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Trail Communication in the Ant *Megaponera foetens* (Fabr.) (Formicidae, Ponerinae)*

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The African ponerine ant *Megaponera foetens* conducts well organized group raids on termites. Observations of raids in western Africa, together with laboratory experiments, confirm previous reports that recruitment is based on a scout system and trail pheromones. One component of the trail signal derives from the poison gland. We discovered a second trail pheromone which originates from the pygidial gland. The latter secretions have a more powerful recruitment effect whereas poison gland secretions contain a much longer-lasting orientation cue. The secretions of the sternal gland, Dufour's gland and hind gut contents do not elicit trail-following. The long bristles surrounding the tip of the gaster are innervated and probably serve as mechano-receptors during trail-laying. No evidence could be found that the conspicuous stridulatory sounds produced by the ant columns serve intraspecific communication. In the field, stridulation by raiding ants was observed exclusively as a response to disturbance. In the laboratory, strong vibrations of the ground as well as air currents elicit stridulation. Air/CO_2 mixtures are significantly more efficient in releasing stridulation compared to pure air. We suggest that these sounds are aposematic warning signals aimed at potential vertebrate predators.

Ponerinae ants Pheromone glands Trail communication Stridulation Aposematic signal

INTRODUCTION

The Matabele ant *Megaponera foetens* is an African ponerine which exclusively hunts termites (Collart, 1927; Wheeler, 1936; Lévieux, 1966; Longhurst *et al.*, 1978; Longhurst and Howse, 1979). Colonies conduct highly organized predatory raids (Lévieux, 1966) during which foragers move in columns, guided by a scout who follows a chemical trail laid while returning from the prey (Fletcher, 1971). The organization of this group foraging behavior has been analyzed in great detail by Longhurst *et al.* (1978, 1979) and by Lepage (1981). According to Longhurst *et al.* (1979), the major source of the trail pheromone in *M. foetens* is the poison gland, but trail following could also be elicited with secretions from the Dufour's gland and with hind gut contents.

In recent years the study of chemical communication has received a new impetus following the discovery of many previously unknown exocrine glands, especially in the Ponerinae, and several of these glands were subsequently shown to be the sources of pheromones (for review see Hölldobler and Wilson, 1990). Following a recent report of several intersegmental glands in *Megaponera* (Fanfani and Valcurone, 1986) we studied the histology of the exocrine glands in greater detail and investigated their role, and the significance of the scout in trail communication. We also conducted a neuro-anatomical study of the particularly long bristles surrounding the tip of the gaster, which appear to be sensory hairs involved in the trail-laying process.

In this context we also studied the conspicuous stridulation sounds emitted by Megaponera workers. The first observations of such stridulation sounds were reported by Prell, Forel and Bequaert (cited in Wheeler, 1936). However, the biological function of these signals remains unknown, although the mechanism of producing stridulatory sounds in ants is well understood (see Markl, 1973, 1983). Stridulatory signals have been documented in a number of ant species (Markl, 1973). These signals can be transmitted as substrate-borne vibrations, as air-borne sounds or through direct tactile contacts. In the leaf cutter ant, *Atta*, it is part of a rescue alarm signal, transmitted through substrate vibrations (Markl, 1967, 1968), and also serves as a recruitment signal during leaf cutting (Roces *et al.*, 1993). In *Aphaenogaster* (*Novomessor*) and *Messor* stridulation enhances the

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effectiveness of recruitment pheromones (Markl and Hölldobler, 1978; Hahn and Maschwitz, 1985; Baroni-Urbani *et al.*, 1988), while in the harvester ant, *Pogonomyrmex*, stridulatory signals play a role during mating behavior and are transmitted by direct tactile contacts (Markl *et al.*, 1977). There is no evidence that air-borne sound has any intraspecific communicatory function in ants, but recently it has been demonstrated that honeybees can detect and make use of air-borne sound signals (Kirchner *et al.*, 1991). It was tempting to speculate that in *Megaponera*, stridulation may be involved in maintaining cohesiveness of the columns by transmitting air-borne sound or substrate-borne vibrations from ant to ant. We therefore studied in laboratory and field experiments whether stridulation serves intraspecific communication during column formation and movement.

MATERIALS AND METHODS

The field experiments were conducted in the Comoé National Park, Ivory Coast from March to August 1992 and from February to May 1993. The raiding behavior of two colonies was observed on a long-term basis, and a total of more than 100 raids of these and five other colonies were observed. Seven colonies were excavated and used for laboratory experiments in Würzburg, Germany. One additional colony was collected during May 1991 in the Shimba Hills reserve (Kenya). In the laboratory, the colonies were housed in plastic containers with moistened filter paper provided as nesting material. Since we had no termites available for food we fed the ants with mealworms and cockroaches.

Histological investigations of head, alitrunk with petiole, and gaster, followed the technique described in Hölldobler *et al.* (1994).

