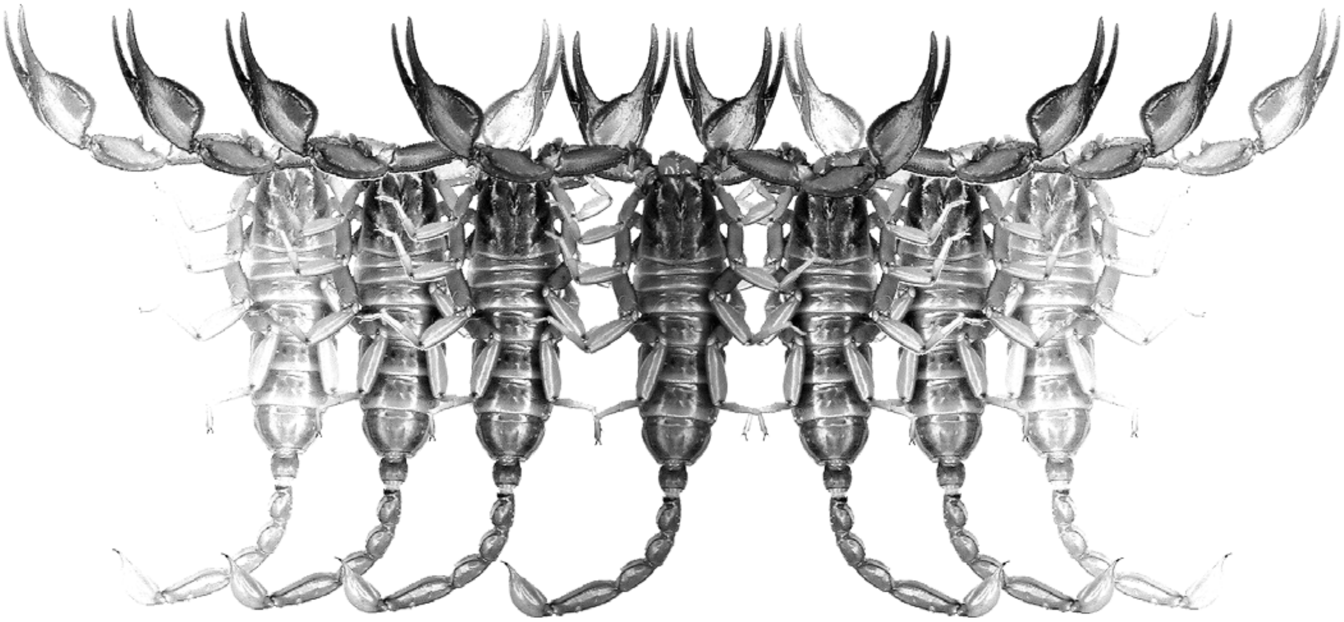
Euscorpius

Occasional Publications in Scorpiology



Proceedings of the 3rd Scorpiology Symposium

(American Arachnological Society,
28th Annual Meeting,
Norman, Oklahoma, June 24, 2004)

December 2004 – No. 17

Euscorpius

Occasional Publications in Scorpiology

EDITOR: **Victor Fet**, Marshall University, **'fet@marshall.edu'**

ASSOCIATE EDITOR: **Michael E. Soleglad, 'soleglad@la.znet.com'**

Euscorpius is the first research publication completely devoted to scorpions (Arachnida: Scorpiones). *Euscorpius* takes advantage of the rapidly evolving medium of quick online publication, at the same time maintaining high research standards for the burgeoning field of scorpion science (scorpiology). *Euscorpius* is an expedient and viable medium for the publication of serious papers in scorpiology, including (but not limited to): systematics, evolution, ecology, biogeography, and general biology of scorpions. Review papers, descriptions of new taxa, faunistic surveys, lists of museum collections, and book reviews are welcome.

Derivatio Nominis

The name *Euscorpius* Thorell, 1876 refers to the most common genus of scorpions in the Mediterranean region and southern Europe (family Euscorpiidae).

Euscorpius is located on Website **'http://www.science.marshall.edu/fet/euscorpius/'** at Marshall University, Huntington, WV 25755-2510, USA.

The International Code of Zoological Nomenclature (ICZN, 4th Edition, 1999) does not accept online texts as published work (Article 9.8); however, it accepts CD-ROM publications (Article 8). *Euscorpius* is produced in two *identical* versions: online (ISSN 1536-9307) and CD-ROM (ISSN 1536-9293). Only copies distributed on a CD-ROM from *Euscorpius* are considered published work in compliance with the ICZN, i.e. for the purposes of new names and new nomenclatural acts. All *Euscorpius* publications are distributed on a CD-ROM medium to the following museums/libraries:

- **ZR**, Zoological Record, York, UK
- **LC,** Library of Congress, Washington, DC, USA
- **USNM**, United States National Museum of Natural History (Smithsonian Institution), Washington, DC, USA
- **AMNH**, American Museum of Natural History, New York, USA
- **CAS**, California Academy of Sciences, San Francisco, USA
- **FMNH**, Field Museum of Natural History, Chicago, USA
- **MCZ**, Museum of Comparative Zoology, Cambridge, Massachusetts, USA
- **MNHN**, Museum National d'Histoire Naturelle, Paris, France
- **NMW**, Naturhistorisches Museum Wien, Vienna, Austria
- **BMNH**, British Museum of Natural History, London, England, UK
- **MZUC**, Museo Zoologico "La Specola" dell'Universita de Firenze, Florence, Italy
- **ZISP**, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia
- **WAM**, Western Australian Museum, Perth, Australia
- **NTNU**, Norwegian University of Science and Technology, Trondheim, Norway

---

Publication date: 24 December 2004

Euscorpius — Occasional Publications in Scorpiology. 2004, No. 17

Proceedings of the 3rd Scorpiology Symposium

(American Arachnological Society,
28th Annual Meeting,
Norman, Oklahoma, June 24, 2004)

Table of Contents

Preface

Scorpions (Arachnida: Scorpiones) have been slowly emerging since the 1950s as the excellent and exotic animal model group, not only to be feared due to their high mammal-specific toxicity but also exhibiting a veritable smorgasbord of unique features—such as true viviparity, blatant cannibalism, unbelievably high densities, amazing chemosensory systems and circadian clocks, amorous square dancing, etc. etc., topped by the psychedelic fluorescence under UV light. This list undoubtedly can, and will, be continued.

I.

The first idea to host a symposium specifically dedicated to scorpions came to Dr. Jerry Rovner who suggested, in his letter to Gary A. Polis dated 30 July 1984, that such a symposium could be a part of the (ninth) Annual Meeting of the American Arachnological Society (AAS) in 1985. Rovner wrote:

> "…My hope is to have much or all of one afternoon of papers at the Los Angeles meeting next year devoted to scorpions. This may well be identified as the first such symposium on the biology of scorpions in the U.S.A…."

In his reply, Gary Polis confirmed: "This will indeed be the first formal symposium on the biology of scorpions". The enthusiastic response from Dr. Polis, and his great organizational and interpersonal skills, resulted in **the first "Scorpion Symposium**" held in Los Angeles County Museum of Natural History, on **June 25, 1985.** Foreign scientists were represented by Wilson Lourenço (France) and Guenther Fleissner (Germany).

Here is the list of presentations at the Los Angeles symposium (**12 talks by 12 authors**):

Due, D. The biology of *Vaejovis littoralis* Williams, an intertidal scorpion from Baja California, Mexico.
Farley, R.D. Innervation and pharmacology of the heart of the desert scorpion, *Paruroctonus mesaensis* Stahnke.
Fleissner, G. The circadian clock of the scorpion: a challenge to neurobiology.
Francke, O.F. Life history strategies: inter- and intraspecific trends.
Hadley, N.F. Scorpion cuticle: a structure-function analysis.
Lourenço, W.R. Systematics and biogeography of some Neotropical scorpions.
Myers, C. A. Burrowing biology and spatial distribution of desert scorpions.
Polis, G.A. Competition and predation among desert scorpions.
Root, T.M. The neural control of scorpion locomotion.
Sissom, W.D. Phylogeny of the Vaejovidae (Arachnida: Scorpiones): preliminary synthesis.
Stockwell, S.A. & O.F. Francke. The scorpions of Costa Rica.
Toolson, E.C. Reproductive biology of scorpions.

Abstracts of this symposium were published in *American Arachnology* newsletter No. 32 (October 1985). It has to be noted that some of the scorpion scientists presented at the first (Los Angeles scorpion symposium were authored of the chapters in the famous 1990 book, edited by Gary A. Polis, *The Biology of Scorpions*. (Stanford, California: Stanford University Press, 587 pp.).

II.

The **second symposium** devoted to scorpions was organized in 1991 by Gary Polis and Philip Brownell under the title "Scorpions as Model Biological Systems". It was, however, not affiliated with AAS but instead was a part of the Annual Meeting of the American Society of Zoologists (now Society of Integrative and Comparative Biology) in Atlanta, on **December 28, 1991**. Five foreign zoologists were represented: Locket (Australia), Lourenço (France), Mahsberg, and Gerta and Günther Fleissner (Germany). The following **14 talks and posters by 15 authors** were presented:

Brownell, P.H. Sensory specialization of a nocturnal predator.
Brownell, P.H. Organized central mapping of chemosensory systems in two arachnid orders (Scorpionida, Solpugida) (poster)
Gaffin, D.D. Scorpion pectines: a model system for physiological studies of olfaction and taste.

Farley, R.D. Regulation of internal organs and tissues.
Fet, V. Molecular approaches to biogeography.
Fleissner, G. & G. Fleissner. What scorpions tell us about the organization of circadian rhythms.
Hadley, N. Scorpions as experimental models for studies of water and metabolic relations.
Gaffin, D.D., L.L. Wennstrom & P.H. Brownell. Water detection in the desert sand scorpion *Paruroctonus mesaensis* (poster).
Locket, A. Scorpion eyes.
Lourenço, W.R. Scorpion species biodiversity in tropical South America and its application in conservation programs (poster).
Mahsberg, D. Scorpion sociobiology and the evolution of sociality in arthropods.
Polis, G.A. Scorpions as model vehicles to advance theories of population and community ecology.
Root, T.M. Scorpion locomotion as a model system (poster).
Sissom, W.D. Scorpions as tools in historical biogeography.

Many of the studies by those who presented at the 1991 Atlanta symposium or attended it were published in 2001 as chapters in another scorpion book, edited by Philip H. Brownell and Gary A. Polis, *Scorpion Biology and Research*. (Oxford, UK: Oxford University Press, 448 pp.).

Tragically, Gary did not live to see this book. His marvelous personality and rich ideas, however, continued to inspire the next generation of scorpion scientists.

III.

Almost 12 years after the second scorpion symposium, an opportunity for the **third** one emerged. It was organized by Douglas D. Gaffin and held on **June 24, 2004** at the University of Oklahoma (Norman, Oklahoma, USA) as a part of the 28th Annual Meeting of the American Arachnological Society. This symposium (addressed in the program of the meeting as a “Scorpiology Symposium”), included **19 talks and posters by 27 authors**, which made it the most representative symposium on scorpions ever conducted. The majority of the authors were from the USA, with four foreign collaborators: Gantenbein (Switzerland), Gromov (Kazakhstan), Grothe (Germany), and Stathi (Greece).

The abstracts of all presentations of this AAS meeting are to be published online in *American Arachnology*, No. 70 (http://www.americanarachnology.org/AAS_AA.html).

