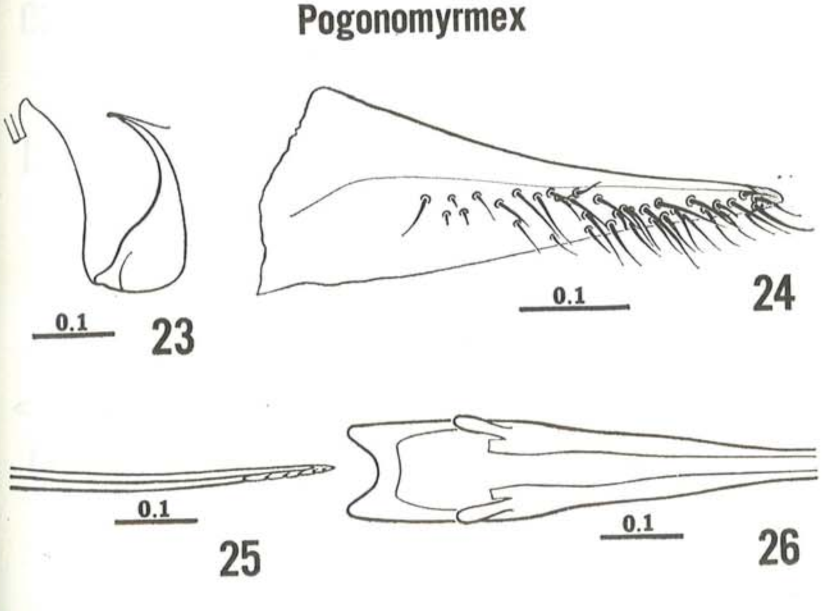
Figs. 7-8. *Amblyopone pallipes* (continued); 7. furcula, posterior view; 8. poison gland, Dufour's gland and sting. Figs. 9-11. *Myrmica emeryana;* 9. spiracular plate; 10. oblong plate; 11. gonostylus.

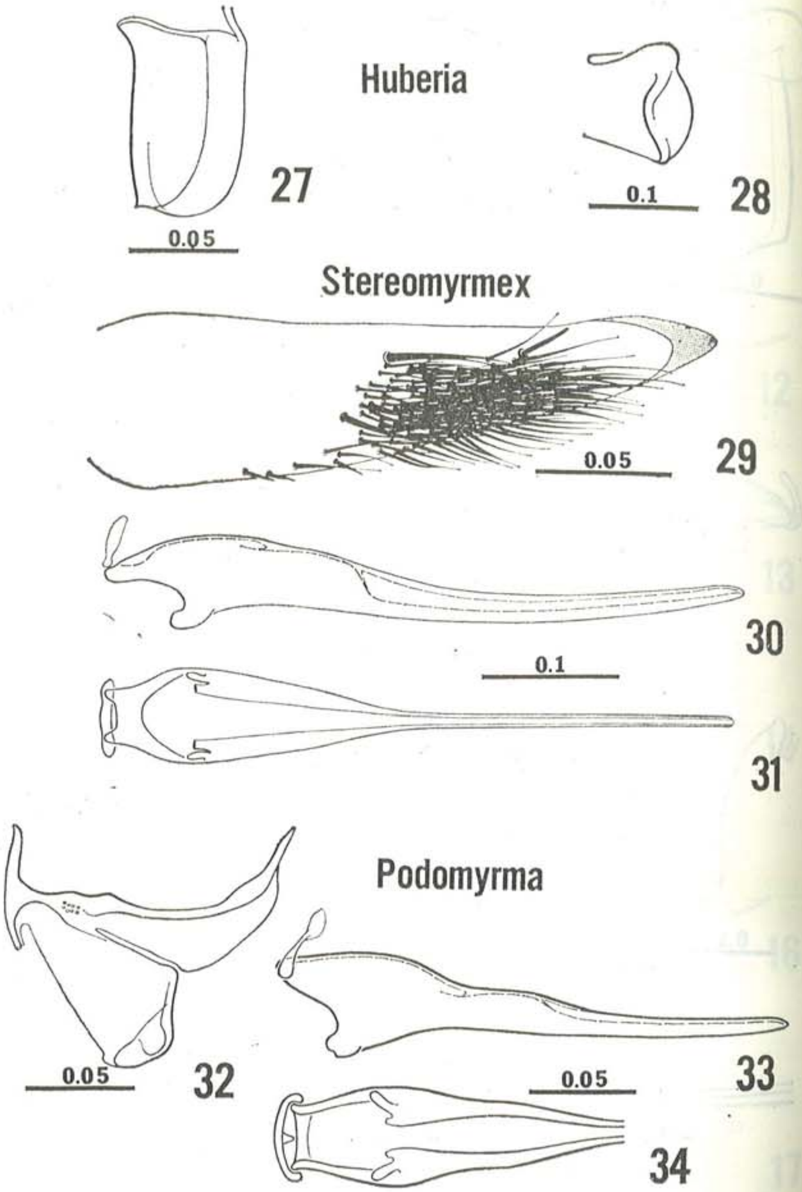


Figs. 12-14. *Myrmica emeryana* (continued); 12. triangular plate, lancet; 13. sting, furcula; 14. ventral sting, furcula. Figs. 15-17. *Manica bradleyi;* 15. ventral arm of oblong plate; 16. caudal half of lancet; 17. sting, furcula.

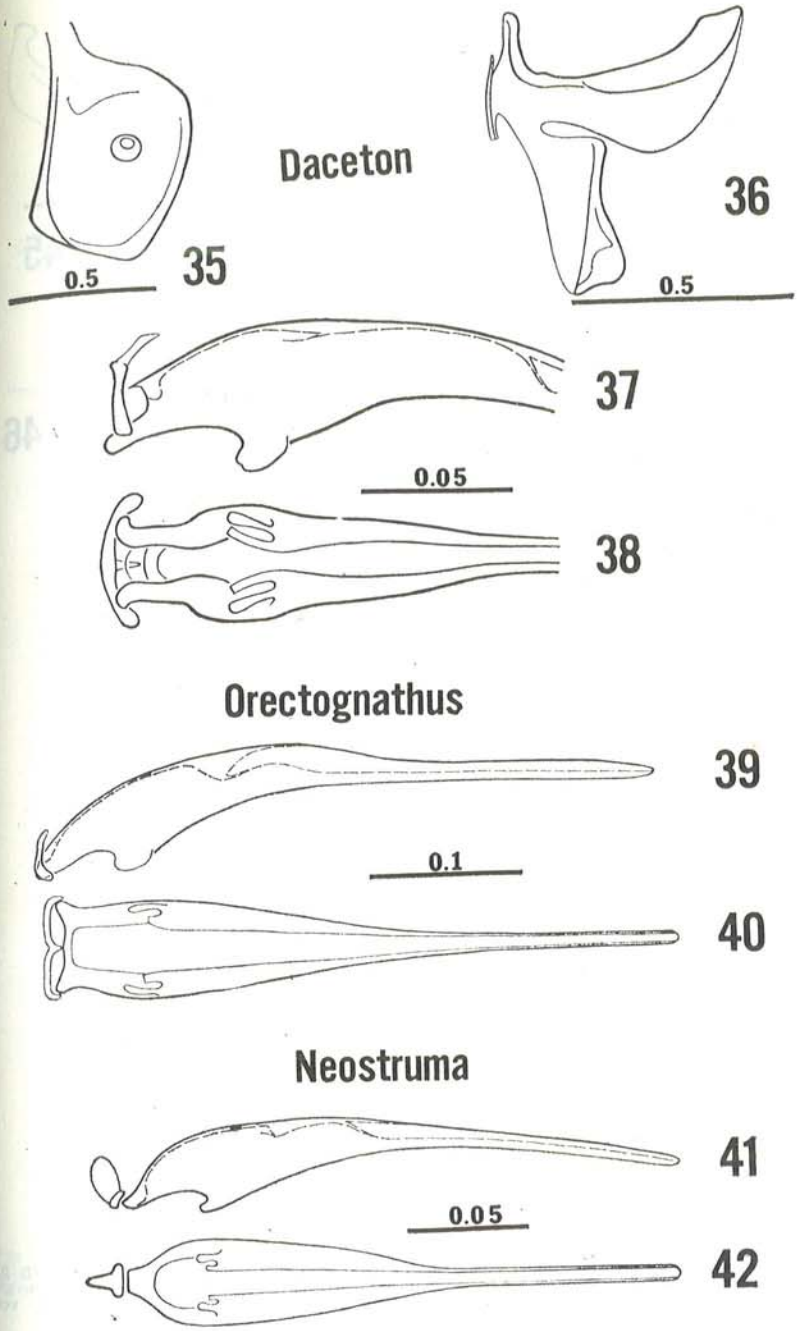




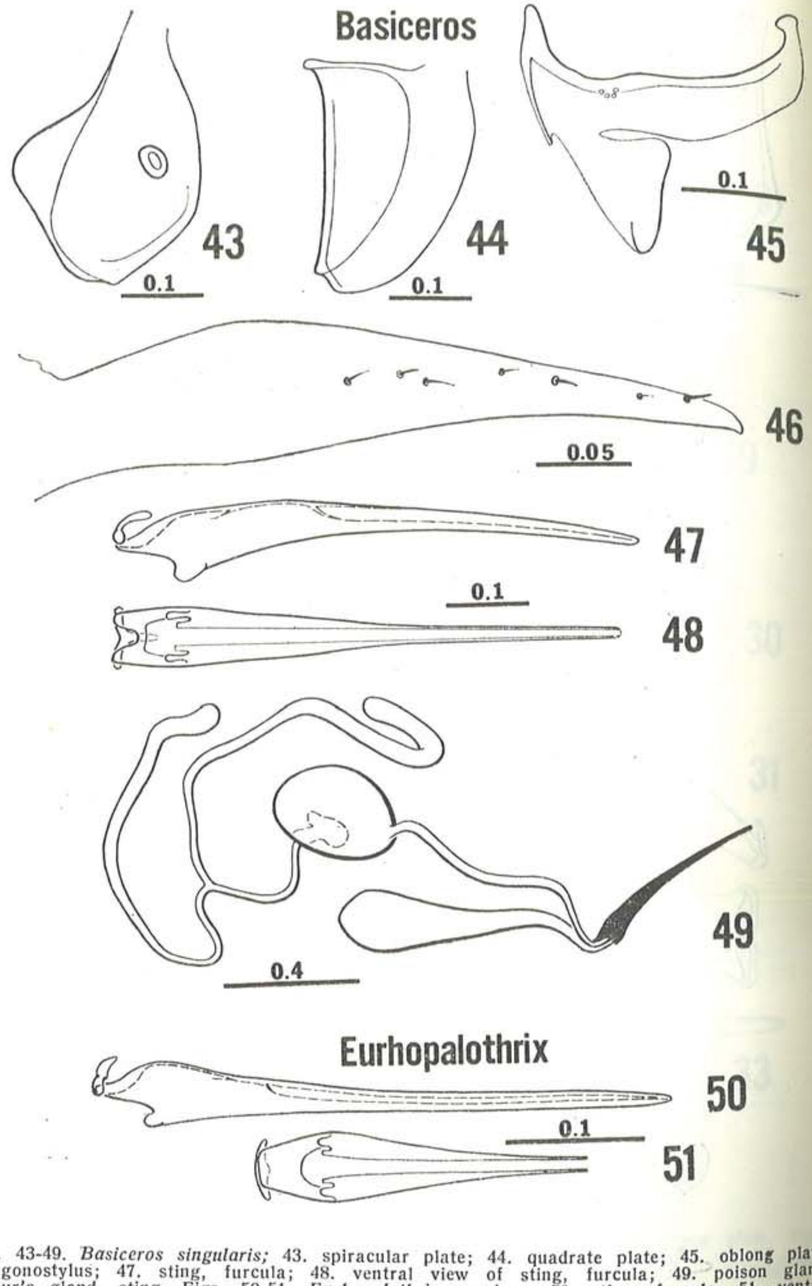
Figs. 18-22. *Ephebomyrmex;* 18. quadrate plate, *E. naegeli;* 19. ventral arm of oblong plate, *E. imberbiculus;* 20. ventral arm of oblong plate, *E. naegeli;* 21. gonostylus, *E. imberbiculus;* 22. sting and furcula, *E. imberbiculus.* Figs. 23-26. *Pogonomyrmex badius;* 23. ventral arm of oblong plate; 24. gonostylus; 25. caudal half of lancet; 26. ventral sting.



