

**Comparative Anatomy and Chemistry of the
Venom Apparatus and Mandibular Glands in
Dinoponera grandis (Guérin)¹ and *Paraponera clavata* (F.)
(Hymenoptera: Formicidae: Ponerinae)**

HENRY R. HERMANN,² MURRAY S. BLUM,² J. W. WHEELER,³
W. L. OVERAL,⁴ J. O. SCHMIDT,⁵ AND JUNG-TAI CHAO²

Ann. Entomol. Soc. Am. 77: 272-279 (1984)

ABSTRACT The venom apparatus of *Dinoponera grandis* is anatomically similar in certain key characteristics to that of *Paraponera clavata* and other ponerines, and also to myrmecines. The furcula in these two species is X shaped. The gonostyli are bilobed, with the distal gonostylar lobe the smaller of the two. Very large mandibular glands attach to the mesal side of each mandible and extend into the cephalic chamber to an area adjacent to the antennal sockets. Dufour's gland secretion in *D. grandis* workers contains a series of saturated, monounsaturated, and diunsaturated hydrocarbons in the range from C₁₃ to C₁₉, with pentadecane being the major alkane present. The mandibular gland secretion consists of 2,5-dimethyl-3-*n*-propylpyrazine and 2,5-dimethyl-3-isopentylpyrazine. Dufour's gland secretion of workers of *P. clavata* is dominated by nonadecadiene, pentacosadiene, and heptacosadiene, with a series of alkanes and alkenes from C₁₆ to C₂₆ also present. Mandibular gland secretions consist of a mixture of 4-methyl-3-heptanone and 4-methyl-3-heptanol. Workers of *P. clavata* and *D. grandis* exhibited no reactions when exposed to either extracts of their cephalic glands or the neat compounds.

Dinoponera grandis (Guérin), anatomically the largest known species of the family Formicidae (our specimens measure 34 mm in length), is found in the jungles of South America. Our specimens were collected at both Pebas, Peru, and Belém, Brazil. In Brazil, this ant species is known by the Huitoto Indians as "Isula Grande" because of its size.

Very little is known about its foraging habits, but there are accounts of this species sometimes foraging in some type of column (Allard 1951, Bates 1892). It is well known as a vicious stinger (Allard 1951, Bates 1892), although the pain associated with a sting from this species apparently is not comparable to that of *Paraponera clavata* (F.).

These two species are members of the subfamily Ponerinae, which has been linked by numerous characters to the Myrmeciinae through a common ancestor (Brown 1954). Although *Dinoponera grandis* and *Paraponera clavata* are both extremely large ponerines and superficially look very much alike, they have been taxonomically separated into two separate tribes (Brown 1954, 1958, Emery 1911). Originally put in a separate tribe

Paraponerini in the Emery-Wheeler classification as referred to by Brown (1958) solely on the basis of its large size, *Paraponera clavata* is now treated as a member of the tribe Ectatommini (Brown 1958). *Dinoponera grandis* belongs to the Ponerini (Emery 1911).

Anatomical, behavioral, and chemical studies on this latter species are lacking in the literature. This paper compares the venom sclerites of this species with those of *P. clavata* (Hermann and Blum, 1966), as well as with other ponerines and myrmeciines. In addition, it compares the Dufour's gland and mandibular gland chemistry of these two ponerines.

Materials and Methods

Anatomy. *Dinoponera grandis* workers were collected in 70% EtOH and dissected from this medium for slide mounting. Because only a dozen specimens were collected for a study of the venom sclerites, no histological studies were performed. The venom apparatus, its Dufour's gland, and mandibular glands were subsequently studied grossly under a binocular dissecting microscope. In addition, whole mounts of the entire apparatus and its individual parts were prepared with Hoyer's medium and Permount without the use of stains. All measurements on figures are in millimeters. Similar preparation was used with workers of *Paraponera clavata*.

Chemistry. Dufour's glands and mandibular glands from both *P. clavata* and *D. grandis* were dissected from 24 freshly collected live specimens.

¹ *Dinoponera grandis* (Guérin) is synonymous with *Dinoponera gigantea* (Perty).

² Dept. of Entomology, University of Georgia, Athens, GA 30602.

³Dept. of Chemistry, Howard University, Washington, DC 20059.

⁴ Divisao de Invertebrados, Museu Paraense Emilio Goeldi, C.P. 399, 66.000 Belem, Para, Brasil.

⁵ Bee Research Laboratory, ARS, USDA, 2000 East Allen Rd., Tucson, AZ 85731.

each and placed
sequent chemical
these extracts.

Analyses were performed on a gas chromatograph-mass spectrometer installed aboard the α -Helix. Samples were analyzed on a 1.8-m \times 0.25-mm i.d. column programmed from 40 to 250°C at 10°C/min. Compounds were identified by comparing their mass spectra (He-3) with those of standard compounds. Analyses of many of the compounds at the University were confirmed by GC-MS, using 10% SP-1000 program for SP-1000) at

Bioassay. Worms were exposed to methylene chloride vapor in glass heads or Dufour-type chambers of mandibular gland extracts were applied to the worms were placed 2 cm from the source. The chambers consisted of filter paper and methylene chloride. In the control, worms were treated with 10% methylene chloride. These ketone-treated worms were removed from the nest and placed in 100 mm squares served as controls. The worms to the treated worms were monitored and the results of the treatment. All experiments were replicated.

