

## Water detection in the desert sand scorpion, *Paruroctonus mesaensis* (Scorpionida, Vaejovidae)

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**Summary.** For the sand scorpion, *Paruroctonus mesaensis*, substrate moisture is a powerful and fast-acting stimulus of discrete behaviors related to localization and imbibitory uptake of water. These behaviors are readily observed in the field and quantified in the laboratory when free-roaming animals encounter sand substrates dampened by small amounts of water. Of 10 behaviors we monitored in laboratory tests, 5 (pedipalp-pull, rototiller-digging, prolonged stops, headstand, and backing-up) occurred only after contact with a moistened substrate. These water-stimulated behaviors were selectively blocked when all 8 tarsal leg segments were coated with wax; coverings of the chemosensory pectine appendages had little to no effect. Electrophysiological recordings from chemoreceptor organs on the tarsi showed that neurons innervating the dorsal tarsal organ, were highly sensitive to humid air stimuli while the numerous, pore-tipped hairs on the ventral surface were responsive to aqueous solutions applied directly to their tips. Selective blocking of the 8 tarsal organs had no effect on water sensitive behavior indicating that the chemosensory hairs mediate detection of substrate moisture. Such localized, sensory triggering of a robust and directed behavior presents a useful model for further neuroethological studies.

**Key words:** Scorpion – Water – Chemoreception – Behavior – Electrophysiology

### Introduction

Water is of obvious importance to all living things; its gain and loss are powerfully regulated, especially in spe-

cies living under chronic water stress. Desert arthropods have provided several interesting examples of physiological adaptations that conserve total body water by minimizing its rate of loss (Edney 1974; Hadley 1970, 1974), but less is known about sensory mechanisms for detection and orientation to substrate water or humid air (Altner et al. 1983; Steinbrecht 1984). Although sensory detection is a prerequisite for orientation to moist microenvironments, the mechanisms involved in the detection of water are likely to be diverse and difficult to localize experimentally.

In this regard, psammophilic scorpions, which live in the driest of desert environments, may be excellent subjects for sensory and behavioral analysis. Under normal circumstances these animals show a simple repertoire of locomotory behaviors which can be used in the field or laboratory to assess responsiveness to a variety of stimuli. Anecdotal field observations show that simulated rain or localized application of water to the substrate evokes unusual behavior from *Paruroctonus*, including en masse emergence from burrows and cheliceral-chewing of the dampened sand. Physiologically, water is a potent stimulus for chemosensory neurons in the pectines, two antenna-like, ventral appendages that intermittently touch the substrate as the animal walks (Brownell 1988; Gaffin and Brownell 1990). Additionally, on the tarsi of each leg there are numerous chemosensory hairs on the ventral surface and a single tarsal organ approximately mid-length along the dorsal surface (Foelix and Schabronath 1983). These organs are similar to those found in spiders where more extensive structural and physiological studies indicate they are chemoreceptors that may be sensitive to water (Foelix and Chu-Wang 1973; Dumpert 1978). Abushama (1964) demonstrated that sensitivity to humid air in the scorpion *Leiurus quinquestriatus* was destroyed by cutting off the terminal (tarsal) leg segments. This would suggest that sensory structures on the tarsus are necessary in water detection and that the pectines are not sufficient for triggering this mode of water-orientating behavior.

**Abbreviations:** *H* headstand; *PP* pedipalp-pull; *RD* rototiller-digging; *B* backing-up; *C* wall-climbing; *P* pause; *W* walk-through; *S* stop; *T* turn; *R* rest; *PST* pacific standard time; *SEM* scanning electron microscopy

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In this study we have examined the behavioral responses of *P. mesaensis* as they encountered localized areas of water-dampened sand in a test arena. We describe several stereotyped behaviors stimulated by substrate water and use electrophysiological procedures to determine which of the tarsal sensory organs are responsive to water and humid air.