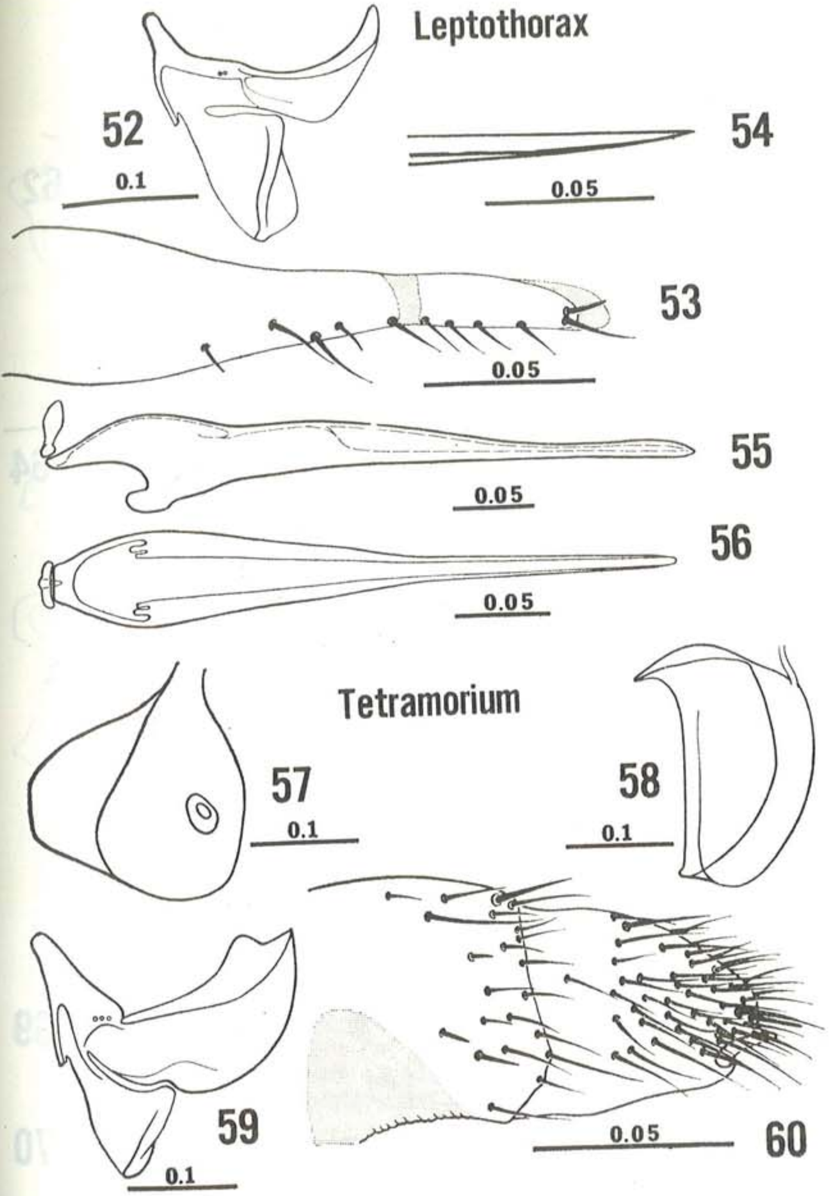
Figs. 27-28. *Huberia striata;* 27. quadrate plate; 28. ventral arm of oblong plate. Figs. 29-31. *Stereomyrmex horni;* 29. dorsolateral gonostylus; 30. sting, furcula; 31. ventral sting, furcula. Figs. 32-34. *Podomyrma abdominalis;* 32. oblong plate; 33. sting, furcula; 34. anterior half of sting, furcula, ventral view.



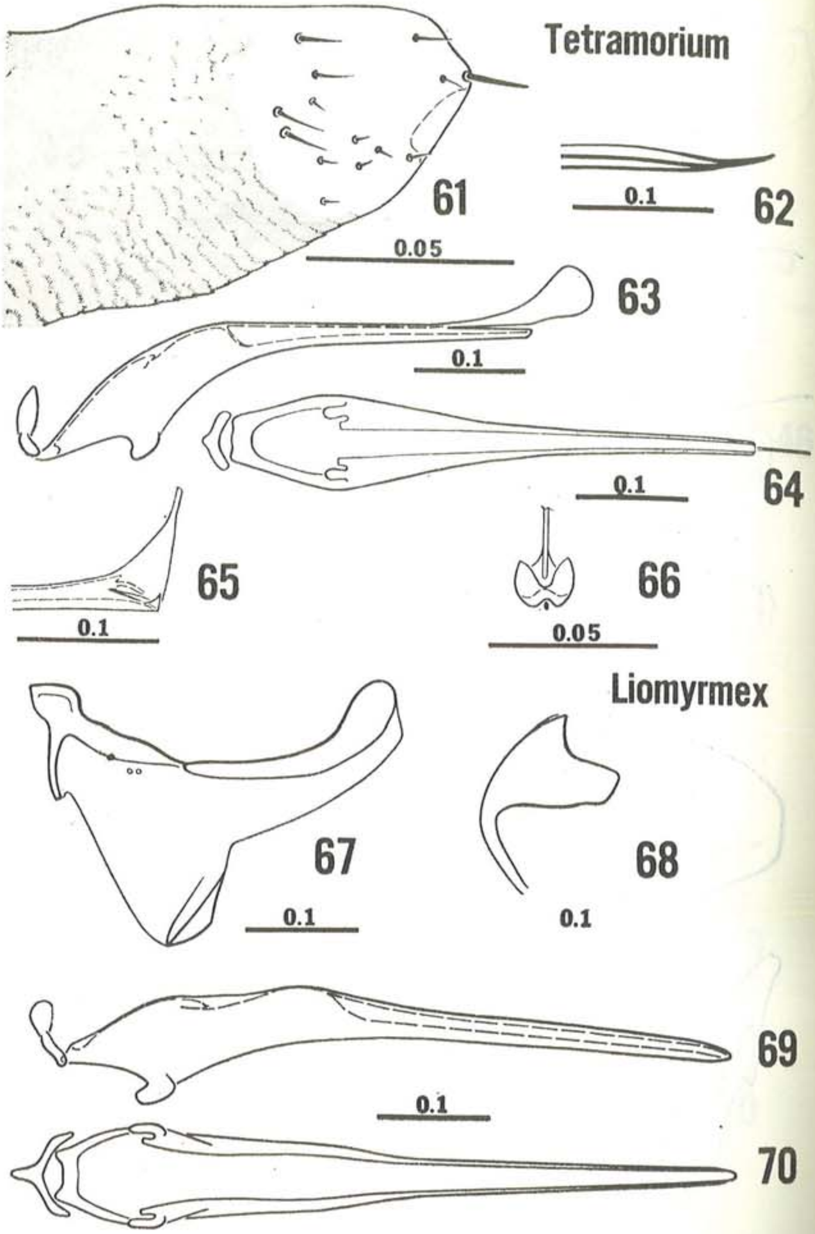
Figs. 35-38. *Daceton armigerum;* 35. spiracular plate; 36. oblong plate; 37. anterior third of sting, furcula; 38. ventral view of anterior third of sting, furcula. Figs. 39-40. *Orectognathus sarasini;* 39. sting, furcula; 40. ventral sting, furcula. Figs. 41-42. *Neostruma metopia;* 41. sting, furcula; 42. ventral sting, furcula.



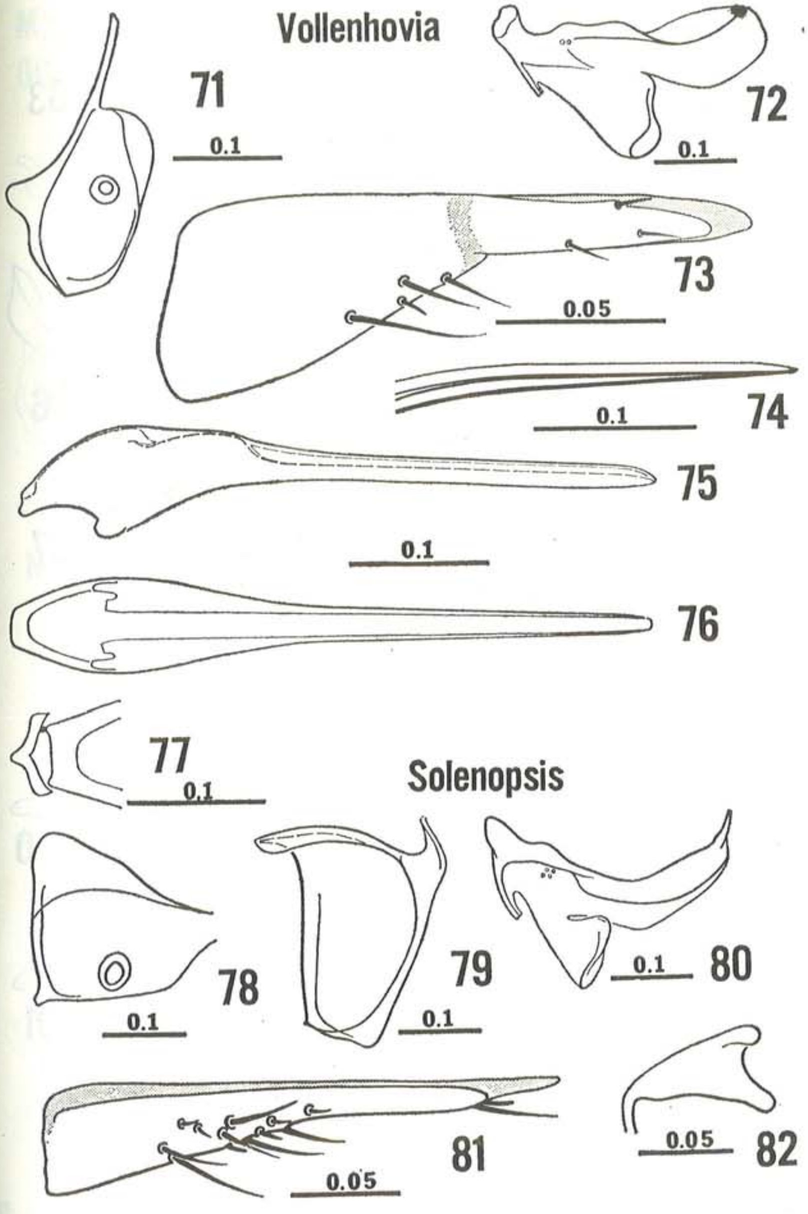
Figs. 43-49. *Basiceros singularis;* 43. spiracular plate; 44. quadrate plate; 45. oblong plate; 46. gonostylus; 47. sting, furcula; 48. ventral view of sting, furcula; 49. poison gland, Dufour's gland, sting. Figs. 50-51. *Eurhopalothrix speciosa;* 50. sting, furcula; 51. ventral view of anterior half of sting, furcula.



