1967

A Comparative Study of the Hymenopterous Poison Apparatus.

Henry Remley Hermann Jr

Louisiana State University and Agricultural & Mechanical College

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Louisiana State University and Agricultural and Mechanical College, Ph.D., 1967
Entomology

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A COMPARATIVE STUDY OF THE HYMENOPTEROUS POISON APPARATUS

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Entomology

by

Henry Remley Hermann, Jr.
M.S., Louisiana State University in Baton Rouge, 1965
May, 1967
ACKNOWLEDGEMENTS

I wish to express my sincere appreciation to a number of people for their assistance in this investigation. I first thank my wife, Patricia, for her constant interest in the subject and assistance in the preparation of material. Dr. Murray S. Blum, advisor and close companion, is especially acknowledged for his continuous support and genuine interest in many problems which arose and for his many efforts in procuring specimens from many areas in the world. Special thanks also go to the following: Dr. William L. Brown, Cornell University, Ithaca, New York, and Dr. E. O. Wilson, Harvard University, Cambridge, Massachusetts, for many ant species of particular interest and for information related to the taxonomic position of some species of ants; Dr. Howard Evans, Museum of Comparative Zoology, Harvard University, for several wasp species; Dr. D. H. Kistner, Chico State College, Chico, California, for Old World dorylines; Dr. C. W. Rettenmeyer, Kansas State University, Manhattan, Kansas, Lawrence, Kansas, for several New World dorylines; Dr. Daniel Janzen, University of Kansas, Lawrence, Kansas, for several species of pseudomyrmecine ants; Dr. L. D. Newsom, Department Head, Louisiana State University, for his interest and support during the investigation; Drs. J. H. Roberts, George H. Lowery, Walter Harman, L. D. Newsom and M. S. Blum, committee members, for their review and worthy criticism of the dissertation.
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ABSTRACT

The results of a comparative study of the sclerites and associated organs that compose the poison apparatus in hymenopterous insects are presented. Species of all 10 subfamilies of the Formicinae and a few wasp species in three families are included in this investigation.

Although there is generally a similarity in the basic structures of the poison apparatus of hymenopterous insects, there are individual characteristics which seem to be significant in determining phylogenetic relationships between the various groups. Certain characters are unique among individuals of a given group. The presence of external convolutions of the convoluted gland is a unique character among members of the Formicinae. There is also a tendency in this subfamily to develop a bilobed Dufour's gland. In all of the aculeate Hymenoptera studied in this investigation, with the exception of the Dorylinae, Formicinae, Dolichoderinae, some Ponerinae and Cerapachinae, a sclerite known as the furcula is present. This small structure is probably the most important single sclerite in the hymenopterous poison apparatus when considering the sclerites as structures useful in the study of phylogeny. Its form varies considerably among the various groups and may correlate, to some extent, with the biology of a given species. Other characters that may be important in classification and phylogeny are the position of extension of the free filaments from the poison sac, the shape and size of the free filaments, the reduction of various structures associated with the apparatus (e.g., sensory pegs
and setae), and the reduction and elaboration of the sting sclerites themselves (especially within the Dolichoderinae and Formicinae). While all of these seem to be important phyletic characters, other characters may be of little, if any, significance in this respect. The presence or absence of lancet barbs seems to have little taxonomic significance, since their presence in one or more groups of aculeate hymenopterans is indeed unpredictable. Branching of the free filaments seems to be present in all species of the Formicidae and thus cannot be used as a phyletic tool unless the extent of branching in any particular group could be of some importance.

Following an explanation of the structures composing the poison apparatus and a comparative explanation of the soft parts and sclerites, a discussion of how this investigation correlates with the current trends of thought in formicid phylogeny is presented. Evidence resulting from this investigation indicates that the poison apparatus may indeed be a significant tool in the study of hymenopterous phylogeny.
The sting of hymenopterous insects is a modified ovipositor. The sclerites that make up the sting of stinging forms are also present in those insects that use the sclerites for the deposition of eggs. It is generally believed that some hymenopterous insects (Fig. 1, A) have retained the ability to utilize these sclerites for oviposition (parasitic forms such as braconid, ichneumonid and mutillid wasps), whereas the reproductive system of many of the higher hymenopterous groups has completely lost any functional association with the sclerites involved in oviposition (Fig. 1, B). Therefore, during the progression of evolution in some hymenopterous species, the sclerites that have arisen from the 8th, 9th and 10th abdominal segments have altered their function from that of oviposition to that of a defensive and offensive nature. The sting of aculeate forms plays an important role in affecting the ethological activities among the various hymenopterous species. Because of this ability of numerous species of ants to sting, many humans have learned to recognize and avoid certain ant species (e.g., Solenopsis saevissima and certain members of the Ponerinae). The evolution of a sting in certain Aculeatae has also created some interesting relationships between the various sclerites and their resulting functions.

There has been considerable interest by morphologists in the hymenopterous poison apparatus throughout much of the past two centuries. Individual studies of a number of species have indicated that there may indeed be some taxonomic significance in a study of
the sting sclerites and associated structures. The purpose of this investigation was to examine comparatively the gross anatomy of the sclerites and some of the soft parts that compose the poison apparatus. An attempt has been made to illustrate some relationships among the Hymenoptera by indicating various similarities and differences among species in this study and in those hymenopterous insects that have previously been examined.

It is interesting to note that taxonomists have, in most cases, ignored the sting in their work, although male genitalia have been used extensively in species descriptions. The failure to employ the sting as a taxonomic structure in the Hymenoptera may be due to a number of factors: 1) upon first exposure to these structures, the composition seems somewhat difficult to understand (i.e., the sclerites represent only parts of the original tergal and sternal plates and their respective gonapophyses). 2) there is some difficulty in distinguishing closely related species, although generic variances are significantly differentiated to distinguish one from another. With this in mind, the poison apparatus seems to be most valuable in indicating gross evolutionary trends rather than showing relationships at the species level. These evolutionary trends are of primary concern in the present investigation. 3) the significant differences and similarities among species are not well understood until many species are examined. Usually, taxonomists deal chiefly with external structures since external characters are much more accessible and the specimen need not be dissected (and essentially destroyed in many cases) for taxonomic placement.

In the Hymenoptera, the same morphological character does not
always illustrate the important trends in evolution. For example, Dufour's gland seems to be one of the important structures in the Formicinae, while the furcula or an homologous structure is extremely important throughout most of the stinging forms. Certain structures that show modification among different groups seem to have no significance in their phyletic relationships. The presence or absence of barbs on the lancets of certain species is one such character.

Often, the biology of aculeate Hymenoptera is reflected in the structure of the sting. Many interesting correlations can be made between certain formicid groups merely by regarding the poison apparatus as playing a significant ethological role in their daily habits, whether a sting is present or absent.
Figure 1.--The evolutionary change from a connection between reproductive system and ovipositor to a separation between the reproductive system and sting in the Hymenoptera. A - Lateral view of reproductive system and base of ovipositor of Habrobracon juglandalis showing a definite connection between the two (Redrawn from Bender 1943). B - Lateral view of the reproductive system and base of sting of Solenopsis saevissima showing a definite separation between the two (Redrawn from Hermann and Blum 1965).

LITERATURE REVIEW

Some of the historical background concerning the hymenopterous poison apparatus has been summarized by Hermann and Blum (1966) and will briefly be reviewed here along with a discussion of additional material.

The first detailed description of the sting of an aculeate hymenopteran was probably made on *Apis mellifera* L. by Johann Svanmerdam (1752). Subsequently, many investigators contributed to the understanding of the structures involved in the act of stinging. Figures of the stings of several aculeates appeared in the articles of Brandt and Ratzeburg (1883) and Siebold (1848). Descriptions of ant, bee and wasp stings and a functional explanation were presented by Fenger (1863) and Sollman (1863) respectively. Forel's work on the poison apparatus of ants (1878) and that of Janet (1898) on the sting of *Myrmica rubra* L. represent two of the major contributions to this field, and these two studies have provided a substantial foundation for all subsequent investigations. Prior to Janet's work, Kraepelin (1873) investigated the postembryonic development of the sting in *Apis* and also redescribed the muscles of the adult. Following Janet's investigation, various accounts of the hymenopterous poison apparatus were presented by Holz (1883), Chesshire (1885), Zander (1899, 1911), Cook (1904), Snodgrass (1910, 1925, 1933b, 1942), Phillips (1916), Trojan (1922), Betts (1923), Bischoff (1927), Morison (1927), Salman (1929), Rietschel (1937), Duncan (1939), Michener (1944), Haupt (1952) and others. A comparative study of the
apparatus in ants, as well as a schematic functional description of the musculature, was made by Foerster (1912). A thorough investigation of the morphology of Iridomyrmex humilis Mayr, was presented by Pavan and Ronchetti (1955). In that study, both sclerites and associated organs were illustrated and described. Snodgrass (1933b) presented one of the first accurate descriptions of the sting muscles of Apis, and some of the musculature of four species of Hymenoptera was described by Rietschel (1937).

Recent investigations concerning the hymenopterous poison apparatus were presented by Whelden (1957, 1958a, 1958b, 1960, 1963), Callahan et al. (1959), Blum and Callahan (1963), Mathewson (1965), and Hermann and Blum (1966, 1967a, 1967b). Some mention of parts of the poison apparatus has been presented by Trojan (1922), Rietschel (1937), Wilson et al. (1956), Cavill et al. (1964), Cavill and Robertson (1965), Wheeler and Wheeler (1965) and Cole (1967).

The degenerate stings of some ants and bees have been described by Forel (1878), Dewitz (1878), von Ihering (1886), Beyer (1891), Foerster (1912), George (1934), Schwarz (1948) and Kerr and de Lello (1962).

The internal organs associated with the sting have been investigated by Forel (1874, 1878), Dewitz (1878), Carlet (1884, 1890), Chesshire (1885), Bordas (1887), Janet (1898), Breslau (1905-1906), Zander (1911), Bishop (1920), Snodgrass (1925, 1933b), Forbes (1938), Maschwitz (1964) and Hermann and Blum (1966, 1967a, 1967b).

Information concerning the chemical nature of the venom has been presented by Adrouny et al. (1959), Stumper (1960), Blum and Callahan (1963), Blum et al. (1964), Cavill et al. (1964) and Hermann and Blum

The effect to humans of ant stings has been discussed by McCook (1879), Spruce (1908), Bequaert (1926), Weber (1937, 1939) and Hermann and Blum (1966, 1967a, 1967b). Effects of the sting of ants have also been mentioned by Creighton (1950), Caro et al. (1957), Faust and Russell (1961), Williams and Williams (1964, 1965) and others.
MATERIALS AND METHODS

Specimens used in this investigation were obtained from various sources. Whenever possible, live material was used. Many specimens, however, were taken from preserved laboratory collections while the more uncommon material was procured from dry, pinned material.

