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Evidence of Chemical Signaling in the Sand Scorpion, *Paruroctonus mesaensis* (Scorpionida: Vaejovida)

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Abstract

This study presents evidence of intraspecific chemical communication in scorpions. The subject of our investigation was the nocturnal sand scorpion, *Paruroctonus mesaensis*. During the mating season, mature males show a sex-specific wandering behavior ostensibly directed at locating conspecific females that remain in the vicinity of their home burrows. Searching behavior was stimulated in the laboratory by releasing males onto substrates that had previously been occupied by females. Receptive males exhibited changes in locomotory behavior that favored occupation of the female-exposed area. Males occasionally displayed a precourtship behavior, called juddering, indicating the presence of a pheromone on the substrate. Juddering, and two newly described behavior patterns, tail-wagging and pedipalp-reaching, were also induced by solvent extracts of female cuticle. Most behavioral responses began vigorously within the first few s of stimulus contact and gradually adapted within 10 min. The potential importance of specialized sensory appendages, the pectines, for mediating chemosensitivity is discussed. These results are consistent with the hypothesis that mate identification and localization in sand scorpions are mediated in part by a contact sex pheromone.

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Introduction

Given the importance of pheromonal signaling in stimulating and directing behavior of mandibulate arthropods (Tumlinson & Teal 1987; Kaissling 1987), it is surprising that so little is known about intraspecific chemical communication in the other great division of the phylum, the chelicerates. Arachnids in particular are a diverse and ancient group of terrestrial arthropods with several large forms that can be easily studied, yet the whole of our understanding of arachnid pheromonal communication is based on investigations of ticks, phytophagous mites (Sonenshine 1985) and spiders (Tietjen & Rovner 1982; Pollard et al. 1987). Notably lacking are studies of scorpions, among the earliest of terrestrial animals and the order believed by some workers to be ancestral to other arachnid

groups. KJELLESVIG-WAERING (1986) notes that the general body form of scorpions and the structure of a putative chemosensory organ, the pectines (ventral antenna-like appendages), changed very little as Devonian aquatic forms began to invade land more than 300 million years ago. From this perspective a study of scorpionids may give insights into the evolution of chemical communication and related behaviors in terrestrial chelicerates.

Apart from their evolutionary significance, scorpions offer special advantages for behavioral analysis and experimentation owing to their longevity, large size, fluorescent cuticle, and ease of maintenance in captivity. The desert sand scorpion, *Paruroctonus mesaensis*, has become a particularly important species for ethological study due to the simplicity of its dune environment and the substantial body of physiological, ecological and natural history literature that has accumulated on this species (BROWNELL 1977; BROWNELL & FARLEY 1979; HADLEY & WILLIAMS 1968; POLIS 1979, 1980; POLIS & FARLEY 1979a, b, 1980; ROOT 1985; STAHNKE 1966). As part of an integrative investigation of chemical communication in arachnids, we have conducted morphological (BROWNELL 1989), neurophysiological (GAFFIN & BROWNELL 1990), and biochemical (BULSECO & BROWNELL 1989) studies of the sand scorpion chemosensory systems and behavior. The present study demonstrates the existence of chemical signaling in this species and describes some aspects of the chemical signals involved and the behaviors they release.

The natural reproductive behavior and environment of *P. mesaensis* suggest that it uses some form of chemical signaling to increase the probability of a reproductive encounter. This is a solitary, cannibalistic species that seldom wanders farther than 1 m from its home burrow (POLIS 1980). Most between-individual interactions occur during the reproductive season when, for a few weeks each year, mature males abandon their burrows and wander across the dune at night apparently in search of potential mates (POLIS & FARLEY 1980). Since at least some, and perhaps all, matings occur on the surface of the dune, the chance of a successful encounter is dependent on the synchrony of male and female surface activities. Furthermore, as a heavily predated species, *P. mesaensis* is a "time-minimizer," emerging from its burrow on less than 40 % of nights and then for only a few h (HADLEY & WILLIAMS 1968; POLIS & FARLEY 1979b). Thus, most matings occur during times when nightly surface densities of mature males and females are about 35 and 40 individuals per ha, respectively (POLIS 1980). At these densities random movements by the males are not likely to account for the number of successful matings observed. Another obstacle to successful mating is the tendency of larger females to cannibalize the smaller males (POLIS 1980); successful encounters occur only after an elaborate courtship dance (POLIS & FARLEY 1979a) when males presumably signal their status as potential mates and suppress the predatory responses of females. One behavior that may signal courtship intention is "juddering", an abrupt lurching of the body that produces substrate vibrations (ALEXANDER 1959; see POLIS & FARLEY 1979a for review). Juddering may itself be released by chemical stimuli since KRAPF (1986) observed that an adult male of the African species *Pandinus imperator* judders following contact with objects transferred from the container of a female conspecific.