Below follows the list of the presentations of the 2004 symposium, which we suggest to designate, for preservation of continuity, as the “*3d Scorpiology Symposium*”:

Bost, K.C. & D. D. Gaffin. Proposal: behavioral assay to identify the important sensory cues involved in sand scorpion navigation to their home burrows.
Brown, C.A. Compensatory growth in the scorpion *Centruroides vittatus.*
Brownell, P.H. & B. Grothe. Vibration sensing in sand scorpions, slit by slit to the CNS.
Farley, R.D. A comparison of ventral mesosomal changes in scorpion embryos.
Formanowitz, D.R., Jr. The adaptive value of the scorpion’s sting.
Fet, V., M.E. Soleglad, D.P.A. Neff & I. Stathi. Tarsal armature in the superfamily Iuroidea (Scorpiones: Iurida) (poster).
Fet, V., M.E. Soleglad & B. Gantenbein. The Euroscorpion: genus *Euscorpius* (Scorpiones: Euscorpiidae).
Fet, V., M.E. Soleglad, B. Gantenbein & E.V. Fet. Systematics and molecular phylogeny of *Euscorpius* from the Julian Alps of Slovenia (Scorpiones: Euscorpiidae) (poster).
Fet, V., M.E. Soleglad & A.V. Gromov. The platypus of a scorpion: genus *Pseudochactas* (Scorpiones: Pseudochactidae).
Habibulla, M. Studies on the brain modulation of circadian rhythms in the scorpion *Heterometrus swammerdami*.
Henson, R. Scorpion diversity of two desert islands in the Northern Chihuahuan Desert.
Porterfield, J.Z. & D.D. Gaffin & C. Porterfield. Screening for scorpions: a non-invasive approach to tracking the movements of arachnids in sand.
Santiago-Blay, J.A., V. Fet, M. E. Soleglad & S.R. Anderson. A new genus and subfamily of scorpions from Cretaceous Burmese amber (Scorpiones: Chaerilidae) (poster).
Shultz, J. New perspectives on the skeletomuscular anatomy of the scorpion prosoma.
Gaffin, D.D., P. McGowan & M.E. Walvoord. Scorpion peg sensilla: are they the same or are they different?

Miller, A. Genetic variation in *Paruroctonus boreus* and data suggesting the possible sister taxa.
McKee, R. & D.D. Gaffin. Non-visual orientation of sand scorpions (poster).
McReynolds, C.N. Temporal patterns and microhabitat use for the scorpion *Centruroides vittatus.*
Yamashita, T. Surface activity, biomass, and phenology of the striped scorpion, *Centruroides vittatus* in Arkansas.

A selection of seven papers, based on some of the talks presented at Norman, is published on the following pages as the "*Proceedings of the 3d Scorpiology Symposium*". We hope that both the Symposium and these Proceedings will serve to further promote the study of various aspects of scorpion biology, and collaboration among the world's scorpion scientists. We thank everybody who contributed to this Symposium and the Proceedings. We also thank Jerry Rovner for sharing with us the historical documents of his correspondence with Gary Polis.

Victor Fet, Douglas D. Gaffin

Euscorpius — **Occasional Publications in Scorpiology. 2004, No. 17**

Sand scorpion home burrow navigation in the laboratory

Karen C. Bost[1] and Douglas D. Gaffin[1]

[1]Department of Zoology, University of Oklahoma, Norman, OK 73019-0235, USA

Summary

Many organisms can navigate their return to a previously experienced location. This ability is beneficial and often a necessary component of an organism's life strategy. Sand scorpions (*Paruroctonus utahensis*, Vaejovidae) typically leave their home burrows at night and subsequently return, suggesting navigational capabilities. Sand scorpions present an ideal system for navigational study in that they exist in ecologically simple dune environments, are abundant, are easily obtained, are easily maintained in the laboratory, and fluoresce under ultraviolet light. Additionally, behavior observed in the laboratory is generally consistent with that observed in the field, allowing comparable laboratory and field study. The work presented in this paper is a laboratory setup in which scorpions successfully navigate to their established home burrow. The ability to induce scorpion navigation in a laboratory setting will be useful in future study. Using this design, scorpion navigation can be assessed when navigational cues are present absent or manipulated.

Introduction

Navigation to a previously experienced location is an ability that has independently evolved throughout the zoological taxa. Convergent behavioral evolution across phylogenetically distinct taxa suggests an associated selective advantage. Undoubtedly, the ability to return to a desirable location such as a good food source, a successful mating location, or a site of refuge is advantageous.

Several different navigational mechanisms have been described in a variety of organisms. Many of these studies have focused on various arthropods owing to their large radiation and consequent, diversity of navigational abilities (for review see Wehner, 1992). Arthropods are model organisms for study in that they offer a variety of mechanisms to study in nearly every habitat.

Psammaphilic scorpions are ideal for navigational study in that they are abundant, easy to obtain, and easily maintained in the laboratory, and they live in environments which are comparatively ecologically simple. Among their most spectacular features is that they fluoresce under ultraviolet light, providing a built-in tracking mechanism for these nocturnal animals.

Although behavioral studies of scorpions are rare, the desert scorpion *Smeringurus mesaensis* (Stahnke, 1957) (Vaejovidae) occurring in the Mojave Desert of southern California has been the focus of several behavioral studies. These scorpions leave their home burrows at night to forage and subsequently return to the same burrow, suggesting navigational capabilities (Polis et al., 1985). Females and immature males use the same home burrow for long periods and may travel several meters away, although they typically remain within a meter of their burrow (Polis et al., 1985).

The sand scorpion *Paruroctonus utahensis* (Williams, 1968) (Vaejovidae) is a related species with a largely similar niche. These scorpions live in sandy burrows in shifting sand environments throughout Chihuahua (Mexico), northern Arizona, New Mexico, Utah, and western Texas (Sissom, 2000). Numerous field observations have indicated that *P. utahensis* scorpions exhibit similar homing behavior (Gaffin, pers. comm., pers. obs.). Following a disturbance, scorpions usually remain motionless for a brief period of time and then move short distances with intermittent pauses and frequent directional changes. This behavior occurs for a brief period of time (30 sec-5 min) and is followed by a rapid movement to the burrow with only minor deviations from a direct path. Complementing its homing ability, prior study of sand scorpion behavior has shown that behavior observed in the laboratory is generally consistent with that observed in the field, allowing comparable laboratory and field study (Gaffin & Brownell, 2001). These characteristics make *P. utahensis* a model organism for navigational study.

To understand how sand scorpions navigate to their home burrow, we must determine which environmental cue(s) they exploit for directional information in their home bound journey. We aim to design in a system in which scorpion navigation can be successfully induced in the laboratory. Once such a system is established, navigational ability can be reassessed with manipulated and/or deleted sensory cues. A loss of navigational ability in the absence or manipulation of a particular environmental cue will suggest dependence.

Methods

Scorpion collections and care

Paruroctonus utahensis specimens were collected from Winkler County Park northeast of Kermit, Texas, in fall of 2003 and summer of 2004. Scorpions were maintained in the laboratory with temperature ranging from 78-86°C with relative humidity ranging from 35%-45% and a light-dark phase of 2000-0700 h dark and 0700-2000 h light. Scorpions were housed in 3.8 L glass jars containing approximately 4 cm sand from their collection site and a broken piece of flowerpot clay. Scorpions were routinely fed crickets and given water in the form of a diffuse spray which lightly moistened the sand surface.

Home burrow navigation experiments

Experimental arenas: Experiments were conducted using 15 individual circular arenas, each with a diameter of 76 cm and a height of 30.5 cm. Arena bottoms were constructed of medium density fiberboard, and the sides were composed of translucent acrylic. Each arena floor was covered with 4 cm sand from the collection site. A hanging 20-watt 120-volt halogen light was positioned 60 cm above the center of each arena. The lights were set to a light-dark phase of 1700-0400 h dark and 0400-1700 h light. A cylinder (15 cm diameter and 8 cm tall) was positioned at random along the outer wall of each arena (Fig. 1). These cylinders were used to confine scorpions to a small portion of the larger arena. A broken piece of flowerpot was placed in the middle of each cylinder to encourage scorpion burrow formation.

Experimental preparations: Six days prior to each experimental trial, a recently fed scorpion was placed inside each home cylinder and allowed to form a home burrow. Two days prior to each trial, the cylinders were removed, allowing the scorpion to explore the remainder of each arena at will. Each afternoon before the burrow lights turned off, the sand within each burrow arena was lightly sprayed with water, providing the surface texture conductive to burrow formation.

Experimental procedure: Experiments occurred in the laboratory at the University of Oklahoma in summer of 2004. Prior to trial, scorpions were removed from each arena and placed individually in black film canisters. Each canister was rotated 360° five times and placed in the middle of each respective arena for at least 5 minutes. Arena sand was not disturbed, allowing any potential visual or chemical cues to remain, but arena lights were dimmed to encourage scorpion movement. Trials began immediately after film canisters were removed, leaving scorpions in the center of each arena. Scorpion activity was videotaped using a Sony Digital Video Camera Recorder (DCR-TRV 120) suspended from the ceiling on a rope pulley system in nine separate filming sessions, each session filming the activity in one or two arenas at a time. The camera's infrared Night Shot capability was used during recording due to the dim lighting. The camera was connected to a color television monitor in the adjacent room for immediate viewing by the experimenters. Scorpion directional choice was observed when the animal crossed an imaginary line delimiting a circle, 46 cm in diameter, in the center of each arena (Fig. 1). Trials ended as this line was crossed.

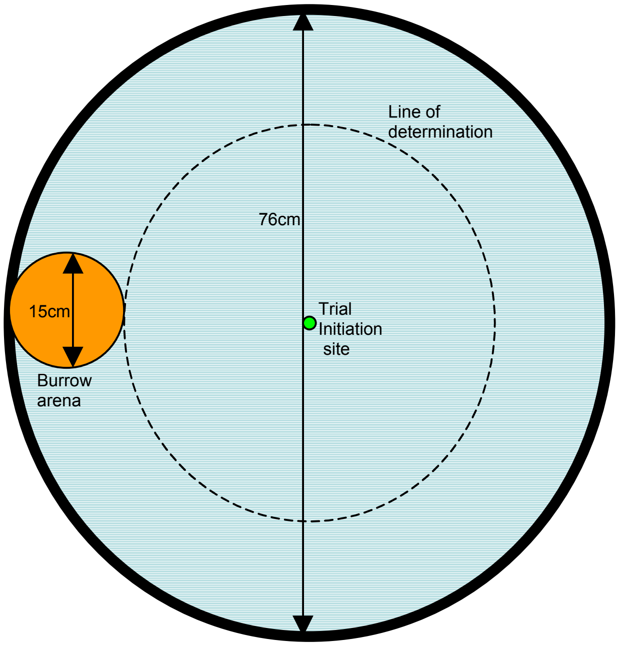


Fig. 1: Circular test arena including the removable burrow arena, site of trial initiation, and line of determination marking directional choice.

Analysis: Scorpion directional choice was quantified using a Batschelet test for circular uniformity (Zar, 1999). This test was used to determine if the initial chosen walking direction was uniform about the arena or if there was a bias in the mean walking direction in relation to the home burrow. Direction was quantified by comparing the center of the cylinder area (normalized to 0°) with the position that the scorpion crossed the circular line of determination. Scorpions that crossed the line of determination within 22.5° of the cylinder area center (1/8 of the total arena circumference) were considered to be within the burrow area.

Results

Thirteen of fifteen scorpions formed burrows within the cylinders (or within the area of the cylinders after day four after cylinder removal) during the six allotted days prior to trial. These observations were made each afternoon while spraying the cylinder areas with water (arena lights were on). Scorpions that did not form burrows were consistently found on top of the piece of flowerpot in the cylinder area throughout the six-day period. Two days prior to trial, all scorpions were found within the burrow-cylinder area, including those that did not form burrows.

Trials were run to elicit home burrow navigation after displacement to the center of the arena. Upon trial initiation, most scorpions remained motionless in the center of their arena for one minute to two hours. Two scorpions quickly ran to the side of the arenas as soon as the film canisters were lifted. These trials were removed from the analysis because the rapid movement was a presumed panic response and not a reliable measure of directed movement. Two scorpions did not move after two hours and were also removed from the analysis. Upon the initiation of movement, the remaining scorpions crossed the line of determination within 43 s. Two basic movement patterns were observed (Fig. 2). Some scorpions initiated a series of turns and pauses before making a more directed movement across the line of determination, whereas others initiated movement with one directed movement that took them across the line of determination.