Dissections of live material were made in normal saline so that the soft parts (e.g., poison sac, free filaments and Dufour's gland) could be examined easily while fresh. After examination, the soft parts were dehydrated in alcohol, cleared in xylene, and mounted on slides with Permount. The sclerotized regions were treated in a different manner, since their shape is preserved without dissection in saline. The pertinent sclerites were severed from the rest of the abdomen and fixed in 70% ethyl alcohol. Dehydration was followed by clearing in xylene and mounting on slides with Permount.

Very small specimens (e.g., Leptanilla and Aneuretus) were processed through xylene before dissection. Loss of such valuable specimens would often occur if dissection preceded dehydration and clearing. After dissection in xylene, each apparatus was transferred directly to the slide and mounted.

Illustrations were prepared chiefly with the use of a binocular microscope. Some clarification was made in the determination of fine structures by use of the low and high powers of a compound microscope. Measurements were made with an ocular micrometer.

Since the synthesis of the poison gland components must first involve the production of proteins, it seemed desirable to determine
what areas of the poison apparatus were involved in the manufacture of venom. This would then isolate the glandular areas that actually biosynthesize the toxic materials. This objective was achieved by employing a tetrazolium salt, a standard histochemical reagent that is routinely used to detect dehydrogenases (Pearse 1961).

The following substrates were employed to determine whether dehydrogenases that are critical to the synthesis of proteins in cellular systems were present: sodium succinate, sodium malate, sodium glutamate. The incubation system contained 0.15 ml of 3-(4,5-dimethyl-thiazolyl-2)-2,5-diphenyl tetrazolium bromide (MTT), 0.05 ml of CoCl$_2$ (0.5 M), 0.05 ml of NaN$_3$, 0.15 ml of substrate (0.5 M), 0.25 ml of tris buffer (pH 7.19), 0.05 ml of MgCl$_2$ (0.05 M) and 0.10 ml of distilled water.

Tissues were frozen for 24 hours in tris buffer in order to remove the normally occurring substrates. Tissues were then added to the incubation system and observations were made through a dissecting microscope to determine whether the various dehydrogenases were present.

Table I lists 61 species studied. It is evident that most consideration has been devoted to the Formicidae with only a few additional aculeate Hymenoptera represented.
### TABLE I

**SPECIES INVESTIGATED**

Superfamily Sphecoidea

Family Sphecidae

Subfamily Sphecinae

- *Sceliphron cementarium* (Drury)

Subfamily Nyssoninae

- *Bembex texana* (Cresson)

Superfamily Scolioidea

Family Mutillidae

Subfamily Typhoctinae

- *Typhoctes peruliaris* (Cresson)

Family Tiphiiidae

Subfamily Tiphiiinae

- *Diamma bicolor* Westwood

Family Formicidae

Subfamily Myrmeciinae

- *Myrmecia auriventris* Mayr
- *Myrmecia simillima* F. Smith
- *Myrmecia tarsata* F. Smith
- *Myrmecia vindex* F. Smith

Subfamily Ponerinae

- *Amblyopone australis* Erichson
- *Ectatomma ruidum* Roger
- *Leptogenys elongata* (Buckley)
- *Neoponera villosa* (Fabricius)
- *Onychomyrmex hedlevi* Emery
- *Pachycondyla harpax* (F. Smith)
- *Paraponera clavata* Fabricius
TABLE I (CONTINUED)

SPECIES INVESTIGATED

<table>
<thead>
<tr>
<th>Species</th>
<th>Author</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhytidoponera metallica</td>
<td>F. Smith</td>
</tr>
<tr>
<td>Simopelta oculata</td>
<td>Brown and Gotwald</td>
</tr>
<tr>
<td>Sphinctomyrmex steinheili</td>
<td>Forel</td>
</tr>
<tr>
<td>Termitopone commutata</td>
<td>Roger</td>
</tr>
</tbody>
</table>

Subfamily Cerapachyinae

<table>
<thead>
<tr>
<th>Species</th>
<th>Author</th>
</tr>
</thead>
<tbody>
<tr>
<td>Syrco typhla</td>
<td>Roger</td>
</tr>
<tr>
<td>Acanthostichus sp.</td>
<td>Mayr</td>
</tr>
<tr>
<td>Phyracaces bicolor</td>
<td>Forel</td>
</tr>
</tbody>
</table>

Subfamily Leptanilloidae

<table>
<thead>
<tr>
<th>Species</th>
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</tr>
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<tbody>
<tr>
<td>Leptanilla swani</td>
<td>Wheeler</td>
</tr>
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Subfamily Dorylinae

<table>
<thead>
<tr>
<th>Species</th>
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</tr>
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<tbody>
<tr>
<td>Aenictus gracilus</td>
<td>(F. Smith)</td>
</tr>
<tr>
<td>Cheliomyrmex morogus</td>
<td>F. Smith</td>
</tr>
<tr>
<td>Dorylus (Dorylus) brauni</td>
<td>Emery</td>
</tr>
<tr>
<td>Dorylus (Anomma) molestus</td>
<td>(Gerstaecker)</td>
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<tr>
<td>Dorylus (Typhlopoone) sp.</td>
<td>Fabricius</td>
</tr>
<tr>
<td>Eciton drepaniforum</td>
<td>F. Smith</td>
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<tr>
<td>Eciton dulcius</td>
<td>Forel</td>
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<tr>
<td>Eciton hamatum (Fabricius)</td>
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</tr>
<tr>
<td>Eciton rapax</td>
<td>F. Smith</td>
</tr>
<tr>
<td>Eciton vagans (Olivier)</td>
<td></td>
</tr>
<tr>
<td>Labidus praedator</td>
<td>F. Smith</td>
</tr>
<tr>
<td>Neivamyrmex nigrescens</td>
<td>(Cresson)</td>
</tr>
<tr>
<td>Nomamyrmex esenbecki</td>
<td>(Westwood)</td>
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Subfamily Pseudomyrmecinae

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<tr>
<td>Pseudomyrmex belti</td>
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<td>Pseudomyrmex brunea</td>
<td>F. Smith</td>
</tr>
<tr>
<td>Pseudomyrmex ferruginea</td>
<td>F. Smith</td>
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<tr>
<td>Pseudomyrmex spinicola</td>
<td>Emery</td>
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Subfamily Myrmicinae

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<tr>
<td>Atta cephalotes</td>
<td>(L.)</td>
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<tr>
<td>Atta texana</td>
<td>Buckley</td>
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<tr>
<td>Myrmicarria cruchetii</td>
<td>Santsh.</td>
</tr>
<tr>
<td>Myrmica americana</td>
<td>Weber</td>
</tr>
<tr>
<td>Pogonomyrmex badius</td>
<td>(Latreille)</td>
</tr>
<tr>
<td>Pogonomyrmex barbatus</td>
<td>(F. Smith)</td>
</tr>
</tbody>
</table>
TABLE I (CONTINUED)
SPECIES INVESTIGATED

**Pogonomyrmex comanche** Olsen
**Pogonomyrmex occidentalis** (Cresson)
**Xiphomyrmex** sp. Forel

Subfamily Aneuritinae

**Aneuretus simoni** Emery

Subfamily Dolichoderinae

**Dorymyrmex pyramicus** (Roger)
**Iridomyrmex pruinosus** (Roger)
**Monacis bispinosa** Olivier

Subfamily Formicinae

**Acanthomyops claviger** (Roger)
**Camponotus abdominalis** Fabricius
**Camponotus pennsylvanicus** (DeGeer)
**Camponotus sericiventris** (Guerin)
**Formica pallidefulva** Mayr
**Lasius sitkaensis** Pergande
**Polyergus** sp. Latreille
HOMOLOGIES AND TERMINOLOGY

Table II lists the various sclerites of the poison apparatus, their origin and significance. Table III lists muscle associations, their origin, insertion and function. Daly (1955) points out the agreement between Snodgrass (1931), Michener (1944) and Gustafson (1950) that the first and second valvulae (lancet and sting respectively) are gonapophyses of the apterygotan ovipositor. It is also generally agreed that the valvifers (triangular and oblong plates) had a coxal origin. There is some controversy, however, over the origin of the gonostyli (third valvulae). Snodgrass and Gustafson claim that elongations of the second gonocoxites have produced the gonostyli while Michener believes the gonostyli are actually styli that arose from the second gonocoxites.

Terminology used throughout this investigation is the same as that used by Hermann and Blum (1966, 1967a, 1967b) in their studies on the poison apparatus of Paraponera clavata, Pogonomyrmex badius and Eciton hamatum respectively. Terms that I have introduced subsequent to the beginning of this investigation are as follows:

Anterior extension of the sting bulb (AE) -- This structure has been found in all New World dorylines, two species of the Ponerinae and three species of the Cerapachyinae.

Anterolateral extensions of the sting bulb (A-L E) -- These structures exist in the Old World dorylines and in some myrmicines. In the myrmicines, a furcula articulates with the anterolateral extensions, whereas a furcula does not exist in the dorylines.
Free filaments (FF) -- These structures have been called the poison glands by previous authors. However, the name has been changed because through chemical testing it was found that venom synthesis occurs chiefly in the convoluted gland. This does not rule out the possibility that the free filaments are also glandular.