## Materials and methods

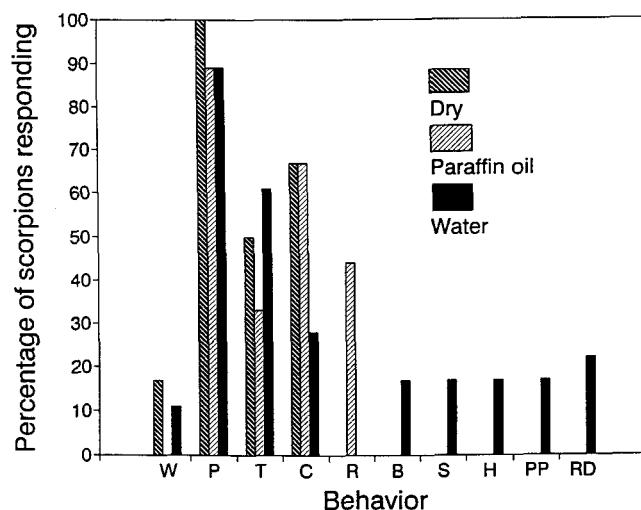
The animals used in this study were adult male and female *Paruroctonus mesaensis* collected from the Mojave Desert near Indio, California in San Bernadino County. They were housed in an environmental chamber (27 °C; 15:9 L/D) in individual containers of clear plastic containing sand from the site of capture and fed biweekly with wax worm larvae (Northern Bait Co., Chetek, WI).

All behavioral observations were recorded by a video camera (Sony V9, 8 mm format) using ultraviolet light (15 W fluorescent black lights) to illuminate the test site; scorpion cuticle fluoresces bright yellow-green under UV illumination giving sharp video images of their movements in the dark without noticeably disrupting their behavior. All trials were conducted in cylindrical arenas of clear plexiglas (13.5 cm in diameter, 8 cm in height) placed over natural desert sand that had been cleaned by baking (220 °C, 2 h) after each use. For 15 min prior to the beginning of each trial each test animal was confined to one quadrant (randomly determined) of an arena by an opaque partition. At the end of this adjustment period a stimulus substance (0.5 ml water or paraffin oil) was placed in the quadrant opposite the scorpion and the partition removed. All trials were carried out in a darkened room and the camera and arenas were enclosed in a black felt tent to reduce visual cues for orientation. Trials were recorded 4 at a time, and the tapes were subsequently reviewed and scored by an observer unaware of the experimental treatments for each trial. A trial ended after 2 h or after an animal had occupied the quadrant for 3 min (cumulative time).

For ablation experiments, behaviors of experimental (sense organs covered) and control (unaffected) animals were scored each time they crossed the site of water application. Scores were assigned as follows: 0, no behavior change; 1, altered behavior (non-specific); 2, altered behavior (water-specific). A trial ended after 2 h or 10 crossings of the stimulus application site unless a score of 2 was achieved in which case the trial was terminated immediately. A minimum of 2 crossings were required for a legitimate trial. For each trial the cumulative score for an animal was divided by the number of crossings it made of the treated site. This response index for individuals was rank-ordered and differences between experimental and control groups were tested for significance by Mann-Whitney analysis.

For electrophysiological investigations, scorpions of either sex were paralyzed by cooling and immobilized in a recording chamber using wax. Electrolytically-sharpened tungsten electrodes were inserted at the tip of the tarsus (indifferent electrode) and through the cuticle of the tarsal organ (Fig. 5) or at the base of single chemosensory hairs on the tarsus (recording electrodes). Alternatively, saline filled (10–150 mM NaCl) glass electrodes slipped over the tips of individual hairs (Fig. 4) were used to detect the presence of water and/or salt sensitive units within these structures. Electrical signals were amplified and stored on audio cassette tapes for subsequent playback and computer analysis (TSG software, Gaffin and Jubran 1991).

Scanning electron microscopy was of unfixed tarsal cuticle lightly coated with gold and viewed at 7 kV in an AmRay 1000A SEM. In most instances the cuticle surface was cleaned by applying a thin layer of polyethylene film (Hobby Technik, W-7850 Lörrach, Germany) and stripping-off the hardened shell once it dried.



**Fig. 1.** Behavioral responses of *P. mesaensis* to dry sand ( $n=6$ ) and sand moistened with water ( $n=18$ ) or paraffin oil ( $n=9$ ). For each treatment group, histogram bars show percentage of animals displaying each of 10 behaviors: Walk-through (W); Pause (P); Turn (T); Pedipalp-pull (PP); Rototiller-digging (RD); Stop (S); Headstand (H); Wall-climbing (C); Backing-up (B); Rest (R)