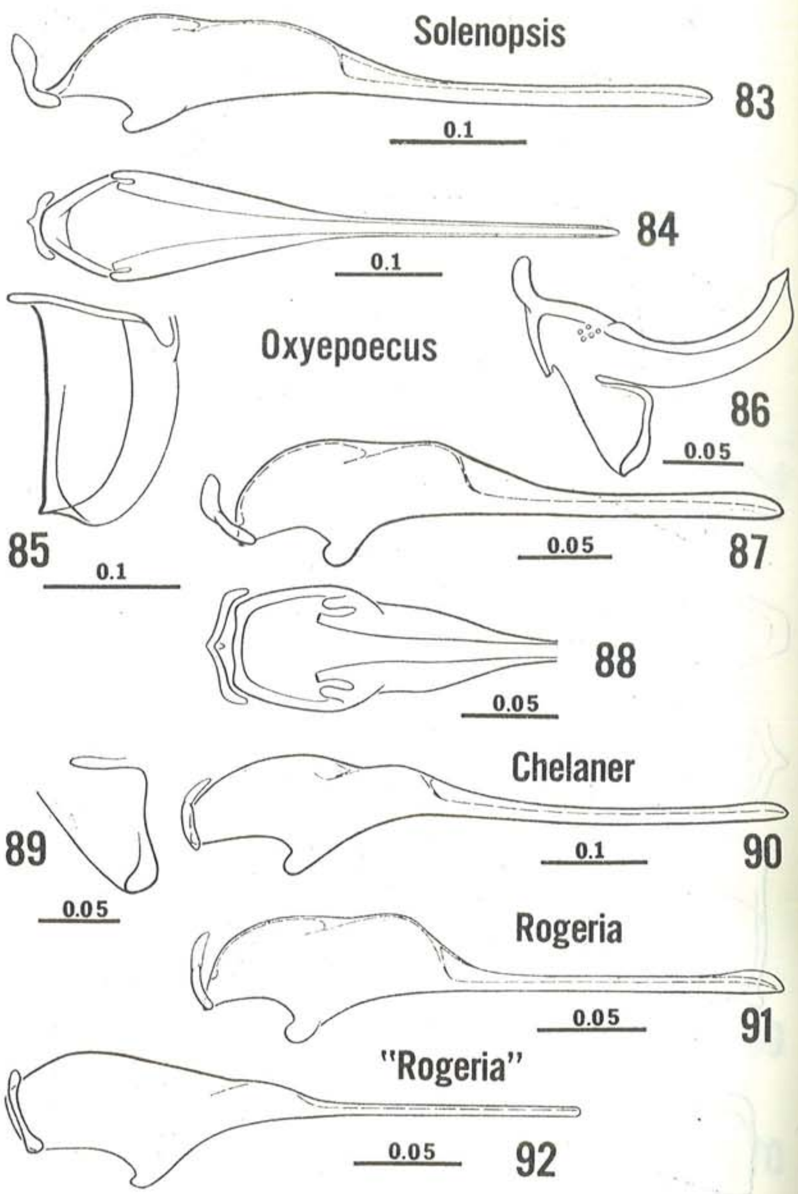
Figs. 52-56. *Leptothorax longispinosus;* 52. oblong plate; 53. dorsolateral gonostylus; 54. distal fifth of lancet; 55. sting, furcula; 56. ventral view of sting, furcula. Figs. 57-60. *Tetramorium;* 57. spiracular plate, *T. grassii;* 58. quadrate plate, *T. pacificum;* 59. oblong plate, *T.* cf. *insolens group;* 60. gonostylus, *T. caespitum.*



Figs. 61-66. *Tetramorium* (continued); 61. gonostylus, *T. tenuicrine;* 62. distal half of lancet, *T. pacificum;* 63. sting and furcula, *T. grassii;* 64. ventral view of sting, furcula, *T. grassii;* 65. end of sting, *T. pacificum;* 66. posterior view of end of sting, *T spinosum.* Figs. 67-70. *Liomyrmex* cf. *aurianus;* 67. oblong plate; 68. triangular plate; 69. sting, furcula; 70. ventral view of sting, furcula.

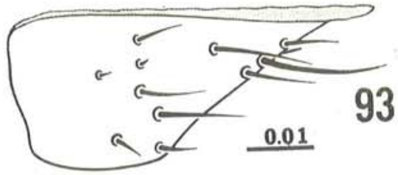


Figs. 71-77 *Vollenhovia;* 71. spiracular plate, V. *sp*. 1; 72. oblong plate; *V*. cf. *pedestris;* 73. gonostylus, *V. sp*. 1; 74. distal end of lancet, *V*. cf. *pedestris;* 75. sting, *V*. *sp*. 1; 76. ventral sting, *V*. *sp*. 1; 77. ventral sting base, furcula, *V*. of *pedestris*. Figs. 78-82. *Solenopsis geminata;* 78. spiracular plate; 79. quadrate plate; 80. oblong plate; 81. gonostylus; 82. triangular plate.



Figs. 83-84. *Solenopsis geminata* (continued); 83. sting, furcula; 84. ventral sting, furcula. Figs. 85-88. *Oxyepoccus rastratus;* 85. quadrate plate; 86. oblong plate; 87. sting, furcula; 88. ventral sting bulb, furcula. Figs. 89-90. *Chelaner sp.* 1; 89. ventral arm of oblong plate; 90. sting, furcula. Fig. 91. *Rogeria inermis* sting, furcula. Fig. 92. *"Rogeria" sp.* 2 (*stigmatica* group) sting, furcula.

Monomorium (Holcomyrmex)



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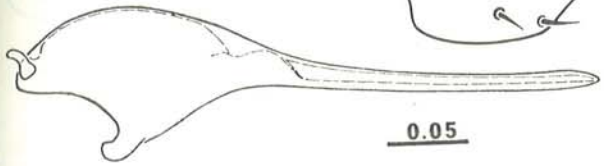

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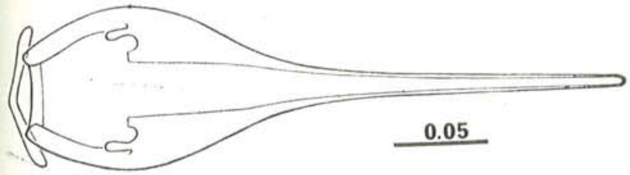

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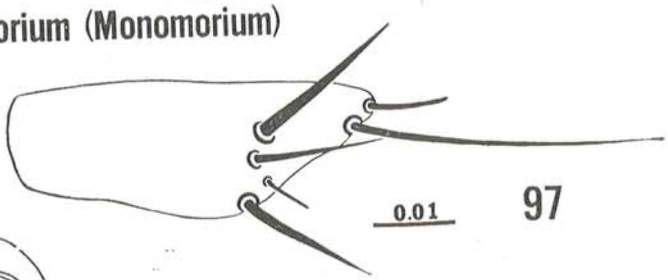
Monomorium (Monomorium)



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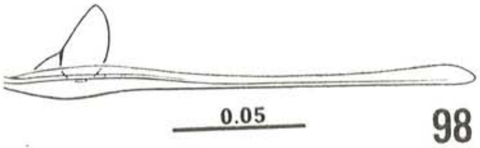

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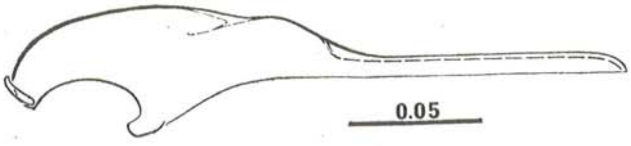

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Figs. 93-95. *Menomorium (Holcomyrmex) scabriceps;* 93. ventral gonostylus; 94. sting, furcula; 95. ventral sting, furcula. Figs. 96-99. *Monomorium (Monomorium) minimum;* 96. spiracular plate; 97. gonostylus; 98. distal end of lancet; 99. sting and furcula.

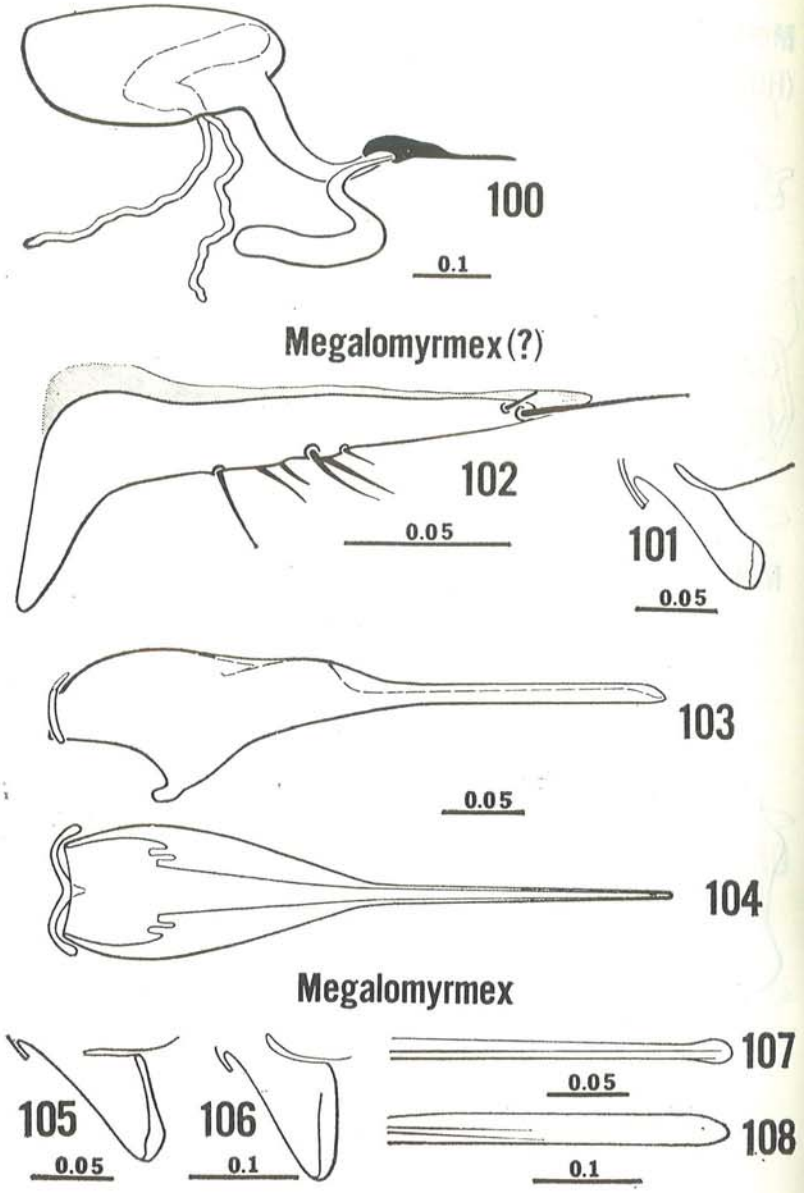

Fig. 100. *Monomorium (Monomorium) minimum* (continued), poison gland. Dufour's gland, sting. Figs. 101-104. *Megalomyrmex(?) sp.* 1; 101. ventral arm of oblong plate; 102. gonostylus; 103. sting, furcula; 104. ventral sting, furcula. Figs. 105-108. *Megalomyrmex;* 105. ventral arm of oblong plate, *M.* near *incisus;* 106. ventral arm of oblong plate, *M. modestus;* 107. distal two-thirds of lancet, *M.* near *incisus;* 108. distal half of lancet, *M. modestus.*