Laboratory colonies were maintained in plastic cages at a temperature of 72 to 80°F, on a 14:10 hr light:dark cycle. Filter paper was moistened with 10 μ l of methylene blue solution. Salivary glandular glands. The salivary glands, 1 cm of the nest entrance, were observed

Res

Nonaggressive E

Dinoponera g base of stumps. I on the ground, n of *P. clavata* (He 1980, Young and did not observe uals, Allard (195 ing them "mar thickets." Whet nest is not certa known to leave gating just outsi up a tree away dem, often follo workers in pre 1973). However, when the ants re tree canopy. Suc

each and placed in methylene chloride. All subsequent chemical analyses were undertaken on these extracts.

Analyses were done with an LKB 2091 mass spectrometer interfaced to a gas chromatograph aboard the α -Helix research vessel. Samples were analyzed on a 1.83-m column of 3% SE-30 by programming from 70 to 300°C at 10°C/min. Compounds were identified by comparison with standard compounds or comparison with published mass spectra (Heller and Milne 1980). Subsequent analyses of many of the same extracts at Howard University were accomplished on a Finnigan 3200 GC-MS, using 1.8-m columns of 3% OV-17 and 10% SP-1000 programmed from 50 to 300°C (200°C for SP-1000) at 10°C/min.

Bioassay. Workers of *P. clavata* were exposed to methylene chloride extracts of either worker heads or Dufour's glands corresponding to one pair of mandibular glands or one Dufour's gland. The extracts were applied to 1-cm² filter papers which were placed 2 cm from the nest openings. Controls consisted of filter paper squares treated with methylene chloride. In addition, 1-cm² filter papers were treated with 10 μ l of 4-methyl-3-heptanone, and these ketone-treated papers were positioned 2 cm from the nest opening. Untreated filter paper squares served as controls. The reactions of workers to the treated and untreated filter papers were monitored and recorded for 10 min after each treatment. All experimental treatments and controls were replicated six times.

Laboratory colonies of *D. grandis* were maintained in plastic trays (25 by 20 cm) at a temperature of 72 to 82°C and a light program of LD 14:10. Filter paper squares were treated with 10 μ l of methylene chloride extracts of the mandibular glands. These papers were placed within 1 cm of the nest entrance, and the reactions of workers were observed for 10 min.

Results and Discussion

Nonaggressive Behavior

Dinoponera grandis was found to nest at the base of stumps. It was encountered foraging singly on the ground, unlike the more arboreal foraging of *P. clavata* (Hermann 1975, Hermann and Young 1980, Young and Hermann 1980). Although we did not observe columns of *Dinoponera* individuals, Allard (1951) and Bates (1892) reported finding them "marching in single file through the thickets." Whether these columns were near the nest is not certain. Individuals of *Paraponera* are known to leave their nest in groups after aggregating just outside the nest entrance. Movement up a tree away from the nest entrance is in tandem, often following the assemblage of 50 or more workers in preforage aggregations (Hermann 1973). However, these groups apparently dissipate when the ants reach their true foraging area in the tree canopy. Such running in tandem apparently

is not analogous to the group raiding of other ponerines, although group raiding may have begun by way of simple tandem groups.

Paraponera apparently maintains a degree of aggregative behavior in terrestrial environments also possible in relation to a food source. This species has been reported in a territorial dispute involving groups of individuals 6 to 7 m or more from their nest (Jorgenson et al. 1984). Overt conspecific aggression was expressed between workers for over 5.5 h. Similar behavior has not been reported for *Dinoponera*.

Upon disturbing individuals at the nest entrance, *D. grandis* workers most often responded in a nonaggressive manner by going deeply into tunnels leading to their nest. In contrast to an apparent lack of aggressiveness in *D. grandis*, two or more workers of *P. clavata* are generally seen guarding their nest entrance. Disturbance of the nests of this latter species elicits defensive charging by guard ants and by other colony workers, terminating with investigating behavior by these ants within 20 to 30 cm of the nest entrance (Hermann and Young 1980). Even during nest excavation and with beating on the nest stump, *D. grandis* workers usually were reluctant to attack. Most encounters with this species that were reviewed by Bates (1892) and Allard (1951) were away from the nest.

Anatomy

The sting of *D. grandis* workers (Fig. 1) is distinctly exsertile, sometimes extending 2 to 3 mm from the posterior tip of the gaster. The sting shaft in lateral view is ascendant like those of myrmeciines (Hermann and Blum 1981, Kugler 1980, Robertson 1968) and other ponerine ant species (Hermann 1968, 1969) (Fig. 2-4). Venom apparatus sclerites in *D. grandis* workers are strongly sclerotized and generally more elongate in appearance (Fig. 1) than those of *P. clavata* (Fig. 2). Also, the sting shaft (SS; Fig. 1 and 2) is slightly more elongate and ascendant than it is in the latter species.

Overall length of the entire sclerotized venom apparatus in *D. grandis* (from anteriormost tip of triangular plate to posteriormost tip of sting) (Fig. 1) is 5.5 mm (ca. 3.5 mm in *P. clavata*). Variation in measurements is slight, due to the monomorphic condition of adults. A venom reservoir (VR) that is 4 mm in length (1.9 mm in *P. clavata*) and 2 mm in diameter (1 mm in *P. clavata*) extends from the sting bulb (SB) by a duct (Dt) that is an additional 3 mm long (Fig. 6). Details of the venom reservoir and its respective glands, as well as Dufour's gland, were not obtained in *Dinoponera*, because much of the internal anatomy was obscure in our alcohol-preserved specimens.