For tracing the sensory afferents of the abdominal setae, some of these hairs were carefully scraped off avoiding other damage to the surrounding cuticle and anterogradely labeled with a 2–5% aqueous solution of Neurobiotin tracer (Vector). After a diffusion period of several hours, the gasters were fixed and reacted with avidin-cascade-blue conjugate (Vector; for details see Gronenberg and Peeters, 1993).

Air-borne sounds emitted by stridulating ants were recorded using Brüel and Kjaer 1/2 and 1/8″ microphones, a B&K 2639 preamplifier and a B&K 2610 measuring amplifier on the HiFi audio track of a Panasonic AG 7500 video tape recorder. The behavior of the stridulating animal was recorded simultaneously on video. Playback sound signals were analyzed using a CED 1401 laboratory interface together with an AT computer. Simulated stridulatory sounds were played back using a Philips PM 5133 function generator together with a homemade power amplifier and an electrostatic ultrasonic loudspeaker. For playback of substrate-borne vibrations we employed a B & K 2706 power amplifier and a B & K 4810 vibration exciter. Vibrational amplitudes were measured using a B & K 4375 accelerometer.

For the laboratory investigation of the stimuli eliciting stridulation air currents were produced using compressed air and CO_2. Pure air was tested against a mixture of 75% air and 25% CO_2.

Details for the field experiments, the behavioral tests of glandular secretions, and the sound playbacks will be given in the Results section.

RESULTS

Tergal and sternal glands in Megaponera workers

The most common intersegmental gland in ponerine ants is the pygidial gland. It is located between the 6th and 7th abdominal tergites and consists of two lateral clusters of glandular cells. Each cluster is connected to a reservoir sac formed as an invagination of the intersegmental membrane. Ducts lead from the glandular cells and penetrate the membrane of the reservoir. This pygidial tergal gland has been discovered in all ponerine species investigated by Hölldobler and Engel (1978) and by Jessen *et al.* (1979), and has also been detected in *M. foetens* workers (Villet *et al.*, 1984; Fanfani and Valcurone, 1986). Each consists of 50–70 glandular cells. The cuticle of the adjacent 7th abdominal tergite (pygidium) has a complex grooved surface structure (Fig. 1). Presumably the contents of the pygidial gland reservoir can be released into these grooves to facilitate its dispersion.

A ventral intersegmental gland has been detected by Fanfani and Valcurone (1986) near the tip of the gaster, between the 6th and 7th abdominal sternites. We found the morphological features of this sternal gland very similar to those of the dorsal pygidial gland, although the cell clusters appear to be smaller (30–40 glandular cells in each cluster) and the cuticular structure on the 7th sternite is less pronounced (Fig. 1).

Fanfani and Valcurone (1986) also noted intersegmental sternal glands between the 4th and 5th, and 5th and 6th abdominal sternites, and two pleural glands in the 4th and 5th abdominal segments. We found these glandular structures to be considerably smaller than the two glands described above; one possible function is lubrication. Additional glands occur in the gaster, between petiole and alitrunk, between the coxae and thorax, and between head and thorax; a detailed description appears in Hölldobler *et al.* (1994). Here we determined whether the secretions from the pygidial gland and the last abdominal sternal gland (between 6th and 7th sternites) can induce trail-following.

Bioassays of glandular secretions: trail-following

We tested the trail-following response of *Megaponera* workers to artificial trails drawn with glandular secretions from the poison gland, Dufour's gland, pygidial gland, sternal gland and with hind gut contents. The respective organs were dissected out of ants killed by placing them for a few minutes in a freezer. Extracts were prepared by placing 10 glands of each kind in

