The Hymenopterous Poison Apparatus. X. Morphological and Behavioral Changes in *Atta texana* (Hymenoptera: Formicidae)[1]

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ABSTRACT

Atta texana (Buckley) and other members of this genus no longer utilize the 8th and 9th gonapophyses as part of their defensive system. Although the sclerites that comprise the stinging apparatus in most aculeate Hymenoptera are present in this species, they seem to function only in the deposition of trail pheromones. A mechanical and chemical defense, through the utilization of a sting and associated venom components, has been replaced in attines by a new mechanical defensive system, primarily the powerful mandibles. The morphology of structures responsible for the deposition of trail pheromones is discussed along with the new means of defense and associated behavioral characteristics.

Atta texana (Buckley), commonly known as the Texas leaf-cutting ant in much of the literature or as the town ant by residents of infested areas in Louisiana and Texas, has been the subject of many publications since Buckley (1860) first investigated its habits. Most of the recent information concerning the biology of *A. texana* has been presented by Moser (1967b) and Weber (1966).

This species and most other members of the tribe

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Attini are well known for their phytophagous habits. To provide food for the colony, *A. texana* workers construct fungus gardens in the ground and provision them with green leaves cut into bits ca. 2 mm diam. On the resultant flocculent leaf mass, they plant a fungus that grows rapidly, producing bromatia on the mycelia which the ants cut and harvest (Batra and Batra 1967). Such bromatia never form without a direct intervention by the ants.

While foraging for leaves, attines deposit chemical odor trails that are followed by other members of the colony to the leaf source. These odor trails are highly persistent, stable, and are detectable by the ants in minute quantities. In 1963, Moser and Blum determined that the trail pheromone of *A. texana* is formed in the gland responsible in most aculeate Hymenoptera for the production of venom. The pheromone is deposited on the ground through the gonapophyses (1st and 2nd valvulae). Fluid from Dufour's gland was inactive in trail pheromone tests. It later was determined that trail pheromones are produced in the "poison gland" of other attine species and that they too pass through the gonapophyses in these species to be deposited on the ground. The various species in this tribe never have been observed to share trails in the field; paradoxically, they readily follow extracts from each other's poison glands in the laboratory (Blum et al. 1964). Moser and Silverstein (1967) showed that at least 2 pheromones, one volatile and one nonvolatile, are present in the venom reservoir of *A. texana.*

Heretofore, the poison apparatus of *A. texana* has been investigated only superficially, though Moser (1967a) indicated its position and some anatomical details. The function of the apparatus is especially interesting in attines because they are phytophagous and incapable of using the sclerites in the act of stinging. The present investigation was initiated as part of a comparative study of the hymenopterous poison apparatus and indicates how closely the sclerites of the 8th–10th abdominal segments of this species, both worker and alate female, resemble comparable structures in the poison apparatus of a stinging formicid without functioning as a sting.

MATERIALS AND METHODS

A. texana workers and alate females were collected near Pineville, Rapides Parish, La., during preswarming activity in May and June (Moser 1967b). Live specimens were dissected in normal saline for an examination of the glandular and reservoir regions. The pertinent sclerites were dissected from the gaster, dehydrated in ethyl alcohol, cleared in xylene, and mounted in Permount®. Sclerites from several specimens were disarticulated from one another to facilitate detailed observations. Both sclerites and soft parts were examined through binocular dissecting and compound microscopes. Measurements for illustrations are in millimeters.

RESULTS

The venom reservoir is globate (PS, Fig. 1 A–C; 3 E, F). The sac wall is composed of simple squamous epithelium, surrounded by a simple layer of striated muscles. These muscles appear weak when compared with those of certain wasp species (Hunt and Hermann 1970). During the stinging act in aculeate species, these muscles contract to force the venom from the reservoir region into the sting. In *A. texana,* these muscles have retained their function as the 1st step in forcing liquids out of the sac. However, these substances are trail pheromones rather than venom.