Sting Base. The sting base (fused second valvulae) is truncate in *D. grandis* (Fig. 1) at its point of attachment with the furcula (Fig. 8), much as it is in *P. clavata*. Its paired ventral sting base

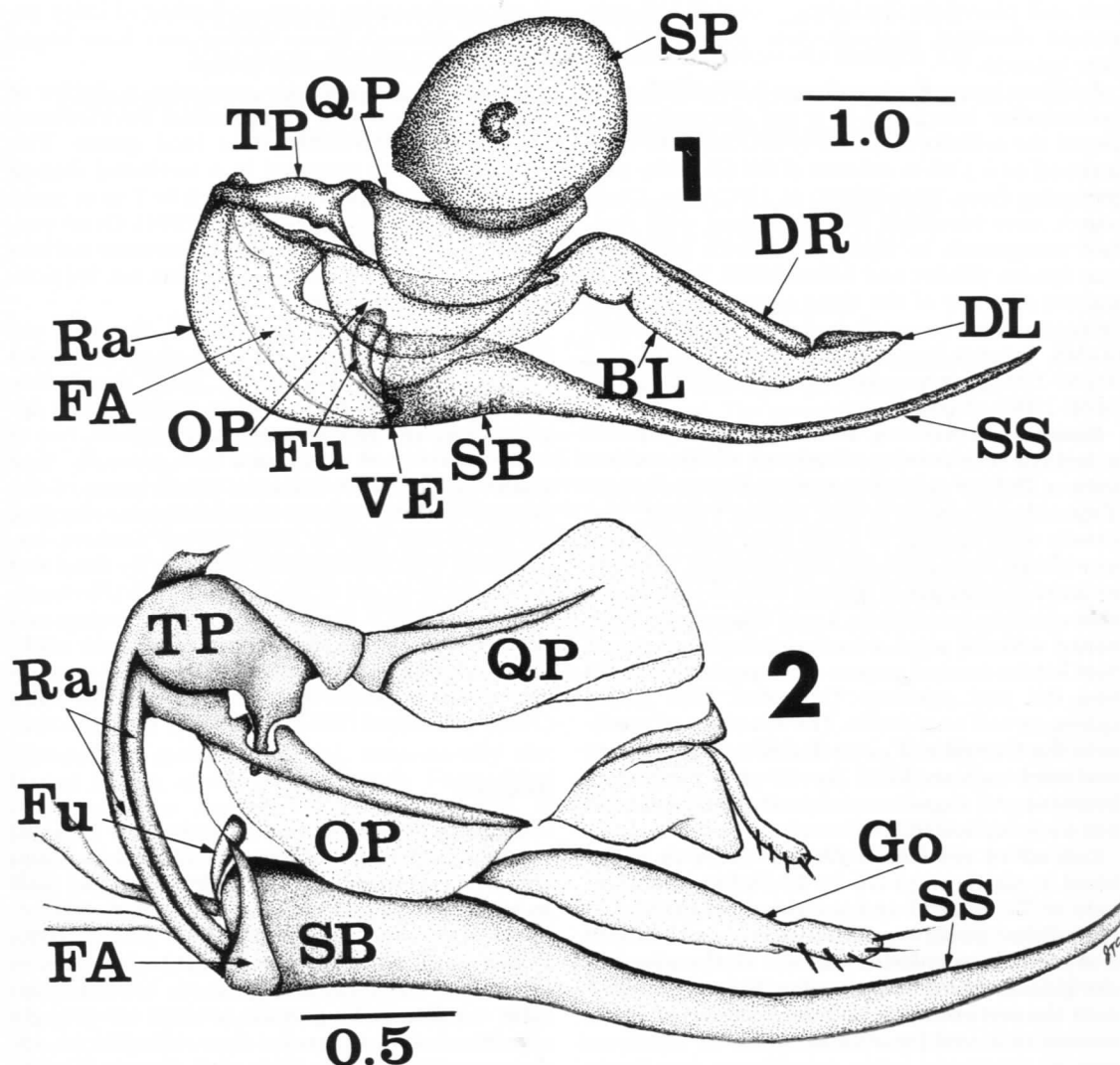


Fig. 1 and 2. Lateral views of venom apparatuses of *D. grandis* and *P. clavata*, respectively. (1) *D. grandis*. Sting shaft is elongate, slender, and ascendant, and gonostyli are distinctly bilobed. BL, Basal gonostylar lobe. DL, Distal gonostylar lobe. DR, Dorsal ridge of gonostylus. FA, Fulcral arms. Fu, Furcula. OP, Oblong plate. QP, Quadrate plate. Ra, First and second rami. SB, Sting bulb. SP, Spiracular plate. SS, Sting shaft. TP, Triangular plate. VE, Ventral extension. (2) *P. clavata* (redrawn from Hermann and Blum [1966]). There is considerable difference between the triangular plates (TP) in this species and those of *D. grandis*. Another minor difference is in the general appearance of the quadrate plate (QP) between the two. In general, there is a strong similarity in these two venom apparatuses, expressed in the form of the gonostyli. Also, there is a strong similarity between these venom apparatuses and those of *Myrmecia*. (Abbreviations same as in Fig. 1.)

extensions (VE, Fig. 1) are well developed, extending anteriorly approximately the same distance as the sting base dorsum.

Gonostyli. The paired gonostyli (=gonoplasts) in *D. grandis* (BL and DL combined, Fig. 1) are distinctly bilobed with an elongate, mostly membranous basal lobe (BL) supported by a dorsal rib (DR) and a smaller distal sensory lobe (DL). The distal lobe is equal to approximately one-fourth the length of the proximal lobe. A bilobed gonos-

tylar structure with the basal lobe largest is typical of primitive ant species of both subfamilies Ponerinae (Fig. 1 and 2) (Hermann 1969) and Myrmeciinae (Hermann and Blum 1981, Kugler 1980). Gonostylar structure is not clear in *Nothomyrmecia* (Go, Fig. 5). The number of gonostylar lobes and their relative sizes appears to be a good taxonomic character, especially in the more primitive formicids. That the ponerines and myrmeciines are very similar in this character indicates a rather

Fig. 3-5. Lateral views of venom apparatuses of (3) *N. macrops* (reconstructed), (4) *N. macrops* (reconstructed), and (5) *N. macrops* (reconstructed).

close relationship. Within the subfamily groups, it is a convergent one.