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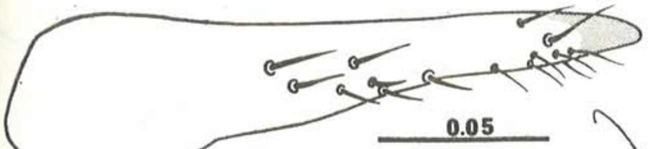
Calyptomyrmex



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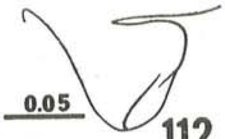

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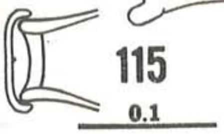

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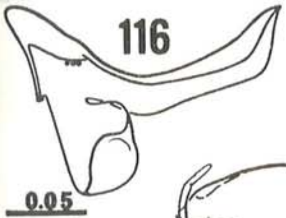
Wasmannia



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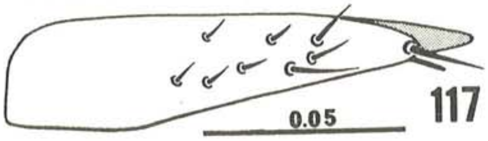

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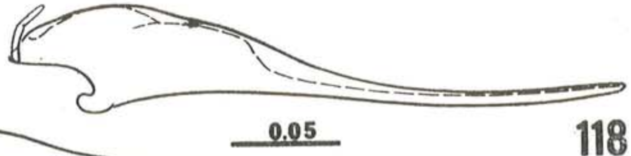

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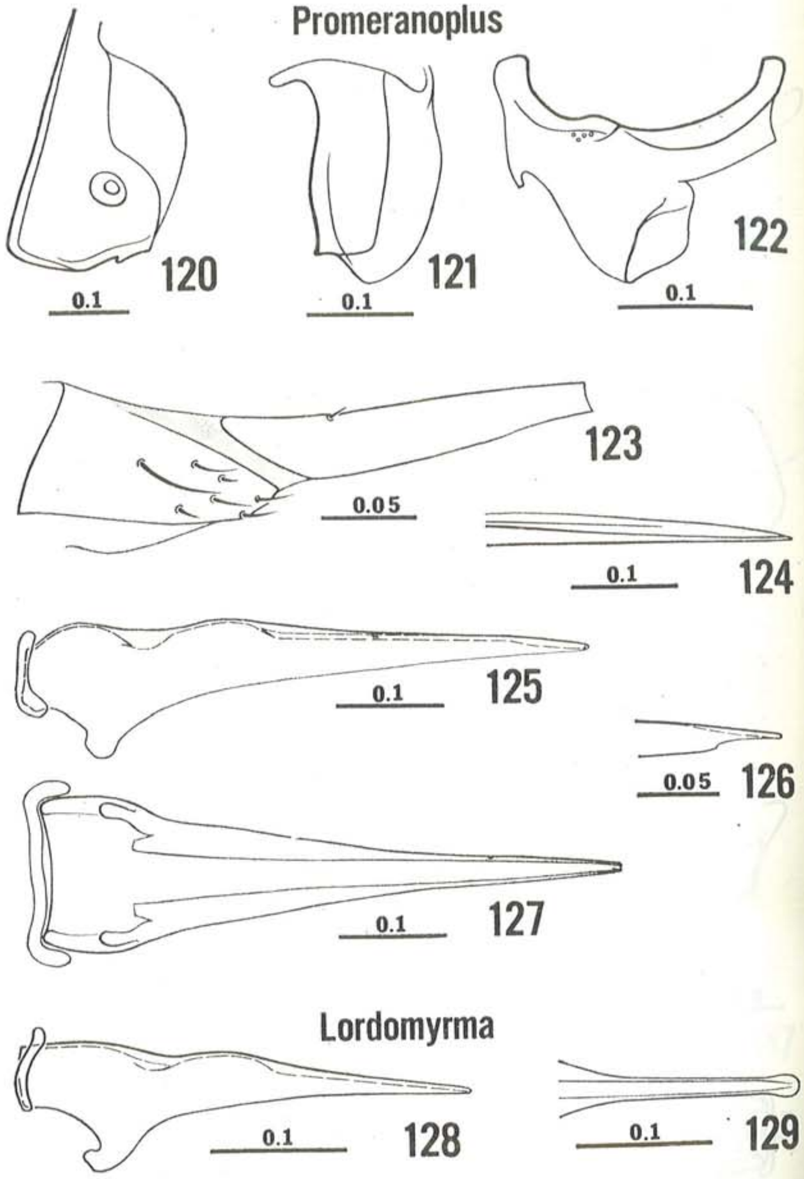
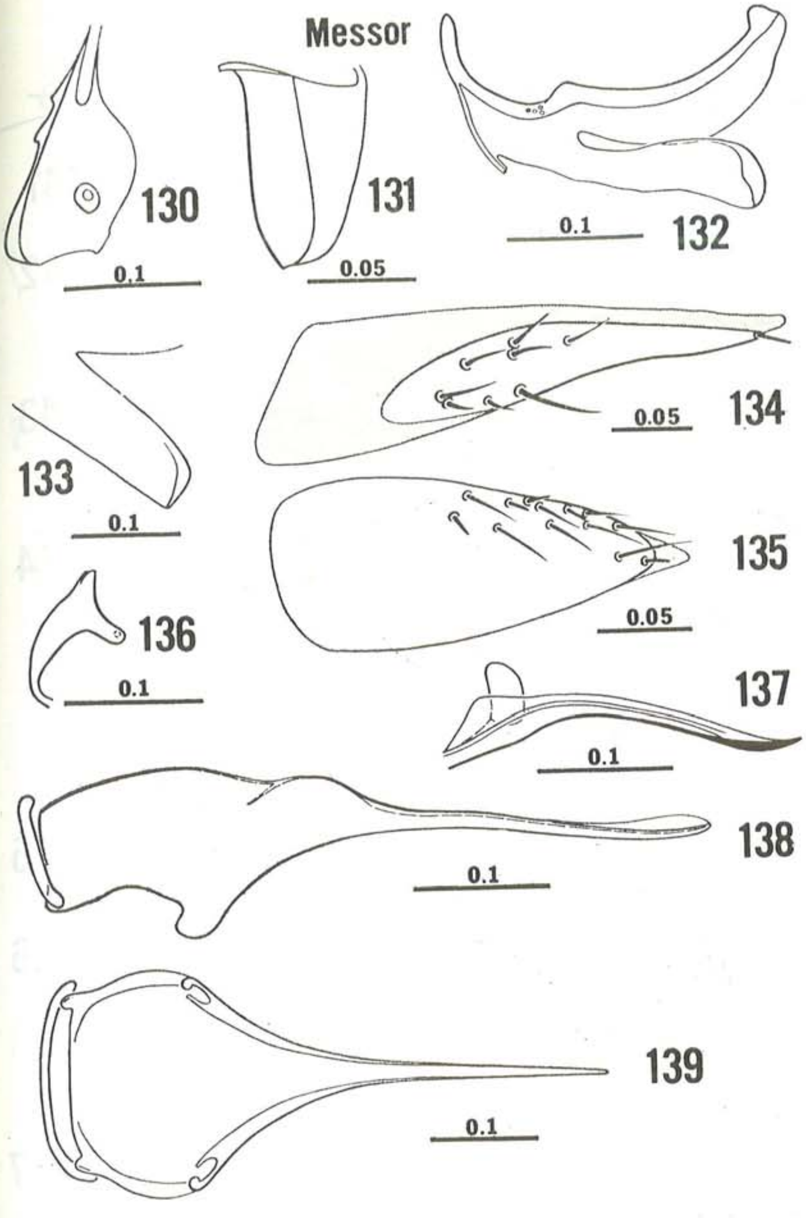
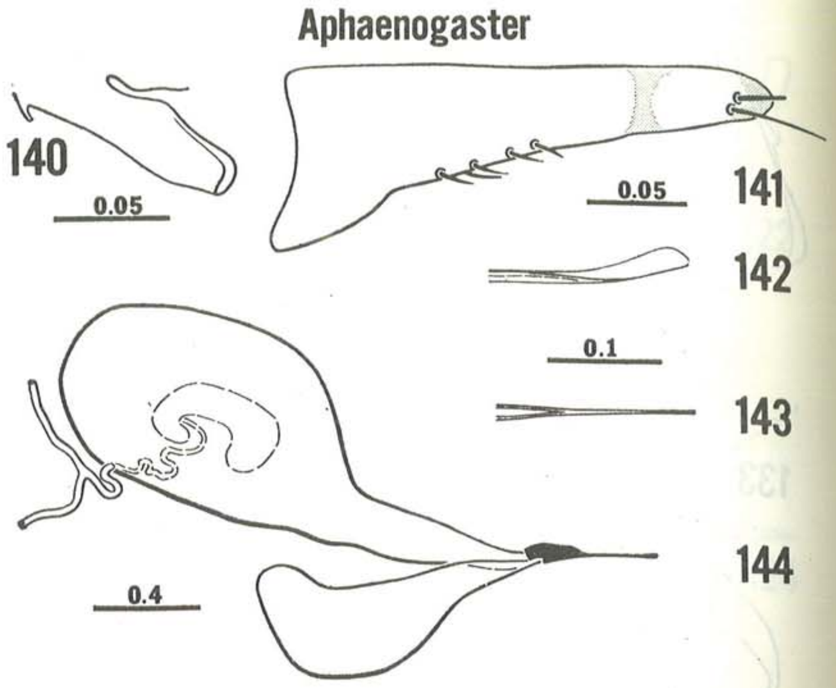
Figs. 109-111. *Megalomyrmex* (continued); 109. sting, furcula, *M.* near *incisus;* 110. distal end of sting, *M. modestus;* 111. ventral sting. furcula of *M.* near *incisus.* Figs. 112-115. *Calyptomyrmex sp.* 1; 112. ventral arm of oblong plate; 113. dorsolateral gonostylus; 114. sting, furcula; 115. ventral sting base, furcula. Figs. 116-119. *Wasmannia;* 116. oblong plate, *W. sp.* 2; 117. ventral gonostylus, *W. sp.* 2; 118. sting, furcula, *W. auropunctata;* 119. ventral sting, furcula of *W. sp.* 2.