Within the reservoir, the convoluted gland (CG) is responsible for the chemical alteration of venom or trail substance precursors which, after being transformed, are later stored in the sac (Blum and Hermann 1969). The convoluted gland is composed of polygonal cells as well as ductules and ducts that function in venom production and transference from the gland to the sac reservoir. The convoluted gland is a structure which has invaginated into the reservoir and is therefore surrounded by an internal and an external cuticula (Fig. 1 B, C).

Articulating with the convoluted gland but extending out of the reservoir are 2 free filaments (FF, Fig. 1 A–C). These slender structures pick up the precursory substances in the ant's gaster and deliver them to the convoluted gland. The filaments characteristically leave the sac as 2 distinct structures in myrmicine and pseudomyrmecine ants. In some of the more primitive subfamilies (e.g., Ponerinae) a common duct external to the sac branches into the individual filaments (Hermann 1969b).

In *A. texana,* the filaments are larger in diameter at their distal end than in the proximal region. In most primitive ants the filaments maintain a uniform diameter throughout their length. However, filaments typical of myrmicine and pseudomyrmecine species have been found in the Ponerinae (Hermann 1969a). The filaments are composed of a simple layer of cuboidal to columnar cells that surround an undulating lumen (Fig. 1 C).

The function of Dufour's gland (DG, Fig. 1 A–D; 3 E, F) in attine species is not known, as is the case for most species in the subfamily Myrmicinae (Wilson 1963). The gonapophyses of the 8th and 9th abdominal segments (Fig. 2 A–H) in *A. texana* and other attines are insertile (i.e., they are entirely hidden within the gaster) (Fig. 2 E, F). Although insertile gonapophyses may be expected in a species that does not sting, they occur also in some stinging groups such as the subfamily Dorylinae (Hermann 1969b). The gaster of attines is constructed in such a way that the sting itself is incapable of extending externally. Although we have observed closely the gaster of *Atta* workers, both during pulsating movements (somewhat simulating stinging movements) as well as during the deposition of trail pheromones, we have not ob-