In some preparations of *macrops* venom apparatuses, a very slight thinning of the sting shaft at about four-fifths the length of an articulated sensilla distribution. That *Nothomyrmecia* (Fig. 5) or ones that show segmentation indicate gonostylar segments. Based on current knowledge, it appears that the p-

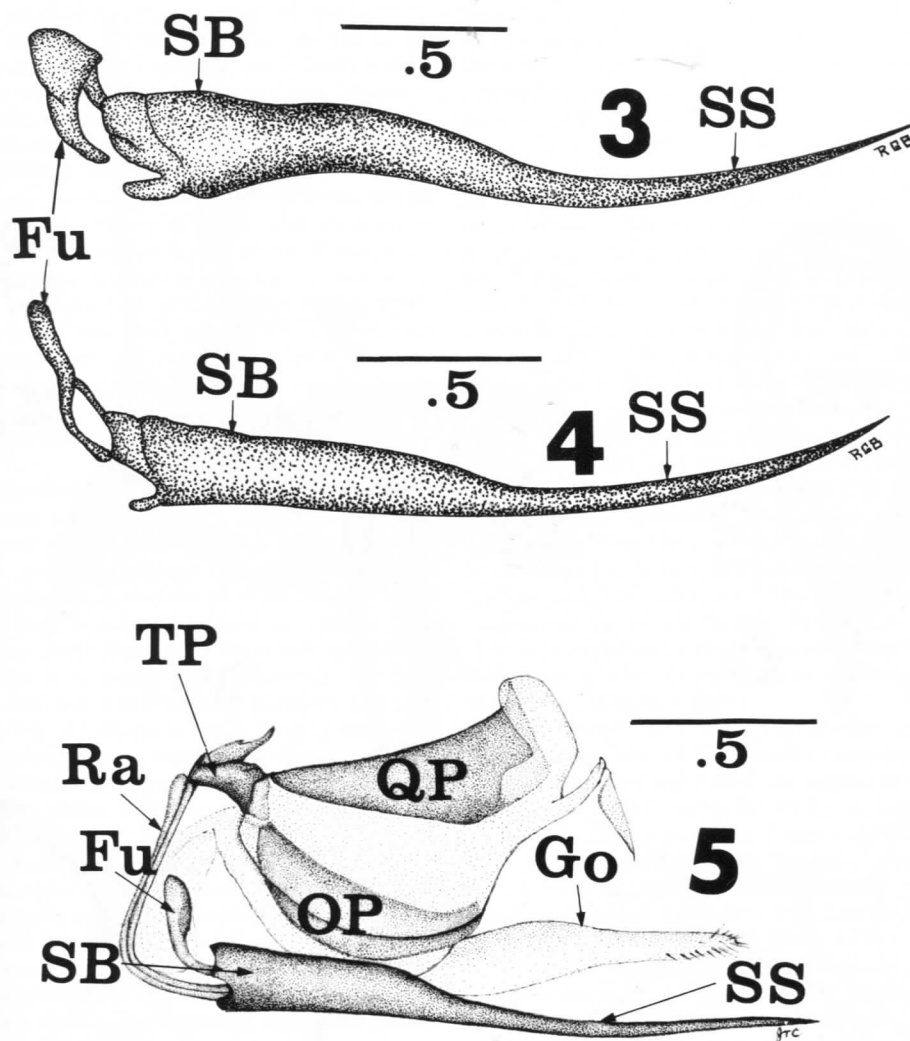


Fig. 3-5. Lateral views of venom apparatus of *M. foetans*, *B. rufipes*, and *N. macrops*. (3) *M. foetans*, showing ascendant sting shaft and robust furcula. (4) *B. rufipes*, with ascendant sting shaft and furcula with thinner body. (5) *N. macrops* (reconstructed and redrawn from Kugler [1980]), showing ascendant sting shaft, robust furcula and unilobular gonostyli. (Abbreviations same as in Fig. 1 and 2.)

close relationship. With such a close likeness in the gonostyli in all investigated species of the two subfamily groups, it is doubtful that this character is a convergent one.

In some preparations of the *Nothomyrmecia macrops* venom apparatus, Kugler (1980) detected a very slight thinning of the dorsal gonostylar wall at about four-fifths its length that may be the vestige of an articulation. He also pointed out that sensilla distribution did not reflect two segments. That *Nothomyrmecia* has unilobular gonostyli (Go, Fig. 5) or ones that have lost all but a trace of segmentation indicates that proximal and distal gonostylar segments are in the process of fusing. Based on current knowledge of aculeate gonostyli, it appears that the presence of unilobular gonostyli

is a derived condition. All of the other ant subfamilies appear to have unilobular gonostyli (Hermann and Blum 1981, Kugler 1978). Although Kugler mentions weak sclerotization between proximal and distal portions of the gonostyli of some myrmecines (e.g., *Myrmica*; see Fig. 11 in Kugler [1978]), the gonostyli of most myrmecine species are distinctly composed of a single lobe. Further reduction in the gonostyli of more derived venom apparatuses in higher ants is most often in length and overall size.

