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CHEMICAL COMMUNICATION IN THE DACETINE ANT *Daceton armigerum* (HYMENOPTERA: FORMICIDAE)

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Abstract—Contrary to previous assumptions, *Daceton armigerum*, the largest ant in the myrmicine tribe Dacetini, employs trail communication. We identified two anatomical sources of trail pheromones: Trails drawn with poison gland contents can last for more than seven days. Trails drawn with the newly discovered sternal glands (in the VIth and VIIth abdominal sternites) are effective but relatively short-lived. In addition, our bioassays revealed that the contents of the mandibular glands elicit alarm behavior, and secretions from the pygidial gland release attraction. When tested with artificial poison gland trails from seven other myrmicine species, *Daceton* did not exhibit trail following behavior. We confirmed, however, previous findings that *Atta* respond to *Daceton* poison gland trails and *Solenopsis* follow *Daceton* Dufour's gland trails.

Key Words—Ants, Dacetini, *Daceton armigerum*, Hymenoptera, Formicidae, poison gland, pygidial gland, sternal gland, mandibular gland, trail communication, alarm communication.

INTRODUCTION

The myrmicine tribe Dacetini is worldwide in distribution, and its 24 genera and 250 species vary enormously in size, morphology, and behavior. The analysis by Brown and Wilson (1959) of the Dacetini was one of the first attempts to correlate the evolution of social behavior with species-level adaptations in feeding and has been supplemented by more recent studies by Dejean (1980a,b; 1985a,b) and Masuko (1984) (see review in Hölldobler and Wilson, 1990).

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These comparative studies suggest an evolutionary tendency of dacetine species to move from open, even partly arboreal foraging, to cryptic mostly terrestrial and subterranean foraging. The ancestral habits may be retained in the genera *Daceton* and *Orectognathus* today. In fact, *Daceton armigerum*, the only species of the genus, is strictly arboreal and has been considered the most primitive dacetine species (Brown and Wilson, 1959; Wilson, 1962). A more detailed study of these genera is therefore of special interest.

The division of labor within colonies of *Daceton* and *Orectognathus versicolor* has been studied by Wilson (1962) and Carlin (1981), respectively. In addition, Hölldobler (1981) discovered in *O. versicolor* chemical communication employed during nest emigrations and alarm behavior. These genera have the most complex division of labor known for the Dacetini. Very little, however, has hitherto been reported on the communication behavior in *Daceton armigerum*.

In the present laboratory study of *D. armigerum* we investigated the glandular morphology of some of the major cuticular glands and conducted a series of bioassays testing the possible behavioral functions of some of the exocrine glandular secretions. The results reveal a new trail pheromone gland in ants and a remarkably diverse array of chemical communication signals.

METHODS AND MATERIALS

A colony of *Daceton armigerum* was collected on May 6, 1988, at the Imataca Forest Reserve, east of El Palmar at the border between Bolivar State and Delta Amacuro Territory, Venezuela. The complete colony contained one dealate queen and 2342 adult workers nesting 6.5 m above ground within a hollow in a tree trunk. Workers outside the nest moved primarily on a route at least 22 m in length, which was stable over the two days of observations. A large subsample of the colony was returned to Cambridge for study.

Worker subcastes were distinguished by size: minors (head width less than 2.2 mm), medias (head width 2.2–4.2 mm), and majors (head width more than 4.2 mm). In the laboratory at Harvard University, the colony was housed in 30 test tubes that had water trapped behind cotton plugs to provide moisture. The nest tubes were piled into two plastic containers (37 × 26 cm). From there the ants had access through cardboard bridges to a large foraging area (150 × 75 cm), where they were offered freshly killed cockroaches, frozen crickets, honey water, and a specially prepared diet (Bhatkar and Whitcomb, 1970). Unfortunately, the queen died several days after the colony had been transported to the laboratory. Although the whole group slowly declined in numbers to about 200 workers when we terminated the experiments, the loss of the queen did not result in a major social disintegration. The workers continued actively patrolling

and foraging in the arena. Some nest workers became fertile, laying viable eggs, which developed into males. Dissections revealed that the workers have two to four ovarioles, each of which can contain one large oocyte.