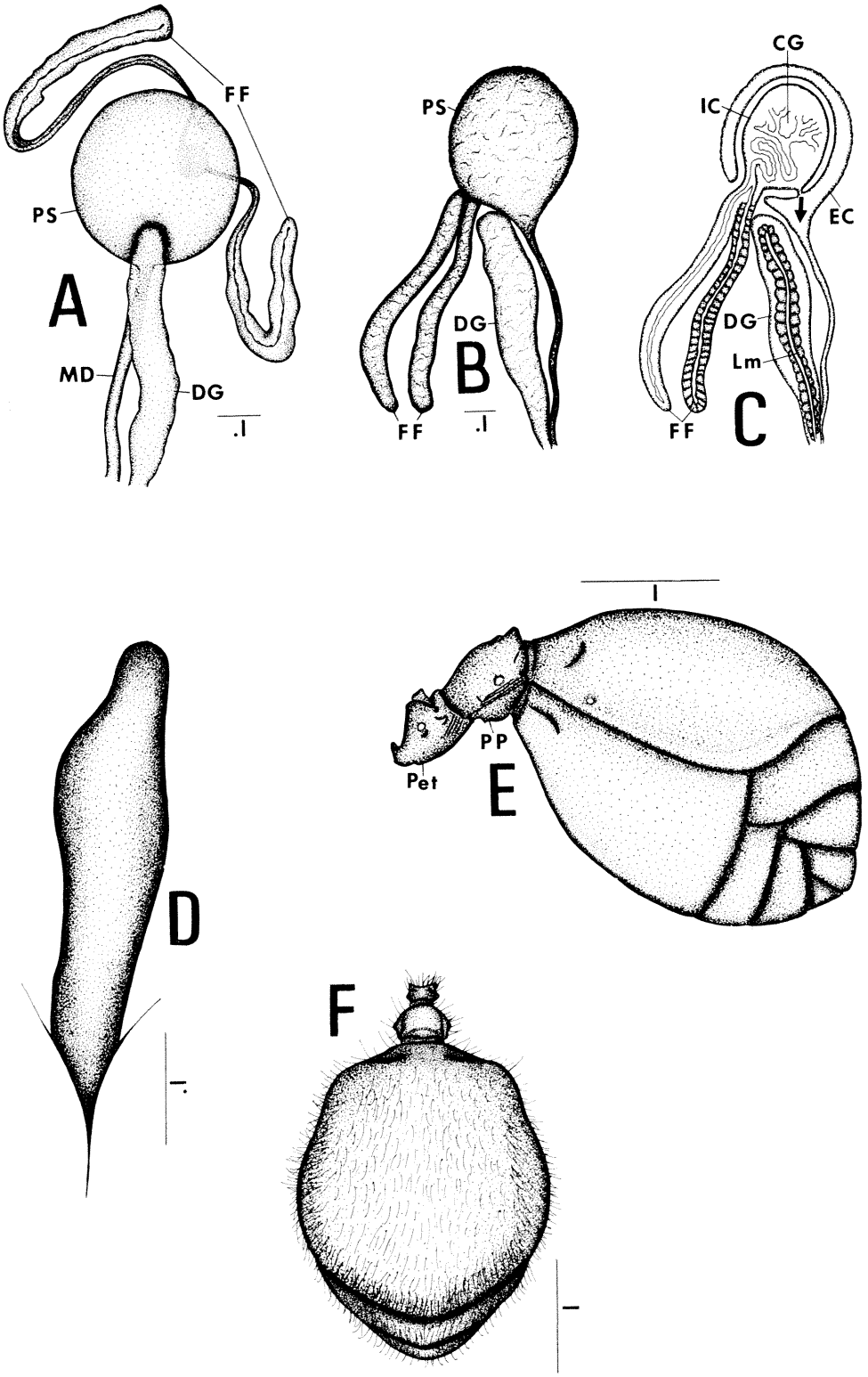

FIG. 1.—Glandular structures associated with the poison apparatus and gaster of an *A. texana* worker. A, Ventral view of Dufour's gland and sac responsible for the production and storage of trail pheromone; B, lateral view of same; C, saggital section of same; D, Dufour's gland; E, lateral view of the gaster of a major worker; F, dorsal view of gaster of a major worker.