Paired Triangular Plates. Each triangular plate (=gonangulum, first valvifer) is more slender in appearance in *D. grandis* (TP, Fig. 1) than in *P. clavata* (Fig. 2). It is associated with an extremely long and slender pair of first rami (Ra; Fig. 1 and

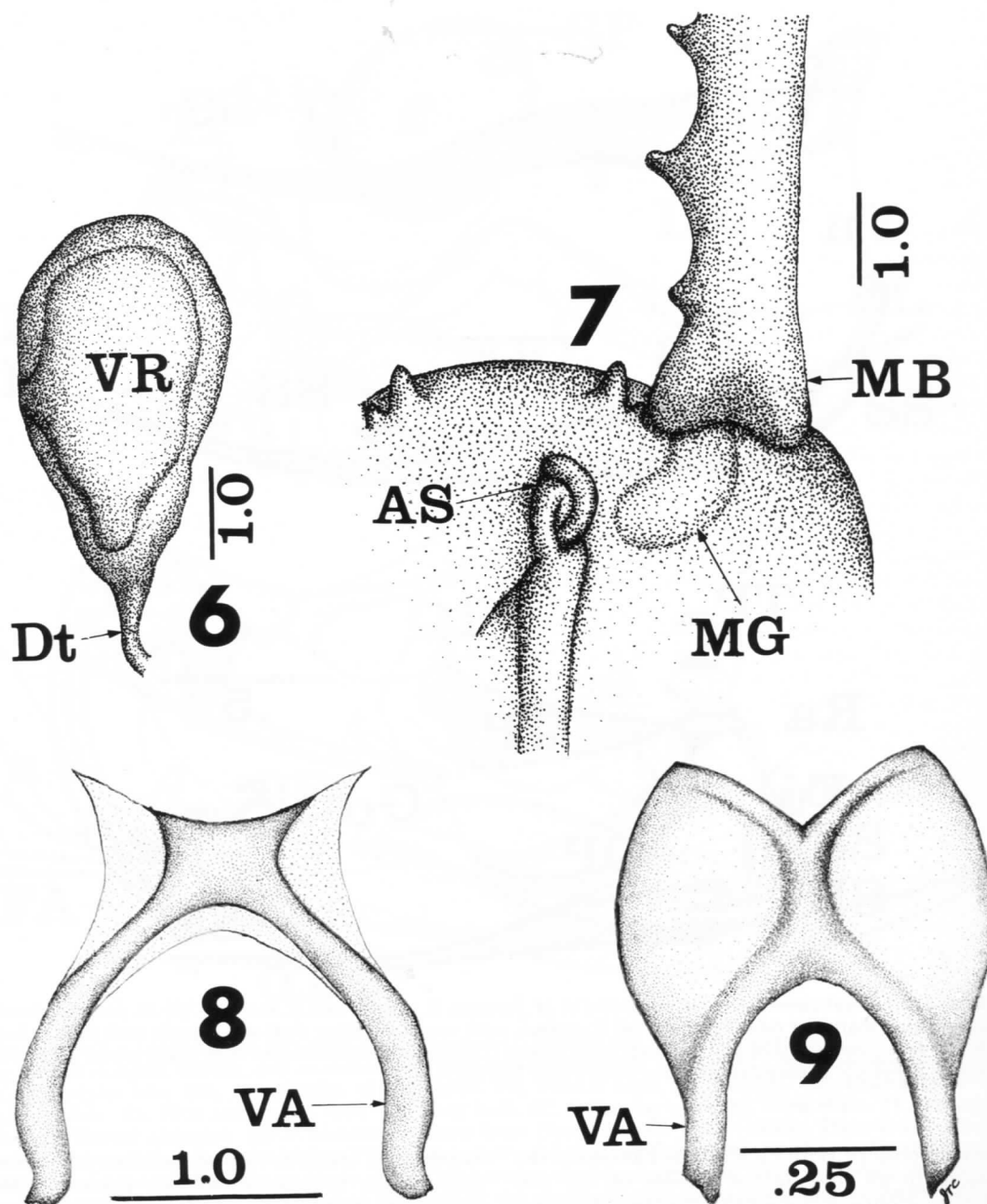


Fig. 6-9. Glands and sclerites of *D. grandis* and *P. clavata*. (6) Venom reservoir, *D. grandis*. (7) Mandibular gland in head of *D. grandis*, dorsal view. (8) Furcula of *D. grandis*, posterodorsal view. (9) Furcula of *P. clavata*, posterodorsal view. AS, Antennal socket; Dt, Duct from venom reservoir; MB, mandibular base; MG, position of mandibular gland inside cephalic capsule; VA, ventral apodeme or ventral articulating arms; VR, venom reservoir.

2) and strongly ascending, paired lancet shafts. Each of the latter structures in *D. grandis* has a well-developed valve at its proximal end and four small barbs at its distal tip. *P. clavata* has 10 lancet barbs. The fourth (proximal-most) barb in *D. grandis* is extremely small and difficult to see.

Furcula. This sclerite (Fig. 8 and 9) is superfi-

cially X shaped in dorsoposterior view. The distal region of the ventral articulating arms (VA) and the shorter dorsal extensions in *D. grandis* are expanded laterally into a thin flare, as is the case in *P. clavata*; sting rotating muscles insert on the dorsal extensions from their point of origin on each of the paired oblong plates. The appearance of this

furcula is rough (Hermann and the furcula in the heres to the upciines (Hermann including *Noth* in Kugler [1980] although some n of a dorsal arm [1980] shows th Y-shaped furcu all known pseu (Hermann and of some poner *Odontomachus* the furcular ap and the dorsola oped.