Eleven legitimate trials yielded five scorpions that crossed the line of determination within 22.5° of the cylinder center (0°, the center of the home cylinder). Batschelet test for circular uniformity indicated that directional choice is not uniformly distributed about the circle and that it is concentrated around 0° (V=0.007, (n=11) (Fig. 3).

Discussion

This design evolved from several preliminary experiments. Initially, directional choice was obtained using rectangular choice chambers. Trials were initiated by placing the scorpion in the center of the rectangular chamber and observing their directional choice, toward or away from the side with their given burrow. The series of turns and pauses associated with movement onset coupled with the thigmotaxic nature of the scorpion rendered inconclusive directional choice. Scorpions commonly hit the arena wall while turning and followed the edge to the corner.

In preliminary tests using circular arenas with a diameter of 76 cm, scorpions were able to make multiple turns in the center of the arenas without hitting the walls. Consequently, scorpions commonly moved toward their burrow after a series of uninterrupted turns and pauses. Additionally, behavior observed during preliminary tests suggested that scorpions may be more loyal to their burrow if they are self-made rather than provided. It was also determined that the burrow forming cylinder must be clear and at least ten cm in diameter, otherwise

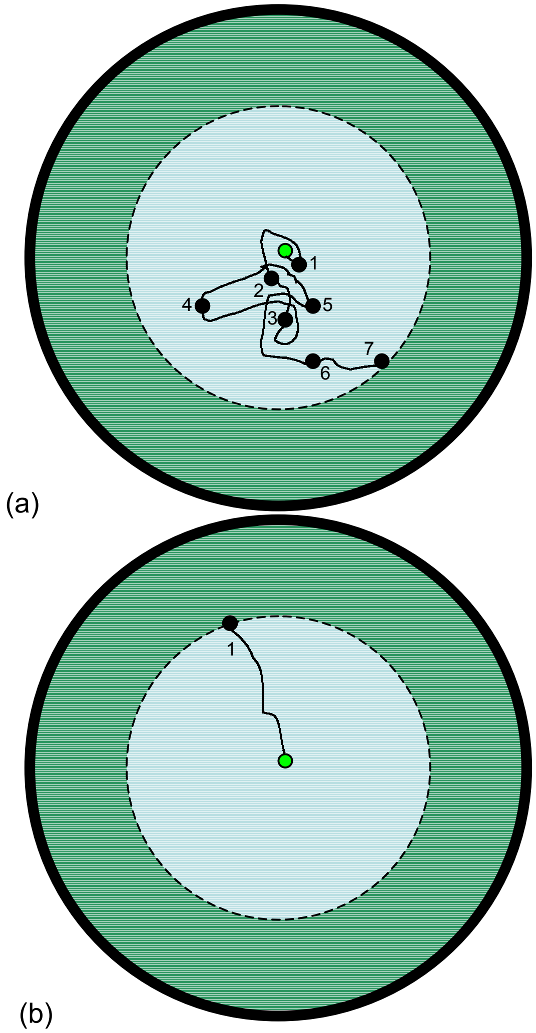


Fig. 2: Typical scorpion movements during trials. Black dots represent scorpion position at five-second intervals. (a) A series of turning and pausing before a seemingly directed movement across the line of determination (b) An initial seemingly directed movement across the line of determination.

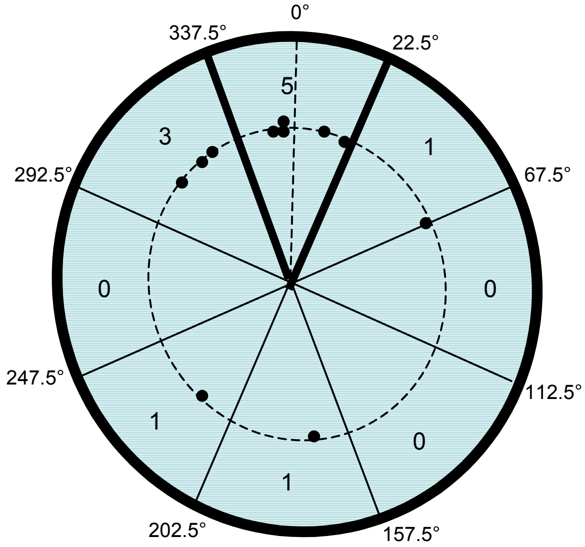


Fig. 3: Circular test arena divided into 45° sections with the burrow cylinder section outlined. The black dots indicate the positions where scorpions crossed the line of determination during experimental trials. The number in each section represents the frequency of scorpion crossing. Note that five of the eleven tested scorpions crossed the line of determination in the section containing the burrow and four additional scorpions crossed in adjacent sections.

most scorpions were not stimulated to form their own burrow.

In this study, *P. utahensis* scorpions exhibited nonrandom directional choice. Furthermore, directional choice was concentrated near the region of the established home burrow. Available cues including light, the Earth's magnetic field, chemical gradients, and humidity gradients may have influenced directional choice. These cues were provided to aid scorpion navigation in attempt to establish a system where it can be observed in the laboratory. These data suggest that scorpions were able to orient themselves in their arenas and navigate towards their home burrows using one or more sensory cues available in the laboratory. These data do not imply that any specific cue or cues present facilitate navigation.

The mechanisms underlying scorpion navigation are currently in the beginning stages of study, thus hypotheses must be formed from information obtained from taxonomically close organisms and from what is known about scorpion sensory systems.

Vision is a likely sensory mechanism used in navigation. Scorpions may use vision to observe landmarks, follow footsteps to retrace their outbound journey, or to potentially use light polarization patterns in navigation. The median and lateral eyes are ocelli bearing a single lens with a few photoreceptors (Locket, 2001). Ocelli are effective in determining light intensity but less capable of allowing shape determination, especially at greater distances. Thus, scorpions may be able to use nearby landmarks or visual cues such as footprints in navigation, but the use of distant landmarks is unlikely. Many arthropods are able to detect light polarization patterns, most notably bees and ants (for review see Wehner, 1997). It has been observed that the microvilli within the rhabdoms are arranged uniformly, and some rhabdomeres occur with differential microvilliar orientation (Locket, 2001). These structures may allow scorpions to exploit polarized light as a navigational tool (Brownell, 2001).

Scorpions possess several sensory structures receptive to chemosensory stimuli, most notably the pectines, which hold many pore-tipped peg sensilla (Gaffin & Brownell, 2001). The ventromedial position of these pectines facilitates contact, and therefore direct chemoreception, between the sensilla and the substrate. Additional chemoreceptive pore-tipped sensilla are common to the mouthparts, chelicerae and distal regions of appendages in arachnids (Foelix, 1985). Contact chemoreception of female chemical deposits has been observed in males of scorpion *Centruroides vittatus* (Buthidae) (Krapf, 1986; Gaffin & Brownell, 1992; Steinmetz et al., 2004). Perhaps similar detection of chemical deposits laid in the sand substrate on the outbound journey provide a chemical trail that the scorpion can follow home.

Detection of moisture and humidity is crucial to desert dwelling sand scorpions. Gaffin et al. (1992) provided evidence that chemoreceptive tarsal hairs detect substrate moisture. Additionally, Abushama (1964) concluded that organs on scorpion tarsi detect humidity. This humidity detection has been associated with the tarsal organ of scorpions, similar to the spider tarsal organ (Foelix & Schabronath, 1983). Prior to experimental trials, scorpion burrows areas were sprayed with water daily. The burrows were sprayed for the last time 24 hours before trial initiation. After trial completion, a HOBO Pro Series device was placed in the burrow area to monitor the level of humidity about the burrow. The HOBO was placed in the burrow for 24 hours, sprayed with the normal amount of water, and removed 24 hours later. Data recorded from the HOBO indicated that relative humidity about the burrow area returned to the initial burrow area humidity (42% RH) within three hours of spraying water (97% RH). These data indicate that a potential humidity gradient established from burrow area moistening had dissipated well before trial initiation, thus it is unlikely that scorpions followed a humidity gradient to their burrows.

It is possible that scorpions are using other environmental cues, including the Earth’s magnetic field, which may aid path integration. Evidence exists for magnetic orientation in several arthropod species, although it has not been shown to be a useful cue in path integration (Nørgaard et al., 2003).

The laboratory design presented here provides a controlled system that can be used to isolate and manipulate potential navigational cues. For instance, controlling the presence, intensity, polarization and wavelength of available light, or providing a fresh sand substrate, or locally disrupting the magnetic field in future trials will provide evidence for the use (or lack thereof) of specific environmental cues in navigation.

Acknowledgments

This work was partially funded by a grant from the University of Oklahoma Graduate Student Senate. We thank Greg Blass for taking care of the specimens and Wendal Porter for assistance in arena construction. Our gratitude also goes out to Ashley Meador and Michel Greene for their assistance in the experimental setup and during trials. We also thank Dr. Mariëlle Hoefnagels for valuable editorial suggestions. The experiments described here comply with the "Principles of animal care", publication No. 86-23, revised 1985 of the National Institute of Health and also with the current laws governing animal care and usage in the United States.

References

ABUSHAMA, F. T. 1964. On the behavior and sensory physiology of the scorpion *Leiurus quinquestriatus*. *Animal Behavior,* 12: 140–153.

BROWNELL, P. H. 2001. Sensory ecology and orientational behaviors. Pp. 159–183, *In* P. H. Brownell & G. A. Polis (eds.). *Scorpion Biology and Research*. New York, NY: Oxford University Press.

FOELIX, R. F. 1985. Mechano- and chemoreceptive sensilla. Pp. 118–137, *In* F. G. Barth (ed.). *Neurobiology of Arachnids*. Berlin: Springer – Verlag.

FOELIX, R. F. & J. SCHABRONATH. 1983. The fine structure of scorpion sensory organs. I. Tarsal sensilla. *Bulletin of the British. Arachnological Society*. 6: 53v67.

GAFFIN, D. D. & P. H. BROWNELL. 1992. Evidence of chemical signaling in the sand scorpion, *Paruroctonus mesaensis* (Scorpionida: Vaejovidae). *Ethology*, 91: 59–69.

GAFFIN, D. D. & P. H. BROWNELL. 2001. Chemosensory behavior and physiology. Pp. 184– 203, *In* P. H. Brownell & G. A. Polis (eds.). *Scorpion Biology and Research*. New York, NY: Oxford University Press.

GAFFIN, D. D., K. L. WENNSTROM & P. H. BROWNELL. 1992. Water detection in the desert sand scorpion, *Paruroctonus mesaensis* (Scorpionida: Vaejovidae). *Journal of Comparative Physiology*, 170: 623–629.

KRAPF, D. 1986. Contact chemoreception of prey in hunting scorpions (Arachnida: Scorpiones). *Zoologischer Anzeiger*, 217: 119–129.

LOCKET, A. 2001. Eyes and vision. Pp. 79–106, *In* P. H. Brownell & G. A. Polis (eds.). *Scorpion Biology and Research*. New York, NY: Oxford University Press.

NØRGAARD, T., J. R. HENSCHEL & R. WEHNER. 2003. Long-distance navigation in the wandering desert spider *Leucorchestris arencola:* can the slope of the dune surface provide a compass cue? *Journal of Comparative Physiology*, 189: 801–809.

POLIS, G. A., C. N. MCREYNOLDS & R. G. FORD. 1985. Home range geometry of the desert scorpion *Paruroctonus utahensis*. *Oecologia*, 67: 273–277.

SISSOM, W.D. 2000. Family Vaejovidae Thorell. 1976. Pp. 503-553. *In* V. Fet, W. D. Sissom, G. Lowe & M. E. Braunwalder. *Catalog of the Scorpions of the World (1758–1998)*. New York: Entomological Society.

STEINMETZ, S. B., K. C. BOST & D. D. GAFFIN. 2004. Response of male *Centruroides vittatus* (Scorpiones: Buthidae) to arial and substrate-borne chemical signals. *Euscorpius*, 12: 1–6.

WEHNER, R. 1992. Arthropods. Pp. 45-144, *In* F. Papi (ed.). *Animal Homing*. London: Chapman and Hall.