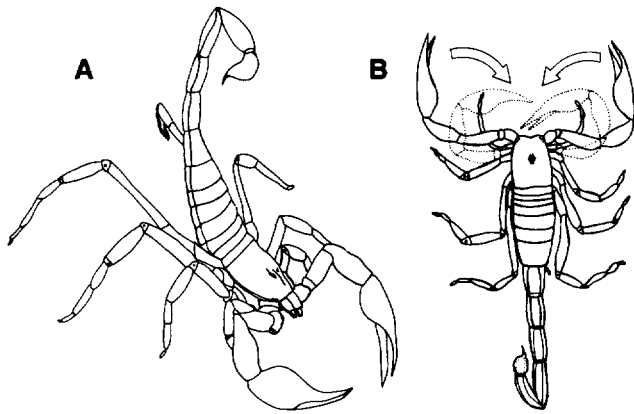
## Results

### Behavioral responses to water

In its natural environment and in captivity, *P. mesaensis* is a nocturnal animal showing peak locomotory activity from 1 to 5 h after sunset (Polis 1980). In the course of these studies we found that animals tested in the late afternoon to early evening (1700 to 2100 PST, Fig. 1) were less responsive to water stimulation than animals tested after 2100 (normal controls in ablation experiments; 27.8% vs. 63.6%, respectively). Nevertheless, significant changes in behavior could be observed at all times.

For the initial description of water stimulated behavior, 10 discrete activities were monitored as each test animal was released from confinement in the test arena. Animals were observed to walk-through (W) a test quadrant without showing overt changes in behavior, or to pause (P) locomotion for less than 2 min or stop (S) for longer time in an alert, standing posture; stops with the body resting on the substrate, usually with the post-abdominal segments and legs retracted, were scored as rests (R). Turns (T) to the left or right, backing-up (B) and wall-climbing (C) were other locomotory behaviors monitored during the test period. When responsive animals encountered dampened sand they displayed several stationary behaviors: headstands (H), where the pre- and post-abdomen were elevated as the chelicera and pre-oral cavity were pressed to the substrate (Fig. 2A); pedipalp-pull (PP), where sand is pulled toward the mouth by the pedipalps (Fig. 2B); and rototiller-digging (RD), where rotary movements of the first 3 leg pairs scrape surface sand away.

As shown in Fig. 1, 5 of the 10 behaviors we scored were only observed when animals encountered water-



**Fig. 2A, B.** Behaviors associated with water detection in sand scorpions. **A** In Headstand behavior, scorpions elevate posterior body segments and tail above the substrate, pressing the pre-oral cavity into the sand while chewing it with the chelicera. **B** In Pedipalp-pull behavior the pedipalps sweep surface sand toward mouth

dampened sand ( $n=18$ ); these behaviors (PP, H, RD, S and B) were not observed in control trials ( $n=6$ ) or trials where non-aqueous material (paraffin oil) was used to wet the sand ( $n=9$ ). Three of these behaviors (PP, H, S) appear to be strictly related to water stimulation while two behaviors (B, RD) have also been observed when animals encounter pheromonal stimuli on the substrate (Brownell 1988; Gaffin and Brownell, in press).

Water responsive animals showed a stereotypical sequence of behaviors when they encountered a small spot of dampened sand. This was characterized by cessation of forward locomotion and initiation of Turning or Backing-up until the chelicerae were directly over the moist sand. At this point the animal would Stop, in some instances for more than 1 h, or immediately display Pedipalp-pulls and Headstand behaviors, often in succession. The PP/H sequence was sometimes interrupted by Backing-up or Rototiller-digging.

#### Localization of water receptors

Since the behavioral responses to water appear to require direct contact with dampened substrate, we conducted a series of behavioral tests on animals with blocked chemosensory organs. The most important contact chemoreceptor organs for *P. mesaensis* are the pectines and a dispersed group of chemosensory hairs on the ventral and lateral surfaces of each tarsus. The numbers of ventro-lateral chemosensory hairs vary between 23 (1st leg tarsi) to 14 (4th leg tarsi) in accordance with anterior-posterior gradient first observed by Foelix and Schabronath (1983) for two species of buthid scorpions. Additionally, each tarsus contains a single tarsal organ on its dorsal surface, which does not contact the substrate directly, but may be sensitive to water vapor (Foelix and Chu-Wang 1973; Foelix and Schabronath 1983). Using various combinations of shrink tubing, low-melting temperature wax and organic adhesives it was possible to selectively block chemosensory function of the pectines,