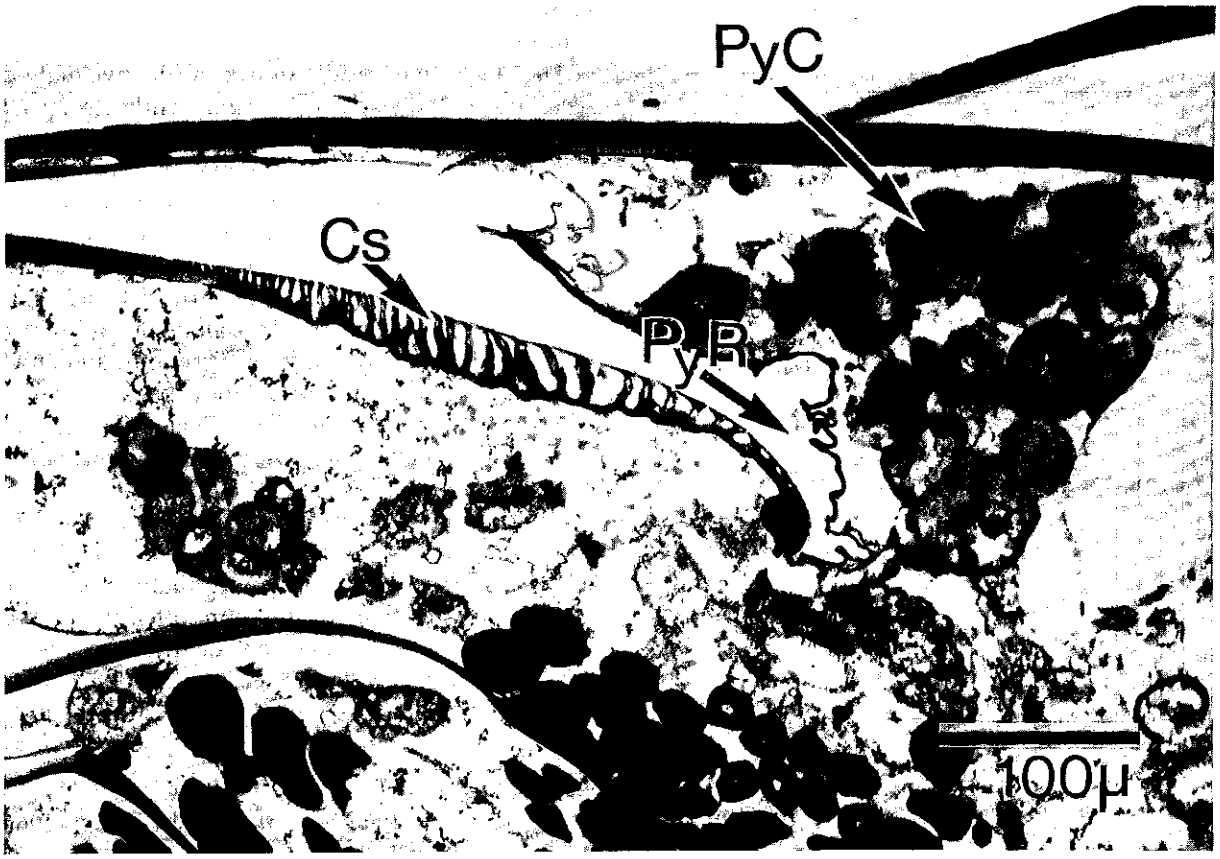

FIGURE 1. Sagittal section through the pygidial gland of *M. foetens*. PyR, pygidial gland reservoir; PyC, pygidial gland cells; CS, cuticular structure on the 7th abdominal tergite.

400 µl diethyl-ether or hexane at room temperature for at least 24 h. With a microsyringe, we laid artificial trails along a 40 cm-long pencil line drawn on sheets of paper, using quantities of extracts that approximated 0.1 to 1 gland equivalents. We also applied freshly dissected glands; one gland of each kind was crushed on the tip of a hardwood applicator stick and smeared once along the pencil line. As a control a second trail was offered simultaneously using either a droplet of distilled water, or the extraction solvent, or one of the other glands. Both test and control trail started at the same point (0.5 cm dia), but diverged at an angle of approx. 40°. All ants crossing a target line at the end of the artificial trails were counted. Each test started when the first ant had entered the arena, and lasted 1 min. In the nest box, most workers were clustered around the queen and brood in a bivouac-like fashion. In most tests the trails originated at the far end of a bridge (60 cm long) that connected the nest box with the foraging arena. When we introduced this bridge, a number of workers usually started moving over it without additional stimulation. When they arrived at the beginning of the artificial trails, they either followed the trails or searched randomly through the arena.

We obtained no substantial differences whether we used 0.1 or 1 gland equivalents of hexane or diethyl-ether extracts, or single glands crushed on applicator sticks. The data presented in Table 1 are pooled from the various tests done with one gland equivalents. Trails drawn with secretions from poison glands and pygidial glands elicited a strong trail-following behavior in *Megaponera* workers, but the ants did not follow trails drawn with secretions from the Dufour's gland, sternal gland, or with hindgut contents. Hindgut trails were offered as controls in preliminary tests with pygidial and poison gland trails. In a total of 6 experiments not a single ant followed the hindgut trail. The major and minor subcastes have the same glandular equipment, and their secretions released the same behavioral response. We also did not detect a substantial difference between the trail-following behavior of majors and minors.

TABLE 1. Trail-following response of *M. foetens* to trails drawn with one gland equivalent of secretions from different exocrine glands

Poison	vs pygidial gl.	Poison	vs Dufour gl.	Pygidial	vs Dufour gl.	Pygidial	vs sternal gl.
15.9 ± 6.8	34.3 ± 16.0	42.8 ± 19.9	0	55.8 ± 12.3	0	54.6 ± 25.6	0
	$n = 11$		$n = 4$		$n = 4$		$n = 5$

Means and standard deviations of the number of ants following the entire 40 cm-long trails within a 1 min period.