WEHNER, R. 1997. The ant's celestial compass system: spectral and polarization channels. Pp. 145–185, *In* M. Lehrer (ed.). *Orientation and Communication in Arthropods*. Basel: Birkhäuser.

ZAR, J. H. 1999. *Biostatistical Analysis*. London: Prentice Hall.

Euscorpius — Occasional Publications in Scorpiology. 2004, No. 17

Scorpion peg sensilla: are they the same or are they different?

Douglas D. Gaffin[1] and Mark E. Walvoord[1]

[1]Department of Zoology, University of Oklahoma, Norman, OK 73019-0235, USA

Summary

Thousands of peg sensilla adorn the ground-facing surfaces of the elaborate chemosensory organs of scorpions called pectines. From external appearances, these sensilla appear identical, however, it is not known if they are functionally the same. The answer to this question will influence our thinking on the organization and function of the pecten chemosensory system. Identical sensilla would suggest a parallel sampling scheme, lending support to an "information enhancement" hypothesis. Conversely, functionally distinct sensilla would support a "segmentation" hypothesis similar to the decomposition of sensory elements in the well-studied mammalian visual processing system. We are using a newly developed chemical delivery approach to test peg response patterns to consistent, repeatable stimulation. We report our findings based on electrophysiological recordings of stimulated peg sensilla of desert scorpions *Paruroctonus utahensis* (Vaejovidae). We also report on other relevant characteristics, including the nature and time course of a typical pecten "sniff" and the density of peg sensilla relative to substrate particle size from the animals' natural sand habitat.

Introduction

Scorpion pectines are featherlike, mid-ventral appendages that form the largest sensory input to the scorpion brain. The pectines are important in guiding males to prospective mates (Gaffin & Brownell, 1992, 2001) and perhaps in spermatophore exchange (Alexander, 1957, 1959) and in relocating stung prey (Krapf, 1986; Skutelsky, 1995). Each pecten is composed of a flexible spine and a series of movable teeth (Fig. 1 A-C; Cloudsley-Thompson, 1955). On the ground-facing surface of each tooth are dense patches of peg-shaped sensilla (Carthy, 1966, 1968; Ivanov & Balashov, 1979; Foelix & Müller-Vorholt, 1983). The peg sensilla are the main chemosensitive elements of the pectines, and previous studies have established their responsiveness to a range of organic molecules (Gaffin & Brownell, 1997a, b). Externally, the pegs appear identical, with their pores directed at the same angle relative to the ground (Gaffin, 2002).

Here we ask the question: are the pegs functionally the same or different? The answer to this question will affect how we think about this organ and its functional organization. In one case, we might find a distinct partitioning of the real world geometrically, where individual pegs contain distinct elements that respond differently to specific chemicals. We term this the *Information Segmentation Hypothesis* (Fig 2A). An example of this type of model is the cochlea in the inner ear, where receptors tuned to different frequencies distribute in an ordered manner along the length of the organ.

A second possibility is that the pegs are essentially repeated units, each possessing the same types of chemosensitive neurons (Fig 2B). This type of arrangement might be useful as a parallel sampling system, amplifying the amount of information received. We term this the *Information Enhancement Hypothesis*. Mammalian taste buds appear to be such a model. Each taste bud contains units that respond to various tastants, and these buds distribute across the tongue.

Initial accounts of peg chemosensitivity have suggested a segregated pattern of responsiveness (Gaffin & Brownell, 1997a). Pegs were stimulated by blowing volatile organic molecules from a syringe tip about a centimeter away as diagramed in Figure 1D. The response pattern for a given peg was consistent within a given stimulant series and orientation, whereas the response patterns for other pegs appeared different (Gaffin & Brownell, 1997a). Still, these results need to be approached with caution since the blowing of stimulant from a distance may have delivered an inconsistent stimulus concentration to different peg tips.

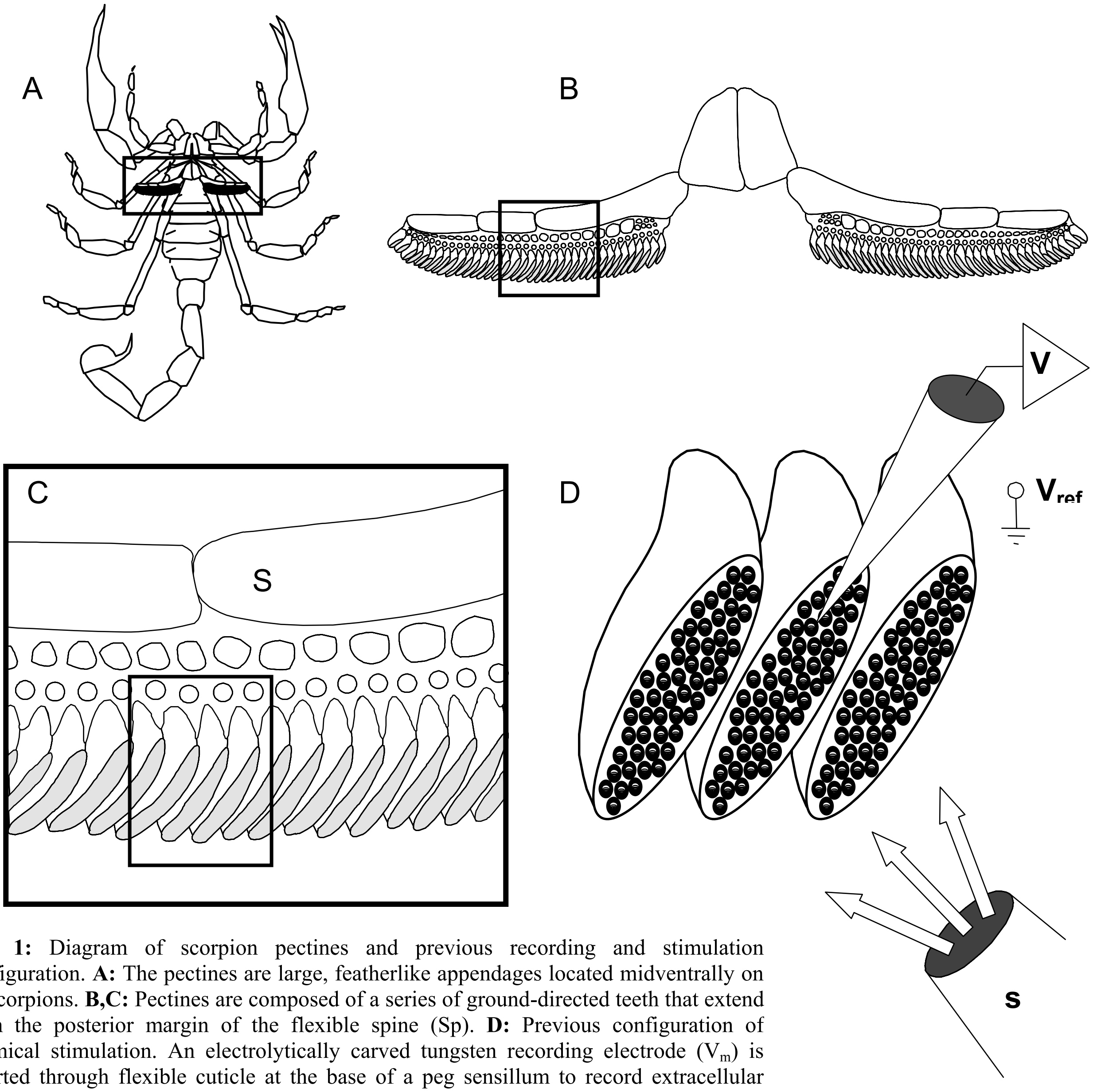


Fig. 1: Diagram of scorpion pectines and previous recording and stimulation configuration. **A:** The pectines are large, featherlike appendages located midventrally on all scorpions. **B,C:** Pectines are composed of a series of ground-directed teeth that extend from the posterior margin of the flexible spine (Sp). **D:** Previous configuration of chemical stimulation. An electrolytically carved tungsten recording electrode (V_m) is inserted through flexible cuticle at the base of a peg sensillum to record extracellular potentials from sensory neurons. Chemical stimuli (st) are blown across peg fields from a distance of about 1 cm (drawing not to scale). A reference electrode (V_{ref}) is placed in contact with hemolymph at some distance from the recording electrode.

While previous studies were important in establishing the chemosensitive nature of peg sensilla, they do not address the functional organization of chemosensitive elements among the peg population. In this study, we investigate this question by using a new method of peg stimulation that depends on stimulant diffusion from a pipette tip within a few microns of the peg pore rather than forceful delivery of stimulant from a distance (Gaffin & Hines, 2003). This method delivers a more controllable and consistent stimulant dose to the pore and allows for better comparison of responses between pegs.

Here, we first describe and characterize this new method of chemical delivery. Next, we use this method to test the sensitivity of adjacent peg sensilla to the identical chemostimulants. In addition, we use high-speed videography to characterize the time course of a typical pectinal brushing ("sniff") of the substrate. Finally, we calculate the density of pegs relative to a sand particle from the scorpions' environment. We use these data to argue that the pegs appear to be functionally redundant, supporting the Information Enhancement Hypothesis.

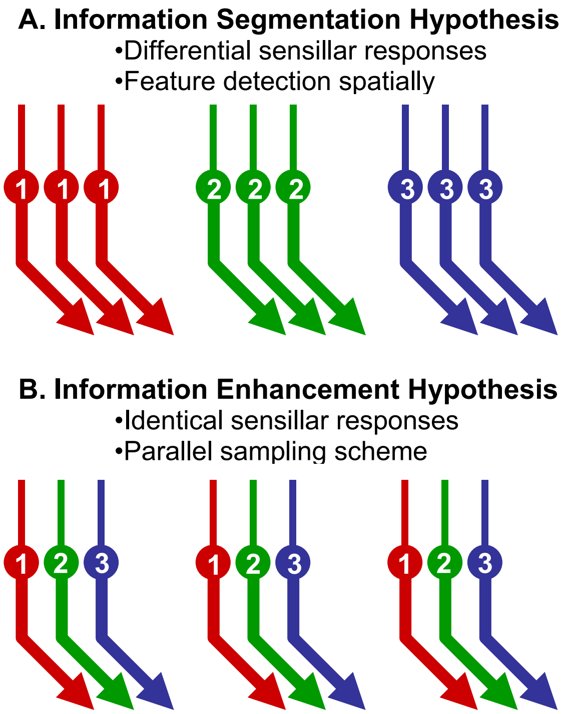


Fig. 2: Alterative hypotheses on the functional neural organization of peg sensilla. **A:** Information Segmentation Hypothesis. In this arrangement, chemical sensitivity is parsed to distinct peg sensilla. **B:** Information Enhancement Hypothesis. In this arrangement, each peg sensillum contains a similar complement of chemically sensitive neurons.

Methods

Animals

Mature *Paruroctonus utahensis* (Williams, 1968) (Scorpiones: Vaejovidae) obtained from sandy regions near Kermit, Texas, were the subjects of these experiments. We housed animals individually in 3.8 L clear glass jars containing 250 ml of sand collected from the scorpions' natural habitat. The jars were kept in a room with consistent temperature (22° C). The room lighting alternated between periods of light (0730-2000 h) and dark (2000-0730 h). Each week, we fed each scorpion one cricket and misted each with 10 ml of deionized water.

Electrophysiology and chemical stimulation

Scorpions used for electrophysiology were immobilized ventral side up in modeling clay on a glass microscope slide. An indifferent silver electrode was inserted between metasomal segments until contact was made with hemolymph. The pectines were then attached to a glass cover slip using double-sided adhesive tape; the individual "teeth" of the pectines were straightened and aligned to facilitate recording. The prepared scorpion was then fastened to the microscope stage and pegs were located using a high-powered (500-1000x) compound microscope (Olympus BX-50WI) equipped with epi-illumination and long working distance objectives.