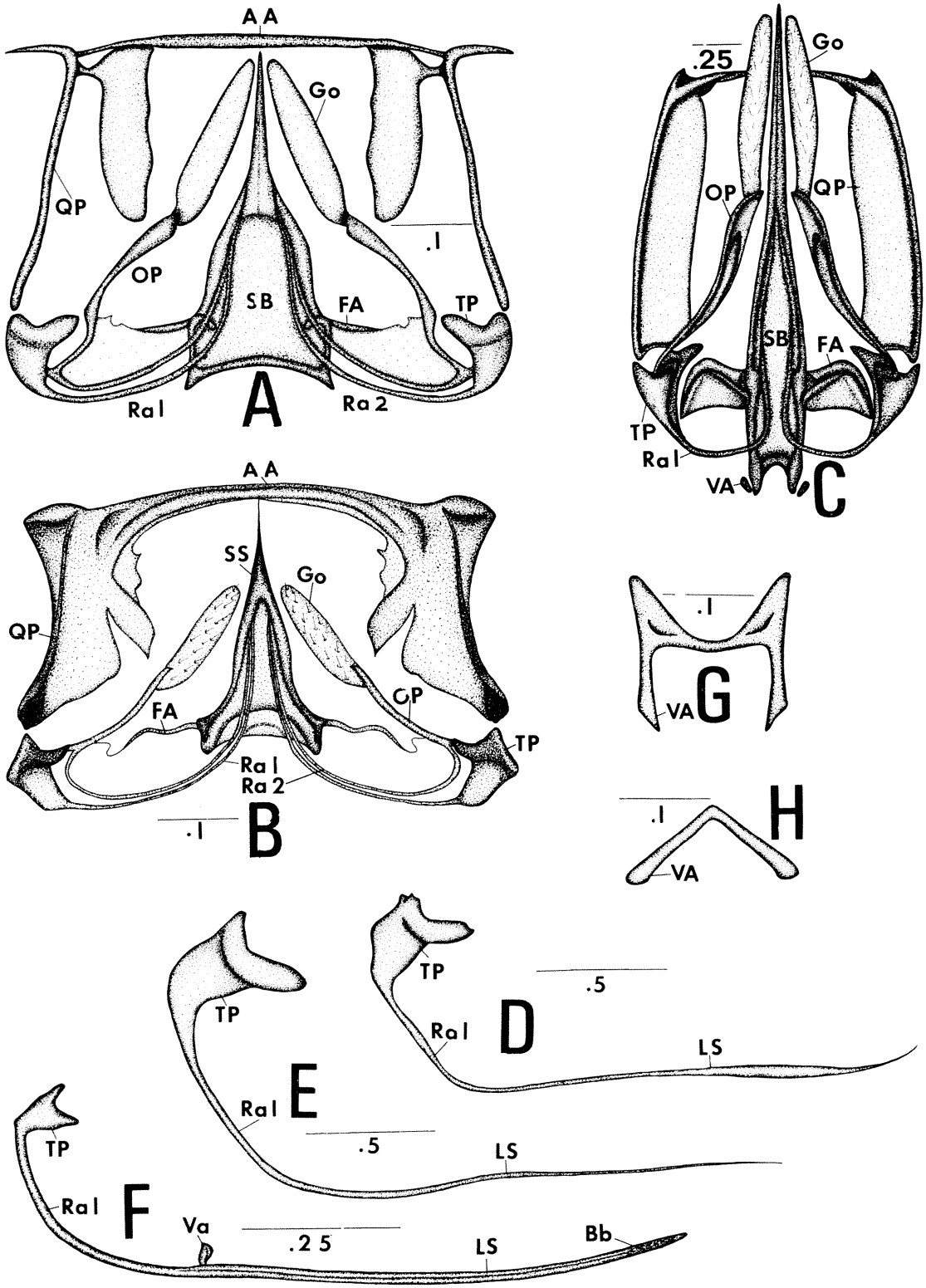

FIG. 2.—Sclerites in the trail depositing apparatus of *A. texana,* and similar structures found in the poison apparatus of stinging myrmicine species. A, Ventral view of the trail-depositing apparatus of an *A. texana* major worker; B, same of an alate female; C, same of *Pogonomyrmex badius* (Latreille); D, lateral view of a lancet of an *Atta cephalotes* (L.) worker; E, same of *A. texana;* F, same of *P. badius;* G, dorsal view of the furcula in an *A. texana* worker; H, same in *P. badius.*