The study presented here supports the hypothesis that substrate-borne chemical signals direct the navigation of male sand scorpions to prospective mates and trigger behavior patterns important to a successful mating.

Materials and Methods

Animals

Field observations and collection of animals for laboratory studies were conducted in sandy regions of the Mojave Desert near Indio, California (San Bernadino Co.) using portable ultraviolet lamps to observe surface activities at a distance of several m. Collected animals were measured and sexed according to the procedures of STAHNKE (1970), and only animals judged to be reproductively active adults (stage 6 instars or older) were used in behavioral experiments. Individuals were kept in an environmental chamber (27 °C; 15L/9D) in separate, clear plastic dishes containing natural sand. They were maintained at capture weight by regular feedings of wax worms.

Apparatus

The test chambers were cylindrical, clear plexiglass arenas (13.5 cm diam., 8 cm height) placed over natural desert sand (80 ml). Sand was cleaned of organic substances by overnight washing in chloroform : methanol (2 : 1, 100 ml per 80 ml of sand) in a reflux apparatus or baked at 250 °C for 4 h. Opaque-plexiglass partitions were used to isolate test animals in specific quadrants within the arenas.

Trials were monitored by a video camera (Sony V9, 8 mm format) positioned above the test arenas. Tapings occurred at night under ultraviolet illumination (single fluorescent bulb: F8T5/BLB Sylvania, 8 W; 50 cm distance). The brightly fluorescent scorpion cuticle gave clear and detailed images for behavioral analysis under this illumination.

We have witnessed successful matings of *P. mesaensis* in the arena environment under UV illumination. All component behaviors described by POLIS & FARLEY (1979a) for matings of this species in the field were observed in laboratory situations including initial female aggression, male juddering, "promenade à deux", and spermatophore exchange. This indicates that the reproductive behavior of *P. mesaensis* is not overtly affected by the arena environment.

Protocol

Two series of experiments were conducted to test the ability of adult male *Paruroctonus mesaensis* to detect (1) natural sand substrates previously exposed to live female conspecifics from the same population, and (2) sand substrates labelled with chloroform : methanol (2 : 1) washes of conspecific female cuticle. For experiments in Series 1, the stimulus female (n = 24, no repeats) was confined to one quadrant of the test arena for at least 24 h where it was constantly in contact with the substrate. The stimulus animal was removed from the arena just prior to release of the test animal (n = 24, no repeats). In this series, 15 of the 24 test animals crossed the exposed quadrant at least once constituting 15 legitimate trials. For trials in Series 2, females (n = 29) were anesthetized by chloroform and cuticular extracts were prepared by submerging tail segments (telson and 5th metasomal segment) of the stimulus female in 1.5 ml of chloroform : methanol (2 : 1) for 2 h. This extract was subsequently dried onto 1.0 g of sand under a stream of nitrogen gas and divided into 0.25 g portions which were placed in test arenas at known location just prior to release of the test animal (n = 43 different males, 19 males repeated after at least 2 d rest for total of 62 trials). 55 legitimate trials (at least one crossing of treated quadrant) were recorded for this series. Trials with pure solvent dried onto sand (n = 16 males, single use; none used in female treated trials) were conducted as a control (14 legitimate trials).

For each trial the test animal was initially fenced in a quadrant of the test arena opposite the area where the stimulus was to be applied. The positions of test animals and stimuli were randomized spatially within the room. A trial was initiated by removing the plexiglass fence that separated the test

animal from the stimulus field. All trials were begun between 19.00 and 24.00 h (normal period of maximal activity) and were recorded for 2 h thereafter. Ultraviolet illumination began 15 min before each trial.

Analysis

Video records of each trial were analyzed and scored for the occurrence of several characteristic behaviors that took place during single "excursions" within the arena. An excursion was defined as an ambulatory movement lasting at least 10 s and containing no pauses greater than 30 s. For each excursion the beginning and ending times, the number of crossings of the treated substrate, and the position of final rest were recorded.