Extracellular recordings were obtained by inserting an electrolytically sharpened tungsten electrode (tip diameter about 1 μm) into the cuticle at the base of the desired peg (Fig. 3). Electrodes were maneuvered into place using a Leitz mechanical micromanipulator. After insertion, the peg was allowed several minutes to recover to a consistent baseline activity. Electrical signals detected by the electrode were amplified 1000 to 10,000 times over a bandwidth of 1-3 kHz, displayed on an oscilloscope, and relayed through digitizing hardware (1401-plus, CED, Cambridge, England) at 20 kHz sampling rate to a computer for storage and analysis. Acquired records were further filtered with a digital high pass filter and analyzed using a spike recognition and analysis program (Spike 2, CED). Spiking events were traced using 100 samples spread evenly across the spike wave (100 points at 20 kHz sampling frequency gives 5 ms between point). Events with peak amplitude above background noise were isolated from the record and categorized to discrete classes using a spike recognition algorithm in the Spike 2 program.

The chemical delivery device consisted of a glass pipette with a tip pulled to a diameter of about 5 μm. The pipette was formed from a glass capillary tube (World Precision Instruments 1.00 mm OD, 0.58 mm ID, 152 mm length, with filament) pulled in a glass micropipette puller (Sutter Instrument Co. Model P-87).

Stimulant pipettes were backfilled by immersing the pipette tip into a vial containing the pure substance to a depth of about 1 cm for 2 hours. This method allowed enough chemical to backfill into the pipette tip to allow several hours of experimentation. We used pure 1-hexanol as the stimulant chemical in this study.

The stimulant pipette was attached to a glass electrode holder and affixed to the head of an electronically controlled micromanipulator (Burleigh step driver PZ-100). The electronic head was mounted to a mechanical micromanipulator for movement of the pipette to within 100 microns of a recorded peg. The left-to-right and up-and-down positioning of the pipette tip was also adjusted using the fine controls of the mechanical micromanipulator. The electronic micromanipulator produced precise in-and-out movements, which allowed us to control the distance of the pipette tip from the tip of the recorded peg. The distance of travel of the pipette tip was monitored by reading the output from the electronic manipulator. This information was sampled at 100 Hz on a second channel of the digitizer and stored on a separate channel in the Spike 2 program.

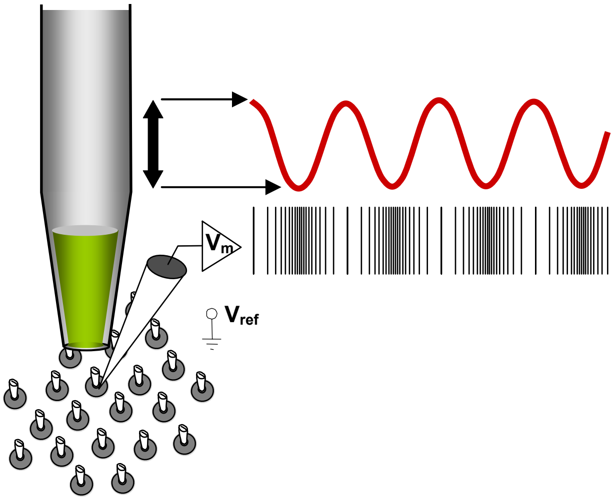


Fig. 3: Recording and stimulation configuration of new static odorant method. Tungsten microelectrode is inserted through flexible base of individual peg sensillum. A glass pipette with tip diameter of about 5 microns is backfilled with a pure substance and maneuvered via an electronically controlled manipulator to within microns of the peg tip. The travel of the stimulant pipette tip is monitored relative to distance from the peg tip while the neural response is recorded.

Once precisely positioned within microns of the peg tip, our experiments consisted of using the electronic manipulator to move the pipette tip close to a recorded peg, away, close, etc. while monitoring the neural response and the position of the pipette as shown in Figure 3.

Videography of a pecten "sniff"

We filmed individual *Paruroctonus utahensis* during the day in a dark room by placing them into a clear, rectangular, Plexiglas container elevated above an infrared (IR) spotlight (Ultrak, model UL-IR-50-FL 12 V, 50 W). This box was 37 cm long, 5.5 cm wide, and 7 cm tall to give enough space for scorpion movement. An IR-sensitive camera (Panasonic CCTV camera model WV-BP314) was focused on the center of the Plexiglas floor through the side of this box. We placed a female scorpion into this box, covered the box with black paper to reduce glare, turned off room lights, and began recording onto a videotape in a time-lapse video recorder (Panasonic model AG-RT600P) set to 8-hour mode. This allowed us to capture sixty frames/second. Video recording took place for approximately 2 hours at a time, before stopping the tape to check for footage of the scorpion traversing in front of the camera.

We reviewed all taped trials, and the single pecten lowering sequence with the clearest view was used in this paper. This trial took place on 20 May 2004 from 1025–1152 hours at 22°C and approximately 78% relative humidity.

Calculation of peg density vs. sand particle size

We directly counted and calculated the density of peg sensilla on tooth 17 of the right pecten of a female *P. utahensis*. We did this by snapping an overlapping series of digital photos using a digital camera (Flexcam Teaching NTSC Rev. 3.0, Videolabs Inc., USA) connected to a frame grabber (Snappy Video Snapshot, Play Inc.) for computer manipulation and analysis. Photos were taken directly from one of the eyepieces on the light microscope used for electrophysiology under high power. We used a similar approach to determine the area of a "typical" grain of sand retrieved from the scorpions' native habitat. Peg density was calculated by dividing the number of pegs on a tooth by the surface

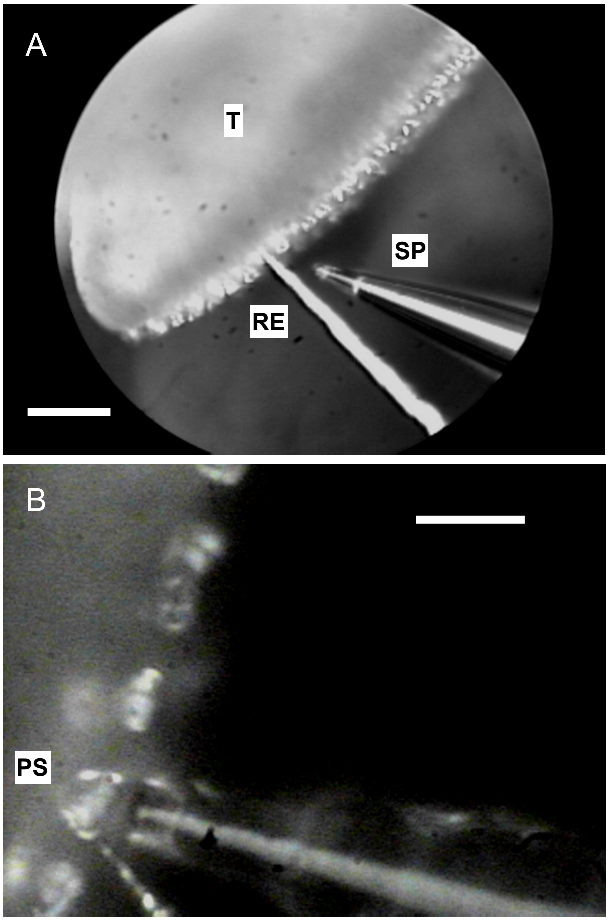


Fig. 4: Stimulus pipette relative to peg and recording electrode. **A:** A pectinal tooth (T) is shown with recording electrode (RE) in place as the stimulus pipette (SP) approaches the recorded peg. **B:** Close up view of tungsten microelectrode inserted in base of peg sensillum (PS) and tip of stimulant pipette manuevered within microns of the peg tip. Scale bars: A: 10 microns; B: 5 microns.

area of the peg field in square microns.

Results

Our extracellular recordings were stable for tens of minutes to hours with little reduction in signal-to-noise ratio. With practice, the recording electrode and stimulus pipette could be configured to avoid crossing each other. We found that the response of peg neurons was highly sensitive to the distance between the pipette and peg tips. Because of this, it was important to move the stimulus pipette as close to the peg tip as possible without making contact. Contact of the tip to the peg usually resulted in flooding of chemical across the peg fields, causing intense firing of peg neurons and several minutes of sensory adaptation. Figure 4 shows the relationship of the recording electrode and stimulus pipette in a typical recording configuration. Figure 5 shows an experimental control recording. Moving an empty pipette tip near to the peg tip had no effect on the spiking activity of the peg neurons.

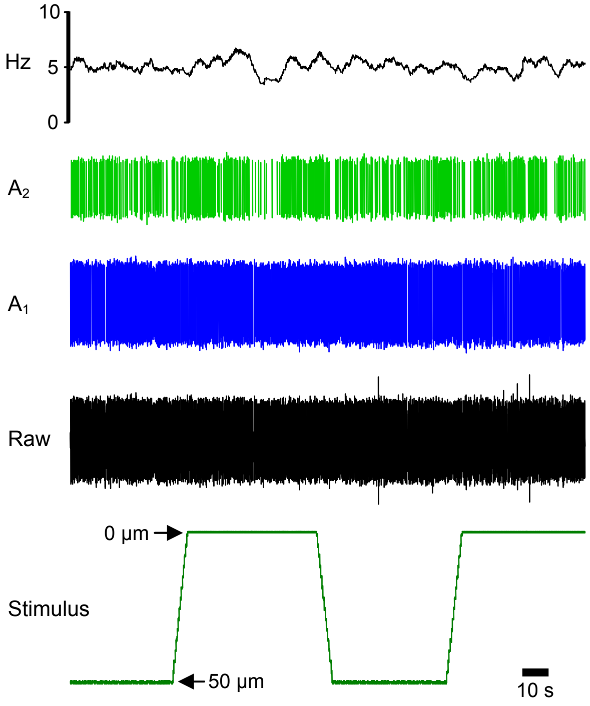


Fig. 5: No stimulus control. The bottom trace shows the travel of an empty pipette tip from 50 microns to within 1 micron of the peg tip and back. The "Raw" trace shows all electrical activity recorded from the peg sensillum while A_1 and A_2 show the isolated activity of two identifiable cells. The top graph depicts the spiking activity of the peg in Hz for the duration of the test.

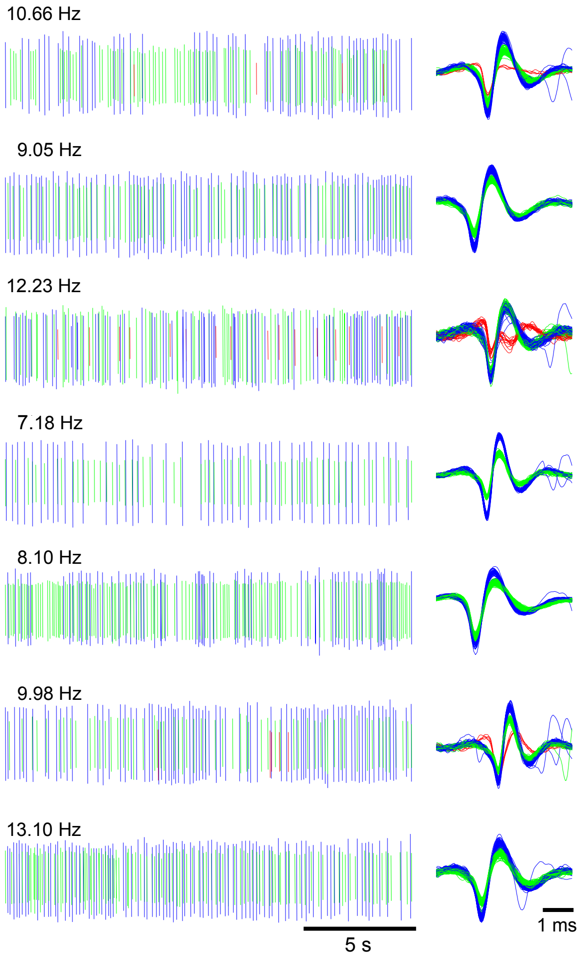


Fig. 6: Baseline series. Shown are no-stimulus recordings of spontaneous activity from seven adjacent peg sensilla. The traces at right show 15 seconds of spiking categorized by spike sorting algorithm. At right are the superimposed waveforms from each record. Spiking frequencies varied from 7.18 to 13.10 Hz in these records.