For histological investigations specimens were preserved in Carnoy's fixative and stored in 80% ethanol. After clearing in toluene, the gasters of workers were embedded in an ultra-low-viscosity epoxy medium (VCD/HXSA) as described by Mascorro et al. (1976) and Oliveira et al. (1983). Blocks were serially sectioned at 2 μm using glass knives and a model MT2-C ultramicrotome (Research Manufacturing Company, Tucson, Arizona). Sections were attached to albuminized glass slides, and plastic was removed prior to staining with toluidine blue–basic fuchsin following Burns and Bretschneider (1981) with slight modifications. Scanning electron micrographs were taken with an AMR 1000A SEM.

Descriptions of individual bioassays are given in the appropriate sections below.

RESULTS

The *Daceton* workers were active in the foraging arena during the daytime with peak activity in the afternoon, and they returned to the nest tubes during the night. Among the worker subcastes, we primarily saw the majors and several size classes of the media groups patrolling the arena and foraging. The minors were rarely seen outside the nest tubes. We did not observe a noticeable recruitment effect when we offered as food honey water (which was readily imbibed by foragers and exchanged among nest mates by regurgitation), or cockroaches and crickets. However, on three occasions (of a total of nine incidents) when we presented termites as prey objects, we noticed that after 10–20 min the number of ants moving over the cardboard bridge into the arena increased markedly. In this situation most ants followed a reasonably well defined route from the nest to the food source in the arena. In fact we observed several workers apparently laying down pheromones. They moved more slowly with their bodies lowered to the ground, so that the last abdominal sternites could touch the surface (Figure 1a). With the aid of a movable operation microscope (Technoscope Zeiss), we were able to confirm these observations and, in addition, noticed that some of the workers extended their sting at irregular intervals.

The observations strongly suggested that *Daceton armigerum* employ chemical recruitment signals and exhibit trail following behavior. The following investigations were designed to test this hypothesis.

Gland Morphology. Daceton workers have a large poison gland that spans approximately one third the length of the gaster. The relatively wide tube lead-

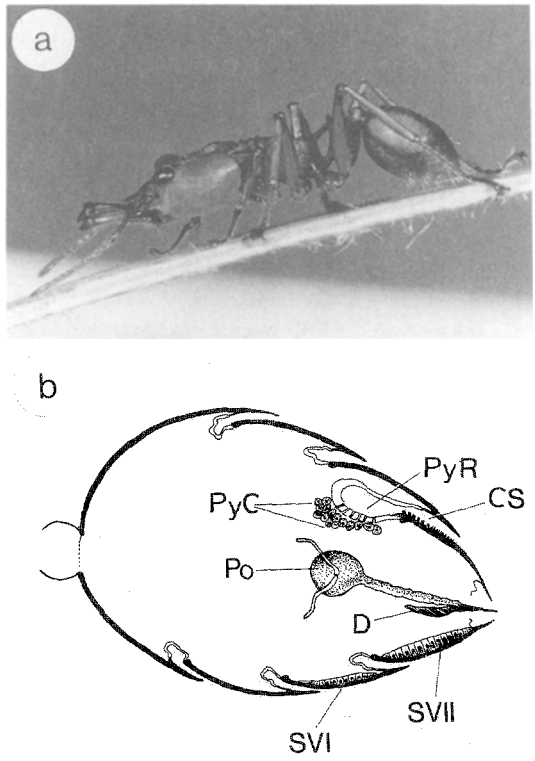

FIG. 1. (a) A worker of *Daceton armigerum* moving over the bridge connecting the nest and foraging arena. The ant closely inspects the substrate with its antennae, apparently following a trail. Its body is lowered, so that the last abdominal sternite can touch the surface. (b) Schematical illustration of a sagittal section through the gaster of a *D. armigerum* worker showing the major exocrine glands. **PyR,** pygidial gland reservoir; **PyC,** pygidial gland cells; **Po**, poison gland; **D,** Dufour's gland; **SVI,** sternal gland in VIth abdominal sternite; **SVII,** sternal gland in the VIIth abdominal segment; **CS,** cuticular structure.

ing from the reservoir to the sting is filled with secretions and appears to be bulging along its entire length. The Dufour's gland is slender and approximately one third the length of the poison gland (Figure 1b).