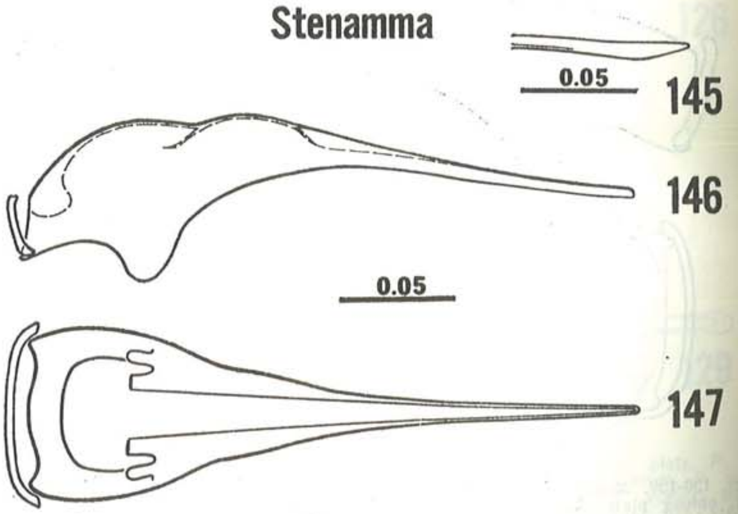


Figs. 120-127. *Promeranoplus;* 120. Spiracular plate, *P. rouxi;* 121. quadrate plate, *P. sp.* 2; 122. oblong plate, *P. sp.* 2; 123. gonostylus, *P. rouxi;* 124. distal two-thirds, *P. rouxi* lancet; 125. sting, furcula, *P. rouxi;* 126. end of sting, *P. sp.* 2; 127. ventral sting, furcula, *P. rouxi.* Figs. 128-129. *Lordomyrma caledonica;* 128. sting, furcula; 129. ventral view of end of sting.

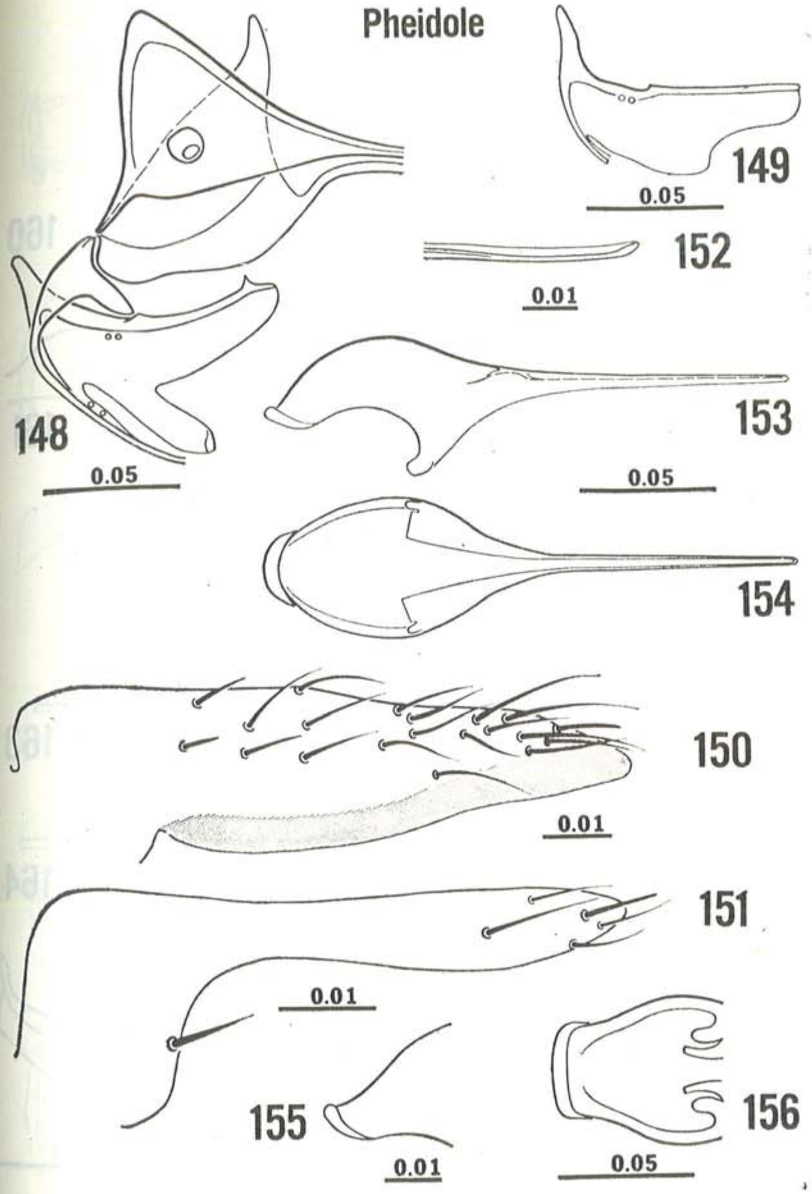


Figs. 130-139. *Messor;* 130. spiracular plate, *M. aciculata;* 131. quadrate plate, *M. aciculata;* 132. oblong plate, *M. sp.* 1; 133. ventral arm of oblong plate, *M. aciculata;* 134. ventral view of gonostylus, *M. aciculata;* 135. dorsal and ventrolateral aspects of gonostylus, *M. sp.* 1; 136. triangular plate, *M. sp.* 1; 137. lancet, *M. sp.* 1; 138. sting and furcula, *M. sp.* 1; 139. ventral sting, furcula, *M. sp.* 1.





Figs. 140-144. *Aphaenogaster;* 140. ventral arm of oblong plate, *A. rudis;* 141. dorsal gonostylus, *A. phalangium;* 142. distal end of sting, *A. phalangium;* 143. ventral view of distal end of sting, *A. phalangium;* 144. poison gland, Dufour's gland, sting of *A. phalangium.* Length of each free filament is 5.0 mm. Figs. 145-147. *Stenamma* near *manni;* 145. distal end of lancet; 146. sting, furcula; 147. ventral sting, furcula.



Figs. 148-156. *Pheidole;* 148. spiracular, quadrate, triangular, and oblong plates of *Ph. sp.* 3 minor worker; 149. oblong plate, *Ph. morrisi* minor worker; 150. ventrolateral gonostylus, *Ph. morrisi* minor worker; 151. dorsal gonostylus, *Ph. sp.* 2 minor worker; 152. distal half of *Ph. sp.* 2 lancet minor worker; 153. sting, furcula, *Ph. morrisi* minor worker; 154. ventral sting, furcula of *Ph. morrisi* minor worker; 155. anterior end of sting, *Ph. sp.* 2 minor worker; 156. ventral view of anterior end of sting, *Ph. sp.* 1 minor worker.

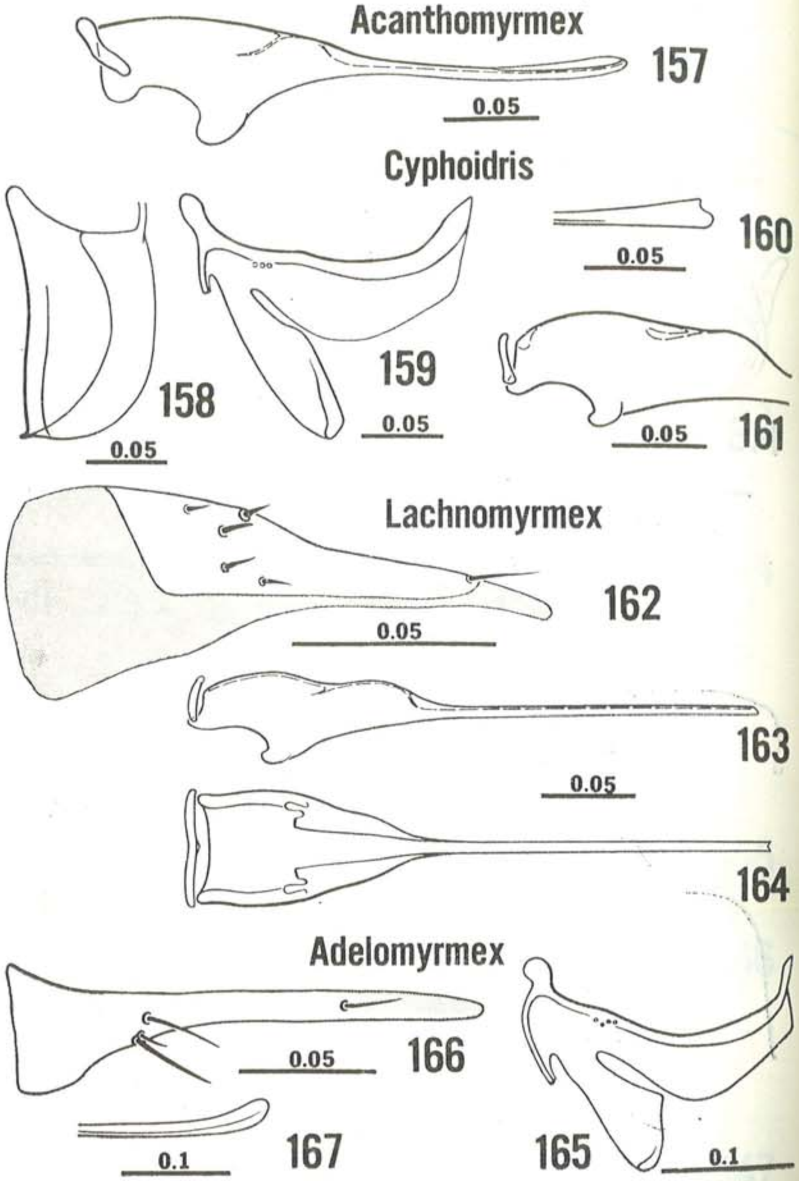
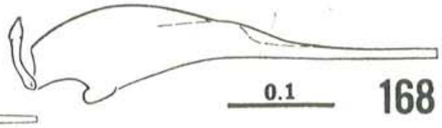


Fig. 157. *Acanthomyrmex* of *notabilis* sting, furcula. Figs. 158-161. *Cyphoidris spinosus;* 158. quadrate plate; 159. oblong plate; 160. end of lancet; 161. sting bulb and furcula, Dundo specimen. Figs. 162-164. *Lachnomyrmex* cf. *scrobiculatus;* 162. gonostylus; 163. sting, furcula; 164. ventral sting, furcula. Figs. 165-167. *Adelomyrmex;* 165. oblong plate, *A. sp.* 2; 166. dorsolateral gonostylus, *A.* near *tristani;* 167. distal end of lancet, *A.* near *tristani.*



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Myrmicaria

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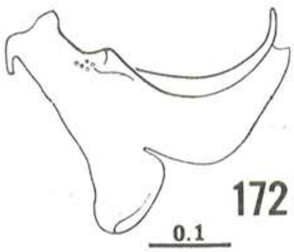

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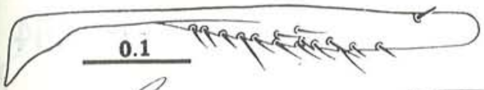