**Table 1.** Statistical comparisons of water-stimulated behavior of scorpions (Response Index) with normal (unblocked) and selectively disabled sense organs (blocked pectines, tarsi or tarsal organs)

| Treatment             | <i>n</i> | Average Response Index (mean $\pm$ SE) | Z-value <sup>1</sup> |
|-----------------------|----------|--|----------------------|
| Unblocked (controls)  | 32       | 0.65 $\pm$ 0.11                        | —                    |
| Pectines blocked      | 7        | 0.47 $\pm$ 0.26                        | 0.231                |
| Tarsi blocked         | 14       | 0.25 $\pm$ 0.08                        | 0.023                |
| Tarsal organs blocked | 11       | 0.49 $\pm$ 0.20                        | 0.265                |

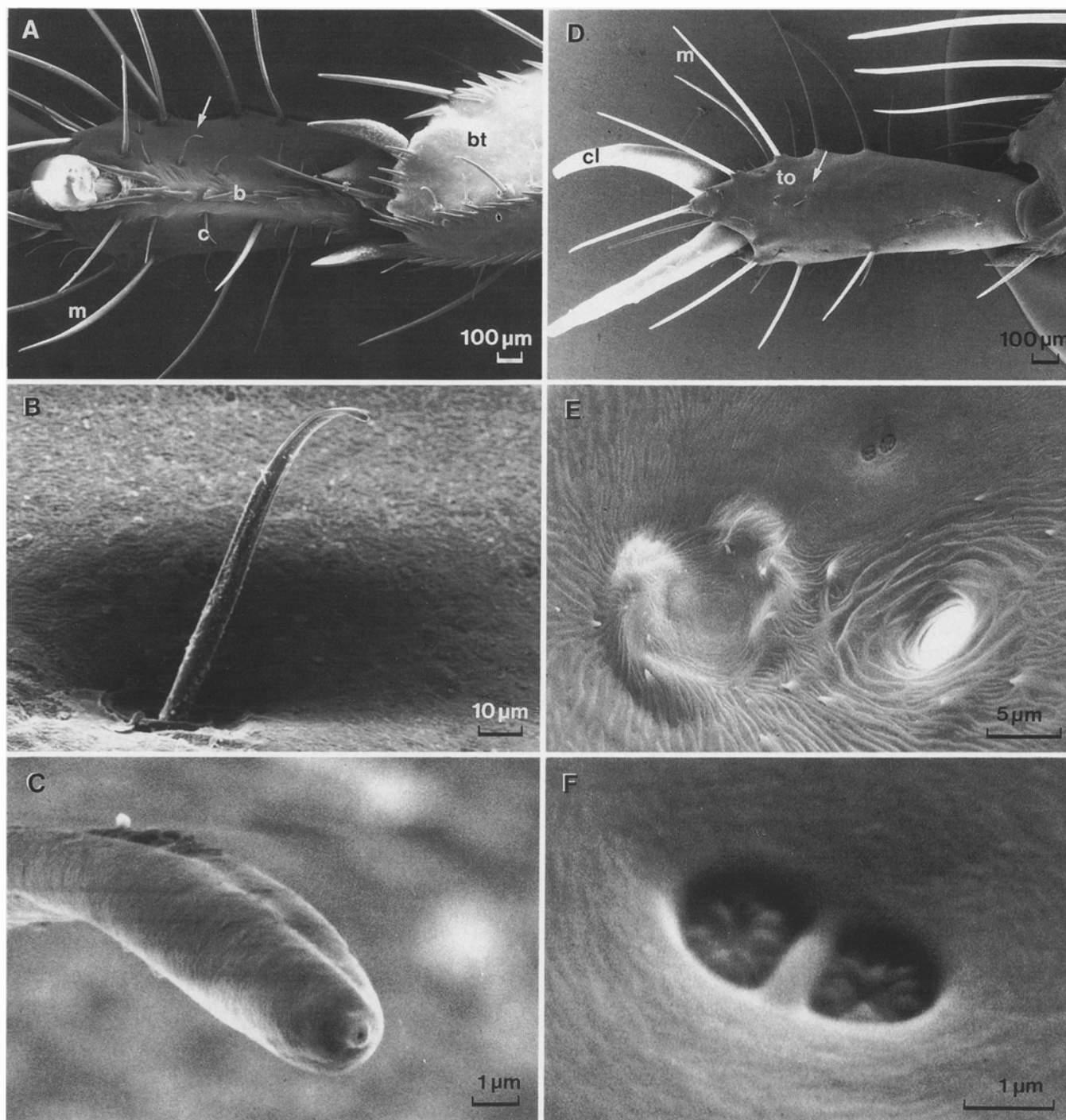
<sup>1</sup> From Mann-Whitney test comparing experimental and control groups

the entire tarsus or the tarsal organs, but the tarsal hairs were too numerous and small to be selectively ablated in this fashion.