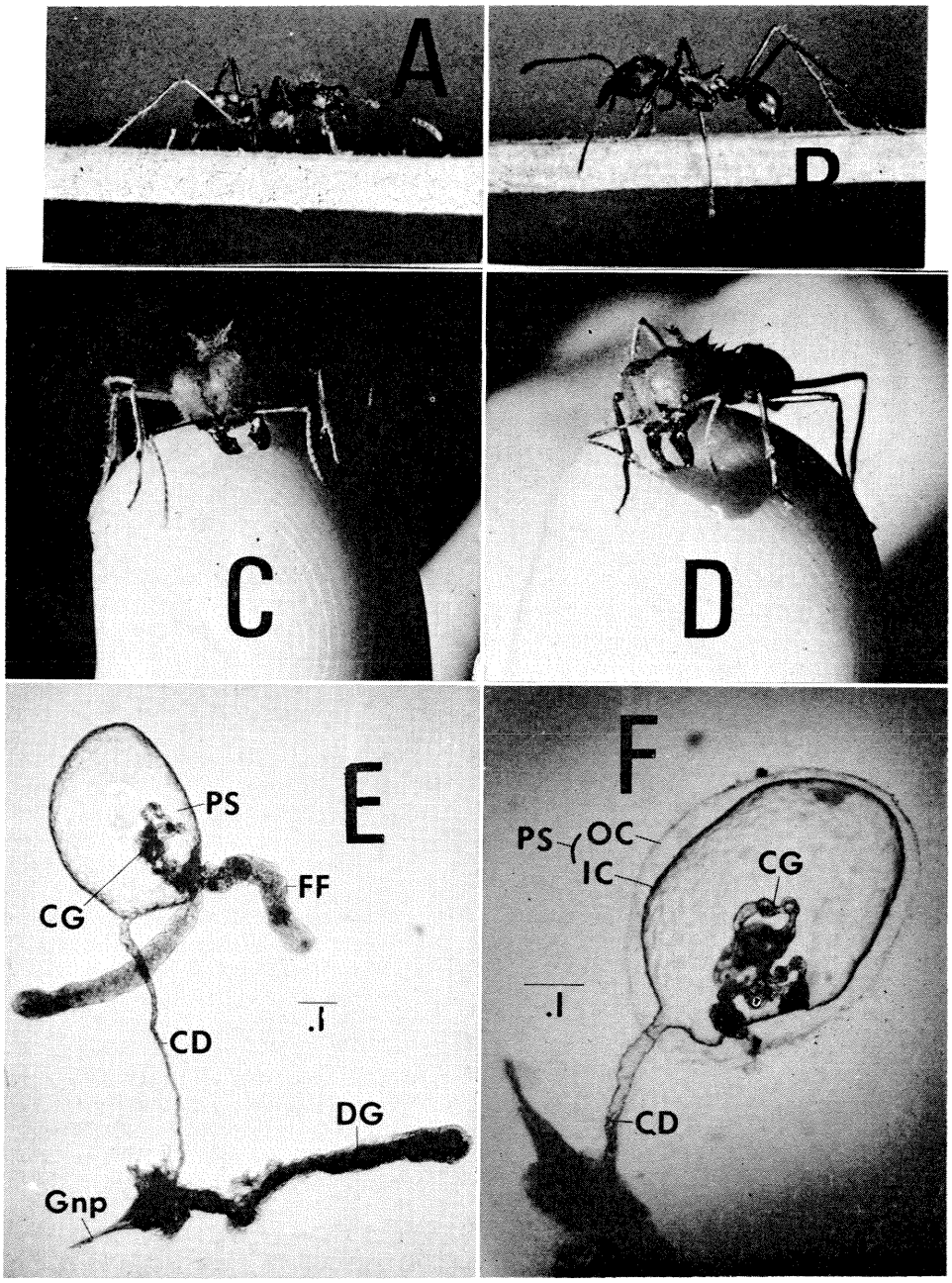

FIG. 3.—Photographs of trail making, defensive behavior, and some glandular structures in *A. texana*. A, An *A. texana* worker with its gaster raised away from the twig during the interphase of trail deposition; B, gaster lowered to the twig for deposition of trail pheromone; C, defensive behavior primarily involves biting with enlarged mandibles; D, when biting human skin, major workers are persistent in producing sawing motions from side to side with their mandibles; if these ants are not removed, they will continue until blood flows from the wound; E, lateral view of sting and pheromone reservoir; F, enlargement of pheromone reservoir to show the convoluted gland.

served an extension of the sting out of the posterior region of the gaster.

The sclerotized portion of the trail-depositing mechanism consists of the entire complement of sclerites that are found in stinging ant species (Fig. 2 A). Certain of the sclerites have become reduced to some degree but not to the extent of being lost.

The stinglike device responsible for the transference of trail pheromone from reservoir to the ground (SB, SS, Fig. 2 A, B) originated in part

from fused gonapophyses (fused 2nd valvulae) of the 9th abdominal segment. In *A. texana,* the sting of both worker and queen has become spatulate and appear's weak (Fig. 2 A, B), whereas in most stinging species the sting appears strong and well sclerotized (Fig. 2 C). In the queen (Fig. 2 B), the proximal end of the sting is more spatulate than in the worker, A. This spatulate appearance of the sting has also been found in some other myrmicines (Hermann, unpublished data) and *Dorylus* (Hermann 1969b), all of which are incapable of stinging.