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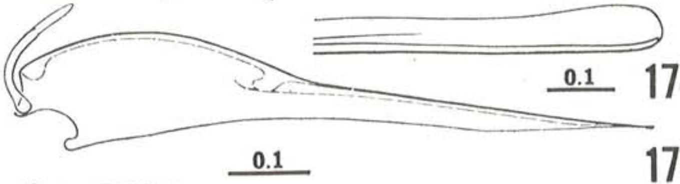

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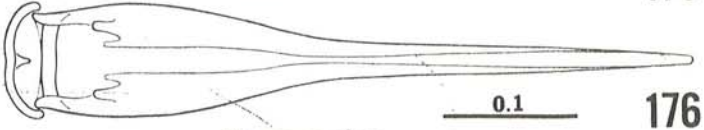

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Meranoplus

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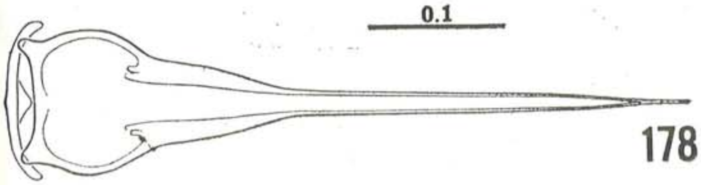

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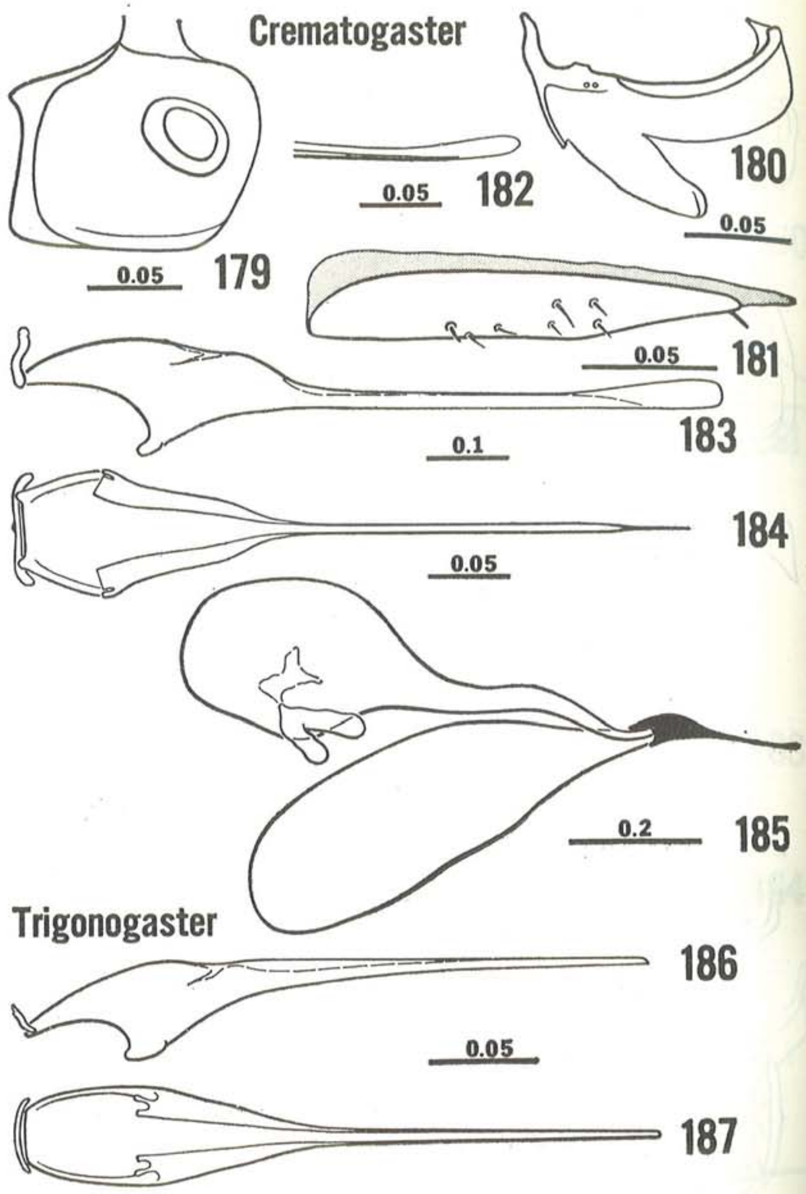
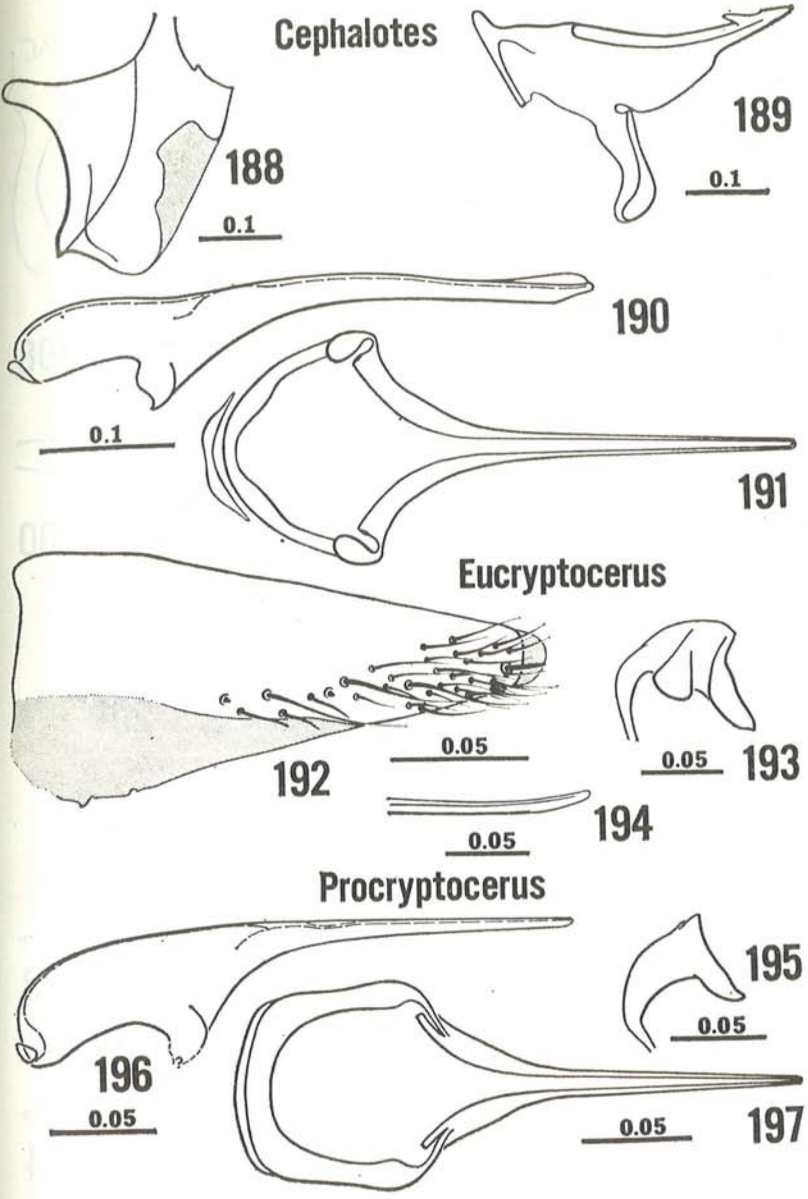
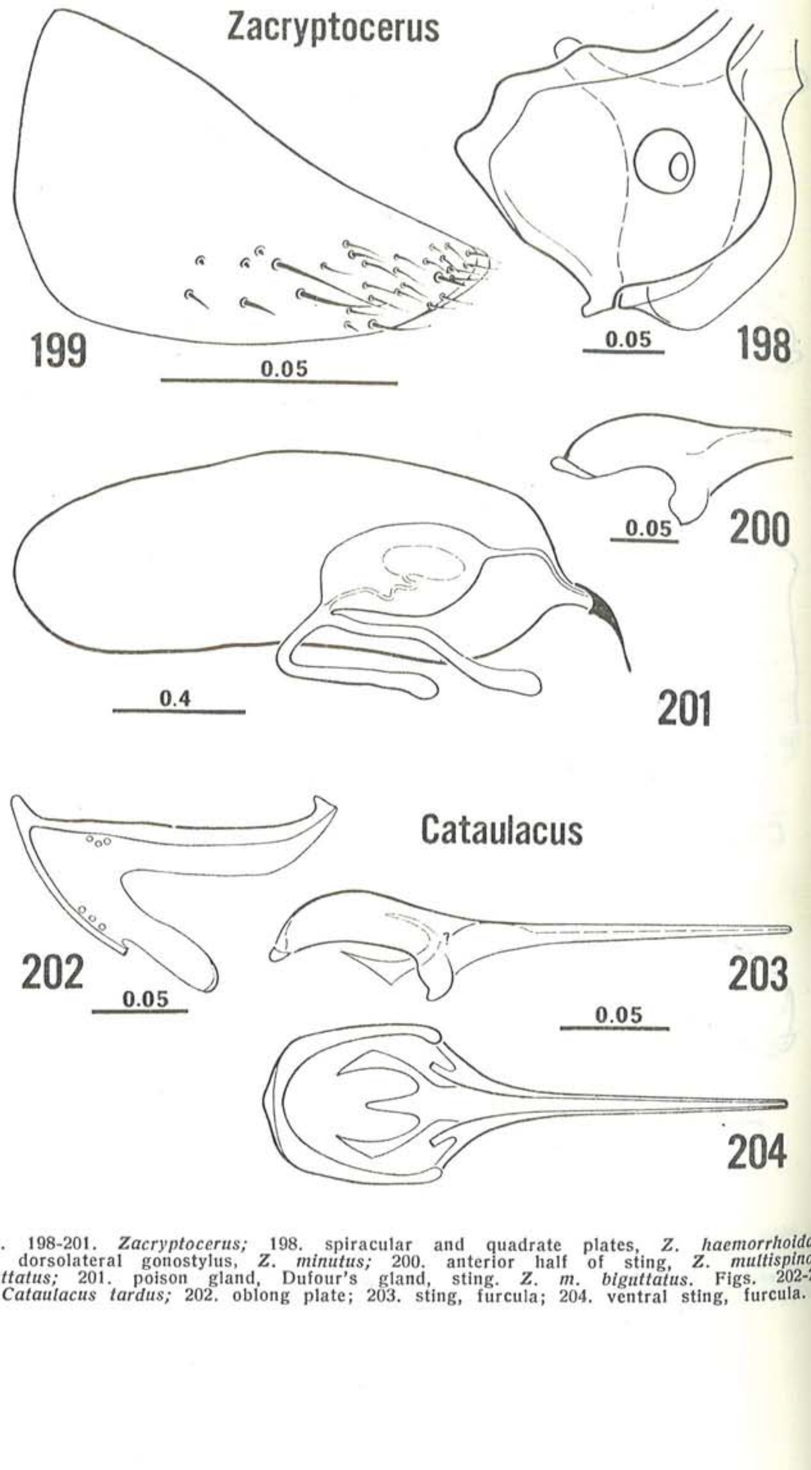
Figs. 168-169. *Adetomyrmex* (continued); 168. sting, furcula, *A.* near *tristani;* 169. ventral sting, furcula of *A.* near *tristani.* Figs. 170-176. *Myrmicaria;* 170. spiracular plate, *M. arachnoides;* 171. quadrate plate, *M. eumenoides;* 172. oblong plate, *M. carinata;* 173. gonostylus, *M. eumenoides;* 174. distal two-thirds of lancet, *M. eumenoides;* 175. sting, furcula, *M. arachnoides;* 176. ventral sting, furcula, *M. arachnoides.* Figs. 177-178. *Meranoplus sp.* 1; 177. sting, furcula; 178. ventral sting, furcula.