Histological and scanning electron microscopic investigations revealed a large, paired pygidial gland. The gland reservoir sacs are formed as invaginations of the intersegmental membrane between the VIth and VIIth abdominal tergites (Figure 2). Ducts lead from clusters of glandular cells that penetrate the intersegmental membrane into the reservoir (Figure 4a). The cuticle of the adjacent VIIth tergite has a complex surface structure, which also occurs in a paired arrangement (Figures 3 and 4). Presumably the secretions of the pygidial gland

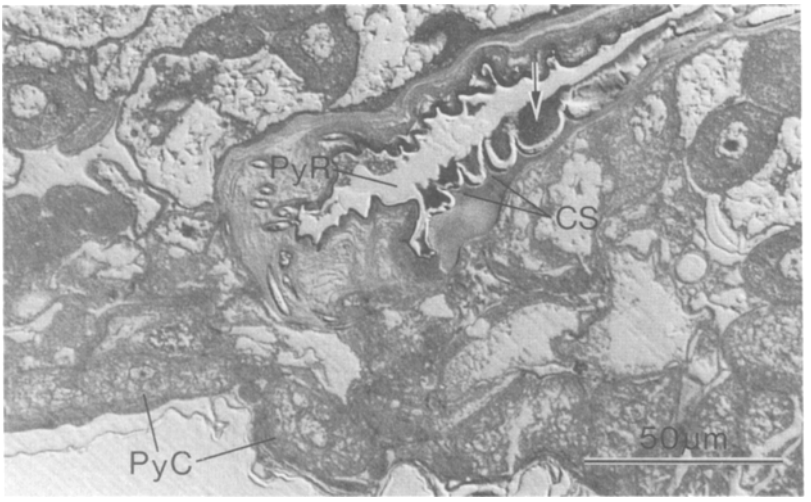

FIG. 2. Sagittal section through the pygidial gland of a *Daceton armigerum* worker. **PyR,** pygidial gland reservoir; **PyC,** pygidial gland cells; **CS,** cuticular structure on the VIIth abdominal tergite; arrow indicates coagulated secretions in the grooves of the cuticular structure.

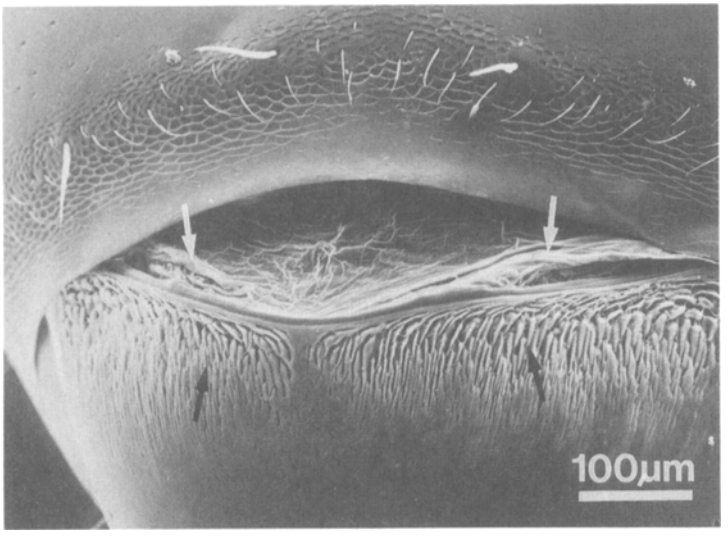

FIG. 3. Scanning electron micrograph of the pygidial gland opening showing the paired cuticular structure (black arrows) on the VIIth abdominal tergite and the intersegmental membrane (white arrows) between the VIth and VIIth abdominal tergites.