Terminology used throughout this investigation has been defined in Appendix A.
<table>
<thead>
<tr>
<th>STING SCLERITES</th>
<th>ORIGIN</th>
<th>SIGNIFICANCE AS PART OF THE POISON APPARATUS</th>
</tr>
</thead>
<tbody>
<tr>
<td>Furcula</td>
<td>Anterior extension</td>
<td>Acts as point of insertion for muscle 3 (deflecting muscle of sting) and muscle 4 (rotating muscle of sting). It is not present in higher ants that do not sting, the Dorylinae, some Ponerinae and Cerapachyinae.</td>
</tr>
<tr>
<td></td>
<td>of sting bulb.</td>
<td></td>
</tr>
<tr>
<td>Fulcral Arms</td>
<td>8th sternum</td>
<td>Act as strengthening structures at the pivot point for the deflection of the sting as a result of the contraction of muscle 3 and during the pivoting action caused by the contraction of muscle 4.</td>
</tr>
<tr>
<td>Anal Arc</td>
<td>10th sternum</td>
<td>May act as a sensory structure (through anal pad) during the stinging act.</td>
</tr>
<tr>
<td>1st valvifer (triangular</td>
<td>8th sternum</td>
<td>Articulates with the dorsal region of the 1st ramus and acts as point of articulation to quadrate plate for the protraction of the lancets. Also articulates with the oblong plate for retraction of the lancets.</td>
</tr>
<tr>
<td>plate)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ramus of 1st valvifer</td>
<td>8th sternum</td>
<td>Joins the dorsal triangular plate to the lancet shaft.</td>
</tr>
<tr>
<td>(1st ramus)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sting Sclerites</td>
<td>Origin</td>
<td>Significance as Part of the Poison Apparatus</td>
</tr>
<tr>
<td>------------------------------</td>
<td>-------------------------------</td>
<td>------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>1st Valvula (lancet shaft)</td>
<td>Gonapophysis of 8th sternum</td>
<td>Articulates with sting bulb by tongue and groove joints to move back and forth during the stinging act. The distal end often has barbs that serve a number of functions.</td>
</tr>
<tr>
<td>2nd Valvifer (oblong plate)</td>
<td>9th sternum</td>
<td>Articulates with the third valvula (gonostylus) posteriorly and with the 2nd ramus anteriorly. Also articulates with the triangular plate near its midpoint to function in the retraction of the lancets through the contraction of muscle 1.</td>
</tr>
<tr>
<td>Ramus of 2nd Valvifer (2nd ramus)</td>
<td>9th sternum</td>
<td>Connects the dorsal oblong plate with the ventral sting bulb. Also possesses sensory pegs near its dorsal end and immediately adjacent the sting bulb. Acts also as origin for muscle 12 (levator muscle of the sting).</td>
</tr>
<tr>
<td>2nd Valvula (sting)</td>
<td>1st gonapophysis of 9th sternum</td>
<td>Functions as the main sting apparatus, the part of the apparatus that enters the wound with the lancets. Articulates with the lancets by tongue and groove joints so that lancets ride back and forth to cut the wound.</td>
</tr>
<tr>
<td>Sting Sclerites</td>
<td>Origin</td>
<td>Significance as Part of the Poison Apparatus</td>
</tr>
<tr>
<td>-------------------------</td>
<td>-------------------------------</td>
<td>------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>3rd valvula (gonostylus)</td>
<td>2nd gonapophysis of 9th sternum</td>
<td>Acts as a pair of sensory structures during the stinging act and as a sheath around the sting.</td>
</tr>
<tr>
<td>9th hemitergite</td>
<td>9th tergum</td>
<td>Acts as point of insertion for muscle 1 (protracting muscle of lancets) and for muscle 2 (retracting muscle of lancets). Articulates with the dorsal apodeme of the triangular plate.</td>
</tr>
<tr>
<td>8th hemitergite (spiracular plate)</td>
<td>8th tergum</td>
<td>Acts as a point of insertion for muscle 8 (1st depressor muscle of the spiracular plate) and muscle 9 (1st elevator muscle of the spiracular plate). Acts as the point of origin for muscle 10 (2nd elevator muscle of the spiracular plate) and muscle 11 (2nd depressor muscle of the spiracular plate). It also represents the last abdominal plate with a spiracle.</td>
</tr>
<tr>
<td>MUSCLE</td>
<td>NAME</td>
<td>ORIGIN</td>
</tr>
<tr>
<td>----------</td>
<td>-------------------------------------</td>
<td>-------------------------------</td>
</tr>
<tr>
<td>1</td>
<td>Protracting muscle of lancets</td>
<td>Dorsal apodeme of oblong plate</td>
</tr>
<tr>
<td>2</td>
<td>Retracting muscle of lancets</td>
<td>Lateral surface of oblong plate</td>
</tr>
<tr>
<td>3*</td>
<td>Deflecting muscle of sting</td>
<td>Mesal border of oblong plate</td>
</tr>
<tr>
<td>4*</td>
<td>Rotating or pivoting muscle of sting</td>
<td>Mesal border of oblong plate</td>
</tr>
<tr>
<td>5</td>
<td>Dilator of the poison canal</td>
<td>Mesoventral border of the fulcral arm</td>
</tr>
<tr>
<td>MUSCLE</td>
<td>NAME</td>
<td>ORIGIN</td>
</tr>
<tr>
<td>--------</td>
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<td>---------------------------------------------</td>
</tr>
<tr>
<td>6</td>
<td>Sphincter of poison canal</td>
<td>Extends from the mesoventral border of one fulcral arm to the other</td>
</tr>
<tr>
<td>7</td>
<td>Aligning muscle of the sting</td>
<td>Extends from the dorsal border of one oblong plate to the other</td>
</tr>
<tr>
<td>8</td>
<td>First depressor muscle of the spiracular plate</td>
<td>Mesal surface of anterodorsal region of 7th abdominal sternite</td>
</tr>
<tr>
<td>9</td>
<td>First elevator muscle of the spiracular plate</td>
<td>Mesal border of anteroventral region of 7th abdominal tergite</td>
</tr>
<tr>
<td>10</td>
<td>Second elevator muscle of the spiracular plate</td>
<td>Posteroverentral region of mesal surface of spiracular plate</td>
</tr>
<tr>
<td>MUSCLE</td>
<td>NAME</td>
<td>ORIGIN</td>
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<tr>
<td>--------</td>
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<td>---------------------------------------------</td>
</tr>
<tr>
<td>11</td>
<td>Second depressor muscle of the spiracular plate</td>
<td>Mesal surface of anterodorsal region of the spiracular plate</td>
</tr>
<tr>
<td>12</td>
<td>Levator muscle of the sting</td>
<td>Posterior border of the second ramus</td>
</tr>
</tbody>
</table>

* Muscle 3 deflects the sting whether we are talking about members of the Ponerinae, Cerapachyinae or Dorylinae. Muscle 4 is known as the rotating muscle in most stinging forms but it is called the pivoting muscle of the sting in the Dorylinae, some Ponerinae and Cerapachyinae.
EVALUATION OF MATERIAL

The importance of using live specimens, especially when freshly collected, cannot be overemphasized. It is extremely difficult, and often impossible, to investigate the soft parts of the poison apparatus, particularly the free filaments, from preserved material. This is, no doubt, what caused Whelden (1958a) to conclude that the free filaments in certain ant species were absent during some periods of adult existence. Because fresh specimens were not always available for examination, the soft parts of many species have not been included in illustrations in this investigation.

In the study of muscle attachments, dried specimens are often superior to freshly collected or preserved material. This is due to the brown coloration that many muscles assume when they become dried. The brown appearance in whole mounts facilitates observations on muscle origin and insertion that may otherwise be extremely difficult.
Several considerations must be evaluated in discussing the soft parts of the poison apparatus: 1) the origin of these structures. 2) their function as part of the poison apparatus. 3) the position at which the free filaments leave the poison sac and the presence of an external common free filament duct. 4) the shape of the various sacs and free filaments.

**Origin.**—Both the poison sac and Dufour's gland represent invaginations of the ectodermal (hypodermal) wall. Although there seems to be considerable variation in these two structures within the Hymenoptera (Bender 1943), all of the Formicidae and most of the wasps contain them. Because of their ubiquitous occurrence in the Hymenoptera, it is likely that these two structures were present in the pre-ant ancestor.

The free filaments, convoluted gland, and poison sac form one continuous structure, although there are cellular differences between the various regions. The convoluted gland has become invaginated into the poison sac and the free filaments presumably represent evaginations from the apical end of the convoluted gland. Such a relationship between these structures has been illustrated by Callahan et al. (1959) and has been discussed by Hermann and Blum (1966).

**Poison Sac** (PS, Figs. 2, 3, 4).—The poison sac functions chiefly as a reservoir for storing venom that has been produced chiefly in the convoluted gland (Fig. 16, G). Due to a simple muscle mass around its periphery, especially in the apical region, it also
functions as the initial structure involved in forcing venom into the sting. The sac empties into the anterior region of the sting bulb through a slender main duct. It is generally oval in shape regardless of the species involved. Within the Myrmeciinae (Fig. 2, F), Ponerinae (Fig. 2, C, E, H), Dorylinae (Fig. 2, I; Fig. 3, A) and Formicinae (Fig. 3, C), the sac is elongate and often pear-shaped in appearance. Its main difference among various groups is concerned with its association with the convoluted gland (CG) and position of the free filaments (FF). The wall of the sac is composed of simple squamous epithelium. Associated with the inside of this epithelial wall is a chitinous structure known as the *tunica propria*.

Usually, the convoluted gland lies within the poison sac, but in members of the Formicinae (Fig. 3, C), the convoluted gland is represented by a long convoluted duct that lies on the periphery of one entire side of the poison sac. Because of the presence of this massive structure, the appearance of the poison sac is characteristically similar in all species of the Formicinae examined.

**Free Filaments** (FF, Figs. 2, 3, 4).—The free filaments are paired structures. These filaments often have been referred to by many authors as "the poison glands" of ants and other hymenopterous insects. Upon testing the soft parts of the poison apparatus by employing tetrazolium salts as hydrogen receptors, it has been demonstrated that dehydrogenase activity is present almost exclusively in the convoluted gland. This is interpreted to mean that the free filaments are not primarily glandular in nature and that the synthesis of venom occurs mainly, if not exclusively, within the convoluted gland. It is probable that the free filaments are important in
picking up precursory materials that eventually move to the convoluted gland for chemical transformation (Fig. 15, G). After the venom is produced, it moves to the reservoir region (poison sac) to be stored until it is used during the stinging act or, in some species, during the deposition of odor trails.

Branching of the free filaments has been found to occur in almost all hymenopterous insects examined in this investigation. Branching of the filaments has previously been reported for Bombus atratus Franklin (Kerr and deLello 1962) and for Paraponera clavata (Hermann and Blum 1966). It is most extensive in the Mutillidae (Fig. 4, C). Specimens may often be recognized as members of the Mutillidae merely because of the extensively branched filaments. In those species in which branching was not found, either too few specimens were examined or the free filaments were difficult to isolate for detailed examination. In an examination of preserved or dried specimens, the location and study of the free filaments is very difficult or impossible to achieve. Indeed, it is difficult to obtain a good set of free filaments during the dissection of the soft parts of some live material because the filaments are very slender and delicate.

In the Myrmeciinae (Fig. 2, F), Ponerinae (Fig. 2, C, E, H), Dorylinae (Fig. 2, I) and Pseudomyrmecinae (Fig. 3, B), a common duct generally extends from the base of the sac before the free filaments branch as two distinct structures. In no case were the filaments in the Ponerinae found to extend from the apical region of the sac as was reported in Rhvridoponera and Stigmatomma by
Whelden (1958a, 1958b). After examining *Rhytidoponera convexa* Mayr, Whelden (1958a) reported that in callow workers two conspicuous branches were found extending from the anterior end of the sac. He also reported that with increasing age, these branches seemed to decrease gradually in size and finally disappear. The presence of these conspicuous branches was also reported by Whelden to extend from the anterior end of the sac in *Stigmatomma pallipes* (Haldeman) (1957) and *Rhytidoponera metallica* F. Smith (1960). Evidently, Whelden was either using preserved material for his studies or his dissections were not very thorough. These filaments are present in all of the adult ants that I have examined. Whelden also erroneously described the free filaments as extending from the anterior end of the sac; the filaments leave the base of the sac in all of the ponerines that I have examined (including the species that he examined). There is no gradual diminution in size of the free filaments during the life of the adult, and upon careful dissection of specimens, I believe it highly probable that the free filaments will be found to exist in all ants.

In the Formicinae, the filaments extend from the base of the sac but the external common duct is not evident (Fig. 3, C). The free filaments extend from the apical region of the sac in the Myrmicinae (Fig. 3, E, F) and Dolichoderinae (Fig. 4, E).