Spontaneous spiking activity

We recorded spontaneous spiking activity from seven adjacent peg sensilla on a single pectinal tooth (Fig. 6). The baseline spiking frequencies of these samples ranged from 7.18 Hz to 13.10 Hz. All seven records contained two large biphasic waveforms, which appear similar to the A1 and A2 waveforms reported for *Smeringurus mesaensis* (Gaffin & Brownell, 1997a). A third, smaller, triphasic waveform (colored red in Fig. 6) was detected in three records. The patterns of spiking activity appeared similar in each of the records.

Chemical Stimulation

To test for similarity in chemical response, we recorded from six consecutive pegs from tooth 19 of a female *P. utahensis*. Several successive advances and retractions of pure 1-hexanol were made for each recorded peg. In each case, the pipette tip was moved immediately adjacent to the peg, then retracted 20 microns, and returned to the peg tip. The advance and retraction rate was 4 microns per second; one complete cycle took 10 seconds. Shown in Figure 7 are samples of seven such advances and retractions. The spiking patterns of each peg were similar, showing a sharp increase in spiking with approach of the stimulus pipette. Spiking frequencies, smoothed by 3-second bins, are displayed above the spikes in each of the peg records. Peak frequencies ranged from 20 to 40 Hz across the records.

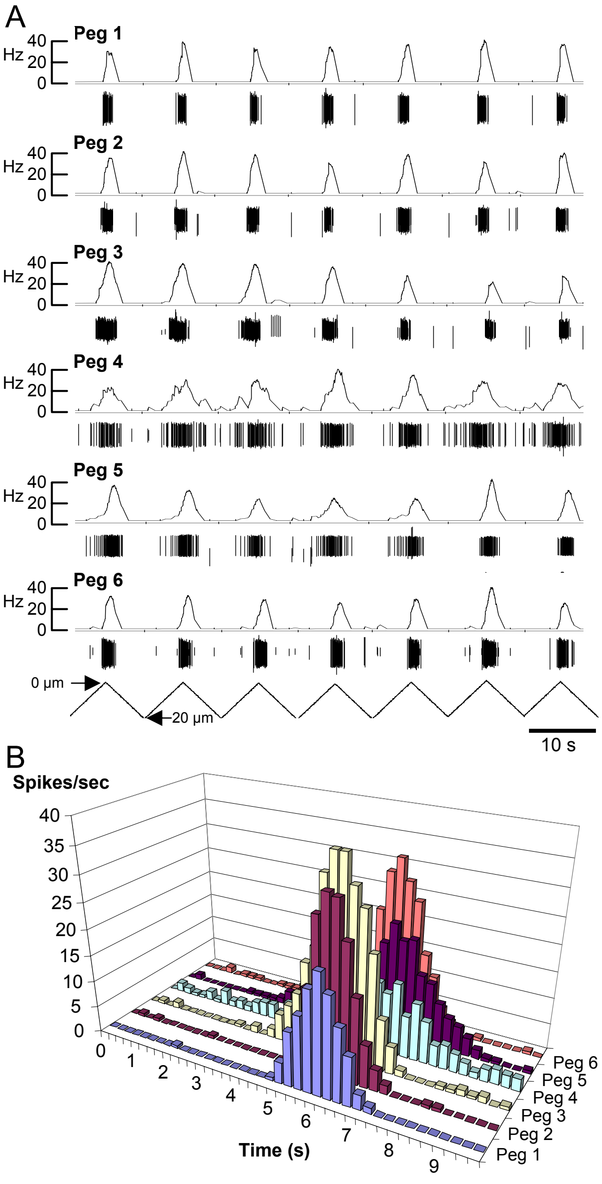


Fig. 7: Hexanol stimulation of six adjacent peg sensilla. **A:** Neural responses of six pegs to seven successive movements of the stimulus pipette from 20 µm to 0 µm (adjacent to the peg tip) and back (pipette travel shown below peg 6 record). For each peg, the bottom trace represents the isolated spiking activity and the top trace the spiking frequency in Hz. **B:** Spiking frequency averaged across the seven stimulus repetitions for each of the six pegs.

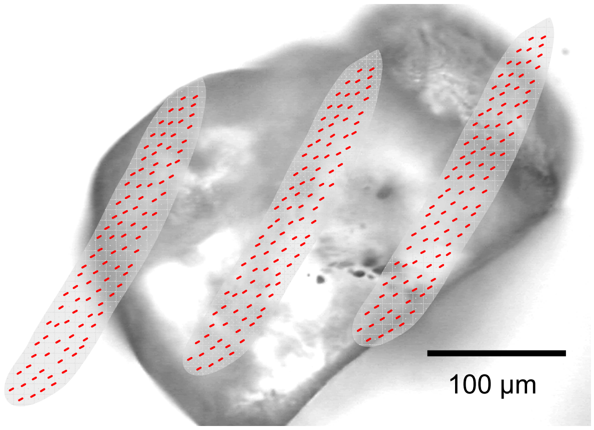


Fig. 8: Peg sensilla density relative to a sand grain. The positions of peg sensilla on a pecten tooth of a female *P. utahensis* was determined using overlapping photos of the peg field taken from high power light microscopy. Here we show this field repeated three times at the appropriate spacing to represent three successive pecten teeth. The fields are superimposed atop a photo of a grain of sand from the scorpion's native habitat.

Peg density vs. sand grain size

The peg density on tooth 17 of a female *P. utahensis* was directly calculated from a series of overlapping photos. We counted 105 pegs on this tooth across a peg field area of approximately 8400 µm^2. This gives a peg density of approximately 0.0125 pegs per µm^2 or 12,500 pegs per mm^2. We also measured the area of a "typical" sand particle from the dune habitat where these animals live. We measured the surface area of this particle directly from the photo as 33,440 µm^2. Put another way, 418 pegs would fit on this sand grain (33,440 µm^2 * 0.0125 pegs/µm^2 = 418 pegs). Figure 8 shows representative peg fields from three pecten teeth superimposed atop the sand grain.

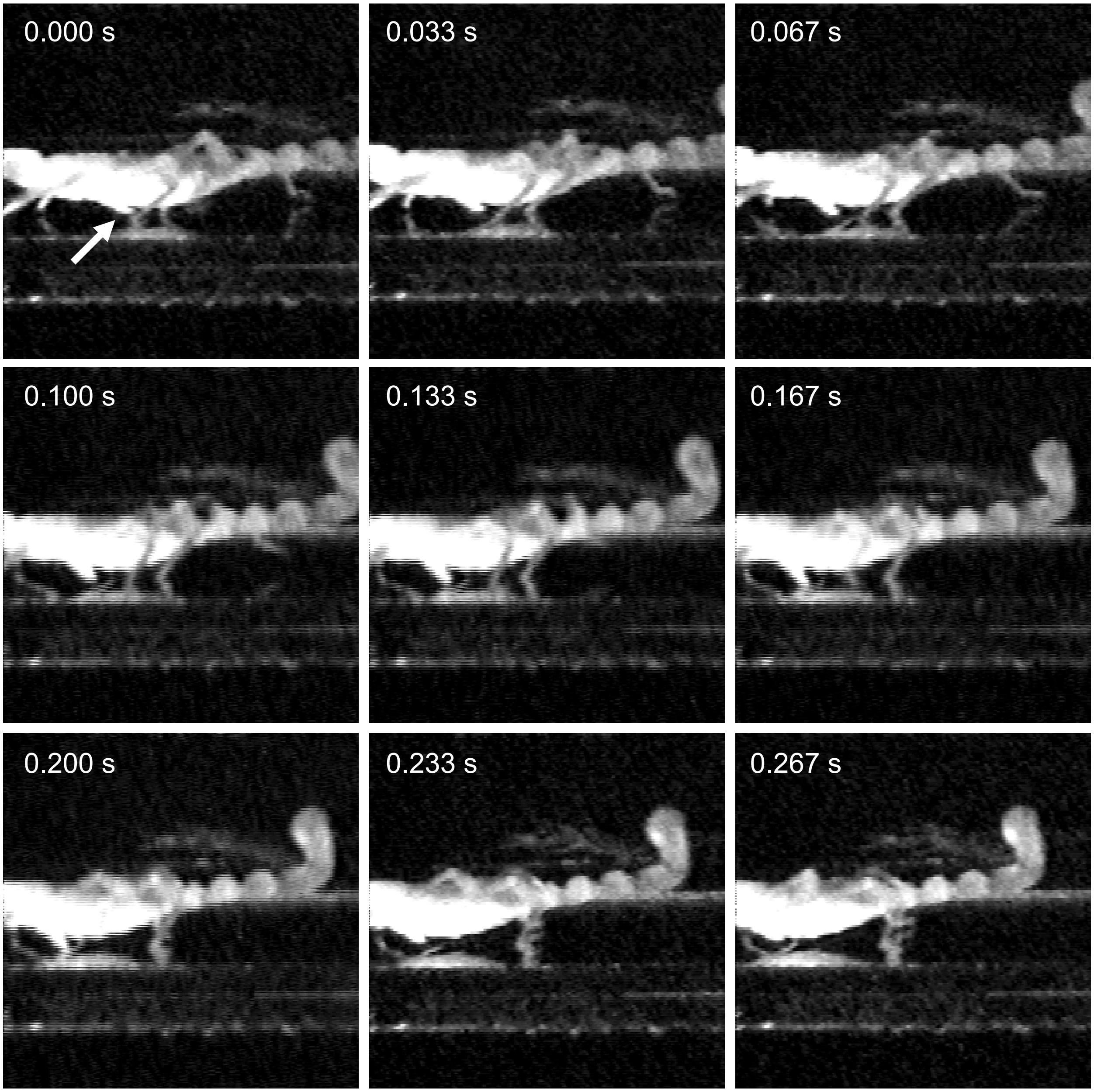


Fig. 9: These pictures represent a time course of a pecten "sniff" in a captive, female *P. utahensis*. Video was recorded at sixty frames/second under infrared (IR) light with an IR-sensitive camera. This time course represents snapshots of the video taken every other frame. The pecten is indicated by the white arrow in the first frame.

Kinematics of a pecten "sniff"

The pecten sniff consisted of a ~0.20-second lowering sequence followed by a ~0.07 second retraction of the pecten upon contact with the substrate (Fig. 9). Contact with the substrate, in this case, lasted at most 0.033 seconds. During other sequences of this and other trials, scorpions displayed another behavior in which they would lower and drag their pectines for a longer period just above or on the substrate before retracting them.

Discussion

Both the activity patterns and types of units present in recordings from peg sensilla are similar between individual pegs during both spontaneous recordings and under consistent stimulation. The new method of presenting a stimulus by moving a static source near a peg tip gives much more consistent response patterns between pegs than during forceful propulsion of the stimulant across the peg field from a distance (Gaffin & Brownell, 1997a). The small departure in stimulant response for some pegs (such as peg 4 in Fig. 7) is more likely a result of the pipette tip not being as close to the peg pore as in the other recordings; we found that distance from pipette to tip greatly influences the peg response and even a micron can have a significant effect.

The data from videography allowed us to observe pecten lowering in a homogenous environment and to determine a time course for one pecten "sniff." We also observed that pectines appear to make contact with the substrate. To fully analyze pecten sniffs or dragging behavior, we need to record more pecten sniffs from multiple animals, classify how many events were "touches" and how many were drags, and record an average time course of these drags. We hypothesize that this dragging behavior may be a response to the smooth, homogeneous surface on which they were traveling. More observations are needed of scorpions active at night in their natural habitat to record the exact sniffing behavior on a normal substrate.

The time course of a single pecten "sniff" is important for approximating the amount of time available for a field of peg sensilla to gather an information sample. On the conservative side, the peg fields are near to the substrate (within microns) for only 0.033 s. We have found that chemical responsiveness of peg neurons to a pure stimulant varies significantly with distance of the stimulant from the peg tip. For example, movement of the pipette tip from 20 μm distant to 1 μm distant resulted in an increase of spiking frequencies from 0 to 40 Hz (see Fig. 7) with most of the change occurring as the tip was within 10 μm.