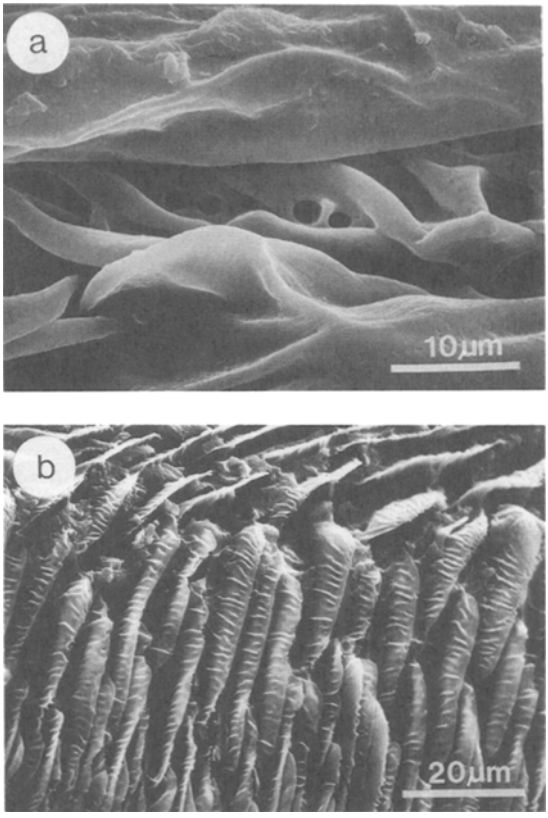

FIG. 4. Higher magnification scanning electron micrographs of details designated by arrows in Figure 3. (a) Area of intersegmental membrane (between abdominal tergites VI and VII) showing pygidial gland duct openings. (b) Grooves of the cuticular structure on abdominal tergite VII.

reservoir can be released into the grooves of this cuticular structure, which, because of its convoluted design, might direct and facilitate the dispersion of the glandular product. In fact, in the histological preparations, one can see coagulated secretions inside the cavities of the cuticular structure (see Figure 2).

Daceton workers possess large glandular epithelia in the last two exposed abdominal sternites. The most posterior sternal gland is especially well developed (VIIth sternite). The epithelium is attached to the cuticle. Intracellular ducts connect to very fine pore capillaries that penetrate the cuticle in dense formation (Figure 5).

Bioassays of Glandular Secretions: Trail Following. In a series of exper-

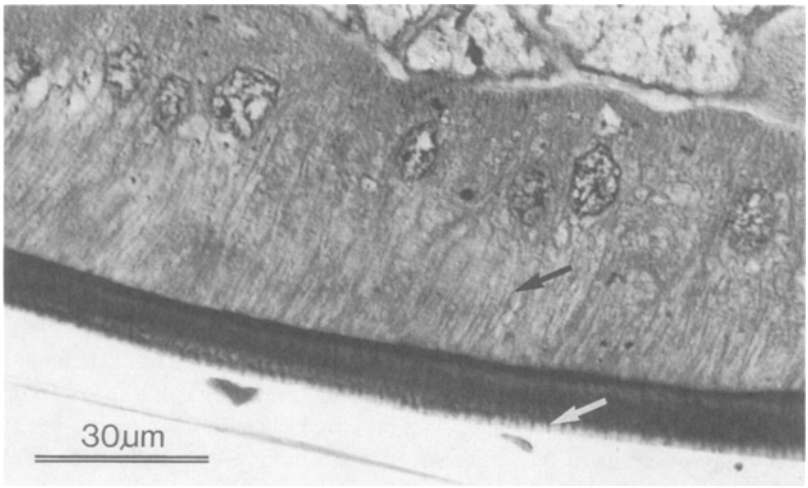

FIG. 5. Sagittal section of the glandular epithelium in the VIIth abdominal sternite (sternal gland). Black arrow points to an intracellular channel. White arrow indicates the opening of a pore capillary in the cuticle.

iments we tested the trail-following response of *Daceton* workers to artificial trails drawn with glandular secretions of poison gland, Dufour's gland, pygidial gland, sternal gland, and hind gut contents. The organs were dissected out of ants killed by placing them for a few minutes in a freezer. For each trail test, one gland of a kind was crushed on the tip of a hardwood applicator stick and smeared once along a 20-cm-long pencil line. The trails were made to originate either from the entrance of a nest tube or from the base of the bridge that connected the nest box with the foraging area. As a control, one or several trails were offered simultaneously that derived either from a droplet of water or from one of the other glands. All ants following the trails to the end during the first 5-min period were counted.