In the Myrmeciinae, Ponerinae, Dorylinae, and Formicinae, the free filaments maintain a relatively uniform diameter throughout their length, and the filaments are generally extremely long. The free filaments in the Pseudomyrmecinae and Myrmicinae gradually become
significantly larger near their distal ends (Fig. 3, B; Fig. 4, A). The external surface of a myrmicine free filament often has an undulating appearance throughout its length. The free filaments in the Dolichoderinae are not filamentous in any respect, but rather bulbous. This globate appearance is unique among hymenopterous free filaments. Pavan and Ronchetti (1955) illustrated the large globular free filaments in Iridomyrmex humilis Mayr and they pointed out the cellular appearance of the filaments in that species.

The free filaments of hymenopterous insects are connected directly or through a slender duct to the convoluted gland. The wall of the filaments consists of a simple layer of cuboidal cells.

**Convoluted Gland (CG, Figs. 2, 3, 4).**—Venom that is stored in the poison sac eventually to be used during the stinging act or in the deposition of an odor trail is synthesized in this gland after precursory materials have been transported from the free filaments (Fig. 15, G). During chemical tests on the convoluted gland to determine the exact area of enzymatic dehydrogenase activity, tetrazolium salt reductions revealed at least two distinctly different areas within the gland of most species. A large portion of the gland reacted to produce a dark coloration whereas the rest of the gland remained light in appearance.

The gland seems to be invaginated into the poison sac in all ants except the Formicinae. In this group, the convoluted gland is represented by a single external extension of the free filaments (Fig. 3, C). Pulling on the base of the free filaments will result in the unraveling of an extremely long duct that lies on the dorsum of the
sac. This type of sac seems to be typical in appearance throughout the Formicinae and has been found in all formicines in this investigation. It has also been illustrated in formicines by other authors.

The convoluted gland in all ants, other than the Formicinae, seems to be composed of polygonal cells that border small ductules. The ductules empty into ducts that in turn empty into the poison sac.

Dufour's Gland (DG, Figs. 2, 3, 4).--The function of this gland is not well known. It was at one time known as the "alkaline gland" and was believed to function in neutralizing fluid from the "poison gland," or "acid gland." It has been found to be the source of a secretion that functions as a releaser of social behavior in the myrmicine genera Pheidole and Solenopsis (Wilson 1963), but no function can be attributed to the products of this gland in any of the other formicid genera. In some cases (e.g., Paraponera), Dufour's gland is much larger than the poison sac (Hermann and Blum 1966).

Dufour's gland is usually an elongate and sacular structure, consisting cellularly of simple columnar epithelium. In the Mutil­lidae it has an extremely crinkled appearance (Fig. 4, I). It is within the Formicinae that this gland seems to illustrate divergence of some phylogenetic significance (Fig. 4, B-J). Lasius sitkaensis possesses a Dufour's gland that may be considered fairly typical among the Formicidae. Wilson (1955) considers this species the most primitive of the subfamily Formicinae. The type of Dufour's gland usually found in the Formicinae is well represented in Formica,
Camponotus, Polyergus and other genera (Fig. 4, F, J), whereas the gland possessed by Acanthomyops (Fig. 4, D) is intermediate in form between the unilobular gland found in Lasius (Fig. 4, B) and the bilobed structure found in the higher formicine taxa.

Other workers have investigated formicine Dufour's glands. Maschwitz (1963) illustrated a bilobed gland in Formica polycetena Först but the gland in Lasius fuliginosus Latr. does not show any indication of being bilobed. Possibly other species within the genus Lasius will be found to possess a Dufour's gland that is not bilobed. The gland of Lasius fuliginosus does not appear to be as elongated (and thus as primitive) as that of Lasius sitkaensis.
SKELETAL COMPONENTS

The stings of hymenopterans may be insertile (positioned fully within the gaster) or exsertile (protruding from the posterior region of the gaster). Certain groups (e.g., Old World dorylines) characteristically have insertile stings and the posteriormost gastral segments fit closely so that none of the sting sclerites are exposed to the outside (Fig. 5, B). The stings of other hymenopterans (e.g., Ponerinae) are usually found extending posteriad from the distal region of the gaster (Fig. 5, A) and in Onychomyrmex the sting extends posteriad for a considerable distance.

All of the sclerotized parts of the poison apparatus are paired structures except the sting, furcula, anal arc, anal pad and sometimes the spiracular plates.

**First Valvifers (Triangular Plates) (TP, Figs. 6, 7, 9-13, 15).**--These are paired structures that are roughly of a triangular appearance. Each plate connects anteriorly with the first ramus (Ra 1) and posteroventrally with an oblong plate (OP). Each first ramus, in turn, articulates ventrally with a lancet (first valvula).

The shapes of the first valvifers vary considerably throughout the Hymenoptera, although they are easily recognizable as triangular plates in all specimens whether the poison apparatus is well developed (as in all stinging forms) or extremely reduced (as in the Dolichoderinae and Formicinae, Fig. 15, E + F). In general, there has been extreme modification of the triangular plates throughout the
Hymenoptera, which has resulted in a diverse array of structures illustrated in the accompanying figures (although the triangular plate in *Dorylus (Anomma) molestus* has remained simple in appearance, Fig. 14, I). These structures tend to be somewhat elongate in some of the Dorylinae (Fig. 9) and reduced considerably in some of the Formicinae (Fig. 15, E). Reduction of the triangular plate is especially exemplified in *Camponotus abdominalis* (Fig. 15, E). Although diversification is well demonstrated in the triangular plates of various hymenopterans, it can be generally said that in all specimens the area of most sclerotization is in the region of articulation with the quadrate and oblong plates.

The close association between the rami of the triangular plates (Ra 1) and the rami of the oblong plates (Ra 2), as is found in all stinging forms, is not present in the Formicinae and Dolichoderinae (Fig. 15, E + F). Since there is no functional sting in the latter groups (and generally no sting at all) the sclerites that remain are not interdependent on one another. However, in some of the Myrmicinae in which the sting is not functional as a defensive organ, the rami have retained their close association (*Atta texana*, Fig. 15, D).

The rami are very long and considerably flexible and their shape depends on the position of associated sclerites (i.e., whether certain muscles are contracted or extended). The flexibility of the rami and varying degree of contractability of the muscles in preserved specimens results in the sclerites being found in a number of positions when the ants are dissected.
Figure 5.--Gasters of ants (lateral view). A - *Termitopone commutata*. B - *Dorylus*. C - *Onychomyrmex hedleyi*. St - Sting. II-VII - Abdominal segments 2 through 7.
It should be noted that in the Mutillidae, even though the sting has undergone a considerable evolution (discussed under second valvulae), the triangular plate and other sclerites have remained virtually in the same position as they have in other hymenopterous insects. In all respects, the triangular plates have maintained the same relative relationships with other sclerites in all of the species examined (except in the highly evolved sting of the Mutillidae). Its close relationship with the oblong plate is illustrated for Eciton hamatum (Fig. 9, B), Formica pallidefulva (Fig. 14, B) and Pseudomyrmex ferruginea (Fig. 13, D).

First Valvulae (Lancets) (Ln, Figs. 13, 14).—The lancets are paired structures that are usually similar in general appearance in most aculeates. Each lancet is joined to a triangular plate (first valvifer) by an anterior articulation to the slender first ramus (Ra 1). The lancets are positioned mesally within the sting and associate lateroventrally with the sting by tongue and groove articulations.

Lancets were present in all of the hymenopterous insect examined, although they were reduced in some Myrmicinae (Fig. 14, C, G), Dorylinae (Fig. 14, I) and especially the Formicinae (Fig. 15, E, F) and Dolichoderinae. Reduction of the lancets involves loss of the valve (Va), a structure that functions during venom release. Loss of the valve or failure to acquire one has occurred in Dorylus (Anomma) molestus, Atta texana and Atta cephalotes. All other stinging species examined possessed this sclerite.

The valves tend to block the poison canal within the sting when
the sting is in a state of rest. They also function to pump the venom into the wound when the lancets are moved back and forth on the tongue and groove articulations within the sting. This process has been described by Hermann and Blum (1966). It is interesting to note that the aculeate specimens that were examined in this investigation and that do not possess valves on the lancets, also do not sting (Anomma and Atta).

The ability of ants and other hymenopterans to sting is also dependent on the condition of the distal tip of the sting. In the aculeates that do not sting (other than the Formicinae and Dolichoderinae), the distal tip of the lancet is membranous (Fig. 14, C, G, I). Usually, the distal tip possesses several barbs that generally function in cutting the wound in order to insert the sting (Fig. 16, F). Not all stinging Hymenoptera possess these barbs but they are generally present in the Ponerinae, Myrmeciinae, and probably in all the Leptanillinae. The barbs seem to be lacking in the Dorylinae and some of the Myrmicinae, and Blum and Callahan (1963) reported them lacking in Pseudomyrmex pallidus. Pseudomyrmex belti (Fig. 13, C), P. brunea, P. ferruginea and P. spinicola possess barbs on the lancet tip. In the Formicinae, the lancet tip has become enlarged and the general appearance of the lancet has been modified (Fig. 15, E, F).

The lancet barbs are located on the lateral and distal portion of the shaft and they sometimes may be examined without dissecting the specimen since the sting often protrudes from the posterior part of the gaster. The number of barbs varies among species ranging
from 2 or 3 to 7 or more. However, there seems to be no correlation with the number of barbs and the phylogenetic relationship between large groups. There may be some significance on the species level but the supraspecies significance is not yet evident, if there is any.

The size of the barbs also varies and may be significant at the species level. The best example of size differentiation in ants is found in *Pogonomyrmex* (Hermann and Blum 1967a). The barbs of *Pogonomyrmex comanche* are large enough to cause the sting to remain at the wound site after the ant has pulled free. The importance of leaving the sting in the wound is discussed under sting autotomy. Sting autotomy has been reported for *Pogonomyrmex badius* and *P. barbatus* (McCook 1878; Hermann and Blum 1967a). This phenomenon has also been reported by Rau (1933) and Rietschel (1937) for other hymenopterous insects.

Second Valvifers (Oblong Plates) (OP, Figs. 6, 7, 9, 10, 13, 15).--The oblong plates are paired structures that articulate anteriorly with the second rami (Ra 2). The second rami, in turn, articulate ventrally with the anterior end of the sting (fused second valvulae). At the extreme posterior end, each oblong plate articulates with the gonostylus.

Oblong plates seem to be present in all hymenopterous insects, although their rami (Ra 2) and valvulae may be reduced or absent in the Formicinae (Fig. 15, E, F) and Dolichoderinae. They are always elongate, slender structures and near the point of articulation with the triangular plate there are a number of setae that presumably
serve a sensory function when the two sclerites articulate with one another. These sensory setae were present in all forms examined whether they were stinging forms or otherwise. The typical number of setae in most ants was 6, although four were found in some higher forms such as *Formica pallidefulva*. Whether this represents a reduction in number can only be determined after many more hymenopterous insects are examined.