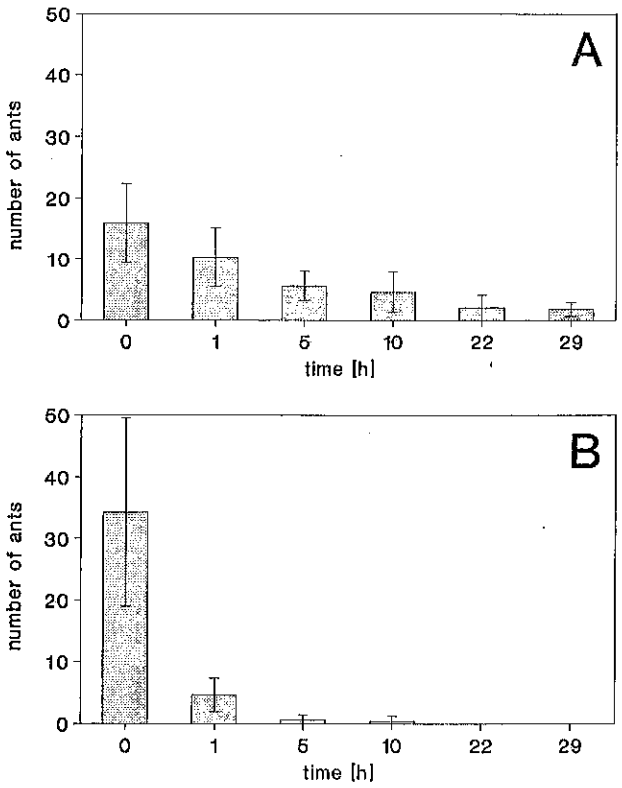

FIGURE 2. Response of *M. foetens* workers to poison gland (A) and pygidial gland (B) trails after different time intervals. The mean and standard deviation are given. Trails were drawn with one gland equivalents along a 40 cm long pencil line.

When fresh poison gland trails were simultaneously offered with fresh pygidial gland trails the ants significantly preferred the latter ($P < 0.01$, t-test). To test their persistency, we prepared a series of poison gland and pygidial gland trails, using one gland for each trail. The papers used as substrate were stored in a drawer at room temperature and presented to the ants at different time intervals from 0 to 29 h. As can be seen from Fig. 2 the poison gland trail is considerably more persistent than the pygidial gland trail. These results were confirmed by another series of experiments. We offered simultaneously poison and pygidial gland trails, but they were drawn 30 min before the test commenced. In this case, significantly more ants had chosen the poison gland trail (poison gland 14.5 ± 5.1; pygidial gland 2.5 ± 2.3; $n = 6$; $P < 0.01$). It is interesting to note that *Megaponera* workers readily followed a hardwood applicator on the tip of which we had crushed a pygidial gland. The tip was moved approx. 5 mm above the ground. When we arrived at the intersection of a poison gland trail and a pygidial gland trail (both 5 h old, diverging at an angle of approx. 40°) and removed the applicator, many ants continued to orient along the poison gland trail for at least a few centimeters and ignored the pygidial gland trail. However, it is important to mention that those ants which had been stimulated with pygidial gland secretions did not show the same persistency in following the poison gland trail. They frequently departed from the trail in searching loops.

The fact that trails drawn with pygidial gland secretions initially released a significantly stronger trail-following response, while poison gland trails had a significantly higher persistency, already suggests that the difference is not due to different sizes of the glands. We confirmed this by an additional series of experiments where we drew trails with two pygidial glands and compared them with trails drawn with one poison gland (three repetitions). The response along the pygidial gland trails declined steeply within the first hour, and only very few ants showed some orientation behavior after 3 h, whereas the orientation effect elicited by the poison gland trail declined more slowly, similar to the time course shown in Fig. 2.

No trail-following could be elicited with secretions from the sternal gland. We noted, however, that *Megaponera* workers inspected a trail drawn with sternal gland secretions significantly more often than a control trail drawn with water or diethyl-ether (controls 4.2 ± 4.4 workers; sternal gland 12.0 ± 5.0 workers; $n = 9$; $P < 0.01$; t-test).

The significance of the scout ant

In contrast to the observations by Lévieux (1966) on *Megaponera* raids in Ivory Coast, we found that the raiding columns (300–700 ants) were always guided by a scout. The scout itself was following its trail laid while returning from the newly discovered termite prey to the nest.

In the field, experimental removal of the scout always led to an immediate stop of the raid. The columns disbanded and after 1 min several ants started to search for prey. When they did not find termites within 1 to 3 min the columns reformed and returned to the nest. In order to study which signal of the scout elicited following behavior, the scout was removed and the secretions of poison and pygidial glands were presented on hardwood applicator sticks (dipped into an extract of 10 glands of ants from the same colony in 400 μl hexane) to guide the column along the trail previously laid by the scout. The experiment was conducted three times with poison gland extract, twice with pygidial gland extract and twice with both extracts combined. In no case did the column continue to follow the trail. After 2 to 4 min they returned to the nest.