As can be seen from Table 1, trails drawn with crushed poison glands or sternal glands (VIIth abdominal sternite) elicited a precise trail-following behavior in *Daceton* workers (Figure 6), but the ants did not follow trails drawn with crushed Dufour's gland, pygidial gland, or hindgut contents.

All worker subcastes have the same glandular equipment, and their secretions release the same behavioral responses. Although there was unequivocal response to trails drawn with sternal glands, the response to poison gland trails was usually stronger ($P < 0.01$; t test; Table 1). Furthermore, trails drawn with crushed sternal glands were only effective for several minutes, whereas poison gland trails can last for several days. In a series of experiments, we

TABLE 1. MEAN NUMBER AND STANDARD DEVIATION ($N = 9$) OF *Daceton armigerum* WORKERS FOLLOWING ARTIFICIAL TRAILS DRAWN WITH CRUSHED EXOCRINE ORGANS DURING 5-MIN PERIOD

Poison gland	Dufour's gland	Pygidial gland	Hindgut	Sternal gland (VIIth sternite)
17.3 ± 9.4	0	0	0	6.3 ± 3.8

tested the trail-following response along poison gland trails of different age. Each trail was drawn with one crushed gland and kept in room temperature (22°C) for increasingly extended intervals (ranging from 1 min to seven days) until it was presented to the ants. We observed clear trail-following behavior along 7-day-old trails (5.0 ± 2.9 ants; $N = 5$). In fact, it is likely that the trails

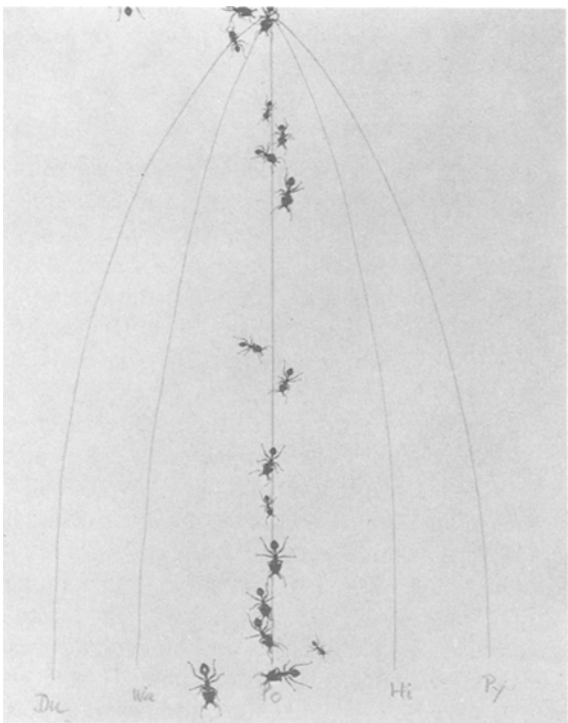

FIG. 6. Trail following response of *Daceton armigerum* workers when five artificial trails were offered at the base of the arena bridge. **Du,** crushed Dufour's gland; **Wa,** water; **Po,** crushed poison gland, **Hi,** crushed hindgut; **Py,** crushed pygidial gland.

TABLE 2. TRAIL-FOLLOWING RESPONSE OF *Atta cephalotes* WORKERS ALONG TRAILS DRAWN WITH GLANDULAR SECRETIONS FROM *Daceton armigerum* AND *A. cephalotes*

Daceton poison gland	vs. *Daceton* Dufour's gland
30.3 ± 17.3[a]	0
	vs. *Atta* poison gland
13.6 ± 4.3[b]	39.2 ± 7.4

[a] $N = 6$.
[b] $P < 0.002$ (paired t test); $N = 5$.

last even longer, because in one test the ants followed a trail which was drawn 10 days previously.

From these experiments we conclude that *Daceton* produce trail pheromones in the poison gland and in the sternal gland. These results differ from previous findings by Blum and Portocarrero (1966), who failed to demonstrate trail-following in *D. armigerum*. Interestingly, however, these authors found that three attine ant genera follow trails drawn with poison gland secretions of *D. armigerum*. Similarly, Wilson (1962) discovered that *Solenopsis invicta* followed trails drawn with Dufour's gland contents of *D. armigerum*.