As shown in Table 1, blocking of pectinal input had little to no effect on water-sensing behavior; these animals continued to orient to damp substrates and to display one or more of the water-specific behaviors (PP, H, S). Selective blocking of the tarsal organ also had no apparent effect on the threshold or expression of these behaviors. Selective ablation or blocking of tarsal chemosensory hairs was not practical, although covering all chemosensory structures on the tarsi significantly blocked water sensitivity without interfering with normal ambulation and searching behavior. The unique importance of tarsi for water detection was confirmed by retrospective examination of video-taped records of responding animals; tarsal contact with the dampened substrate nearly always preceded initiation of water-specific behaviors in these trials.

#### Anatomy of tarsal chemoreceptors

To further localize and identify the tarsal receptors involved in water detection, we used scanning electron microscopy (SEM) to characterize their gross structure and standard electrophysiological procedures to record unitary sensory responses from chemosensory hairs and the tarsal organ. Individual hairs were approximately 100  $\mu$ m long and 7  $\mu$ m in diameter at their base and protruded from a cup-shaped socket approximately 25  $\mu$ m in diameter; most possessed a distinct 30°–90° bend in their shaft near the tip (Fig. 3A, B). SEM inspection clearly showed each of these hairs contained a single, terminal pore approximately 0.1  $\mu$ m in diameter (Fig. 3C). Tarsal organs were readily identified as indentations (10  $\times$  30  $\mu$ m) of the dorsal tarsal cuticle with two morphologically distinct pores spaced approximately 20  $\mu$ m apart (Fig. 3C, D). The larger of the pair (Fig. 3D) has a 4  $\mu$ m diameter opening similar to wax-secreting ducts of other scorpions (Hadley, pers. comm.). The second pore consisted of two D-shaped openings, each approx 1  $\mu$ m diameter, that were occluded internally (Fig. 3E). By appearance, these structures appear to be specialized cuticular sensilla and, thus, the source of the physiological recordings discussed below.



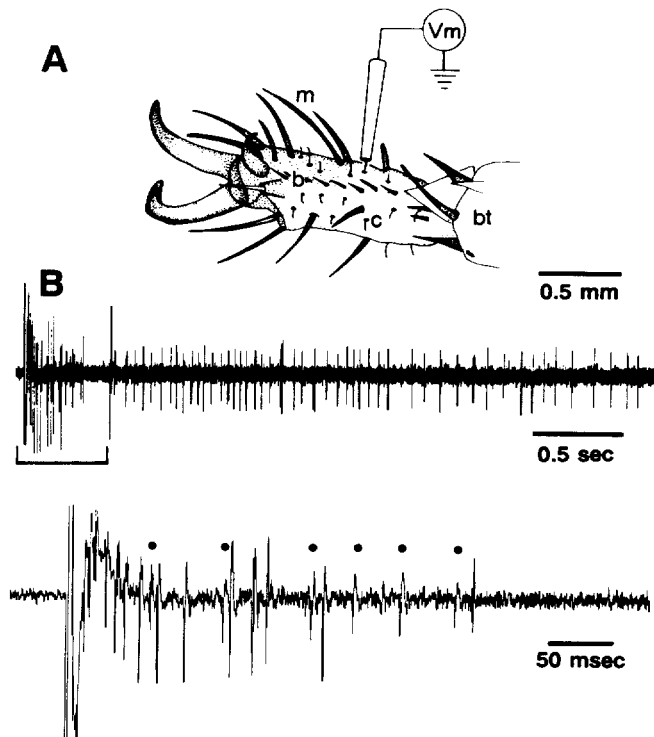
**Fig. 3A–F.** Scanning electron micrographs of tarsal chemosensory sensilla in *P. mesaensis*. **A** Tarsus leg 2, ventral view. **B** Chemosensory hair sensillum (arrow in **A**) showing characteristic curve in hair shaft and single terminal pore (**C**). **D** Tarsus leg 2, dorsal view. **E** Expanded view of tarsal organ (arrow in **D**) showing two distinct

pore morphologies. The larger pore, possibly a wax secreting duct, appears open while the second double-pored opening (**F**) has fine structure of a chemosensory pore. *c* chemosensory hairs; *to* tarsal organ; *m* mechanosensory hairs; *bt* basitarsus; *b* bristle hairs; *cl* claws