The 1st valvulae (Fig. 2 D–F), representing gonapophyses of the 8th abdominal segment and well known as lancets (Fig. 2 D–F) in stinging Hymenoptera, articulate mesally with the 9th gonapods by tongue-and-groove articulations. In many myrmicine species, the 1st valvulae assist the movement of venom or trail substances out of the posterior end of the sting shaft by moving back and forth on these articular processes. This function is primarily a result of the presence of valves normally positioned on the proximal and dorsal portion of the lancet shaft (Va, Fig. 2 F). In *A. texana,* this valve is lacking (Fig. 2 D, E) and the flow of trail pheromone from the reservoir to the ground may be entirely dependent upon the contraction of muscles that surround the reservoir.

The 9th hemitergites or quadrate plates are well developed and connect to the anal arc (QP, Fig. 2 A, B). There is considerable difference between these sclerotized parts in the queen, B, and worker, A. Fulcral arms (FA, Fig. 2 A–C) are represented in the 2 castes as thin sclerites that taper to a point toward their dorsal or distal end. The base of the arms remains the fulcral point for the deflection of the fused 9th gonapophyses.

The gonostyli (Go, Fig. 2 A–C) are not well sclerotized and are simple in structure. Sensory setae are found on much of the surface of each gonostylus.

The furcula (Fig. 2 G) is only slightly sclerotized. In stinging ants, the furcula functions in rotating the sting shaft, thus producing the multidirectional movements of deflection and protraction. In attines, a directional apparatus is not needed, but the furcula retains its function of deflecting the shaft ventrad. This movement assists the deposition of trail pheromones.

Many of the sclerites that once took part in the stinging act now function in conjunction with the deposition of trail pheromones in attines. Trails (Fig. 3 A, B) seem to be deposited by workers of the colony as they move toward the nest and away from the food source. Deposition of a trail from the food source to the nest is typical of trail-laying behavior among social insects. Food, which is a reward for the insect seeking it, stimulates the insect to deposit a trail back to the nest. With *A. texana,* trails seem to be physical as well as chemical because a path is often worn away along the main trail route and part of the attine trail is beneath the surface of the ground.

DISCUSSION

Several steps are evident in the evolution of the hymenopterous poison apparatus from the original ovipositor to the structures that we find in attines (Hermann, in preparation). Some wasps employ the structure which has resulted from a fusion of the gonapophyses as an ovipositor alone, while others retain that function and also use this structure as an offensive or as a defensive weapon. Members of the Formicidae and other social Hymenoptera no longer retain the gonapophyses as an ovipositor but often use it primarily as a defensive mechanism. A modification of this use is seen in many ant species as is well demonstrated in attines. In *A. texana,* as in many other attines, the apparatus has further evolved from a defensive weapon to a communicative device. Besides being well armored, the prime defensive mechanism of this species is now the mandibles, which have developed into formidable and very effective weapons (Fig. 3 C, D). Terpenoid repellents may also play an important part; Blum et al. (1968) found them in mandibular glands in 4 of 6 species investigated.

In considering the evolution of attines and their acquisition of leaf-cutting habits (Weber 1958), it seems likely to assume that the development of powerful mandibles preceded the loss of the ant's ability to sting. We may assume that the predecessors of attines were stinging ants or more closely related to stinging ants, for all members of the family Formicidae are, in general, aculeate forms. Some phyletic correlations between another myrmicine, *Oxyopomyrmex,* and the attine *Trachymyrmex,* have been discussed in another paper (Weber 1958). *Oxyopomyrmex* is closely related to *Messor* of the Old World and to the well-known stingers of the genus *Pogonomyrmex* of the New World. Presumably, the sting had already atrophied when the fungus-growing habits of attines were acquired because the ants in this group are believed to have been phytophagus feeders before they commenced to culture fungus. The phyletic changes from entomophagy to phytophagy are, indeed, very little understood.