Paired Second of the second r the sting and p fers) in *D. gran* that are aligned total of 30 such The double- an arrangement is these two speci *nera* (OP, Fig. *sensilla trichod* Douglas 1976a, b ing triangular pl in the hair plate

Paired Spira shaped spiracula 1) in *D. grandis* otized dorsal bar maining venom general moveme contractions of r quadrate plates

Mandibular G dibular glands in to the mandibul ture's mesal side examined in hyr mesal side of each Each mandibula from the mandib area that is adja Nothing is know dibular gland in species in the sub information is av from ponerine m mann 1978, Herr

Chemistry

Eleven hydroc four's gland secre peared to be stra all hydrocarbons

furcula is roughly similar to that of *P. clavata* (Hermann and Blum 1966). It is not as robust as the furcula in the latter species, and strongly adheres to the upper half of the sting base. Myrmecines (Hermann and Chao 1983, Kugler 1980), including *Nothomyrmecia* (see figure 6 on p. 264 in Kugler [1980]), also have an X-shaped furcula, although some mention in Kugler (1980) was made of a dorsal arm. (figure 4 on p. 264 in Kugler [1980] shows the furcula to be more Y shaped.) Y-shaped furculae are found in some myrmecines, all known pseudomyrmecines, apids, and vespids (Hermann and Chao 1983, Kugler 1978). Furculae of some ponerines are more U shaped (e.g., in *Odontomachus* [unpublished data]), in which case the furcular apex is more truncate in appearance and the dorsolateral apodemes are poorly developed.

Paired Second Rami and Oblong Plates. Each of the second rami (Ra, Fig. 1 and 2) connecting the sting and paired oblong plates (second valvifers) in *D. grandis* supports 40 sensilla trichodea that are aligned in a double row. *P. clavata* has a total of 30 such sensilla, arranged in a single row. The double- and single-row variation in sensilla arrangement is a significant difference between these two species. Each oblong plate in *Dinoponera* (OP, Fig. 1) supports eight closely arranged sensilla trichodea in a hair plate (Hermann and Douglas 1976a,b) adjacent to the paired articulating triangular plates. Fifteen such sensilla are found on the hair plate of *P. clavata*.

Paired Spiracular Plates. The paired, oval-shaped spiracular plates (8th hemitergites) (SP, Fig. 1) in *D. grandis* are joined mesally by a thin, sclerotized dorsal bar. They fit saddle-like over the remaining venom apparatus sclerites, facilitating general movements of the latter structures through contractions of muscles inserting upon the paired quadrate plates (QP).

Mandibular Glands. Each of the paired mandibular glands in *D. grandis* (MG, Fig. 7) attaches to the mandibular base (MB) on the latter structure's mesal side. To date, all mandibular glands examined in hymenopterous insects attach on the mesal side of each mandible (Hermann et al. 1971). Each mandibular gland extends 1.5 μ m cephalad from the mandibular base to a point in the facial area that is adjacent to the antennal socket (AS). Nothing is known about the function of the mandibular gland in this species. This is true of most species in the subfamily Ponerinae, although some information is available on the chemicals secreted from ponerine mandibular glands (Blum and Hermann 1978, Hermann and Blum 1981).

bons coelute on 3% SE-30 and 3% OV-17 columns, alkenes and alkadienes were detected by obtaining the mass spectra of the hydrocarbon mixture and noting the presence of ions that were two or four mass units less than the molecular ions of the corresponding saturated hydrocarbons. Peaks at M-2 and M-4 were considered to be alkenes and alkadienes corresponding to the alkane exhibiting the molecular ion. The major compounds present (molecular ions in parentheses) were pentadecane (m/z 212), pentadecene (m/z 210), heptadecane (m/z 240), heptadecene (m/z 238), and heptadecadiene (m/z 236). Tetradecane (m/z 198), hexadecane (m/z 226), hexadecene (m/z 224), nonadecane (m/z 268), and nonadecatriene (m/z 262) constituted minor products whereas tridecane (m/z 184) was a trace constituent. Reduction of the extracts (Pt/H_2) resulted in the disappearance of all ions corresponding to either 2 or 4 mass units less than the molecular ions in the mass spectra, thus supporting the conclusion that these ions corresponded to alkenes and alkadienes, respectively, in the original mixtures. The positions and stereoisomerism of all double bonds are unknown. The mass spectra of the reduced compounds were identical to the straight-chain hydrocarbon standards (unpublished data).

Extracts of both the mandibular glands and heads of workers of *D. grandis* contained a major constituent that exhibited an apparent molecular ion at m/z 177 (actually M-1), a base peak at m/z 122, with significant fragments at m/z 163, 149, 135, 80, and 42. Both the mass spectrum and GC retention time of the ant volatile were identical to those of authentic 2,5-dimethyl-3-isopentylpyrazine (Wheeler and Blum 1973).

The well-developed Dufour's gland of *P. clavata* contained 17 compounds which also appeared to be straight-chain compounds. The major compounds present were pentacosane (m/z 352), pentacosene (m/z 350), heptacosene (m/z 378), and heptacosadiene (m/z 376). In addition, nonadecane (m/z 268), heneicosane (m/z 296), heneicosane (m/z 294), tricosene (m/z 322), nonacosane (m/z 408), nonacosene (m/z 406), and nonacosadiene (m/z 404) were present as minor constituents. Pentadecane (m/z 212), heptadecane (m/z 240), and heptadecene (m/z 238) were present in trace amounts. All ions corresponding to alkenes and alkadienes disappeared after reduction of the extracts (Pt/H_2) giving mass spectra consistent with the straight-chain hydrocarbons. The positions and stereoisomerism of all double bonds are unknown.