### Electrophysiology

The small, curved hairs on the ventral surface of the tarsi contain both mechano- and chemosensory neurons. Extracellular recordings with metal electrodes inserted at the base of these hairs showed each contained at least one unit responsive to deflections of the hair shaft, but unit

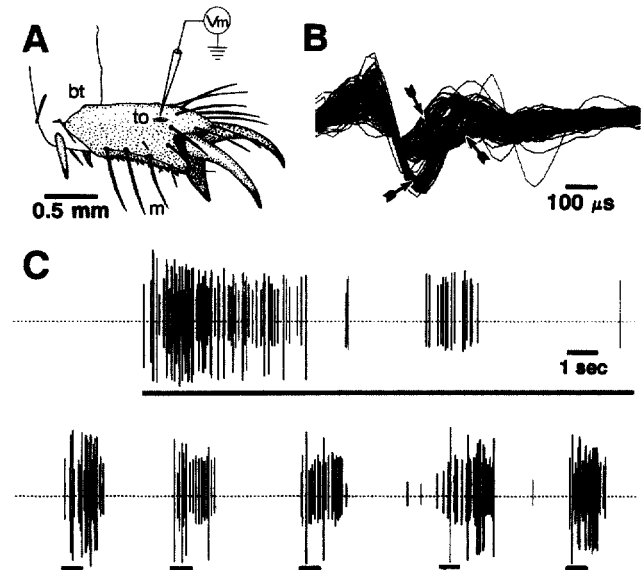
responses to aqueous solutions applied to the hair tip were not well resolved in this recording configuration. Chemosensory units were more clearly seen when glass electrodes containing dilute saline solutions were slipped over the hair tip (Fig. 4). Figure 4B shows the initial seconds of spiking activity after a recording electrode containing 150 mM NaCl made contact with a hair tip.



**Fig. 4A, B.** Electrophysiological response of tarsal chemosensory hairs. **A** Ventral-posterior view of left first tarsus showing location of chemosensory hairs (*c*) and placement of single hair within bore of saline-filled recording pipette. *m* mechanosensory hairs; *bt* basitarsus; *b* bristle hairs. **B** Initial sensory response of sensory hair to contact with 150 mM NaCl solution in recording pipette. Top trace shows first 3 s of electrical activity; bracket indicates initial 0.5 s of response expanded and displayed in bottom trace. Artefact at beginning marks time of stimulus application. A fast adapting (<200 ms) unit of large amplitude can be seen in lower trace along with brief activity of a smaller unit (indicated by dots). A third unit, showing a tonic pattern of excitation, becomes active 0.5 s after stimulus application

At least two distinguishable units were transiently excited within the first 0.5 s of contact (lower trace) while other units showed more delayed and sustained responses (upper trace, Fig. 4B). Mechanosensory units in recordings from the hair tip were easily triggered and distinguished from the chemosensory responses by deflecting the hair shaft side to side with the recording electrode. Tip recordings using saline of lower ionic strength (10, 50, and 100 mM NaCl) gave similar responses indicating that water as it occurs naturally on dampened sand would excite these units.

Extracellular recordings from the tarsal organ (Fig. 5) were obtained by impaling the cuticle near this depression with a bluntly-tapered metal electrode. Sensory neurons in the tarsal organ were notably silent in the absence of stimulation which made it difficult to position the recording electrode. When properly positioned, at least 3 units (Fig. 5B) were highly responsive to humid air stimuli presented either as moist breath blown over the organ or as a moist cotton swab brought to within 1 cm of the tarsus. Spike activity of these units adapted quickly to sustained stimulation (Fig. 5C, top trace) and re-



**Fig. 5A–C.** Electrophysiological responses of tarsal organ stimulated by humid air. **A** Dorsal-posterior view of right second tarsus showing placement of metal electrode through cuticle near tarsal organ (*to*). *m* mechanosensory hair; *bt* basitarsus. **B** Superimposed spike wave forms recorded from tarsal organ during stimulation with humid air. Arrows indicate the presence of at least 3 different spike classes within these records. **C** Computer filtered records (20 s duration) of spiking activity of tarsal organ to near-range water stimulation. *Top trace*: water on tip of a paper swab held stationary 1 cm from the tarsal organ. *Bottom trace*: water on swab tip brought within 1 cm of organ, withdrawn, and returned for 5 repetitions. Black bars indicate approximate duration of stimulus

covered sensitivity rapidly between presentations (Fig. 5C, bottom trace) indicating this is a phasic receptor. These neurons were also strongly excited by direct application of water to the tarsal organ pit even though this mode of stimulation probably does not occur when the tarsus comes in contact with dampened sand substrates.