Abdominal setae and trail-laying

Megaponera workers moving in the raiding column hold their gaster low, so that the long setae surrounding the tip of the gaster frequently touch the ground. We confirmed these observations by video recordings in the laboratory. Morphological investigations demonstrated that the setae are innervated. The axons of the sensory cells associated with the bristles on the caudal tergites and sternites project centrally through nerves that run anteriorly along the cuticle. Many of these fine tributary

nerves merge to form a prominent nerve root of the terminal ganglion complex [see Fig. 3(a)].

Since the abdominal nerve cord of ants has not been described to our knowledge, here we outline the gross organization. The abdomen of ant consists of 7 segments, 2 forming the petiole and 5 comprising the gaster.

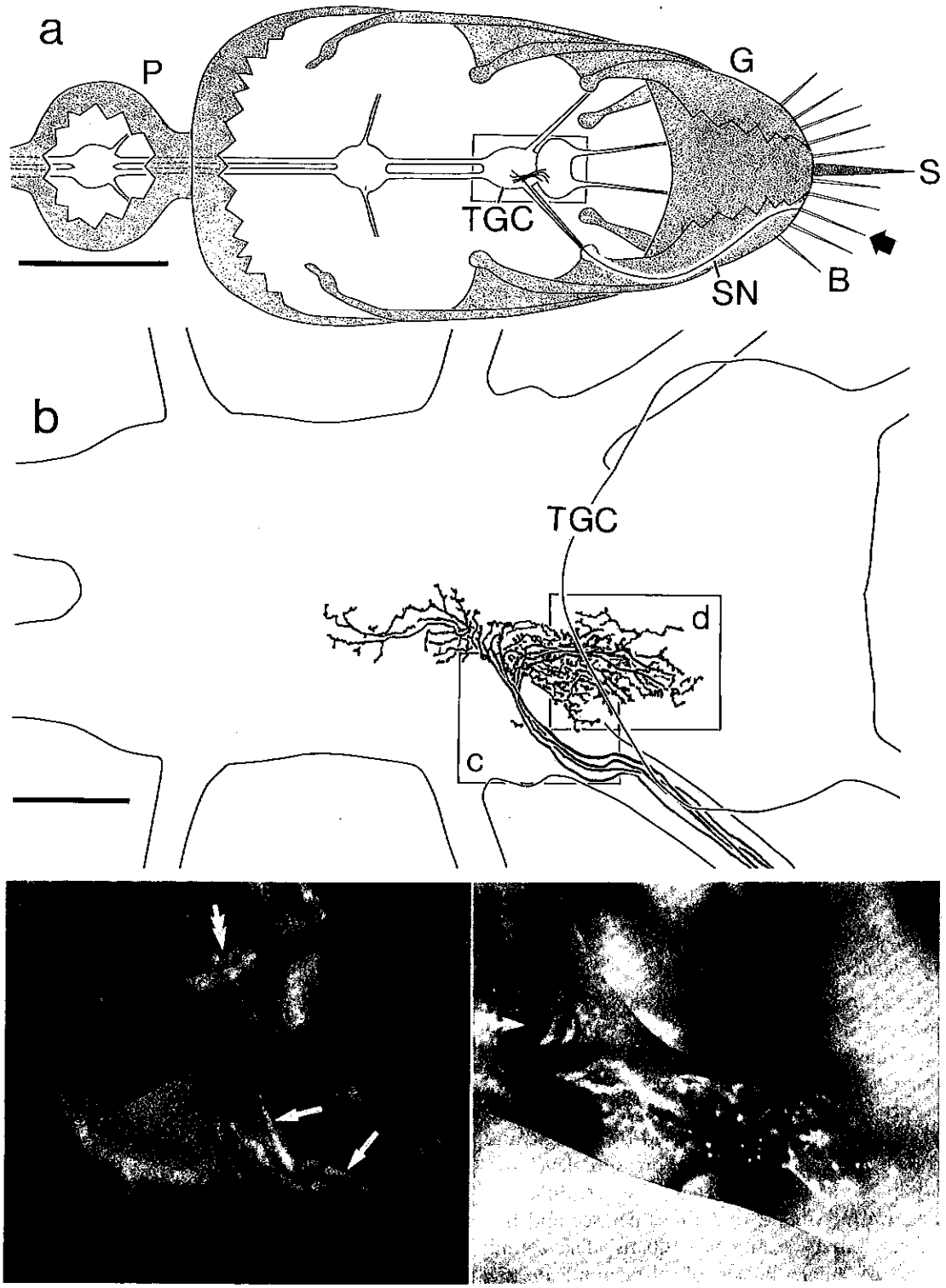

FIGURE 3. Central projections of bristle afferents. (a) Semi-schematical representation of the ventral nerve cord of *Megaponera* within the petiole, P and the gaster, G. B, bristles; S, sting; SN, sensory nerve originating from the sensilla; TGC, terminal ganglion complex. Boxed area enlarged in b. Calibration bar 1 mm. (b) Reconstruction of the afferents originating from bristles on the lateral side of the 7th tergite and schematically indicated by an arrow in (a). Boxed areas (c and d) indicate approximate position and size of the photomicrographs in c and d. Calibration bar 100 μm. (c) Photomicrographic montage showing the sensory afferents (arrows) entering the ganglion via the nerve root; double headed arrow indicates terminal arborizations within the 6th neuromere. (d) Photomicrographic montage showing sensory axon collaterals and terminals within the 7th neuromere. Arrow points at central trachea.

The corresponding ganglia of the ventral nerve cord are organized as follows. The first abdominal ganglion appears to be fused to the metathoracic ganglion in the alitrunk (not shown in Fig. 3). The second abdominal ganglion resides in the petiole and the third abdominal ganglion resides ventrally in the first segment of the gaster (=postpetiole). The remaining 4 abdominal ganglia appear to be fused in a complex residing ventrally somewhere in the middle of the gaster and here referred to as the terminal ganglion complex [TGC in Fig. 3(a and b)]. The 4 nerve roots indicated in Fig. 3(b) reflect the notion that the terminal ganglion complex comprises 4 ganglia.