Scores were assigned to the initial 5 entries into the experimental quadrant as follows: 1 = no alteration of behavior; 2 = slight but noticeable alteration of behavior; 3 = distinct alteration of behavior, specific behaviors include: "back-ups" (cessation of forward locomotion followed by quick backward movement of 1 to 2 steps) and/or increased turning tendency (animal moves away from container walls); 4 = prolonged alteration of behavior, specific behaviors include: "push-ups" (animal's body pushes forward and downward while tarsal segments remain stationary, pectines brush forward and laterally over substrate), "creeping" (distinct change of normal forward stepping movements to shorter forward movements, usually accompanied by increased turning movements), "tail-wags" (described in results section), and/or "pedipalp-reaches" (also described in results section); 5 = presence of juddering. The highest score received constituted the overall score for the trial.

The binomial distribution (Snedecor & Cochran 1967) was used to test the statistical significance of a behavioral pattern (BP) initiated in the treated quadrant (E) compared to a hypothetical random quadrant of initiation. In a random situation, the probability of initiation in quadrant E (p_E) would be $\frac{1}{4}$ while the initiation in any of the other three quadrants would be $\frac{3}{4}$. Thus, we test for H_O: $p_E \leq \frac{1}{4}$ and
H_a: $p_E > \frac{1}{4}$ where:

$$p_E = \sum_{i = x_E}^{N} \binom{N}{i} \left(\frac{1}{4}\right)^i \left(\frac{3}{4}\right)^{N-i} \quad \text{where} \quad \binom{N}{i} = \frac{N!}{i!\,(N-i)!}$$

x_E is the number of scorpions which first exhibited the BP in quadrant E; N is the total number of scorpions exhibiting the BP. Mann-Whitney analysis was used to test for significant differences between trials with female cuticular extracts and solvent controls.

Results

When placed in a foreign environment, such as the test arena of these experiments, *P. mesaensis* were quiescent for several min ($\bar{x} = 18.5 \pm 16.8$ min). Thereafter, most animals began to explore the new environment, generally walking along the walls of the circular arena. These exploratory movements were characterized by quick forward steps interrupted by brief pauses. If no stimulus was encountered during this time the animal eventually began other behaviors in the vicinity of the container walls such as "wall-climbing" (animal attempts to climb container walls) or "rototiller-digging" (first three leg pairs quickly rotate and scrape surface sand away). A strikingly different behavior was observed for male scorpions that encountered substrates that had been exposed to female conspecifics; their exploratory and escape behavior abruptly changed to shorter, creeping movements, with a tendency to turn and move toward areas away from the container walls. As a consequence, stimulated animals tended to spend more time in the quadrant labelled by exposure to the female; a representative example is shown in the tracing of movement over time for one individual in Fig. 1 A.
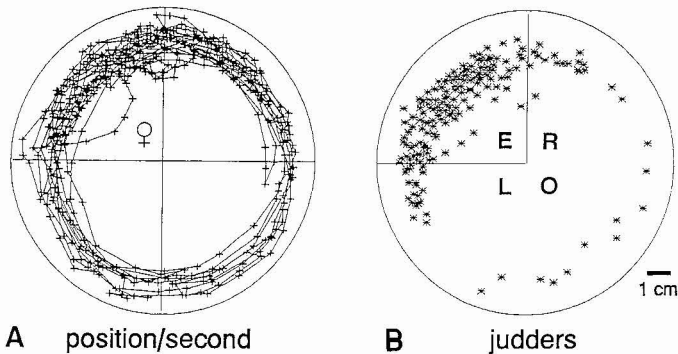
Paruroctonus mesaensis

A   position/second   B   judders

Fig. 1: Behavioral response of an individual male *Paruroctonus mesaensis* to sand previously exposed to a conspecific female. A. Initial 5 min of locomotory movements plotted as position at 1-s intervals. B. Location of juddering behavior during first 10 min of male movement. E: quadrant containing the sand exposed to a live conspecific female for 24 h prior to testing. L, R, and O: quadrants on the left, right and opposite the exposed quadrant

Some stimulated males also displayed juddering behavior (Fig. 2 A) as they traversed substrates previously exposed to a female. Fig. 1 B shows the locations where juddering behavior was performed by the animal depicted in Fig. 1 A. When the animal moved out of the exposed quadrant, creeping and juddering behavior usually ended abruptly as turning behavior continued.