The oblong plate serves as a point of origin for muscles 3 (deflecting muscle of the sting) and 4 (rotating or pivoting muscle of the sting). Muscle 3 moves from its point of origin in an anteriad direction to insert on the furcula in most aculeates (Hermann and Blum 1966) or the sting bulb in the Dorylinae (Hermann and Blum 1967b), some ponerines (*Simopelta* and *Sphinctomyrmex*) and cerapachyines (*Acanthostichus* sp., *Phyracaces bicolor*, *Syscia typhla*, Fig. 11, A, B + C, respectively.

Each ramus of the oblong plates normally articulates ventrally with the sting bulb but in the Formicinae (Fig. 15, E + F) and some Dolichoderinae, the rami are quite reduced. In *Monacis bispinosa*, the rami are present but they are not connected to the sting bulb. *Camponotus abdominalis* (Fig. 15, E), *C. pennsylvanicus* (Fig. 15, F) and *Formica pallidefulva* possessed only a slight indication of second rami. In these higher forms, the oblong plates are similar to those of other hymenopterans but the gonostyli are membranous.

**Second Valvulae (Sting)** (St, Figs. 5-7, 9-11, 13, 15).--The sting represents the fused gonapophyses of the 9th abdominal segment (Hermann and Blum 1966). It forms a crescent shaped structure in
transverse section with the ventral opening being filled by the first valvulae (lancets). The latter structures associate with the sting along their mesoventral wall by tongue and groove articulations. The sting (fused 2nd valvulae) clearly serves several important functions: 1) it acts as the dorsal and lateral portions of the poison canal through which venom passes during the act of stinging and during the process of laying trails. 2) through tongue and groove articulations, it acts as a rigid base for the anteroposteriadi movement of the lancets. 3) its distal end tapers to a point that is inserted into the wound.

The sting generally consists of a proximal sting bulb (SB) and distal sting shaft (SS). It is usually an elongate structure but in some of the Old World dorylines (Fig. 10, C, E, F) and some myrmicine ant species (Atta texana, Fig. 15, D), the sting takes on a broad appearance. A number of other nonstinging myrmicines possess a sting of this type.

The anterior region of the sting is interesting in that it is usually associated with a small sclerite, the furcula (Fu). This sclerite functions in deflection and rotation or pivoting of the sting, and it therefore serves an important function during the stinging act. The significance of the relationship between the furcula and sting bulb becomes evident when members of the Dorylinae (Fig. 9; Fig. 10, A, C-F) and some dorylinelike cerapachyines (Fig. 11) and ponerines (Fig. 10, B) are examined. These ants do not possess a furcula but do have the muscles that normally insert on that structure (muscles 3 and 4, Table III). Further discussion of
this sclerite will be found under an analysis of the furcula's function.

The shape and size of the sting varies considerably among ant species. Wheeler and Wheeler (1965) recently discussed the differences in the size of the sting in some myrmicine ant species. Generally, those hymenopterans that produce a painful reaction possess a relatively large sting whereas those that do not possess a small sting. A relatively large sting is found in most ponerines, some dorylines, pseudomyrmecines and myrmicines, whereas ant species in some of the Dorylinae, Pseudomyrmecinae and Myrmicinae possess small stings.

The distal tip of the sting is generally a simple pointed structure. In Simopelta, however, the tip was found to expand distally after a gradual posterior taper (Fig. 14, E). Such a modification has produced a spear-shaped structure.

Third Valvulae (Gonostyli) (Go, Figs. 6, 7, 9, 10, 13, 15).-- The gonostyli, which represent the 2nd gonapophyses of the 9th sternum, are paired structures that articulate anteriorly with the posterior region of the oblong plates (second valvifers). They presumably serve a sensory function during the stinging act and also act as a sheath around the sting (Hermann and Blum 1966). In many of the Hymenoptera, each gonostylus is separated into distal and proximal sclerites by a narrow nonsclerotized region and usually by a peripheral constriction.

The distinction between proximal and distal portions is well illustrated in the Mutillidae (Fig. 6, A), Myrmeciinae (Fig. 6, D, E)
and Ponerinae (Fig. 7, A-E; Fig. 15, A) but not in the Tiphilidae (Fig. 6, C), Dorylinae (Fig. 9, C, D; Fig. 10, A, D), Pseudomyrmecinae (Fig. 13, A, B), Myrmicinae (Fig. 15, B, C, D), Dolichoderinae or Formicinae (Fig. 15, E, F). In the Mutillidae (Fig. 6, A), the distal portion of each gonostylus has become modified in appearance to such an extreme that it no longer resembles a gonostylus. However, the gonostyli in members of the Mutillidae have retained their function as a sting sheath (i.e., the gonostyli have concave mesal borders that allow them to form a sheath around the sting shaft). Indeed, it is in the Mutillidae that the gonostyli are best represented as a sheath, but another function is especially evident in members of that family. Since the gonostyli are not separated from each other at their base, they act as a guide for the sting shaft when the latter structure is being deflected. Such a mechanism is necessary in a stinging hymenopteran in which the sting has evolved as a coiled structure.

**Fulcral Arms (FA, Figs. 6, 7, 9-11, 13, 15).**—These are paired structures that articulate ventrally with the anterior end of the sting. They represent portions of the 8th sternum and are present in all of the hymenopterous species examined. At their point of articulation with the sting they act as points of pivot for the deflection and pivoting or rotation of the sting upon contraction of muscle 3 (deflecting muscle of the sting) and muscle 4 (pivoting or rotating muscle of the sting) (Fig. 12).

The base of each fulcral arm is usually broad and well sclerotized, and the distal tip usually tapers to a point. These sclerites
Figure 12.—Diagrammatic illustration showing results of contraction of muscle 4 in most stinging Hymenoptera and in the dorylinelike members of the Formicidae. A - Transverse section through anterior region of sting and furcula. B - Dorsal view of sting and furcula. C - Transverse section through dorylinelike sting. D - Dorsal view of dorylinelike sting. In the furculate Hymenoptera, contraction of muscle 4 causes a rotation of the sting due to the basal connection of the furcula to the sting (A and B). In the dorylinelike Hymenoptera, contraction of muscle 4 causes a pivoting action of the sting since there is no furcula to produce a rotating motion (C and D). The pivoting point (PP) is at the point of articulation between each fulcral arm and the sting. Fu - Furcula. OP - Oblong plate. PP - Pivoting point. SB - Sting bulb. Muscles: 3 - Deflecting muscle of sting. 4 - Rotating or pivoting muscle of sting.
act as points of origin for muscle 6, the sphincter muscle of the poison canal (Hermann and Blum 1966).

**Quadrate Plates** (9th hemitergites) (QP, Figs. 6, 7, 9, 10, 13, 15).--The quadrate plates are paired structures that have arisen from the 9th tergum. They articulate anteroventrally with the triangular plate (first valvifer) and associate relatively closely on their posteroventral region with the anal arc (remnant of the 10th tergum). Each quadrate plate acts as a point of insertion for muscle 1 (the protracting muscle of the lancet) and muscle 2 (the retracting muscle of the lancet). These plates usually have a well sclerotized central bar with less sclerotized marginal wings. The dorsoposterior end (distal tip) forms a T-shaped apodeme that receives muscles 1 and 2.

**Spiracular Plates** (8th hemitergites) (SP, Fig. 7, A, B; Fig. 13, A).--These plates have arisen from the 8th tergum and function in depressing or elevating the entire sting mechanism chiefly because of the action of two muscle groups originating on the seventh tergum (muscles 8 and 9) and others inserting on the quadrate plate (muscles 10 and 11). The spiracular plates represent the last abdominal structures to possess a spiracle (Hermann and Blum 1966). Often, the spiracular plates are joined to each other dorsally by a dorsal bar. Whether a well sclerotized bar is present or absent, the 8th hemitergites always possess membranous connections with each other.

**Anal Arc** (10th tergite) (AA, Figs. 6, 7, 9, 10, 13, 15).--This structure lies ventrad to the posterior end of the quadrate plates (9th hemitergites) and just dorsad to the posterior end of the oblong plates (2nd valvifers). It possesses an anal pad that
has distal setae, and is often membranous and difficult to see in whole mounts.

**Furcula** (Fu, Figs. 6-8, 13-15).—This structure has been found in many hymenopterous insects. It has either arisen from the anterior end of the sting bulb or has fused with it in the course of evolution. Two muscles that originate on the oblong plate insert on this sclerite. Muscle 3, the deflecting muscle of the sting, originates on the mesal border of the oblong plate, passes postero-dorsad and inserts on the lateroventral surface of the furcula. In all hymenopterous forms, contraction of this muscle results in a dorsal movement of the anterior (proximal) region of the sting. Due to the presence of pivot points on each side of the sting base (PP, Fig. 12), there is a deflection of the distal tip of the sting. The function of muscle 4, the rotating or pivoting muscle of the sting, varies in different hymenopterous groups. In most aculeate Hymenoptera that have been studied, the furcula is a distinct sclerite. In these groups, muscle 4 originates on the mesal border of the oblong plate and inserts on the laterodorsal region of the furcula. Due to a strong articulation between the basal apodemes of the furcula and the proximal region of the sting bulb, sideward movement of the furcula results in a rotation of the sting (Fig. 12, A + B).

In some members of the Formicidae, especially species of the subfamily Dorylinae, the furcula is not present. The base of the sting is either in a prefurculate condition or fusion between the furcula and the anterior region of the sting bulb has resulted in a single structure instead of two sclerites. Species examined that
possess this prefurculate or postfurculate condition are: *Aenictus gracilis* (Fig. 10, D), *Dorylus (Anomma) molestus* (E), *Dorylus (Dorylus) braunsi* (F), *Dorylus (Typhlophone)* sp. (C), *Cheliomymex morosus* (A), *Eciton drepaniforum* (Fig. 9, C), *Eciton dulcius, Eciton hamatum* (B), *Eciton rapax* (E), *Eciton vagans* (D), *Labidus praedator, Neivammyrmex nigrescens*, and *Nomammyrmex esenbecki* (G) in the subfamily Dorylinae, *Sycia typhia* (Fig. 11, C), *Acanthostichus* sp. (A) and *Phyracaces bicolor* (B) in the subfamily Cerapachyinae, *Simopelta oculata* and *Sphinctomyrmex steinheili* (Fig. 10, B) in the subfamily Ponerinae. All other aculeate Hymenoptera examined thus far (except members of the Formicinae and Dolichoderinae) have a furcula.