The sensory bristle afferents in Fig. 3(b) enter the terminal ganglion complex via the 3rd nerve root, thus indicating that they correspond to the 3rd ganglion of the terminal complex (i.e. 6th abdominal ganglion). This coincides with the location of the corresponding bristle on the lateral side of the 6th tergite. Within the terminal ganglion complex however, the axonal terminals are not restricted to neuropil corresponding to the 6th ganglion [Fig. 3(b)]. They extend anteriorly to neuropil associated with the 5th or even 4th abdominal neuromeres, and posteriorly they extend into the last neuromere. This is demonstrated by the photomicrograph in Fig. 3(d), where the trachea indicated by an arrow denotes the (virtual) boundary between the 6th and 7th neuromere; thus all the collaterals shown here are located within the 7th neuromere.

We did not undertake a comprehensive study on the topographic organization of the projections from the bristles on the gaster. The few other successful preparations obtained, however, corroborate the finding that all the bristles are innervated and probably are of a mechanoreceptive nature, that the sensory axons enter the terminal ganglion complex via the nerves corresponding to the segment on which the sensilla reside, and that the axon collaterals are not restricted to a single neuromere.

Stridulatory signals

We attempted to test the hypothesis that stridulation may be involved in maintaining column cohesiveness. The basic parameters of a typical stridulatory sound of a *Megaponera* worker are shown in Fig. 4. Stridulatory signals are produced by female and male ants. The intensity of the air-borne sound emitted by a single ant is in the range of 54–70 dB sound pressure level (or 10–60 mPa) at a distance of 3 cm. The stridulatory sound bursts are repeated 3 to 5 times per sec and the duration of the bursts is approx. 100 ms. The sound bursts consist of single pulses of ultrasound in the frequency range from 20 to 40 kHz. The pulse repetition rate is approx. 1 kHz.

Within the nest box, groups of 300 or more ants were disturbed by breathing towards them, in response to which they produced stridulatory sounds more or less continuously. The intensity of these group signals was around 74 dB sound pressure level (or 0.1 Pa) at approx.

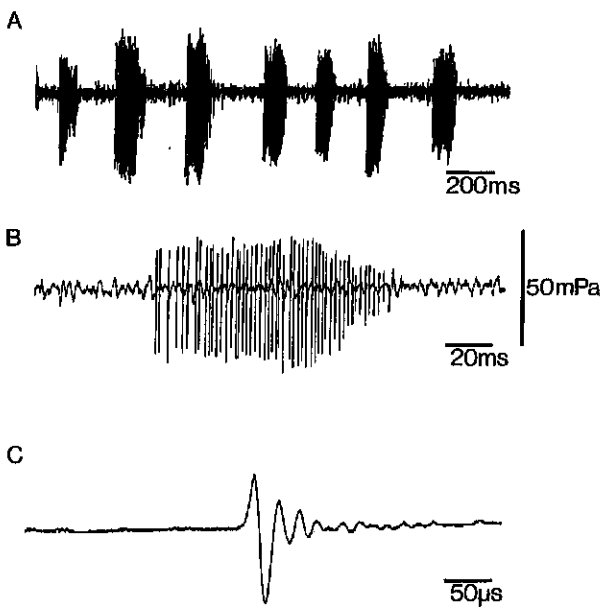

FIGURE 4. The basic parameters of stridulatory sound of *Megaponera*. Scraping of the 2nd tergite of the gaster against the 1st tergite produces bursts of air-borne sound of 100 ms duration, which are repeated 3–5 times per second (A). Each burst (B) consists of a sequence of ultrasonic pulses (C) repeated at a rate of 1 kHz. Bars indicate time and intensity scales (a sound of 50 mPa is equivalent to 68 dB sound pressure level).