These changes in locomotory behavior of males are likely stimulated by substances deposited on the sand by the stimulus female or, alternatively, by mechanical disturbances of the substrate (e.g. tarsal-print patterns) resulting from her movements. To eliminate the latter as a potential cue and to minimize potential variability in the distribution and intensity of the stimulus signal we tested the male's response to organic extracts of conspecific females. When male
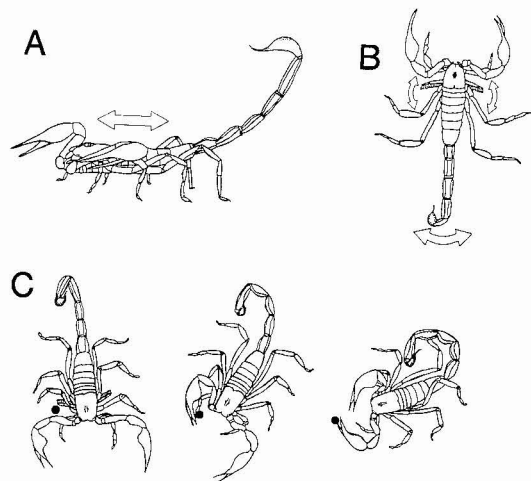

Fig. 2: Three discrete behaviors observed during male contacts with substrates exposed to live female conspecifics or extracts of female conspecifics: A. juddering, B. tail-wagging, C. pedipalp-reaching. The black spot in C indicates a point of the sand touched initially by the right pectine then subsequently by the pedipalp tips at the conclusion of the behavior

scorpions encountered undisturbed substrates with sand grains labeled with these dried extracts they showed distinct changes in locomotory activity and movements of their appendages. Behavioral changes (score of 2 or greater, see Materials and Methods for criteria) were seen in 62 % of the males as they first moved across the extract-treated region (34 of 55 trials). Juddering behavior was elicited in 8 of these trials.

In addition to juddering behavior, female tail extracts also evoked two other behaviors referred to here as "tail-wagging" and "pedipalp-reaching" (Fig. 2). These behaviors have not been previously described for *P. mesaensis* or other scorpions. In tail-wagging (Fig. 2 B), the animal's first four metasomal segments are held low to the substrate and in line with the body axis. The terminal (fifth and sixth) segments of the metasoma are held perpendicular to this axis and rotated approximately 15 degrees side to side at about 1 Hz. The rest of the body remains stationary except for the pectines, which brush forward and backward against the substrate at a frequency similar to that of the tail-wag. In pedipalp-reaching (Fig. 2 C), the pedipalps appear to grasp for an illusory object immediately in front of the chelicera. This behavior was accompanied by a short backing or turning movement of the body, which places the pedipalps in an area where the pectines had been moments before. Pedipalp-reaching and tail-wagging occurred in 6 and 15 of the 55 trials, respectively.
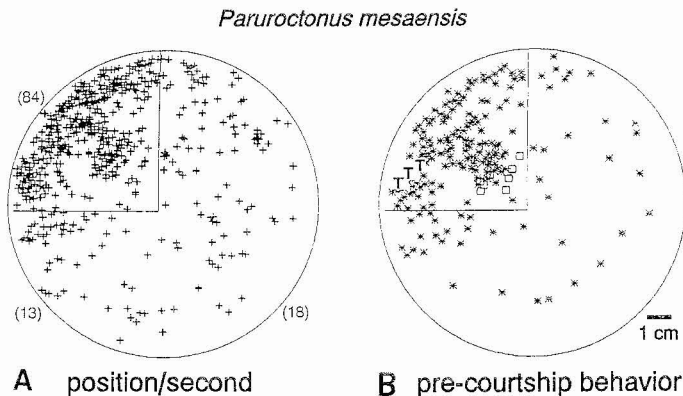
Paruroctonus mesaensis

A   position/second   **B   pre-courtship behavior**

Fig. 3: Response of an individual male *P. mesaensis* to sand treated with chloroform : methanol extract of a female's metasomal segments. A. Scatter plot of male location at each s during 8-min observation. Numbers in parentheses: frequency of pectine-tapping per min by quadrant during the animal's first movement into the treated quadrant. B. Location of juddering (∗), pedipalp-reaching (□), and tail-wagging (T) behaviors for the same 8-min period. The quadrants were labeled according to Fig. 1

Fig. 3 shows a vigorous response of a male to a cuticular extract of a conspecific female in which all three behaviors described in Fig. 2 were performed. For all trials taken together, the sites of initiation of juddering, pedipalp-reaching, and tail-wagging behaviors were significantly associated with the quadrant containing sand treated with extracts of female cuticle. All pedipalp-reaching (n = 6) and juddering behaviors (n = 8), and all except one of the tail-wagging

behaviors (n = 15), began within the quadrant containing the extract (binomial distribution p < 0.001 for each). Also depicted in Fig. 3 is the frequency of pectine contacts with the substrate during the male's initial movement into the treated quadrant. As the male moved through quadrants O and L, pectine-tapping frequency was 18 and 13 taps per min, respectively. Upon initial contact with the treated substrate in quadrant E, pectine-tapping frequency increased to 84 taps per min.