Two compounds were identified in extracts of mandibular glands and heads of workers of *P. clavata*. The major compound present exhibited a molecular ion at m/z 128, a base peak at m/z 57, with additional fragments at m/z 99, 86, 71, and 43. 4-Methyl-3-heptanone possessed a GC retention time and mass spectrum identical to those of the ant-derived volatile. A minor concomitant

Chemistry

Eleven hydrocarbons were observed in the Dufour's gland secretion of *D. grandis*, and all appeared to be straight-chain compounds. Because hydrocarbons having the same number of car-

showed a weak molecular ion at m/z 130 and a base peak at m/z 59, with additional fragments at m/z 101, 83, 71, 70, 58, 55, 45, 43 and 41. Both the mass spectrum and GC retention time of this compound were congruent with those of 4-methyl-3-heptanol.

Bioassay

Workers of *P. clavata* exhibited no obvious responses when they encountered objects treated with 4-methyl-3-heptanone, 4-methyl-3-heptanol, or mixtures of the two compounds. The ketone did not appear to be repellent, and except for occasional antennation of the treated papers, the workers ignored them. Similarly, workers of *P. clavata* demonstrated no consistent reactions when they encountered papers treated with extracts of their mandibular glands or Dufour's gland. In a few cases, workers moved the papers with their mandibles, but for the most part the treated papers were ignored.

The Dufour's glands of *P. clavata* and *D. grandis* contain mixtures of hydrocarbons, and it is possible that this class of compounds is typical of ponerine species (Cavill and Williams 1967). The functions of these alkanes, alkenes, and alkadienes remain to be determined.

Both 4-methyl-3-heptanone and 4-methyl-3-heptanol are used by myrmicine species in several genera as alarm pheromones (Blum and Hermann 1978). This pair has also been detected as mandibular gland products of one ponerine species, *Neoponera villosa* (Duffield and Blum 1973), in which both 4-methyl-3-heptanone and the derived alcohol are releasers of alarm behavior.

Alkylpyrazines have been demonstrated to function as alarm pheromones for ponerine species in a wide range of genera. Both of the pyrazines identified as mandibular gland products of *D. grandis*—2,5-dimethyl-3-isopentylpyrazine and 2,5-dimethyl-3-*n*-propylpyrazine—have been identified previously in ponerines, and these compounds appear to be somewhat characteristic of ponerine species in the genera *Odontomachus* (Wheeler and Blum 1973), *Ponera*, *Hypoponera* (Duffield et al. 1976), *Anochetus*, and *Brachyponera* (Longhurst et al. 1978). The identification of a variety of alkylpyrazines as mandibular gland products of ponerines demonstrates that this class of compounds has been frequently used as signaling agents.

Workers of both *P. clavata* and *D. grandis* are exceptional in not exhibiting any detectable responses to their mandibular gland products. Although other ponerine species exhibit alarm behavior when exposed to the compounds produced by *D. grandis* and *P. clavata*, these two ponerines do not appear to communicate alarm with their volatile mandibular gland products. Significantly, the workers of neither species exhibit well-developed extra-nidal interactions, and it is likely that

group interactions to external stimuli have not been well evolved by either species. Disturbances of the nest of *D. grandis* result in the workers withdrawing singly into the nest. In the case of *P. clavata*, in response to a disturbance, workers will egress either singly or in pairs, but no evidence of a group defensive response is evident. Thus, it is possible that species that do not display well-developed interactions outside the nest do not use pheromones as frequently as species that exhibit pronounced extra-nidal interactions.

Acknowledgment

This research was supported in part by NSF Grant 7605271 as part of Phase 7 or the Alpha Helix Research program in the spring of 1977 and by project RF 76086 GA AS 7704 by the Rockefeller Foundation.