In the Old World dorylines (Fig. 10, C-F), anterolateral projections (A-L E) receive muscle 3 while muscle 4 inserts in a more mesal position on the base of the sting bulb. In the New World dorylines (Fig. 9; Fig. 10, A), there is an anterior extension of the sting bulb (AE) upon which both muscles 3 and 4 insert. Although *Simopelta oculata* is a member of the subfamily Ponerinae (a subfamily in which the furcula is usually represented as a strong and well developed sclerite), it possesses a dorylinelike sting. In that species there is no furcula and muscles 3 and 4 insert on a well developed extension of the sting bulb. Although *Sphinctomyrmex steinheili* does not have an anterior bulb extension or anterolateral extensions, muscles 3 and 4 nevertheless insert on the sting bulb (Fig. 10, B). Species of the Cerapachyinae are similar to the Ponerinae in that they do not possess an anterior bulb extension (except to a minor degree in *Sycia typhia*) but are like the dory-
line species in that muscles 3 and 4 insert on the sting bulb instead of a furcula (Fig. 11).

The furcula varies considerably among species of ants and wasps. Members of the Ponerinae (Fig. 8, B, C) and Myrmeciinae (Fig. 8, A, D) generally have a well developed furcula but this sclerite in some members of the Myrmicinae is almost membranous in appearance (e.g., *Atta texana* and others, Fig. 8, G, E). It is slender in species of Pseudomyrmecinae (Fig. 8, J) and reaches its maximum diversity in the Mutillidae (Fig. 8, H, I).

In members of the family Mutillidae, the function of the furcula has become extremely modified in the course of evolution. As the sting evolved to an anterodorsal position, the furcula became elongated so that now it fulfills a different role in the stinging process. Upon contraction of muscle 3 in the Mutillidae, the furcula articulates along much of its posterior border with the anteriorly positioned sting (Fig. 16, E). The posteriad movement of the furcula forces the sting to acquire a more straightened form, resulting in the exaggerated protraction of the sting.

Regardless of the form of the furcula in stinging Hymenoptera other than the Mutillidae, this sclerite and its associated muscles seem to function in a similar manner (deflection and rotation of the sting). If a furcula ever existed in the Dolichoderinae and Formicinae, it has been lost in those groups along with other sting sclerites (Fig. 15, E, F).

The fact that members of the Dorylinae and some species of the Ponerinae and Cerapachyinae do not possess a furcula raises some
Figure 16.—Diagrammatic illustrations.

A through E - Steps in the evolution of the mutillid sting. "A" represents the position of the sting in most aculeate Hymenoptera. The sting began to evolve dorsad, and "B" represents the stage now present in some Tiphiidae. As the sting moved more dorsad (C and D) it also became more elongated and finally the sting pushed anteriad (E) so that the present-day mutillid sting is completely modified to be thrust a considerable distance from the gaster. Instead of merely deflecting the distal tip of the sting, as in most hymenopterans, the furcula in the Mutillidae functions in uncoiling the entire sting during the act of egg deposition.

"F" represents the procedure of sting insertion by hymenopterans that possess barbs on the distal tip of their lancets. The lancets cut the wound and the barbs aid in holding to the tissue. If the barbs are especially large, sting autotomy often results.

"G" represents the poison sac of most hymenopterous insects, how materials are picked up and transformed in the production of venom. Precursory materials are picked up by the free filaments (1) and transferred (2) to the convoluted gland (3). In the convoluted gland, enzymatic reactions necessary for venom production occur. The synthesized venom passes out of the convoluted gland (4) into the poison sac for storage. When venom is needed during the stinging act, it passes posteriorly through the main duct of the poison sac (5), through the sting and into the victim.
important questions. It has been suggested that both the ponerines and dorylines have a common poneroid ancestor (Brown 1954). However, it is not clearly established that the dorylines have arisen from poneroid stock, although based on behavioral and morphological considerations, dorylines and some ponerines share a number of common characters. A number of ponerine genera demonstrate what Wilson (1958) defined as army ant behavior (group raiding and nomadism). Simopelta oculata is such a species, and its dorylinelike sting has already been mentioned. Another species that has been listed by Wilson as having army ant characteristics is Onychomyrmex hedleyi, and Brown (per. comm.) states that members of this genus, along with species of Simopelta, seem to have many army ant attributes, both behaviorally and morphologically. After careful examination of the sting sclerites in Onychomyrmex hedleyi, I have found that this species possesses a well developed furcula, a condition found in none of the doryline species.

Autotomy of the sting.---The acquisition of a mechanism that is fatal to the bearer upon employment rarely occurs in the Insecta. The loss of the entire poison apparatus, and usually the seventh tergal and sternal sclerites, insures the death of the individual losing it. Such autotomy, investigated as early as 1933 by Rau, is due to the presence of enlarged barbs on the distal end of the first valvulae (lancets) (Fig. 16, F).

Autotomy of the sting has been reported by Rau (1933) for Synoeca surinama var. cyanea (Fabricius), Polybia similima F. Smith and Tatuia tatua (= Epipona) (Cuvier). The loss of the sting after
use has been known to occur in the case of the honeybee (Rietschel 1937) for many years, and it also occurs to some extent in ants. Hermann and Blum (1967a) have reported on autotomy in *Pogonomymex* species, especially *P. comanche*. The stings of *P. barbatus* and *P. badius* have also been found to become severed from the posterior abdominal region.

Although the individual gains no particular advantage in losing its sting, there may be considerable advantage gained by the colony. In attacking prey, or in defending the colony, the principle function of the individuals is to sting and subsequently inject enough venom to immobilize the prey or otherwise discourage any intruders. Autotomy of the sting facilitates the procuring of prey or discouragement of an intruder because the sting mechanism continues to function after autotomy has occurred. Likewise, the seventh abdominal sclerites are associated with the 8th hemitergites (spiracular plates) by muscle attachments that affect the function of the stinging process. All of the muscles involved in the stinging act remain with the sclerites at the site of the wound. Because of this, all of the important functions of the sting (e.g., deflection and rotation or pivoting of the sting, cutting of the wound and injection of venom) continue for a period of time after autotomy occurs. It seems clear then, that autotomy of the sting may be a direct and definite advantage to the colony as a whole.

Although enlarged lancet barbs within the Formicidae are best known in *Pogonomymex* species, other members of this family possess barbs that are by no means small. The lancets of *Leptonilla swani*
are relatively very large, and it would not be surprising if it is found that members of the Leptanillinae lose their sting after the stinging act. However, the habits of the species of this subfamily are not well known. Indeed, the number of pinned and preserved specimens in museum collections is very small due to their secretive habits and subsequent lack of availability to collectors.
Phyletic relationships within the Formicidae have previously been based almost entirely on external characters (with the exception of the proventricular investigation, Eisner and Brown 1958). Several internal characters that may be important phylogenetically have been found in this investigation.

In the Formicinae, Dufour's gland is bilobed in most cases. It is only in the primitive *Lasius sitkaensis* and *Lasius fuliginosus* that it resembles the Dufour's gland present in most formicids. This gland in *Acanthomyops* appears to be intermediate between the unilobular gland of *Lasius* and the bilobed structure of higher forms. A comparative study of Dufour's gland in the Formicinae may reveal some interesting correlations since there is some diversity in the structure among species.

The phyletic relationship between the Ponerinae and Dorylinae has been the subject of much investigation (Brown 1954; Eisner and Brown 1958). The sclerites, muscles and other associated parts of the poison apparatus of the Dorylinae are essentially the same as those found in other aculeate hymenopterans. Some specific differences between the poison apparatus of dorylines and most other species of the Aculeateae are: 1) the position of departure by the free filaments from the poison sac, 2) the lack of barbs on the distal end of each lancet, and 3) the absence of a furcula that articulates with the anterior end of the sting bulb in other aculeates.
The free filaments extend from the base of the poison sac in this subfamily, a condition that also occurs in the Myrmeciinae, Ponerinae, Pseudomyrmecinae, and Formicinae. The free filaments extend from a position near the apex of the sac in myrmicines and dolichoderines. The slender appearance of the filaments in the Dorylinae is also a condition found in the Myrmeciinae, Ponerinae, Pseudomyrmecinae and Formicinae, whereas in the Myrmicinae, the filaments have a larger diameter/length ratio. In the Dolichoderinae, the free filaments are oval in appearance.

At present, it is difficult to comment on the significance of these data since the phylogenetic relationships of all the groups within the Formicidae are not well understood. The data accumulated in this investigation will have to be correlated with additional information in the future before much comment can be made on formicid phylogeny. It appears that the poison apparatus of certain groups (e.g., subfamilies) does fit a characteristic pattern in many cases. Further investigations of these characters will determine whether these patterns are consistent in each subfamily. Although it is not evident at this time, the position and gross appearance of the free filaments may indicate some phylectic relationships in the future.

The lack of barbs on the lancets of doryline ants does not have any obvious significance since there is no constant pattern among any members in the Formicidae. Thus, barbs are present on the lancets of many myrmicines, although they are absent in Myrmica americana. They are present in some pseudomyrmecines but have been reported to be absent in Pseudomyrmex pallidus (Blum and Callahan 1963). They are
generally present in the Ponerinae but are lacking in all the doryline species that I have examined.

The lack of a furcula in species of the Dorylinae does have some interesting implications that may be very important in establishing the phylogenetic relationship of the army ants.

The origin of the hymenopterous furcula has not been previously suggested. Other than for members of the Dorylinae and two species of the Ponerinae, all of the stinging Hymenoptera that I have examined possess this sclerite. None of the dorylines, including New World members of the genera Eciton, Labidus, Neivamyrmex, Nomamyrmex and Cheliomyrmex as well as Old World genera Dorylus (subgenera Dorylus, Typhlones and Anomma) and Aenictus, possess a furcula. There is an anteriorly extended portion of the sting bulb in all New World dorylines examined and anterolateral extensions in the Old World dorylines. The presence of muscles 3 and 4 in these doryline species and their insertion on the anterior and anterolateral extensions of the sting bulb indicates that the furcula and anterior region of the sting bulb are homologous structures. Since these structures are homologous, it seems evident that either the furcula has arisen from the anterior region of the sting bulb or fusion between the furcula and anterior region has taken place to produce the condition found today in the dorylines, some ponerines and cerapachyines.

The suggestion that the furcula may have arisen from the sting bulb must be reconciled with several important considerations. First, it has been suggested that the dorylines may have arisen from poneroid stock (Brown 1954). Structural modifications of Onychomyrmex
larvae and the wing venation in *Typhlomyrmex* are suggestive of doryline characters. Also, it has been pointed out that a number of ponerine species illustrate doryline behavior such as group raiding and nomadism (Wilson 1958). If the dorylines have arisen from poneroid stock, the presence of a furcula would be the primitive condition, and fusion of the furcula to the sting bulb must have been the subsequent evolutionary step.

Secondly, the separation of a furcula from the sting bulb (sclerite elaboration) does not follow the rule of evolutionary reduction (Brown 1965). This rule states that "evolutionary change in a given character is more likely to be a reduction rather than an elaboration." According to this rule, fusion of the furcula to the sting bulb would support the rule whereas the elaboration of a furcula from the sting bulb would not.