Our studies confirmed these findings of interspecific responses. We offered *Atta cephalotes* and *Solenopsis invicta* trails drawn with either poison or Dufour's gland secretions of *D. armigerum*. As Tables 2 and 3 show, *Atta* follow poison gland trails and ignore Dufour's gland trails, whereas *Solenopsis* follow the Dufour's gland trails but not the poison gland trails. However, when we offered *Solenopsis* or *Atta* a choice between the effective *Daceton* trail and a trail drawn with the test species' own trail gland, the ants significantly preferred their own species' trails. *Daceton*, on the other hand, is very specific in its trail-following response. It only followed its own poison gland secretions,

TABLE 3. TRAIL-FOLLOWING RESPONSE OF *Solenopsis invicta* WORKERS ALONG TRAILS DRAWN WITH GLANDULAR SECRETIONS FROM *Daceton armigerum* AND *S. invicta*

Daceton poison gland	vs. *Daceton* Dufour's gland
0[a]	32.8 ± 16.4
Daceton Dufour's gland	vs. *Solenopsis* Dufour's gland
15.9 ± 6.3[b]	42.2 ± 9.2

[a] $N = 5$
[b] $P < 0.001$ (paired t test); $N = 9$.

ignoring those of *Atta cephalotes*, *Solenopsis invicta*, *Tetramorium caespitum*, *Aphaenogaster cockerelli*, *Pheidole desertorum*, *Pheidole dentata*, *Pogonomyrmex occidentalis*, and *Pogonomyrmex badius*.

Bioassay of Glandular Secretion: Chemical Alarm and Attraction. Although *Daceton* did not follow trails drawn with crushed pygidial glands, we noticed an attraction to pygidial gland secretions. This was revealed by the following bioassays:

We offered at the entrance of a nest tube alternately either an applicator on which we had crushed the Vth abdominal tergite (control) or an applicator on which we had crushed the VIIth tergite (with the pygidial gland attached). The applicators were held approximately 1 cm above the surface so that the ants could not touch them. The number of ants were counted that left the nest tube within a 2-min period after the applicators were presented.

From a total of six tests, the mean number of ants leaving the nest tube when the control was offered was 4.8 ± 5.5 ($\bar{X} \pm$ SD), which was significantly ($P < 0.02$; paired t test) different from the mean number of leaving ants (13.3 ± 5.9) when crushed pygidial glands were offered. The response toward pygidial gland secretions not only was attraction, but also an increase in locomotory speed.

We also noticed that the mandibular gland contents had a strong smell. When filter paper on which mandibular glands or whole heads of *Daceton* workers were crushed were presented to the ants, they responded with attraction, increase in locomotory speed, and aggression, charging the paper with widely opened mandibles. In another experimental series, two applicator sticks, one plain, the other contaminated with the mandibular gland secretions of one ant, were placed into the arena (approximately 10 cm apart). After 60 sec the number of ants assembled at the sticks were counted. From a total of 10 tests, the mean number of ants assembled at the contaminated stick was 10.6 ± 3.7 ($\bar{X} \pm$ SD). This was significantly ($P < 0.001$; paired t test) different from the mean number of ants at the control stick (2.4 ± 2.3). At the contaminated stick the ants behaved aggressively, charging and biting the stick repeatedly.

Finally, we tested the response of *Daceton* workers towards Dufour's gland secretions. As already reported, *Daceton* workers did not follow trails drawn with Dufour's gland secretions. Neither did they exhibit an obvious alarm behavior when exposed to crushed Dufour's glands. However, when the secretion was offered on small disks (4 cm diameter) of filter paper in the arena (eight repetitions), the mean number of ants inspecting these disks with their antennae in five consecutive snapshot counts during a 5-min period was significantly higher (3.3 ± 0.5) than the mean number of ants inspecting a simultaneously offered control paper (0.8 ± 0.3; $P < 0.001$; paired t test). Thus, *Daceton* workers pay some attention to the Dufour's gland secretions, but it is not clear to us whether this secretion has signal function and in what context it might be discharged.

DISCUSSION

Daceton armigerum are the biggest ants in the myrmicine tribe Dacetini, living in large arboreal colonies. Almost nothing was known about communication in this species. We were able to study the chemical communication in the laboratory using a large portion of a *D. armigerum* colony.