## Discussion

Our results indicate that point sources of dampened sand release a series of stereotyped behaviors in *P. mesaensis* directed toward localization and imbibition of substrate-associated water. Selective masking of candidate water receptors gave behavioral evidence that chemosensory hairs on tarsal leg segments are the most important sensory structures for detection of substrate moisture. Morphological and physiological analysis of these sensilla further support our conclusion that the robust behaviors associated with water localization and uptake are triggered by this relatively simple and localized sensory system.

Like many desert arthropods, *P. mesaensis* is under chronic water stress in its natural dune environment (Hadley 1970). Although standing surface water or dampness rarely occurs on sandy substrates, behaviors that increase the likelihood of finding and utilizing ingestible water may have adaptive value for animals that encounter infrequent rainstorms. Hadley's (1971) field

observations of *Centroides sculpturatus* show it is capable of imbibition of standing water and Polis and Seely (1990) have observed *Parabuthus villosus* drinking precipitated fog in the Namib Desert. In the current study the stereotyped Headstand and Pedipalp-pulling behaviors were clearly discernable attempts to bring dampened sand to the vicinity of the mouth.

In addition to detection of substrate water, our electrophysiological investigations of *P. mesaensis* indicated the tarsal organs are very sensitive to water vapor and may mediate orientation to high-humidity environments. In this regard, it is noteworthy that the burrows of *P. mesaensis* maintain a steep humidity gradient ranging from almost 0% near their entrances to near saturation 30–50 cm below the sand surface (Edney et. al. 1974; Polis and Farley 1980). Previous studies by Abushama (1964) on *Leiurus quinquestriatus* show that these animals were capable of orienting to humidity gradients and that ablation of the tarsi on all legs destroys this sensitivity. Stahnke (1966) observed that ground scorpions living in desert washes follow the receding moisture line as summer progresses, indicating the preference for higher humidity microclimates is expressed behaviorally in the field. These results indicate the tarsal organs are likely to be essential for such detection.

The location of chemosensory hairs on the ventral surfaces of the tarsi is appropriate for detection of substrate moisture and close examination of the behavioral responses reported here confirm this view. In one instance we observed a responding animal as it contacted a small spot (50  $\mu$ l) of water with its second right leg. This animal immediately turned to the right, found the precise location of the moisture, and began performing Pedipalp-pulls. The location and size of tarsal chemoreceptive sensilla in *P. mesaensis* were similar to that described by Foelix and Schabronath (1983) for two species of buthid scorpions although *P. mesaensis* had fewer sensilla per tarsus and gradation in number between first and fourth leg pairs was not as steep as in the buthids. It remains to be determined, however, if functional and/or morphological differences exist among these hairs as described for chemosensory hairs of insect tarsi (Dethier 1976). The buthid chemosensory hairs are innervated by 22–23 bipolar neurons, 4 of which terminate at the hair base in a manner typical of mechanoreceptor cells (Foelix and Schabronath 1983). Our electrophysiological investigations are consistent with this arrangement since recordings made from the base of individual hairs showed units distinctly responsive to deflection of the hair shaft while tip recordings with saline-filled electrodes did not show large-amplitude mechanoreceptor responses. Analysis of extracellular action potential wave-forms for water responsive units revealed 3 or more distinguishable units in tip recordings, many fewer than the number believed to innervate individual hairs. Other neurons in these sensilla are not spontaneously active and may require more specific stimuli for activation.

The dorsally-located tarsal organ does not come in direct contact with the substrate although its proximity to the surface and high sensitivity to humid air clearly

leave open the possibility of indirect detection of substrate moisture. Foelix and Schabronath (1983) describe the organ in buthid scorpions as a two-pored structure of unknown function situated inside a small oval depression of the cuticle ( $16 \times 22 \mu$ m). We found a similar depression in the dorsal tarsal cuticle of *P. mesaensis* and a double-pored opening (approx  $1 \times 3 \mu$ m) of unique appearance. This organ is most likely to be the source of hygrosensitivity detected in our physiological recordings. Direct contact of these pores with water (saline-filled electrodes as used in hair-tip recordings) produced vigorous multi-unit responses with summed spiking frequencies of approximately 180 nerve impulses/s for the first 200 ms which abruptly decreased to about 50 impulses/s for the following few seconds. Though such direct stimulation of the tarsal organ is unlikely to occur in freely behaving animals, the number of discrete units seen following strong stimulation of this kind is consistent with morphological description of 6 to 9 sensory neurons per pore (Foelix and Schabronath 1983).