It is not clearly established that the dorylines have arisen from poneroid stock, although on the basis of behavioral and morphological considerations, dorylines and some ponerines share a number of common characters. In the last few years, more information on the doryline-like ponerines has been accumulated, and Brown (per. comm.) feels that there can be no reasonable doubt that *Onychomyrmex*, *Simopelta* and the mass-foraging species-group of *Leptogenys* originated separately from all or any of the ponerine tribes. *Simopelta* and *Onychomyrmex* seem to have most army ant attributes, both behaviorally and morphologically. Based on the present investigation, the following interesting results were obtained: *Onychomyrmex hedlevi* has a well developed furcula. *Simopelta oculata* possesses a dorylinelike sting
that lacks a furcula and has an anterior extension of the sting bulb that is the point of insertion of muscles 3 and 4. *Sphinctomyrmex steinheili* does not possess an anterior extension of the sting bulb but muscles 3 and 4 are nevertheless inserted on the anteriormost region of the sting bulb.

A consideration of all these data leads me to conclude that the ponerine-doryline similarities may indicate a phylogenetic relationship between the two groups. However, the possession of a furcula by *Onychomyrmex* seems to indicate that similarities between it and the Dorylinae may represent nothing more than the convergence of characters.

Because many characters support the rule of evolutionary reduction, especially meristic ones, it is by no means impossible to find exceptions to the rule. In support of the fact that the anterior bulb extension and furcula are homologous structures is the presence of the pair of muscles (3 and 4) that insert on these structures. In aculeate Hymenoptera, other than the Dorylinae and some of the dorylinelike ponernies and cerapachyines, muscle 4 tends to rotate the sting rather than pivot it. It is decidedly advantageous for an ant to be able to rotate its sting since rotation permits the sting to be thrust in a number of directions. A pivoting sting, such as is found in all the doryline species examined, is much more limited in the direction of its thrusts. Because of the obvious importance of the sting in the biology of ants, it would operate as a selective disadvantage to lose a structure (the furcula) that contributes so markedly to the efficiency of action of the sting. This considera-
tion would tend to support the hypothesis that the anterior bulb extension may have given rise to the furcula.

In a predatory group of ants such as the dorylines the lack of an effective stinging mechanism would prove to be a very strong liability unless the ants had been selected for the development of another highly efficient method of immobilizing prey. This problem appears to have been admirably solved by the Dorylinae through the use of their mandibles which are extensively and effectively employed in killing other arthropods. It may be more than coincidental that the Old World dorylines, which have lost completely the ability to sting, are considered to bite with a severity that is never encountered in the New World dorylines, all of which can sting.

If the furcula has arisen from the anterior bulb extension, it would seem that one of two conditions prevailed in the early history of these ant species: 1) ants arose from wasps as two independent stocks (i.e., in a prefurculate, or dorylinelike, form and a furculate form). Although the prefurculate condition has not been reported in modern wasps, further investigations of wasp stingings may reveal prefurculate species. 2) ants arose from a prefurculate-type ancestor and the furcula has evolved independently in wasps and ants. All wasp species previously investigated possess this sclerite (including the Taphiidae).

That the ants are diphyletic has little support other than the possibility suggested by the prefurculate-furculate evidence presented here. At present, neither morphological nor behavioral data provide any compelling evidence that indicates that the Formicidae are diphy-
letic. The possibility that the furcula evolved independently in ants and wasps seems to have some support. Selection pressure for the development of a furcula may have been, and still may be, great in those ants and wasps in which stinging plays an important ethological role. In the mutillid wasps, for example, selection has played an important role in the evolution of the furcula so that this sclerite has become extremely modified in both shape and function (Fig. 6, A). Therefore, if the furcula did arise independently in the two groups, it seems as though the dorylines and a few ponerines and cerapachyines have retained the single primitive prefurculate form.

In conclusion, I feel that the furcula may be an important tool in understanding the phylogenetic sequence through which aculeate hymenopterans have evolved. Based on whether a prefurculate or a furculate condition is present, as well as on other morphological and behavioral evidence, it seems likely that the ponerine-doryline relationship may be close in some cases. I believe that much more morphological evidence is needed to support any hypothesis as to whether the anterior bulb extension is a pre- or postfurculate structure.
SUMMARY

Generally speaking, the poison apparatuses of all hymenopterous insects examined in this investigation are similar in respect to the fact that the sclerites that compose the sting are derived from the same abdominal segments. These sclerites are the same as those employed by parasitic species for egg deposition. The basic differences between species and higher taxa involve the relative diameter of the free filaments, the presence of an external common duct that connects the free filaments to the convoluted gland, the position on the poison sac from which the free filaments extend, the shape of Dufour's gland, the distinction between distal and proximal regions on the gonostylus, the presence of barbs on the distal ends of the lancets, the number of sensory setae on the oblong plate near the latter structure's articulation with the triangular plate, the relative shapes and sizes of all sclerites and the diversity of form of a sclerite known as the furcula.

Evolution of the mutillid sting is discussed briefly. In that family, the sting has become coiled in order that it may be thrust a considerable distance from the posterior region of the abdomen. The mutillid furcula is employed in the thrusting action of the sting. Because of the various modifications in the mutillid sting, it is probably the most highly evolved poison apparatus currently described in the Hymenoptera.

The function of the lancets in cutting a wound and sting autotomy
are discussed. Large barbs on the lancets sometimes cause the sting to remain in the wound which may result in sting autotomy, an important function in the colony. Although the sting is lost by individuals in the colony, the poison apparatus continues to function in venom injection.

An explanation for the process of venom production is presented. Based on the reduction of tetrazolium salts, it was possible to determine what structures appear to be involved in the synthesis of venom. Precursory materials are presumably picked up from the hemocoel by the free filaments and transferred to the convoluted gland via a slender common duct. The venom is synthesized in the convoluted gland and stored in the poison sac until it is used. When the sting is in use, muscles around the sac constrict and force the venom through the sting and into the wound.

The presence or absence of a furcula may indicate some important relationships between some members of the Ponerinae, Cerapachyinae and Dorylinae. None of the dorylines examined possessed a furcula. This sclerite is also absent in *Simopelta oculata* and *Sphinctomyrmex steinheili* in the Ponerinae; the cerapachyines *Sycia typhla*, *Acanthostichus* sp. and *Phyracaces bicolor* also lack this sclerite. Future investigations may determine whether the condition found in these ants is a pre- or postfurculate one. Based on the position of the furcula in the poison apparatus and on sting efficiency, the furcula is postulated to have arisen from the anterior extension of the sting bulb.
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APPENDIX A

Anal Arc (AA) - This structure lies dorsad to the anus and represents the only remaining structure from the tenth abdominal segment. A structure called the anal pad is connected to the ventral region of the anal arc.

Anterolateral Extensions of the Sting Bulb (A-L E) - These projections are found in the Old World Dorylinae and in some of the Myrmicinae (e.g., Atta texana). However, in the Myrmicinae a furcula articulates with these extensions, whereas a furcula does not exist in the Dorylinae.

Anterior Extension of the Sting Bulb (AE) - The anterior region of the sting bulb of some ants (e.g., the New World Dorylinae) which is the point of insertion for muscles 3 and 4. Such an extension has been found to occur in all of the New World doryline species examined as well as in Simopelta oculata, a member of the Ponerinae, and in one of the Cerapachyinae species. The Ethiopian Dorylinae possess anterolateral extensions rather than an anterior extension.

Barbs of the Lancets (Bb) - The sawlike teeth present on the distal end of the lancet of many aculeate Hymenoptera. These structures assist in cutting a wound in the victim and often are responsible for the sting remaining in the wound (sting autotomy), such as is the case with the honeybee and some Pogonomyrmex species. The presence or absence of lancet barbs is not constant in any of the subfamily groups. They have generally been found in the Myrmicinae.
but are missing in *Myrmica rubra* and the Attini. They are generally
ground in the Pseudomyrmecinae but have been reported absent in *Pseu-
dodomyrmex pallidus*. Lancet barbs seem to be present in the Ponerinae
and Leptanillinae, but absent in the Dorylinae as well as in groups
that possess a much reduced poison apparatus (e.g., the Dolichoderinae
and Formicinae).

Branches of the Free Filaments (Br) - The small or large offshoots
from the main structure of the free filaments. Branching of the free
filaments has been found in most hymenopterous groups and seems to
occur most extensively in the Mutillidae.

Bursa Copulatrix (BC) - The copulatory pouch of the female,
usually the chamber that receives the male genitalia during copula-
tion.

Calyx (Cal) - The enlarged anterodorsal portion of the lateral
oviducts that receives the ova from adjacent and surrounding ovarioles.

Circular Muscle (CM) - Muscle found on the periphery of the poison
sac (PS), Dufour's gland (DG), and around various parts of the repro-
ductive system. All muscle is of a skeletal nature.

Columnar Epithelium (CoE) - The epithelium often found lining
Dufour's gland of some ants and which is often found lining the
reproductive tract in the female.

Cuboidal Epithelium (CuE) - The epithelium usually found through-
out the free filaments (FF), inside the sting bulb (SB), and also
in parts of the lining of the reproductive tract.

Convoluted Gland (CG) - The convoluted gland is the region of
the poison apparatus in which the venom is produced. Precursory
materials picked up by the free filaments (FF) are received and metabolized here. Venom flows from this region to the poison sac (PS) for storage. A convoluted gland has been found to occur in all hymenopterous insects.

Dorsal Apodeme of the Oblong Plate (DA) - This structure serves as the origin for muscle 1, the protracting muscle of the lancets. It represents the dorsal portion of the second ramus (Ra 2) and the anteriormost region of the oblong plate.

Dorsal Bar of the Spiracular Plate (DB) - A dorsal connecting structure joining the two spiracular plates (SP), structures that are often found to be hemitergites of the eighth abdominal segment.

Duct Exit (DE) - The region of the main duct and Dufour's gland that is found within the sting bulb.

Dufour's Gland (DG) - Not much is known about this structure. It nevertheless enters the sting bulb (SB) just ventrad to the main duct (MD) of the poison sac (PS). Although the secretion from this gland functions as a releaser of social behavior in the myrmicine genera *Pheidole* and *Solenopsis* (Wilson 1963), no function can be attributed to the products of this gland in any of the other formicid genera.

Free Filaments (FF) - These usually slender structures extend from the poison sac (PS) and are believed to function in picking up precursors of the venom in various parts of the gaster. These materials then move to the convoluted gland (CG) in the poison sac (PS) where venom synthesis occurs. The filaments characteristically extend from the base of the sac in the Myrmeciinae, Ponerinae, Dory-
linae, Pseudomyrmecinae, and Formicinae but at a position near the apex in the Myrmicinae and Dolichoderinae. They are generally of a uniform diameter throughout their length in the Myrmeciinae, Ponerinae, Dorylinae and Formicinae. The diameter/length ratio is greater in the Myrmicinae and Pseudomyrmecinae. In the Dolichoderinae, the free filaments are bulbous in appearance.