The peg density for the pecten tooth we measured on a female *P. utahensis* was approximately 0.0125 pegs per μm^2. This calculation is in line with what Brownell (2001) reported for another vaejovid scorpion species, *Smeringurus mesaensis*. Why are there so many pegs? This is an important question, given that the particle size of the animal's habitat is orders of magnitude greater than the inter-peg distances.

The answer to this question may come from a closer examination of the chemical response data. First, we find that the inter-peg distances are approximately 8 μm, which is in line with the proximity of the stimulus pipette tip for which we see significant neural responses. Also, while our frequency graphs of neural activity suggest that individual pegs can track the stimulant within this distance, we obtained those graphs by averaging over 3-second bins. If calculated across a more realistic time window of 0.033 seconds (the time course of a pecten "sniff," calculated above), spiking averages of peg neurons would not be able to resolve stimulant distance with any degree of confidence. Put another way, to achieve the stimulant distance resolution for a single peg sensillum as implied by Figure 7, the animal would need to hold its pectines to the ground for at least three seconds – and the animal simply does not do this.

Taken together, these data support the *Information Enhancement Hypothesis*, with the peg sensilla being functionally repeated units. It appears that the peg fields function in a parallel sampling system, delivering to the brain information sampled from a quick "sniff." In essence, such a system could provide the same resolution of stimulant location as can be obtained from a single sensillum presented with seconds of prolonged chemical stimulation.

Acknowledgments

We thank Drs. J. Bastian and M. Hoefnagels for their valued suggestions, technical advice, use of equipment, and encouragement. We would also like to thank P. McGowan, M. Hines, and G. Blass for assistance during the research project. An Associates Presidential Professorship and the *Life Fund* of the University of Oklahoma Foundation provided funding for this project. The experiments described here comply with the "Principles of animal care," publication No. 86-23, revised 1985 of the National Institute of Health and also with the current laws governing animal care and usage in the United States.

References

ALEXANDER, A. J. 1957. The courtship and mating of the scorpion, *Opisthophthalmus latimanus*. *Proceedings of the Zoological Society, London*, 128: 529–544.

ALEXANDER, A. J. 1959. Courtship and mating in the buthid scorpions. *Proceedings of the Zoological Society, London*, 133: 145–169.

BROWNELL, P. H. 2001 Sensory ecology and orientational behaviors. Pp. 159–183 *In* P. H. Brownell & G. A. Polis (eds.). *Scorpion Biology and Research*. New York, NY: Oxford University Press.

CARTHY, J. D. 1966. Fine structure and function of the sensory pegs on the scorpion pecten. *Experientia,* 22: 89–91.

CARTHY, J. D. 1968. The pectines of scorpions. *Symposium of the Zoological Society, London*, 23: 251–261.

CLOUDSLEY-THOMPSON, J. L. 1955. On the function of the pectines of scorpions. *Annals and Magazine of Natural History*, 8: 556–560.

FOELIX, R. F. & G. MÜLLER-VORHOLT. 1983. The fine structure of scorpion sensory organs. II. Pecten sensilla. *Bulletin of the British Arachnological Society*, 6: 68–74.

GAFFIN, D. D. & P. H. BROWNELL. 1992. Evidence of chemical signaling in the sand scorpion, *Paruroctonus mesaensis* (Scorpionida: Vaejovidae). *Ethology,* 91: 59–69.

GAFFIN, D. D. & P. H. BROWNELL. 2001. Chemosensory behavior and physiology. Pp. 184–203, *In* P. H. Brownell & G. A. Polis (eds.). *Scorpion Biology and Research*. New York, NY: Oxford University Press.

GAFFIN, D. D. & P. H. BROWNELL. 1997a. Response properties of chemosensory peg sensilla on the pectines of scorpions. *Journal of Comparative Physiology, A,* 181: 291–300.

GAFFIN, D. D. & P. H. BROWNELL. 1997b. Electrophysiological evidence of synaptic interactions within chemosensory sensilla of scorpion pectines. *Journal of Comparative Physiology, A,* 181: 301–307.

GAFFIN, D. D. & M. A. HINES. 2003. A new approach to chemostimulation of scorpion peg sensilla reveals high resolution response properties to near-range chemostimulants. *Abstracts/27th Annual Meeting of the American Arachnological Society. Denver, Colorado, 24–28 July 2003*.

IVANOV, V. P. & Yu. S. BALASHOV. 1979. [The structural and functional organization of the pectine in a scorpion, *Buthus eupeus*, studied by electron microscopy]. *In*, Balashov, Yu. S. (ed) *Fauna i ekologiya* paukoobraznykh [*The Fauna and Ecology of Arachnida*]. *Trudy Zoologicheskogo Instituta, Leningrad,* 85: 73–87 (in Russian).

KRAPF, D. 1986. Contact chemoreception of prey in hunting scorpions (Arachnida: Scorpiones). *Zoologischer Anzeiger*, 217: 119–129.

SKUTELSKY, O. 1995. Flexibility in foraging tactics of *Buthus occitanus* scorpions as a response to above-ground activity of termites. *Journal of Arachnology*, 23: 46–49.

Euscorpius — **Occasional Publications in Scorpiology. 2004, No. 17**

Screening for scorpions: A non-invasive approach to tracking the movements of arachnids in sand

James Z. Porterfield[1], Douglas D. Gaffin[1], Caitlin Porterfield[1] & Curtis Johnston[1]

[1]Department of Zoology, University of Oklahoma, Norman, OK 73019-0235, USA

Summary

Piezoelectric materials are highly sensitive devices capable of transducing mechanical energy into electric voltage. They find application as sensors in a wide variety of commercial and academic fields. Borrowing from the use of these materials in geophysics to measure the transmittance of a wave front through a substrate, and the principles used to locate the epicenter of an earthquake, we are investigating the use of an array of piezoelectric transducers on a much smaller scale to triangulate the position of a scorpion, in sand, as it leaves its burrow to hunt. Such an approach relies on the ability to resolve the surface waves created by a scorpion's footsteps and uniquely identify them against a background of other such waves. Such a passive form of measurement has the benefit of eliminating environmental factors associated with other monitoring systems, such as camera lights, that could change the scorpion's behavior. The work to date has yet to yield a fully functional tracking system but has identified the major obstacles that, when resolved, should yield a sensitive, accurate, and dependable technique. Much progress has been made in resolving issues of sensitivity and reproducibility of signal measurement with the piezoelectric materials currently in use.

Introduction

Scorpions are well suited for scientific study. Their relatively clear ancestral origin makes them ideal for comparative studies, and their unique physiology offers an exceptional platform for investigating the "broader questions of organismal biology" (Brownell, 2001). One of the very interesting aspects of scorpion sensory biology, seemingly unique among terrestrial animals, is their use of vibration-sensitive structures for hunting. These structures, called the basitarsal slit sensilla, are located near the tarsal joint on each of the scorpion's eight legs and can sense the mechanical waves generated by the movements of its prey (Brownell, 2001). In the 1970s and 1980s, Philip Brownell published a series of papers detailing this sensitivity to vibration and how such information is vital to the way scorpions hunt (Brownell, 1977, 1984). Scorpions can determine with remarkable accuracy both the direction of and distance to the origin of a set of waves. Brownell reports that within a distance of 20 cm these estimates are reliable enough to capture a prey item in a single movement, and that signals generated from as far away as 50 cm can be sensed and used for hunting (Brownell, 1977).

This ability is made possible by the wave conduction properties of sand. Unlike many other solids, where seismic velocities are typically on the order of several kilometers per second (Manghnani & Ramananantoandro, 1974), measured velocities in unconsolidated sand are closer to 40–120 m/s (Brownell, 1977) with a theoretical minimum of 13 m/s, as reported by Bachrach et al. (1998). Nervous systems were once thought to be too insensitive to discern the differences in arrival times of waves with the greater velocities measured in solids (Brownell, 1984). Accordingly, when an earthquake strikes, a human can tell when the seismic waves have passed by feeling the "shaking" of the ground, but cannot determine which leg felt the wave first. No known example exists of an organism with sufficient resolution to use mechanical vibrations in a solid substrate to orient itself. In sand, however, the lessened velocity of the waves allows the scorpion to judge the passing of the wave front across each of its legs, making sand a plausible medium for transmitting a biologically useful and unique sensory cue.

Inspired by the ability of a scorpion to triangulate the position of an object of interest based on vibration, we became interested in devising a method of tracking the scorpion itself in a similar manner—a case of hunting the hunter, so to speak. With an array of sensors sufficiently sensitive to resolve the seismic waves generated by a scorpion's footsteps, it seems possible that one could track the movements of a scorpion in a non-invasive way. Traditional approaches to monitoring such movements use a low-light or IR camera for filming. With such methods, however, a certain amount of light is necessarily introduced into the environment. In experiments where total darkness may be desired to limit the scorpion's reliance on visual cues, no completely satisfactory method exists for determining the position and movement of the study organism. With vibration sensors buried within the substrate, measurements would be taken in a passive way, eliminating the need for light sources or other behavior-altering stimuli. It has been the focus of this project to determine if such a technique can be developed, based on preliminary experimentation with inexpensive materials.

Piezoelectric materials

Piezoelectric crystals are transducers that convert mechanical energy into a voltage and vice versa (Mason, 1950). As such, they can be used as sensors by producing a voltage proportional to the amount of strain applied or, with applied voltages they can be used as micromanipulators or motors. The major characteristic common to all materials exhibiting the piezoelectric effect is the lack of a center of symmetry in the crystal structure (Mason, 1950).

These materials are quite common, being used in such varied applications as crash sensors in automobiles, micromanipulators, "key finders" activated by whistling, and in electronic circuitry as filters for eliminating extraneous signals (Mason, 1950; Anonymous, 2004). For our purposes, the most appealing characteristic of these materials is their acute sensitivity, which makes them a candidate for the sensors required to register the very low energy waves that will be produced by a scorpions footsteps.

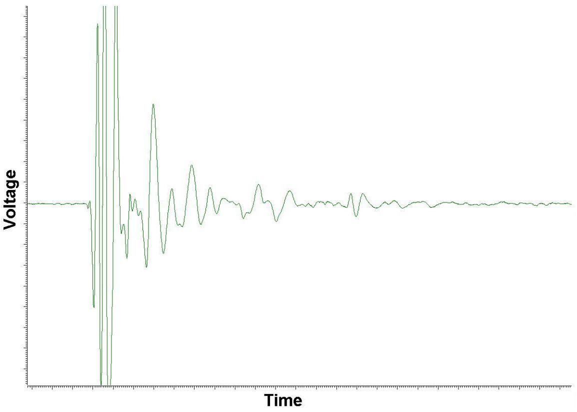
Piezoelectric materials can be specially manufactured to suit a particular application. As an inexpensive alternative, we have been using materials harvested from pre-existing commercial sources (see Methods).

Theory of triangulation

Theoretically, to determine the position of a scorpion, one needs at least three transducers arrayed so as to measure the passing waves from three different positions. The transducers are only able to measure the difference in arrival times of various waves, but from this information two methods for determining the position of the scorpion are available.

The first takes advantage of the fact that packets of waves are typically produced when the surface of the substrate is disturbed. Traditionally, these packets are referred to as primary, secondary, and long waves. Each has a characteristic transmission velocity and thus the tranducer will register their passage at different times—first the primary wavefront, then the secondary, and finally the long waves. If the waves have traveled any appreciable distance, the temporal separation between the arrivals of the various waves should be measurable. The farther the waves have had to travel, the greater the separation in time between their respective arrivals. This separation is predicted to vary linearly with distance traveled, but can appear nonlinear if the distances and depths of transmission are great. The latter factor involves the increasing velocity of the waves with depth, due to the increased compression of the substrate (Longwell & Flint, 1955).