3 cm distance. Group stridulation was not synchronized, i.e. the group signals did not show the temporal pattern of the sounds made by single ants, but they exhibited a similar frequency spectrum.

To study in more details the stridulation-eliciting effect of human breath, currents of air and air/CO_2 mixtures were tested in two colonies. Each of the colonies was stimulated 28 times with air and 28 times with an air/CO_2 mixture for 3 s. The ants responded to these stimuli by strong group stridulation. The durations of these responses were significantly longer with an air/CO_2 mixture compared to pure air (colony 1:

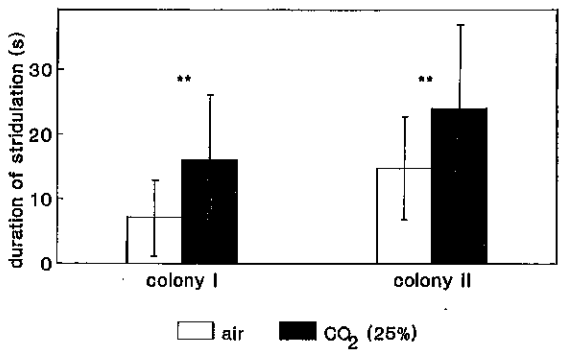

FIGURE 5. Stridulatory responses of two colonies of *M. foetens* to disturbances by air currents (air and air/CO_2 mixture). Each colony was stimulated 28 times with air and 28 times with an air/CO_2 mixture (3:1). The duration of the stridulatory group response was measured, the means and standard deviations are given, **indicates a significant difference at the 1%-level (t-test).

16.1 ± 9.9 vs 7.1 ± 5.8 s; $P < 0.01$; colony 2: 24.0 ± 13.0 vs 14.8 ± 8.0 s; $P < 0.01$; Fig. 5).

The ants did not react to air-borne sounds played back to them while excluding vibrations of the substratum. We tested different vibrational intensities. We then produced vibrations by using a thin rod connected to the vibration exciter on one end with the other end buried in the soil. Only with high vibrational amplitudes ($> 10\ m/s^2$) was digging behavior sometimes observed close to the source of the vibrations.

We finally tested whether substrate-borne vibrations can affect column formation. We constructed a Y-shaped, 60 cm-long cardboard bridge which connected the nest with the foraging arena. The two branches leading into the arena were separated from each other and from the first part of the bridge by 2 mm-wide gaps. This made it possible to vibrate one branch, whilst the other part of the bridge remained "silent". During the test series we alternated in a haphazard sequence the vibrating and silent branch. A total of 5 tests did not reveal any preference for the vibrating branch.

Another series of tests examined whether vibrations have a modulatory effect on the trail pheromones. As in the previous experiments, one of the branches of a Y-shaped cardboard bridge was vibrated but on both branches a trail had been drawn using gland extracts. No preference for the vibrating branch could be found, either in 12 trials using poison gland extract or in 12 trials using pygidial gland extract. With poison gland extract, 18.8 ± 5.3 out of the first 40 ants crossing the bridge chose the vibrating branch; with pygidial gland extract 21.5 ± 6.6 ants did so.

During the field observations of raids, we rarely noticed stridulation unless the ants were disturbed. Disturbances occur naturally by predators or other animals such as millipedes crossing the path of the raid. Experimentally, stridulation could be elicited by strong vibrations or strong wind (simulated with a fan). While all these responses were generally weak and local, breathing onto the columns always induced a strong stridulatory response spreading throughout the column for up to 1 m in both directions; sometimes the entire group of hundreds of individuals stridulated for up to a minute. Stridulation was always accompanied by behavioral changes: the columns disbanded and the ants showed aggressive behavior such as walking faster, raising head and antennae, and opening the mandibles. Majors spread out and examined the source of disturbance. After about 1 min without further disturbances the columns reformed and continued their raid.