Fulcral Arms (FA) - Paired structures extending dorsally from the base of the sting bulb. They act as supporting structures, as a pivot point (PP) for the deflection of the sting and for the laterad pivoting found in the Dorylinae. There are also muscle attachments (muscles 5 and 6) on each of their ventral borders.

Furcula (Fu) - Of primary significance in this work, the furcula may have originated from the anterior extension (AE) of the sting bulb (SB). It varies in size among the Formicidae and is absent in the Dorylinae and in some non-doryline species. It is fork-shaped and functions in the deflection and rotation or pivoting of the sting by two sets of muscles that originate on the oblong plate (muscles 3 and 4).

Furcula Socket (FS) - A concave region of the sting bulb that receives the ventral arms of the furcula in some ants (e.g., Paraponera clavata).

Germarium (Gm) - The anterior end of an ovariole that contains the primary oogonia.

Gonapophyses (Gp) - Mesal processes of the bases of the gonopods, perhaps endites, forming the first and second valvulae (lancets and sting respectively) of the ovipositor or sting.
Gonopore (Gon) - Either one of the paired primitive openings of the lateral oviducts, or the median opening of the median oviduct (oviductus communis). Snodgrass 1935.

Gonostyli (Go) - A pair of structures that are sensory in nature and extend posteriad from the posterior end of the oblong plate (OP). Also known as sting palps, they arise from the lateral gonapophyses of the ninth abdominal sternum (gonapophysis 2 of sternum 9). The gonostyli are often found to be divided into a distal and proximal region, a feature that has reached its maximum diversification in the Mutillidae. They possess a concave mesal wall that enables them to form a sting sheath when they are brought together.

Lancet (Ln) - A pair of structures, each of which represents the fused triangular plate, ramus 1, and the lancet shaft, all three of which are discussed under their individual titles. Each lancet has several functions due to the presence of a valve near the base of the first ramus and barbs at the distal tip. The valves serve to block the poison canal during the period when the sting is at rest. It also functions as a pump during the stinging act. The lancet barbs assist in cutting into the victim and also aid in sting autotomy.

Lancet Shaft (LS) - This structure represents the first valvula (Vlv 1) which articulates with the fused second valvulae (sting shaft) by a tongue and groove articulation. Each of the paired shafts articulates with a ramus (Ra 1) on its anterior end. Each lancet shaft stems from a gonapophysis of the 8th sternum. It is the shaft of the lancet that possesses barbs on its distal end.
Lateral Oviduct (LO) - Also known as oviductus lateralis, these structures converge from their anterior enlarged calyces to form a common duct, the median duct or oviductus communis.

Lumen (Lu) - Any lumen found in the poison apparatus or reproductive system. It usually refers to the lumen of the soft structures of the poison apparatus such as the poison sac, poison canal, main duct, Dufour's gland or any of the chambers of the reproductive system.

Main Duct of the Poison Sac (MD) - The duct that connects the poison sac (PS) with the sting bulb (SB). Its cellular make-up is of simple squamous epithelium.

Median oviduct (MO) - A common duct that receives the two lateral oviducts anteriorly. Also known as the ductus communis, it is usually very short in the Hymenoptera.

Meroistic Insect - One which has both oocytes and nurse cells occurring within the oviduct, including acrotrophic and polytrophic types.

Nurse Cell (NC) - Also known as trophocyte, these cells follow the oocytes within the ovariole of meroistic insects.

Oblong Plate (OP) - The oblong plates are paired and represent the lateral parts of the ninth sternum (second valvifers). See "Valvifer 2." Each oblong plate acts as the point of origin for muscles 3 and 4 (deflecting and rotating or pivoting muscles of the sting respectively) and muscle 2 (protracting muscle of the lancet). On their distal ends they articulate with the gonostyli (3rd valvulae).
Oocyte (Oo) - The egg cell before maturation.

Ovariole (Ov) - One of several secondary divisions of each of a pair of ovaries that consists of a terminal filament, egg tube, and pedicel.

Ovary (Ov) - One of a pair of structures composed of a number of ovarioles that contain developing oocytes. The number of ovarioles in each ovary may range from a couple to several hundred depending on the species.

Ovum (Ovm) - The mature and unfertilized egg cell.

Pedicel (Pcl) - A short stalk connecting the ovariole to the calyx of the lateral oviduct.

Poison Canal (PC) - The path followed by venom from the main duct of the poison sac through the sting. The poison canal is held closed by muscle 6 (sphincter of the poison canal) and is blocked by the valves of the lancets when the sting is in a state of rest. The canal is opened by muscle 5 (dilator of the poison canal). Venom is forced through the canal and out of the sting by the moving valves of the lancets and contraction of the muscles surrounding the poison sac.

Poison Sac (PS) - This structure acts as a reservoir for venom produced in the enclosed convoluted gland. It is composed of a tunica propria and a simple layer of squamous epithelium. It is surrounded by a layer of muscle that functions in forcing the stored venom from the sac, through the main duct and poison canal and out of the sting. The free filaments extend from the sac and are believed to collect precursory materials that are used in the synthesis of venom by the
convoluted gland (CG), which is located within the poison sac.

Quadrate Plate (QP) - This structure articulates on its proximal and anteriormost end with the dorsal apodeme of the triangular plate (TP). It acts as a point of insertion for muscle 1, the protracting muscle of the lancets, and for muscle 2, the retracting muscle of the lancets. The quadrate plates, also called the 9th hemitergites, represent the 9th abdominal tergal segment.

Ramus 1 (Ra 1) - Each slender first ramus connects the triangular plate (TP) with the lancet shaft (LS).

Ramus 2 (Ra 2) - Each slender second ramus connects the oblong plate (OP) with the sting bulb (SB). On its posterior border in a dorsal region and at its base are found sensory pegs.

Sensory Pegs (SnPg) - Peglike structures found in two positions on the second ramus (ramus of the sting), one group at the dorsal region and the other near the junction with the sting bulb.

Sensory Setae (SnSt) - These structures are often numerous on the third valvulae (gonostyli) and presumably serve a sensory function during the stinging act. Other sensory setae are located on the oblong plate (OP) near the articulation with the triangular plate (TP).

Spermatheca (Spm) - Also known as the receptaculum seminis, this is the sperm receptacle (sperm storage area) in the female. It is located above the vagina in the Hymenoptera, between the anterior uterine pouch and posterior bursa copulatrix.

Spermathecal Duct (SD) - This duct passes from the anterior border of the uterine pouch and enters the spermatheca in a dorsal location. It is traversed by sperm that are stored in the spermatheca.
Spiracle (Sp) - The external opening of the tracheal system of any segment but specifically referred to here as the opening on the 8th hemitergites (spiracular plates, SP).

Spiracular Plate (SP) - Each of the 8th hemitergites or merely the plates of the 8th abdominal tergites that function in movement of the entire poison apparatus. The spiracular plates are the last abdominal structures to be associated with spiracles.

Squamous Epithelium (SE) - The epithelium usually found covering the poison sac, main duct, and Dufour's gland. It may be found in the female reproductive tract in the region of the vulva.

Sting (St) - The sting is also known as the fused 2nd valvulae. It is composed of the sting bulb (SB) anteriorly and sting shaft (SS) posteriorly. It represents the fused 1st gonapophyses of the 9th sternum.

Sting Bulb (SB) - This is the anteriormost and bulbous region of the sting (St) or terebra and actually represents a part of the fused second valvulae. This latter structure originates from gonapophyses of the ninth sternum.

Sting Shaft (SS) - The sting shaft, which provides a dorsal and lateral cover for the poison canal and also holds the lancets in position, represents fused gonapophyses of the 9th abdominal tergites. The sting shaft is the structure that is inserted into the wound of the victim after an incision has been made by the lancets.

Terminal Filament (TF) - The cellular anterior end thread of an ovariole.
Triangular Plate (TP) - Also known as the first valvifer (Vlf 1), this structure originates from the 8th sternal plate. Although it is roughly subtriangular in most hymenopterous insects, the shape and size of this structure may vary considerably.

Uterine Pouch (UP) - A dorsal extension of the uterus. The spermathecal duct often leaves the anterior border of this pouch in ants.

Uterus (Ut) - A region of the genital tract in which embryonic and sometimes partial postembryonic development may take place. In the Hymenoptera, this region is located between the median oviduct (oviductus communis) and vagina.

Vagina (Va) - A part of the definitive egg passage posterior to the uterus and anterior to the vulva.

Valve (Va) - A dorsally projecting structure on the proximal region of the lancet shaft (LS). It acts in closing the poison canal when the sting is not being used and in assisting the ejection of venom from the sting.

Valvifer 1 (Vlf 1) - Also known as the triangular plate (TP), this structure articulates with the oblong plate (OP) by a posterodorsal projection and with the quadrate plate (QP) by a posterodorsal projection. It forms an enlarged structure on the dorsal portion of Ramus 1 (Ra 1).

Valvifer 2 (Vlf 2) - Also known as the oblong plate (OP), this structure extends posteriad from the dorsal portion of Ramus 2 and articulates posteriorly with the gonostylus. It also makes a sensory articulation with the triangular plate (TP) near the middle of
the shaft and several sensory setae are usually located on the oblong plate at that point.

Valvula 1 (Vlv 1) - This is also known as the lancet shaft (LS) and is discussed under that title.

Valvula 2 (Vlv 2) - This is also known as the sting (fused second valvulae) and is discussed under that title.

Ventral Apodeme of the Sting Bulb (VA) - This pair of structures extends anteriorly and sometimes slightly dorsad from the ventral region of the sting bulb (SB).

Ventral Groove of the Sting (VG) - The open ventral portion of the sting that is usually filled by the pair of lancets.

Vulva (Vu) - The posteriormost region of the female reproductive tract. It is bordered anteriorly by the vagina, dorsally by the bursa copulatrix, and exits posteriorly through the gonopore.
Henry Remley Hermann, Jr., was born in New Orleans, Louisiana, on September 6, 1935. He attended grammar school in the public school system of that city and attended Delgado Trades School from September, 1951, to February, 1954, graduating on the latter date as a machinist. On March 7, 1954, he entered the United States Air Force and served as reporter and editor of three Air Force newspapers until being honorably discharged in November, 1957. He served inactively in the Air Force reserve until March, 1962. He entered Louisiana State University in New Orleans in September, 1958, and graduated in June, 1963, with a Bachelor of Science degree in biology. Mr. Hermann was married to Patricia Ann Watt on August 17, 1963. He entered Louisiana State University in Baton Rouge in September of that same year and graduated in May, 1965, with a Master of Science degree in Entomology. The subject of his thesis concerned the poison apparatus of three species of ants. Mr. Hermann is now a candidate for the degree of Doctor of Philosophy in Entomology.
EXAMINATION AND THESIS REPORT

Candidate: Henry Remley Hermann, Jr.

Major Field: Entomology

Title of Thesis: A Comparative Study of the Hymenopterous Poison Apparatus

Approved:

[Signatures and titles]

EXAMINING COMMITTEE:

[Signatures]

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