Although it has been well documented that many species of the subfamily Myrmicinae employ secretions from the glands associated with the sting apparatus (poison gland; Dufour's gland) for chemical trail communication and orientation (for review see Morgan, 1984; Attygalle and Morgan, 1985; Hölldobler and Wilson, 1990), our finding of trail communication in *Daceton* is only the second case in the tribe Dacetini where this behavior has been demonstrated. In fact, previous studies have failed to show trail following in *D. armigerum*, and therefore it was assumed that this species has no trail communication (Blum and Portocarrero, 1966). A surprising result was the astounding persistence of the poison gland trails of *Daceton*. Trails older than one week still elicited a precise trail-following behavior in *D. armigerum* workers.

Although we did not find *Daceton* workers following trails drawn with Dufour's gland secretions, the Dufour's gland contents of *D. armigerum* are followed by *Solenopsis invicta* (Wilson, 1962), while the poison gland contents are followed by species of *Acromyrmex* and *Atta* (Blum and Portocarrero, 1966). We were able to confirm these interspecific responses. These results suggest that the Dufour's gland of *D. armigerum* contains the farnesene known as a major component of the *Solenopsis* trail pheromone (Vander Meer, 1986) and its poison gland the pyrrole, one of the active trail pheromone components identified in attine ants (Tumlinson et al., 1971, 1972). On the other hand, the trail-following response of *D. armigerum* is highly specific: they do not follow poison gland secretions of *Atta* or of seven other myrmicine species tested.

We discovered large glandular epithelia in the VIth and VIIth abdominal sternites. This structure is especially well developed in the VIIth sternite, where one can detect intracellular ducts connecting with fine pore capillaries in the cuticle. Sternal epithelial glands are known from several ant species (Hölldobler and Engel, 1978; Jessen et al., 1979), but this is the first case where a behavioral response to its secretions could be demonstrated: Workers follow trails drawn with secretions from the VIIth sternite glands. We assume that both poison gland and sternal gland secretions might be involved in trail formation, because behavioral observations indicate that trail-laying ants touch the last abdominal sternites to the ground and at irregular intervals extrude the sting. In fact, in our tests, when we offered poison gland and sternal gland secretions on the same trail, we observed the most precise trail-following behavior, although the number of ants following the trail was not significantly different from those following poison gland trails alone.

There is also the possibility that a recruitment signal is discharged from

the well developed pygidial gland. The secretion of this gland elicits attraction, but no trail-following behavior. In the dacetine species *Orectognathus versicolor* Hölldobler (1981) found workers following pygidial gland trails. In this species the pygidial gland is associated with an epithelial tergal gland in the VIIth tergite (which is absent in *Daceton*). It is possible that in this case the epithelial tergal gland has the same function as the epithelial sternal gland in *Daceton* (which is absent in *Orectognathus*).

Based on the findings in *O. versicolor*, where we discovered the pygidial gland associated with a glandular epithelium in the VIIth abdominal tergite, which resembles pygidial glands in some ponerine ants (i.e., *Pachycondyla laevigata*; Hölldobler and Engel, 1978), Hölldobler (1981), we speculated that the closely related *Daceton* might also have a well-developed pygidial gland of similar construction. In the present paper, we confirm that *Daceton* possesses a well-developed pygidial gland, which resembles that of *Orectognathus*; however, the glandular epithelium in the VIIth abdominal tergite is absent.

In the first behavioral study of *Daceton*, Wilson (1962) observed that workers of *D. armigerum* often moved to areas of excitement, and when a worker ant had discovered prey it moved in "excited broken running patterns" by which other ants in the vicinity might be attracted. Wilson (1962, 1971) hypothesized that this running pattern might serve as a communicative signal of the kind of "Stäger's kinopsis," i.e., the large-eyed *Daceton* worker might respond to the visual stimuli produced by the nestmate moving excitedly. There is no doubt *Daceton* has excellent vision and readily reacts to moving objects in its visual field. Our new results on the response to chemical signals from the mandibular glands and several abdominal glands suggest that these glands are also involved in this behavior. Indeed, chemical communication in *Daceton* is well developed and plays a major social role in this species.

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