When biting human skin during colony defense, the major workers spread their mandibles apart nearly 180°. A rocking of the head results in a sawing motion of the mandibles so that the wound produced is often 3 mm wide and as much as 2 mm deep (Fig. 3 C). This cutting action usually draws blood and causes some pain (Fig. 3 D). During the entire process of cutting a wound, the abdomen is pulsated up and down. Although this pulsation at first brings to mind stinging behavior, the ant is incapable of stinging. Such pulsation is often seen in many species of aculeate Hymenoptera, including males, which never possess a sting. The sting of *A. texana* possesses a weak distal end and the lancet valve is wanting. These are 2 structures that are extremely important in the act of stinging. Another feature of the sting itself, which is generally characteristic of some nonstinging Hymenoptera, is

its spatulate appearance throughout most of its length. Some other myrmicine ants possess this character and it has been found in some species of the Dorylinae (Hermann 1969b).

All evidence indicates that the sclerites originating from the 8th through the 10th abdominal terga and sterna in *A. texana* have been modified considerably from the typical poison apparatus found in stinging Hymenoptera. Although all of the sclerites present in stinging species are present in *A. texana,* several of the major sclerites have been modified so that the sclerites can in no way function in the act of stinging.

Abbreviations Used in Figures

AA	Anal arc	OP	Oblong plate
Bb	Barbs on lancet	Pet	Petiole
CD	Common duct	PP	Post petiole
CG	Convoluted gland	PS	Poison sac
DG	Dufour's gland	QP	Quadrate plate
EC	External (outer) cuticula	Ra	Ramus
		Ra 1	Ramus of 1st valvifer
FA	Fulcral arm		
FF	Free filaments	Ra 2	Ramus of 2nd valvifer
Gnp	Gonopods		
Go	Gonostylus	SB	Sting bulb
IC	Inner cuticula	SS	Sting shaft
Lm	Lumen	TP	Triangular plate
LS	Lancet shaft	Va	Valve of lancet
MD	Main duct of poison sac	VA	Ventral apodeme of furcula
OC	Outer (external) cuticula		

REFERENCES CITED

Batra, S. W. T., and L. R. Batra. 1967. The fungus gardens of insects. Sci. Amer. 217(5): 112–20.

Blum, M. S., and H. R. Hermann. 1969. The hymenopterous poison gland: Probable functions of the main glandular elements. J. Ga. Entomol. Soc. 4: 23–28.

Blum, M. S., J. C. Moser, and A. D. Cordero. 1964. Chemical releasers of social behavior. II. Source and specificity of the odor trail substances in four attine genera (Hymenoptera: Formicidae). Psyche 71: 1–7.

Blum, M. S., F. Padovani, and E. Amante. 1968. Alkanones and terpenes in the mandibular glands of *Atta* species (Hymenoptera: Formicidae). Comp. Biochem. Physiol. 26: 291–9.

Buckley, S. B. 1860. The cutting ant of Texas. Proc. Phila. Acad. Natur. Sci. 12: 233–6.

Hermann, H. R. 1969a. The hymenopterous poison apparatus. VIII. *Leptogenys (Lobopelta) elongata* (Hymenoptera: Formicidae). J. Kans. Entomol. Soc. 42: 239–43.

1969b. The hymenopterous poison apparatus: Evolutionary trends in three closely related subfamilies of ants (Hymenoptera: Formicidae). J. Ga. Entomol. Soc. 4: 123–41.

Hunt, A. N., and H. R. Hermann. 1970. The hymenopterous poison apparatus. XI. *Polistes annularis* (Hymenoptera: Vespidae). J. Ga. Entomol. Soc. (in press).

Moser, J. C. 1967a. Trails of the leafcutters. Natur. Hist. 76(1): 32–35.

1967b. Mating activities of *Atta texana* (Hymenoptera: Formicidae). Insectes Soc. 14: 295–312.

Moser, J. C., and M. S. Blum. 1963. Trail marking substance of the Texas leaf-cutting ant: Source and potency. Science 140: 1228.

Moser, J. C., and R. M. Silverstein. 1967. Volatility of trail marking substance of the town ant. Nature 215(5097): 206–7.

Weber, N. A. 1958. Evolution in fungus-growing ants. Proc. 10th Int. Congr. Entomol. 2: 459–73.

1966. Fungus-growing ants. Science 153: 587–604.

Wilson, E. O. 1963. The social biology of ants. Annu. Rev. Entomol. 8: 345–68.

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