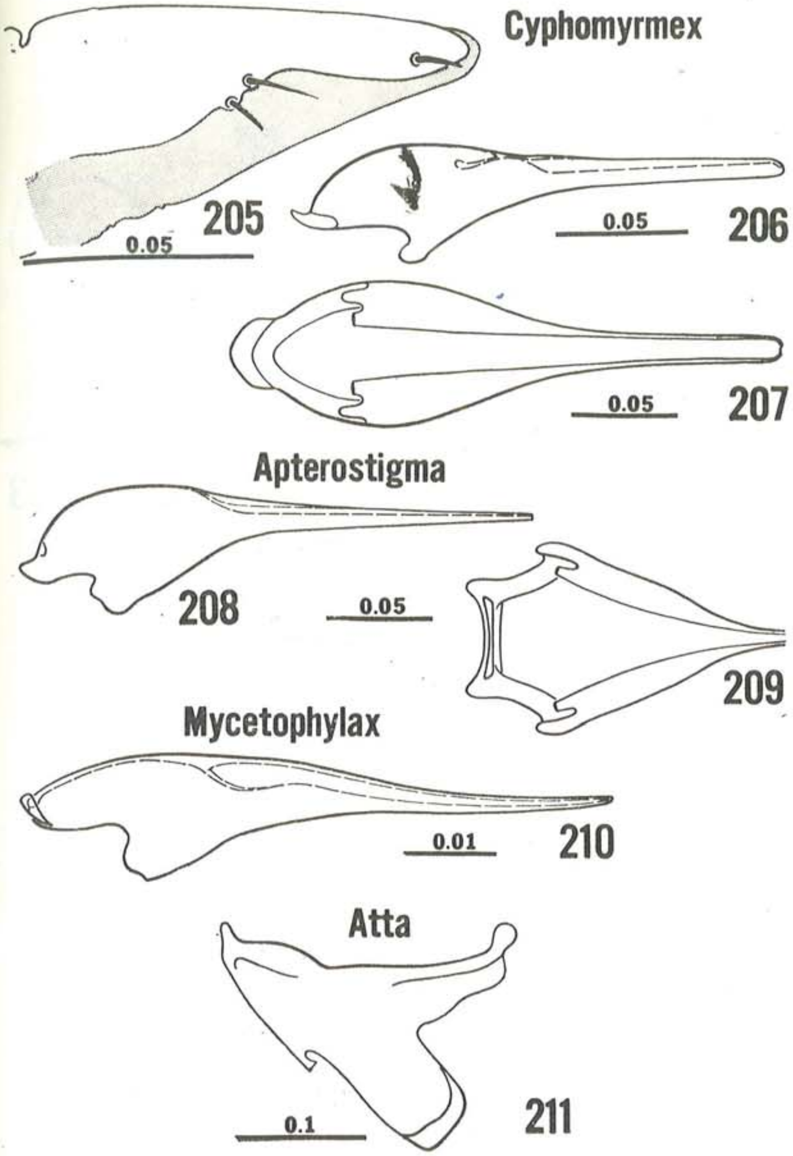
Figs. 179-185. *Crematogaster;* 179. spiracular plate, *C. ashmeadi;* 180. oblong plate, *C. minutissima;* 181. ventral gonostylus, *C. atkinsoni;* 182. distal half of lancet, *C. atkinsoni;* 183. sting, furcula, *C. cerasi;* 184. ventral sting, furcula, *C. minutissima;* 185. poison gland, Dufour's gland, sting, *C. minutissima.* Figs. 186-187. *Trigonogaster recurvispinosus;* 186. sting, furcula; 187. ventral sting, furcula.



Figs. 188-191. *Cephalotes atratus;* 188. quadrate plate, major worker; 189. oblong plate; 190. sting, furcula; 191. ventral sting, furcula. Figs. 192-194. *Eucryptocerus opacus;* 192. dorsolateral gonostylus; 193. triangular plate; 194. distal end of lancet. Figs. 195-197. *Procryptocerus scabriusculus;* 195. triangular plate; 196. sting, furcula; 197. ventral sting, furcula.

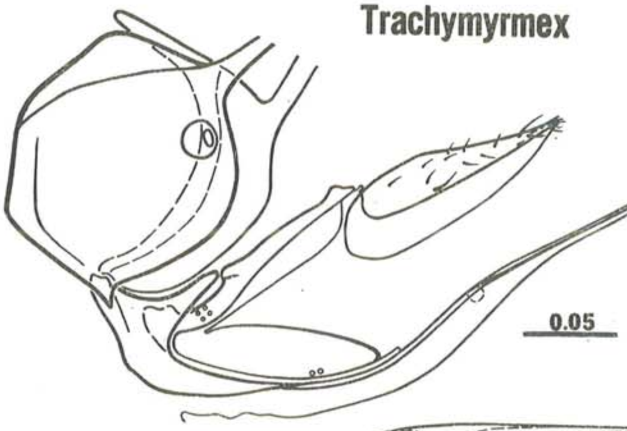


Figs. 198-201. *Zacryptocerus;* 198. spiracular and quadrate plates, *Z. haemorrhoidalis;* 199. dorsolateral gonostylus, *Z. minutus;* 200. anterior half of sting, *Z. multispinosus biguttatus;* 201. poison gland, Dufour's gland, sting. *Z. m. biguttatus.* Figs. 202-204. *Cataulacus tardus;* 202. oblong plate; 203. sting, furcula; 204. ventral sting, furcula.



Figs. 205-207. *Cyphomyrmex salvini;* 205. dorsolateral gonostylus; 206. sting, furcula; 207. ventral sting, furcula. Figs. 208-209. *Apterostigma collare;* 208. sting, furcula; 209. ventral view, anterior end of sting, furcula. Fig. 210. *Mycetophylax emeryi,* sting, furcula. Fig. 211. *Atta cephalotes,* oblong plate.

Trachymyrmex



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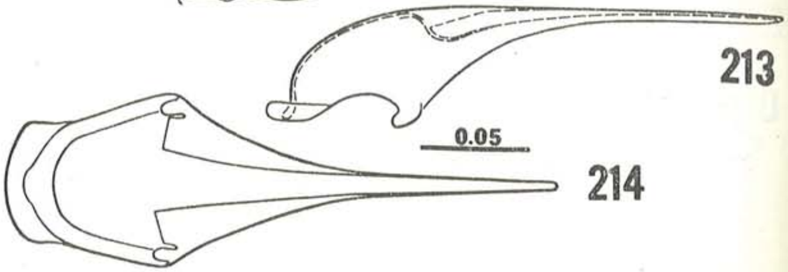

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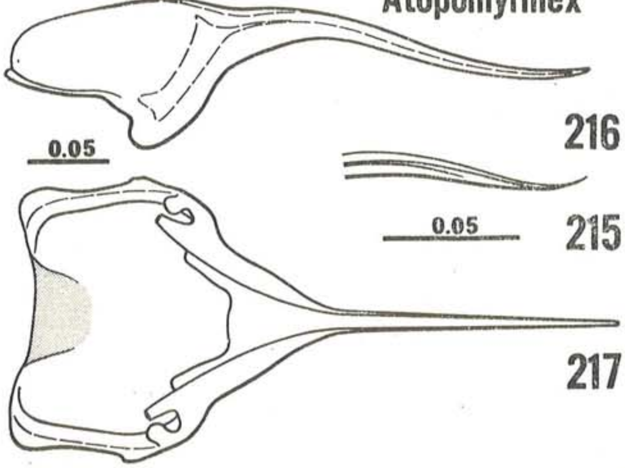
Atopomyrmex