References Cited

- Allard, H. A. 1951. *Dinoponera gigantea* (Perty), a vicious stinging ant. J. Wash. Acad. Sci. 41: 88-90.
- Bates, H. W. 1892. The naturalist on the River Amazon. John Murray, London.
- Blum, M. S., and H. R. Hermann. 1978. Venoms and venom apparatuses of the Formicidae: Myrmecinae, Ponerinae, Dorylinae, Pseudomyrmecinae, Myrmicinae, and Formicinae, pp. 801-869. In S. Bettini [ed.], Arthropod venoms. Handb. Exp. Pharmacol., vol. 48. Springer-Verlag, Berlin.
- Brown, W. L. 1954. Remarks on the internal phylogeny and subfamily classification of the family Formicidae. Insectes Soc. 1: 21-31.
1958. Contributions toward a reclassification of the Formicidae. II. Tribe Ectatommini (Hymenoptera). Bull. Mus. Comp. Zool. Harv. 118: 173-362.
- Cavill, G. W. K., and P. J. Williams. 1967. Constituents of Dufour's gland of *Myrmecia gulosa*. J. Insect Physiol. 13: 1097-1103.
- Duffield, R. M., and M. S. Blum. 1973. 4-Methyl-3-heptanone: identification and function in *Neoponera villosa* (Hymenoptera: Formicidae). Ann. Entomol. Soc. Am. 66: 1357.
- Duffield, R. M., M. S. Blum, and J. W. Wheeler. 1976. Alkylpyrazine alarm pheromones in primitive ants with small colonial units. Comp. Biochem. Physiol. 54B: 439-444.
- Emery, C. 1911. Subfamille Ponerinae. Genera Insectorum, fasc. 118: 1-125.
- Heller, S. R., and G. W. A. Milne. 1980. EPA/NIH mass spectral data base. NBS Publ. NSRDS-NBS 63. U.S. Government Printing Office, Washington, D.C.
- Hermann, H. R. 1968. The hymenopterous poison apparatus. VII. *Simopelta oculata* (Hymenoptera: Formicidae: Ponerinae). J. Ga. Entomol. Soc. 3: 163-166.
1969. The hymenopterous poison apparatus: evolutionary trends in three closely related subfamilies of ants (Hymenoptera: Formicidae). Ibid. 4: 123-141.
1973. Formation of preforage aggregations in ponerine ants (Hymenoptera: Formicidae), a possible step toward group raiding. Ibid. 8: 185-186.
1975. Crepuscular and nocturnal activities of *Paraponera clavata* (Hymenoptera: Formicidae: Ponerinae). Entomol. News 86: 94-98.
- Hermann, H. R., and M. S. Blum. 1966. The morphology and histology of the hymenopterous poison apparatus. I. *Paraponera clavata* (Hymenoptera: Formicidae: Ponerinae). Entomol. Soc. 1: 1-19.
1981. Defensive apparatus of *Paraponera clavata*, pp. 77-199. Insecta. Academic Press, New York.
- Hermann, H. R., and M. S. Blum. 1978. The major components of the hymenopterous poison apparatus. Int. J. Insect Physiol. 24: 337.
- Hermann, H. R., and M. S. Blum. 1979. The structures on the hymenopterous poison apparatus. Ann. Entomol. Soc. Am. 72: 1-19.
- 1976b. Comparison of the sting and the poison apparatus. J. Ga. Entomol. Soc. 1: 1-19.
- Hermann, H. R., and M. S. Blum. 1978. The elicited defensive response of *Paraponera clavata* (Hymenoptera: Ponerinae). Ibid. 71: 43-49.
- Jorgenson, C. D., and M. S. Blum. 1984. Territoriality in the giant tropical ant, *Paraponera clavata* (Hymenoptera: Ponerinae). Ibid. 77: 1-19.

not been
es of the
thdraw-
clavata,
ll egress
a group
possible
oped in-
romones
nounced

NSF Grant
Research
RF 76086

(Perty), a
1: 88-90.
River Am-

3. Venoms
ae: Myrme-
ymecinae,
-869. In S.
Exp. Phar-

rnal phylog-
family For-

ation of the
menoptera).
362.

67. Constit-
gulosa. J. In-

4-Methyl-3-
n *Neoponera*
nn. Entomol.

eeler. 1976.
primitive ants
hem. Physiol.

e. Genera In-

0. EPA/NIH
SRDS-NBS 63,
shington, D.C.
pteros poison
Hymenoptera:
ol. Soc. 3: 163-

paratus: evolu-
subfamilies of
d. 4: 123-141.
ations in poner-
a possible step
86.

ivities of *Para-*
micidae: Poneri-

966. The mor-
opterous poison

apparatus. I. *Paraponera clavata* (Formicidae). Ann. Entomol. Soc. Am. 59: 397-409.

1981. Defensive mechanisms in the social Hymenoptera, pp. 77-197. In H. R. Hermann [ed.], Social insects. Academic Press, Inc., New York.

Hermann, H. R., and J. T. Chao. 1983. Furcula, a major component of the hymenopterous venom apparatus. Int. J. Insect Morphol. Embryol. 12: 321-337.

Hermann, H. R., and M. Douglas. 1976a. Sensory structures on the venom apparatus of a primitive ant species. Ann. Entomol. Soc. Am. 69: 681-686.

1976b. Comparative survey of the sensory structures on the sting and ovipositor of hymenopterous insects. J. Ga. Entomol. Soc. 11: 223-239.

Hermann, H. R., and A. M. Young. 1980. Artificially elicited defensive behavior and reciprocal aggression in *Paraponera clavata* (Hymenoptera: Formicidae: Ponerinae). Ibid. 15(1): 8-10.

Hermann, H. R., A. N. Hunt, and W. F. Buren. 1971. Mandibular gland and mandibular groove in *Polistes annularis* (L.) and *Vespula maculata* (L.) (Hymenoptera: Vespidae). Int. J. Insect Morphol. Embryol. 1(1): 43-49.

Jorgenson, C. D., H. L. Black, and H. R. Hermann. 1984. Territorial disputes between colonies of the giant tropical ant *Paraponera clavata* (Hymenop-

tera: Formicidae: Ponerinae). J. Ga. Entomol. Soc. (in press).

Kugler, C. 1978. A comparative study of the myrmicine sting apparatus (Hymenoptera, Formicidae). Stud. Entomol. 20: 413-458.

1980. The sting apparatus in the primitive ants *Nothomyrmecia* and *Myrmecia*. J. Aust. Entomol. Soc. 19: 263-267.

Longhurst, C., R. Baker, P. E. Howse, and W. Speed. 1978. Alkylpyrazines in ponerine ants: their presence in three genera and caste-specific behavioral responses to them in *Odontomachus troglodytes*. J. Insect Physiol. 24: 833-837.

Robertson, P. L. 1968. A morphological and functional study of the venom apparatus in representatives of some major groups of Hymenoptera. Aust. J. Zool. 16: 133-166.

Wheeler, J. M., and M. S. Blum. 1973. Alkylpyrazine alarm pheromones in ponerine ants. Science 182: 501-503.

Young, A. M., and H. R. Hermann. 1980. Notes on foraging of the giant tropical ant *Paraponera clavata* (Hymenoptera: Formicidae: Ponerinae). J. Kans. Entomol. Soc. 53: 35-55.

Received for publication 2 May 1983; accepted 7 February 1984.