Reversible blocking of the most elaborate chemosensory structure of scorpions, the pectines, had little to no observable effect on their water-sensing behavior. However, normal animals were observed to repeatedly sweep dampened areas with their pectines suggesting these mid-ventral appendages may be used secondarily to assay moisture content of the sand once it has been detected by the tarsi. Electrophysiological studies of individual chemoreceptive sensilla on the pectines are consistent with this view (Brownell 1988, 1989; Gaffin and Brownell 1990).

Thus, the sand scorpion, *P. mesaensis*, appears to have several independent sensory channels capable of detecting substrate-associated water and humid air. The tarsal chemosensory hairs are a small and particularly interesting subset of these receptors in that they are highly effective triggers for stereotyped behaviors associated with imbibition. Future neuroethological analysis of this sensory-motor association may reveal the integrative processes that direct and coordinate water-orienting behavior in this animal.

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## References

- Abushama FT (1964) The behaviour and sensory physiology of the scorpion *Leiurus quinquestriatus* (H. & E.). *Anim Behav* 12: 140–153
- Altner H, Loftus R, Schaller-Selzer L, Tichy H (1983) Modality-specificity in insect sensilla and multimodal input from body appendages. *Fortschr Zool* 28: 17–31
- Brownell PH (1988) Properties and functions of the pectine chemosensory system of scorpions. *Chem Senses* 10: 557
- Brownell PH (1989) Neuronal organization and function of the pectinal sensory system in scorpions. *Neurosci Abstr* 15: 1289
- Dethier VG (1976) The hungry fly. A physiological study of the behavior associated with feeding. Harvard University Press, Cambridge, pp 72–74
- Dumpert K (1978) Spider odor receptor; electrophysiological proof. *Experientia* 34: 754–755

- Edney EB, Haynes S, Gibo D (1974) Distribution and activity of the desert cockroach *Arenivaga investigata* (Polyphagidae) in relation to microclimate. *Ecology* 55:420–427
- Foelix RF, Chu-Wang I (1973) The morphology of spider sensilla. II. Chemoreceptors. *Tissue Cell* 5:461–478
- Foelix RF, Schabronath J (1983) The fine structure of scorpion sensory organs. I. Tarsal sensilla. *Bull Br Arachnol Soc* 6:53–67
- Gaffin DD, Brownell PH (1990) Electrophysiological studies of the pectinal chemosensory system of scorpions. *Chem Senses* 15:579
- Gaffin DD, Brownell PH (in press) Evidence of chemical signaling in the sand scorpion, *Paruroctonus mesaensis* (Scorpionida:Vaejovidae). *Ethology*
- Gaffin DD, Jubran I (1991) Turbo spike grabber: data capture and analysis software. *Biotechnology Software* 8:4–7
- Hadley NF (1970) Water relations of the desert scorpion, *Hadrurus arizonensis*. *J Exp Biol* 53:547–558
- Hadley NF (1971) Water uptake by drinking in the scorpion, *Centruroides sculpturatus* (Buthidae). *The Southwestern Naturalist* 15:504–505
- Hadley NF (1974) Adaptational biology of desert scorpions. *J Arachnol* 2:11–23
- Polis GA (1980) Seasonal patterns and age-specific variation in the surface activity of a population of desert scorpions in relation to environmental factors. *J Anim Ecol* 49:1–18
- Polis GA, Farley RD (1980) Population biology of a desert scorpion: survivorship, microhabitat, and the evolution of life history strategy. *Ecology* 61:620–629
- Polis GA, Seely MK (1990) Imbibition of precipitated fog by Namib desert scorpions. *J Arachnol* 18:362–363
- Stahnke HL (1966) Some aspects of scorpion behavior. *Bull So Calif Acad Sci* 65:65–80
- Steinbrecht RA (1984) Arthropoda: chemo-, thermo-, and hygroreceptors. In: Bereiter-Hahn J, Matoltsy A, Richards KS (eds) *Biology of the integument*, Vol. I. Springer, Berlin, pp 523–553