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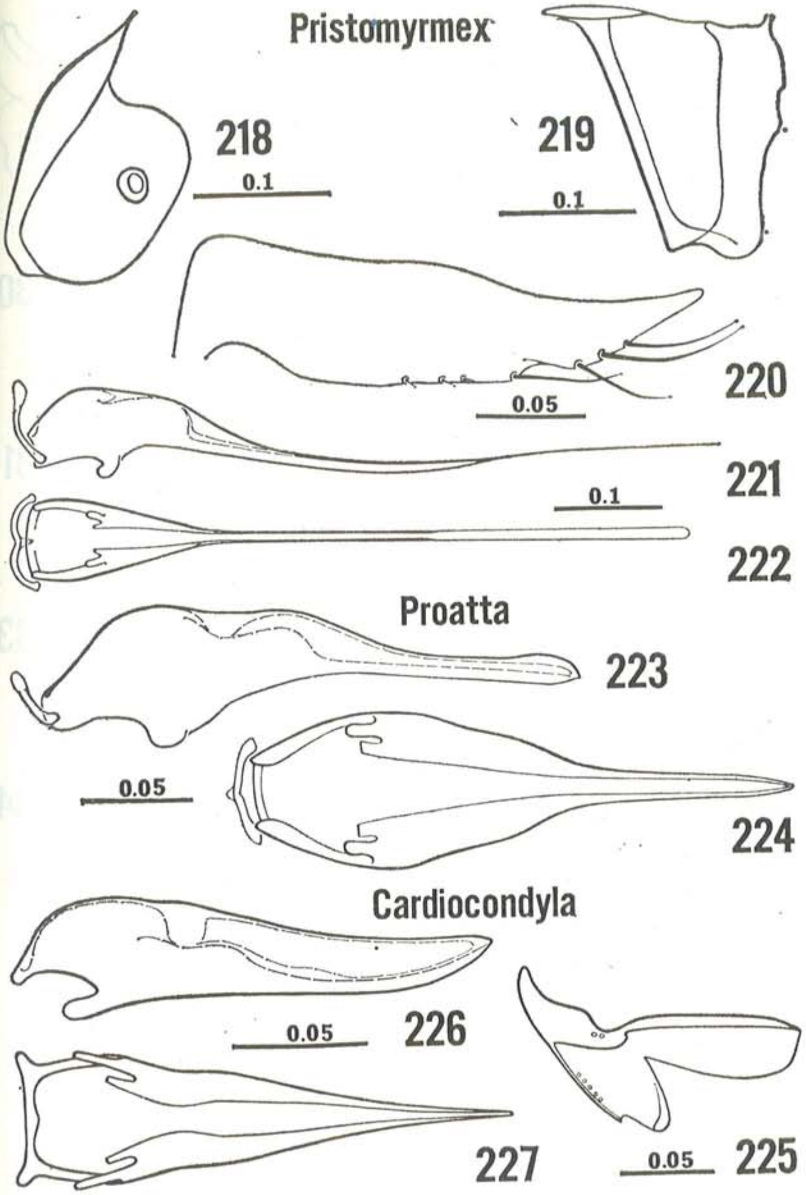
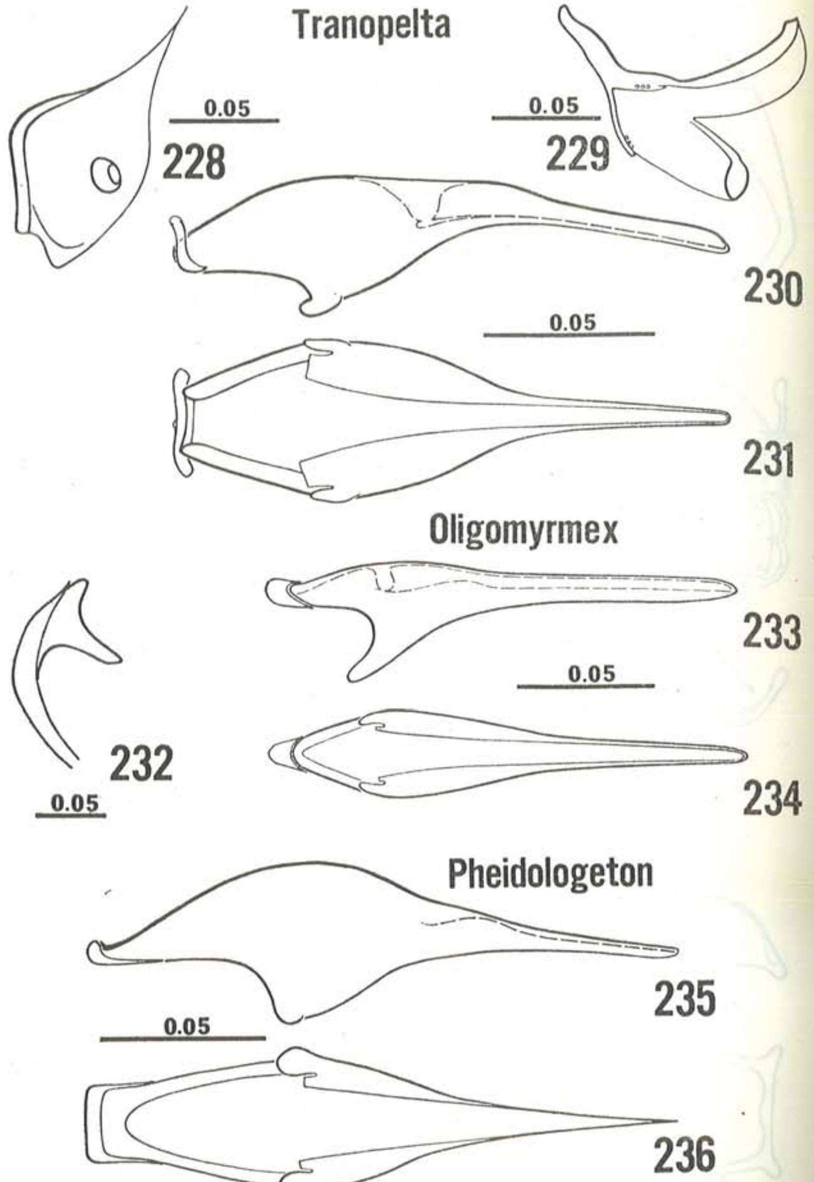
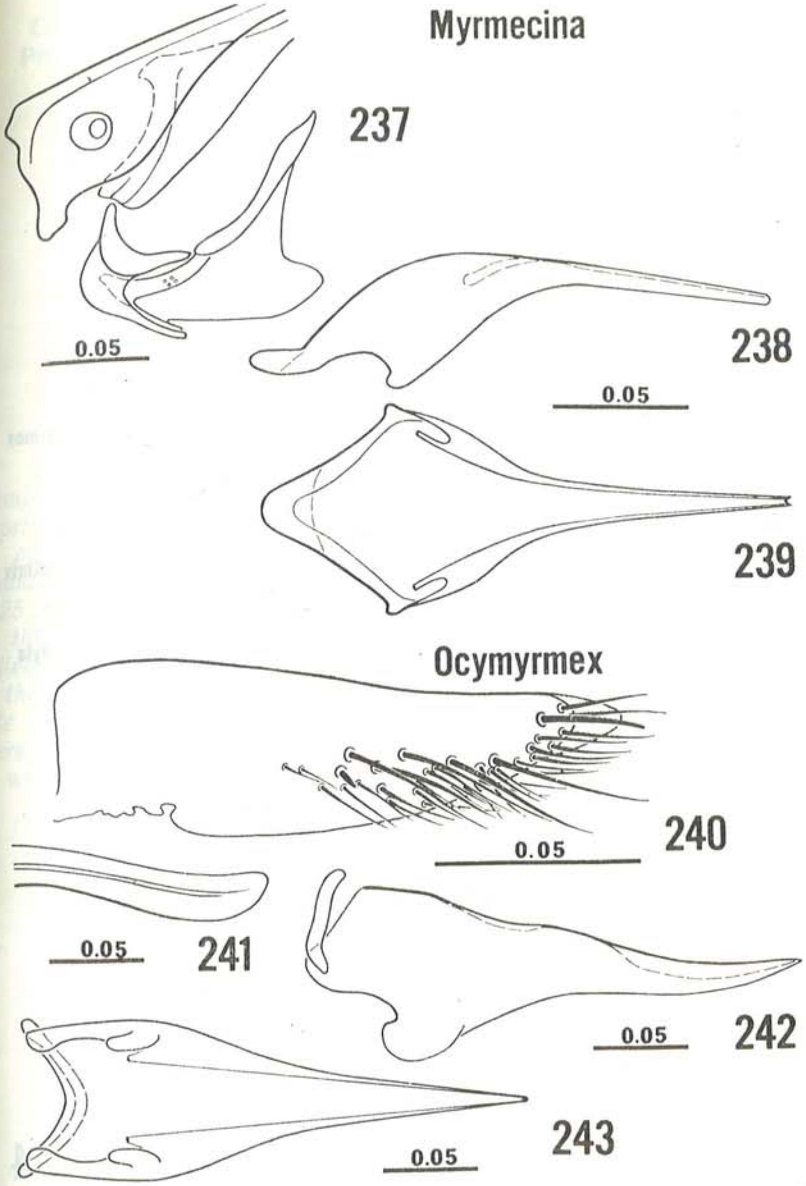
Figs. 212-214. *Trachymyrmex seminole;* 212. spiracular, quadrate, oblong and triangular plates, lancet, ventral view of gonostylus; 213. sting, furcula; 214. ventral sting, furcula. Figs. 215-217. *Atopomyrmex mocquerysi;* 215. distal end of lancet; 216. sting; 217. ventral sting.



Figs. 218-222. *Pristomyrmex brevispinosus;* 218. spiracular plate; 219. quadrate plate; 220. dorsolateral gonostylus; 221. sting, furcula; 222. ventral sting, furcula. Figs. 223-224. *Proatta buttelli;* 223. sting, furcula; 224. ventral sting, furcula. Figs. 225-227. *Cardiocondyla elegans;* 225. oblong plate; 226. sting; 227. ventral sting.



Figs. 228-231. *Tranopelta gilva;* 228. spiracular plate; 229. oblong plate; 230. sting, furcula; 231. ventral sting, furcula. Figs. 232-234. *Oligomyrmex corniger sodalis?*); 232. triangular plate; 223. sting, furcula; 234. ventral sting, furcula. Figs. 235-236. *Pheidologeton* cf. *diversus;* 235. sting, furcula; 236. ventral sting, furcula.



Figs. 237-239. *Myrmecina graminicola;* 237. spiracular, quadrate, triangular and oblong plates; 238. sting, furcula; 239. ventral sting, furcula. Figs. 240-243. *Ocymyrmex* cf. *arnoldi;* 240. dorsolateral gonostylus; 241. distal two-thirds of lancet; 242. sting, furcula; 243. ventral sting, furcula.

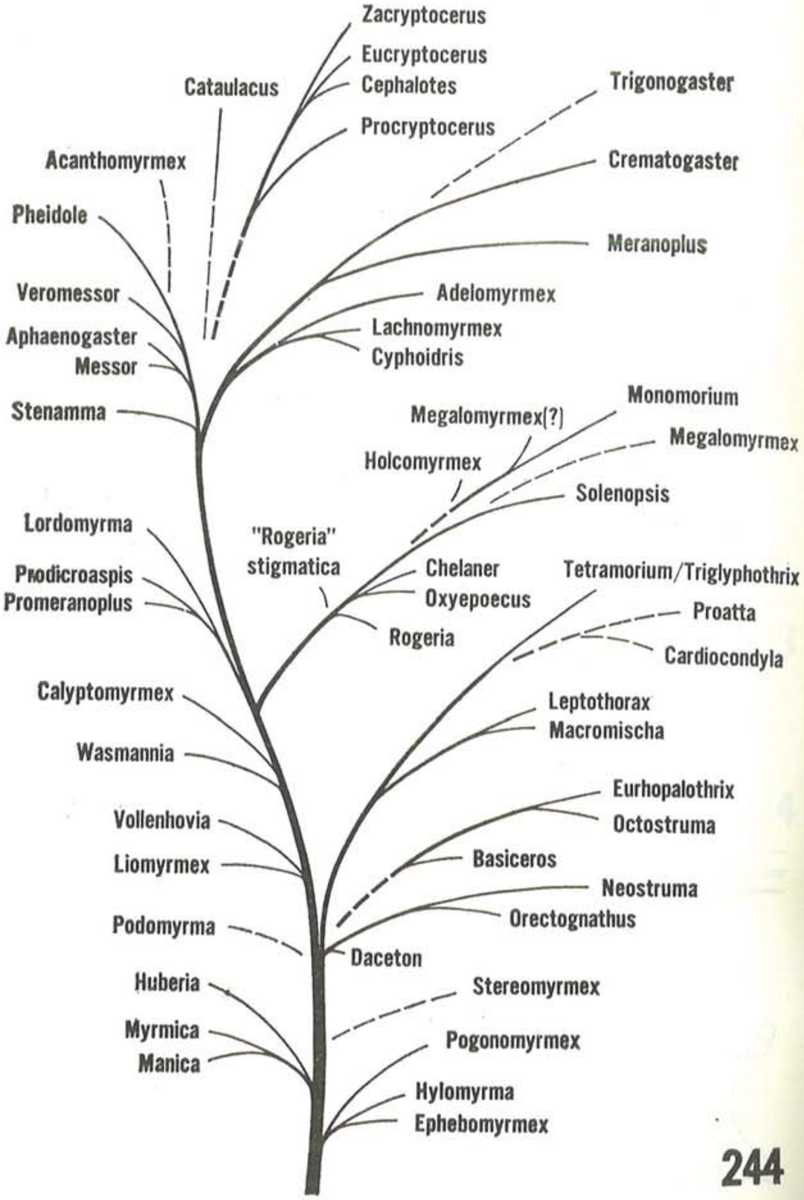


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Fig. 244. Proposed phylogeny of some myrmicine genera based on morphology of the sting apparatus. The following genera are excluded because of poorly known affinities: Attini, *Myrmicaria, Pheidologenton, Oligomyrmex, Ocymyrmex, Atopomyrmex, Tranopelta, Myrmecina, Pristomyrmex.*