DISCUSSION

Group raiding in the termite-hunting ponerine *Megaponera foetens* is organized by complex chemical communication. We confirm the findings by Longhurst *et al.* (1979) that a major chemical trail signal originates from the poison gland of workers. We discovered a second source of recruitment pheromone in the pygidial gland. The secretions of both glands appear to have different properties with complementary functions. The pygidial glands pheromone seems to be a more powerful recruitment signal, but it is relatively short-lived in comparison with poison gland secretions. Trails (40 cm long) drawn with the contents of one poison gland still elicited an orientation effect after more than 29 h. This is in accordance with field observations by Lévieux (1966) that trails in the field can last up to 24 h, but contradicts findings by Longhurst and Howse (1979) and Longhurst *et al.* (1979) who report that scent trails did not last more than 3 h. During trail-laying, the ants deposit the trail pheromone from the poison gland through the extruded sting, the tip of which touches the ground at irregular intervals. Orientation of the gaster appears to be aided by long innervated bristles surrounding its tip. These setae most probably function as mechano-receptors indicating to the trail-laying ant when the gaster touches the ground. We have never observed that the pygidial gland secretions are deposited on the ground. We assume that this recruitment pheromone is released into the air from the cuticular structure on the 7th tergite, and that this stimulates nestmates to follow behind the odor plume emanating from ants running in front of the column.

We were unable to elicit trail-following behavior in *Megaponera* with secretions from the Dufour's gland or with hindgut contents. It is possible that the weak trail-following response reported by Longhurst *et al.* (1979) was due to contamination with pygidial gland secretions. The authors were not aware of the presence of the pygidial gland in *Megaponera* and it is conceivable that it was ruptured during the dissections of the other organs, leading to contamination. The sternal gland, although very similar in its morphology to the pygidial gland, clearly does not produce trail pheromones. We have no clear experimental evidence yet that would suggest a behavioral function of this gland. Since the ants exhibit increased inspection behavior toward sternal gland secretions, perhaps this gland is involved in marking behavior.

Recent studies have demonstrated that the pygidial gland is a major source of pheromones in ponerine ants (for review see Hölldobler and Wilson, 1990). Many ponerine species conduct predatory raids on termites and other arthropods, and generally this is organized by powerful trail pheromones which are often composed of secretions from several glands. In group-raiding *Leptogenys* species one component originates from the poison gland (Fletcher, 1971; Maschwitz and Mühlenberg, 1975), but a second recruitment pheromone derives from the pygidial gland (Maschwitz and Schönegge, 1977; Attygale *et al.*, 1988). Here too, the poison gland secretions seem to have a stronger orientation effect, while the pygidial gland secretions serve as the major recruitment signal (Maschwitz and Schönegge, 1983, Hölldobler, unpublished results). In the termitophagous *Pachycondyla* (*Termitopone*) *laevigata* the trail

pheromone does not, as previously assumed, originate from the hindgut (Blum 1966), but from the pygidial gland (Hölldobler and Traniello, 1980). In this case it seems to serve both as an orientation and recruitment signal. In the myrmecophagous group-raiding *Cerapachys turneri*, the trail pheromone originates from the poison gland, but appears to be reinforced by recruitment signals from the pygidial gland (Hölldobler, 1982). In several species of the legionary and group-raiding genus *Onychomyrmex*, there is a large unpaired sternal gland located in the median line between the 5th and 6th abdominal sternites. Both group-raiding and colony emigrations are organized by trails laid with this sternal gland (Hölldobler *et al.*, 1982). However, chemical orientation in *Onychomyrmex* appears to be supplemented by homing signals discharged from a basitarsal gland in the hindlegs (Hölldobler and Palmer, 1989; Hölldobler, unpublished results).

While in the laboratory the ants followed the trails drawn with poison and pygidial gland extracts, in the field the artificial trails were not sufficient to guide the raiding columns to the prey. Whenever the scout was removed the raid stopped and the ants returned to the nest. This might be due to the variable conditions in the field, or may indicate that at least in the context of raiding, additional behavioral or chemical signals from the scout ant are used.

The biological significance of the stridulatory sounds of *M. foetens* has been completely unknown. Our results show that the stridulation signals produced during raiding do not serve in intraspecific communication. Neither simulation of the airborne sound emitted by the ants nor simulation of vibrations of the substratum had any behavioral effect on the ants. We also did not find any synergistic effect of stridulation and pheromones in the laboratory. Stridulation is clearly a response to disturbance. The finding that the most efficient releaser of group stridulation is a mixture of air and CO_2 strongly supports the idea that it serves as an aposematic signal, warning potential predators such as birds and mammals of the powerful sting a *Megaponera* worker can administer. This phenomenon is well known from other insects, such as mutillids (Masters, 1979, 1980), and even from fresh water crayfish (Sandeman and Wilkens, 1982). This hypothesis is supported by the observed behavioral changes correlated with stridulation, namely the immediate dispersal of the column and increasing walking speed, which also seem to be adaptations to predation by vertebrates, using the dilution effect and the confusion of the predator. Its striking resemblance to the hissing noise of snakes suggests that the ant is exploiting the interspecific communication between snakes and other vertebrates by mimicking the snake's signal. The fact that *Megaponera* itself is well protected against vertebrate predators by its sting may have enhanced this aposematic use of sound signals.

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