Fig. 4: Summary of male behavioral responses to female-derived chemical stimuli. Percent of animals in all trials grouped by behavioral score. Mean values: female deposit 2.01 (n = 15), female cuticular extract trials 2.93 (n = 55), solvent control 1.14 (n = 14). Responses to solvent control differ from female cuticular extract responses at p < 0.001 level (Mann-Whitney analysis)
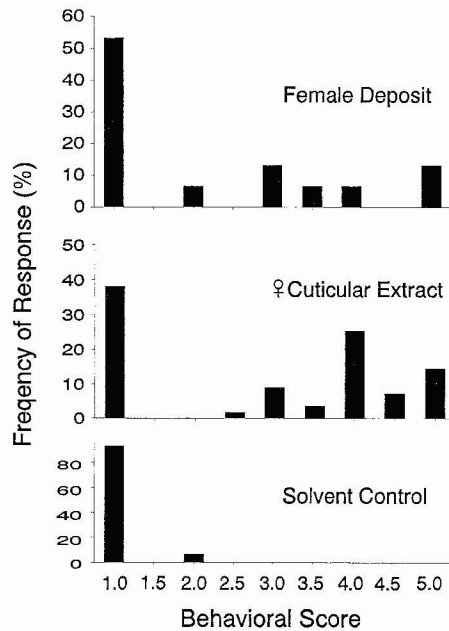
The results of all trials of males to female deposits, female cuticular extracts, or solvent controls as categorized by behavioral score (see Methods for details) are summarized in Fig. 4. Mann-Whitney analysis of trials with female cuticular extract compared with solvent controls was significant at the p < 0.001 level.
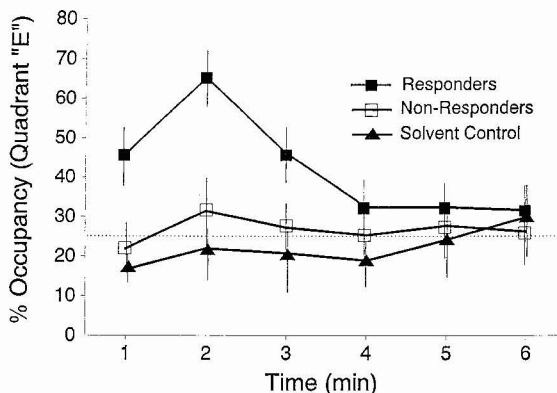

Fig. 5: Adaptation of male's response to female extract-treated sand. Male occupancy of quadrant treated with either female cuticular extract or pure solvent (n = 12) during first 6 min of movement; x̄ ± SEM. Trials with cuticular extract are grouped as responders (behavioral score ≥ 2; n = 21) or non-responders (behavioral score = 1; n = 11). Only trials with at least 10 min of total movement were compiled

Mean behavioral responses to deposits and extracts were 2.1 and 2.9, respectively, reflecting the large number of non-responders (behavioral score = 1) in each group.

The response of males to female cuticular extracts was generally immediate and intense but adapted quickly with continued exposure. The dynamics of adaptation are shown in Fig. 5 as a record of the initial 6 min of occupancy of the experimental quadrant (E) treated with either female cuticular extracts or pure solvent. Most responses decay to spontaneous levels within 3—5 min.

Discussion

This study shows that male scorpions (*P. mesaensis*) markedly alter their locomotory behavior when they encounter substrates previously exposed to female conspecifics. Sand substrates exposed to live females or treated with organic extracts of female cuticle suppressed non-directed locomotory behavior and released mate-searching behavior that was of greatest intensity in the vicinity of stimulus application. The simplest explanation of these observations is that male scorpions are responding to a chemical signal deposited on the substrate from the cuticle of conspecific females. In their natural, sand dune environment such responses would have the effect of congregating male scorpions in areas frequented by females, that is, in the vicinity of a female's burrow. In most instances we only observed changes in the pattern of locomotion although some trials also stimulated behavior related to courtship — juddering, and two previously undescribed behaviors, tail-wagging and pedipalp-reaching. These behavioral observations are consistent with the hypothesis that scorpions, like many other terrestrial arthropods, use pheromonal signals to trigger and direct orientational behaviors related to mating.

The natural history of *P. mesaensis* suggests the need for some means of species-specific chemical communication during reproduction. For most of their 5—7 yr life span, males and females of this species live in solitary burrows; these are generally located among dunegrass and creosote vegetation where thermal and water stresses of the diurnal dune environment are minimized. At night their surface activities are confined to areas near their home burrows, where they lie motionless on the surface in ambush of arthropod prey, some of which are conspecific scorpions of smaller size. During the summer mating season mature *P. mesaensis* males become increasingly mobile and are often seen walking with extended pectines in regions between patches of vegetation. During this time males are heavily predated by larger *P. mesaensis* and the sympatric scorpion, *Hadrurus arizonensis*, indicating that wandering behavior involves substantial risk. Wandering appears to diminish in the vicinity of a female's burrow since clusters of 2 or more immobile males are often seen there (Polis, pers. comm. 1990). Clustering of males is particularly evident in two other species, *P. luteolus* and *P. borregoensis*, that are rarely seen on the surface.

Such observations lead us to hypothesize that some form of chemical signal attracts male scorpions to female burrows. Once within detectable range, surface

vibrations generated by male juddering may function to suppress the female's predatory attack response; *P. mesaensis* is known to be highly sensitive to disturbances of the substrate (BROWNELL 1977; BROWNELL & FARLEY 1979). Near-range behaviors may also be governed by specific qualities of the stimulus. Pedipalp-reaching behavior (Figs. 2, 3), which appears to be a male's attempt to make direct contact with the female, only occurs at the central-most region of the stimulus field.

Nature and Detection of Chemical Cues

Our observations suggest the chemical signal that triggers reproductive behavior is a substance of low volatility and high potency. Males responded strongly to sand that had been exposed to females for a brief period, and extracts of female cuticle dried onto sand and allowed to stand for 3 d were still capable of stimulating changes in locomotory behavior. Furthermore, extracts that produced vigorous behavioral responses (e.g. juddering) on contact during locomotion did not affect test animals from a distance. For instance, the response depicted in Fig. 3 occurred on the animal's second excursion, 39 min after release into the test arena. During the first excursion (26 min post-release) the animal remained in regions away from the treated quadrant, with no indication of behavioral change. These observations are consistent with those of ABUSHAMA (1964) who found no tendency for *Leiurus quinquestriatus* to be attracted to regions of a test chamber in which conspecifics were confined behind a wire gauze barrier. Thus, stimulus detection appears to require direct contact with a substrate bearing a non-volatile signal.

The sensory organs involved in pheromone detection in scorpions are unknown. Chemosensory sensilla are abundant on the cuticular surfaces of *P. mesaensis* and other scorpions but are most concentrated on the pedipalps, the tarsal leg segments and pectinal appendages (HOFFMANN 1967; FOELIX & MÜLLER-VORHOLT 1983; FOELIX & SCHABRANATH 1983; KRAPF 1986). In this regard the sexually dimorphic pectines may be of particular importance. We observed changes in substrate-sweeping activity of the pectines as males wandered in the field or moved across female-treated substrates in laboratory test arenas. During normal ambulatory movements the pectines are swept lightly over the substrate or brushed intermittently against the substrate as the animal pauses between forward movements. When adult males contact a female-exposed surface, pectine tapping increases in frequency and changes to longer sweeping movements over the substrate. These ventromedial sensory appendages support dense arrays of minute peg-shaped sensilla which are structurally similar to contact chemoreceptors found in other arthropods (CLOUDSLEY-THOMPSON 1955; BOECKH et al. 1965; HOFFMANN 1964, 1967; CARTHY 1966, 1968; IVANOV & BALASHOV 1979; FOELIX & MÜLLER-VORHOLT 1983). KRAPF (1986) noted that the pectines may be involved in chemosensory responses to prey. Anatomical and physiological studies of the pectines (BROWNELL 1988, 1989; GAFFIN & BROWNELL 1990) are consistent with the hypothesis that these are the primary chemosensory organs of scorpions and the ones most likely to be involved in detection of a substrate-borne pheromone.

Acknowledgements

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