A typical signal from a piezoelectric transducer registering surface waves is pictured below:



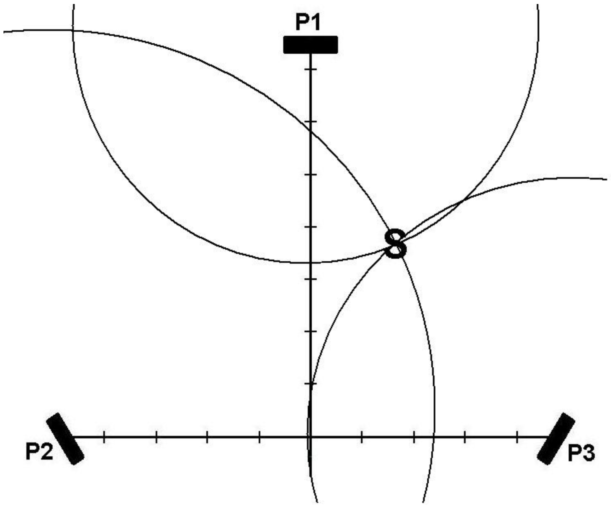
Here, the first few spikes likely represent the passage of compression waves, whereas those that follow are probably due to Rayleigh waves (Mason, 1950). Assuming one can accurately determine the difference in arrival times of these two sets of waves, one can calculate the total distance they have traveled.

Assuming that the increase in separation of the wave fronts is linear with respect to the distance the waves have traveled, one can calculate the distance from their origin to the receiver by solving the following equation for X:

$$X / V_s - X / V_p = t$$

where X = *the distance from the origin to the receiver*
Vs = *the velocity of the second wave to arrive*
Vp = *the velocity of the first wave to arrive*
t = *the time between the arrival of the two waves*

This distance can be represented graphically by a circle of radius X that is centered on the receiver, signifying that the origin of the waves could have been anywhere a radial distance of X from the receiver. If three receivers are used, and three such distances are derived, one can triangulate the position of the scorpion by determining the intersection of the three circles:



Where:

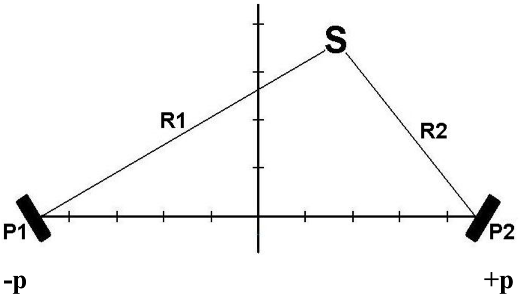
P1, P2, P3 = *Piezoelectric receivers 1, 2, and 3*
S = *Source of the disturbance*

We did not explore this approach for two reasons. First, it relies on the ability to precisely identify the arrival of at least two separate wave types. As will be discussed, one of the greatest difficulties encountered thus far is judging precisely the arrival of a single wavefront. Making two of these judgments for each measurement compounds the difficulty. Second, this approach will require that, beyond the use of surface waves, the more ephemeral compression waves be used. Compression waves spread in three dimensions, as opposed to surface waves that are largely two dimensional, and thus suffer from geometrical spreading to a greater degree than their surface counterparts. Essentially, the energy that interacts with a given receiver diminishes far more quickly with compression waves, making them hard to measure except at close range.

The second approach that can be used to determine the scorpion's position involves looking at the time difference of arrival of the same wave packet at each of the three receivers. One might, therefore, track the arrival of the Rayleigh wave front as it passes across each of the receivers.

If, for example, the source of the waves is equidistant from two receivers, the waves should arrive at the same time. If the source is closer to one receiver than the other, the wave packets will arrive first at the nearer of the two. More quantitatively, for receivers called "1" and "2," placed at "**p**" and "**-p**" on the x-axis respectively, the radial distance from any point in the x-y plane to the first receiver can be expressed as:

$$\mathbf{R1 = SQRT\ [(x-p)^2 + y^2]}$$



Where:

R1 = *the radial distance between the source and the first receiver (P1)*
x = *the Cartesian coordinate of the scorpion on the x-axis*
p = *the known position of the receiver (P1 or P2) on the x-axis*
y = *the Cartesian coordinate of the scorpion on the y-axis*

The distance to the second receiver is thus

$$\mathbf{R2 = SQRT\ [(x+p)2 + y2]}$$

The difference in the distances is

$$\mathbf{R2 - R1 = SQRT\ [(x+p)2 + y2] - SQRT\ [(x-p)2 + y2]}$$

This represents the extra distance the waves must travel to reach the second receiver after contacting the first. This distance can also be expressed as

$$\mathbf{V * t = R2 - R1 = SQRT\ [(x+p)^2 + y^2] - SQRT\ [(x-p)^2 + y^2]}$$

Where

V = *the velocity of the wave used for the calculation*
t = *the time difference between the arrivals at the two receivers*

This yields a relationship between the arrival time difference and the x and y position of the scorpion. The equation itself is that of one-half of a hyperbola, as is more easily seen when rewritten in the more familiar form :

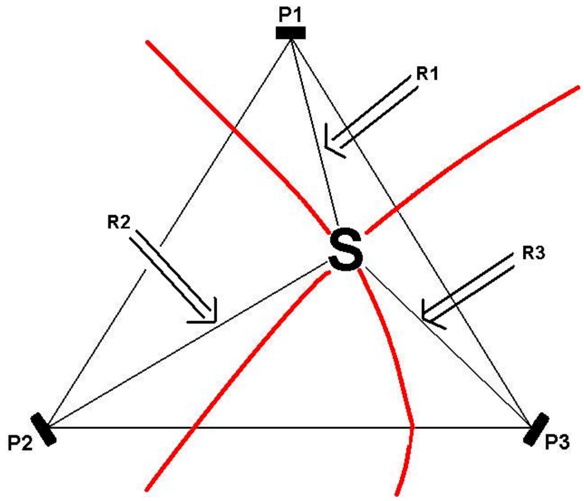
$$\mathbf{\frac{x^2}{t * v/2} - \frac{y^2}{p^2 - t * v/2} = 1}$$

Where

t, **p**, *and* **v** *are constant*

A hyperbola describes the set of points for which the absolute value of R2 - R1 is constant (Demana & Waits, 1990). In our case, we are not concerned with the absolute value of R2 - R1 but rather the true value. A positive value for this difference indicates that the scorpion is closer to P1, whereas a negative value indicates the scorpion is closer to P2. Thus, when plotting the graph of the hyperbola, only half of the points are included; those on the side of the conjugate axis shared with the closest receiver.

For any given time difference between the arrivals at two receivers, a series of possible origination points are found by plotting the half of the hyperbola that used the nearest receiver as a focal point. If three receivers are used and the time differences are found between two pairs, two hyperbolas can be plotted. The intersection of these hyperbolas is the origin of the wave fronts.



Representation of the intersection of two hyperbolas generated by the time differences between P1 - P3 and P2 - P3 (the third possible hyperbola is not pictured). Here,

S = *Position of the scorpion*
P1 = *Receiver 1*
P2 = *Receiver 2*
P3 = *Receiver 3*
R1 = *Distance between S and P1*
R2 = *Distance between S and P2*
R3 = *Distance between S and P3*

Assuming that sensors are sensitive and precise enough to register the vibrations produced by the walking of a scorpion, a series of equations similar to those above could be solved to arrive at a position in the defined Cartesian coordinate system that represents the origin of the waves and thus the position of the scorpion at that moment.

Methods

To develop a reliable system of triangulation for tracking a scorpion, the piezoelectric receivers must be both sensitive and reproducible. Various inexpensive commercial sources of piezoelectric materials were explored including those harvested from an antiquated brand of phonograph cartridge from the Astatic company, and those taken from two brands of electric lighters. Other sources have been examined but not tested to this date.

Each transducer was assessed for sensitivity and reproducibility to a signal generated by disturbing the surface of the sand. As this project is still in its trial stages, no single rigorous assay has been developed for comparing the performance of the various piezoelectric materials or determining the effect of the various alterations made to improve the setup. Most of the "data" to this date are either qualitative or based on simple voltage or signal-to-noise ratio comparisons.

The outputs of the transducers were amplified by an AM Systems differential AC Amplifier (Model 1700) and converted to a digital signal by a 1401-plus Analog to Digital Converter (CED, Cambridge, England). Spike II (CED) was used as the data acquisition and analysis software package.

Sand used in these experiments was collected from sandy regions of the Northern Chihuahuan Desert near Kermit, Texas, from areas with healthy populations of sand scorpions (*Paruroctonus utahensis,* in particular). Several small containers for this sand were experimented with, and the best results were achieved in a thick (approximately 2.5 cm) Styrofoam container, with a square internal diameter of 35 cm, filled with sand to an average depth of 20 cm. Good results were also achieved in an electrically grounded metal cookie tin of about 30 cm circular diameter and an average sand depth of 15 cm.

Several methods were used to disturb the surface of the sand, ranging from driving the tip of a pen into the surface, to dropping a small weight from a known height, to allowing a scorpion to walk across the surface.

To test the characteristics of each piezoelectric material, some effort was required to standardize the measurements and to improve the between-trial reproducibility. Steps were taken to filter out extraneous noise, adjust amplification parameters, and improve the sensitivity of the transducers themselves.

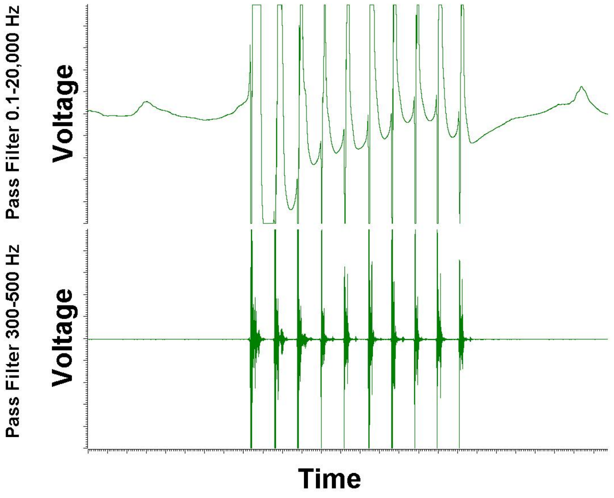
Results & Discussion

The following factors had the most significant effects on the sensitivity and reproducibility of measurement:

- Bandpass filter of the signal from 300–500 Hz to capture the major frequency bandwidth for compression and Rayleigh waves in sand.
- Further insulation of the sandbox from extraneous vibrations.
- Use of a resistor/capacitor (RC) filter to attenuate unwanted frequencies.
- Elimination of unnecessary electromagnetic field effects from the environment.
- Reduction of amplification of the signal to prevent saturation of the amplifier.
- Increasing of the exposed area of the piezoelectric receiving element to improve sensitivity.

Bandpass filtering

The greatest improvement to the signal came by limiting the frequency bandwidth used for amplification. For the AM Systems amplifier, the high pass filter ranges from 0.1 Hz to 300 Hz, and the low pass filter ranges from 500 Hz to 20,000 Hz. With the high pass filter set at 0.1 Hz and the low pass filter set at 20,000 Hz, the signal drifts over a wide range, and distinct wave pulses attributable to a stimulus cannot be identified. Brownell (2001) states that in sand the majority of the signal strength for compression and Rayleigh waves lies in the 300–500 Hz range for distances greater than 10 cm and up to 5000 Hz for lesser distances. On the assumption that either compression or Rayleigh waves would be valuable for triangulation purposes, the signals from the receivers were band passed filtered between 300 to 500 Hz. The result was immediately apparent, yielding a vastly improved signal. It was noted, by independently varying the high and low pass filters, that most of the noise and "drift" was a result of low frequencies. Thus, a high pass filter setting of 300 Hz was necessary, while filtering above 500 Hz was less important. The figure below shows an example of signal improvement with filtering:



Insulation of the apparatus

Most measurements were taken with the sandbox atop a thick foam insulation pad. This reduced the effects of building vibrations but did not completely eliminate them.

To further improve insulation from vibration, the apparatus was placed atop an inertial mass (a very heavy metal sheet) supported by four rubber racquet balls. Theoretically, this should eliminate high frequency noise as the inertial mass will resist high frequency oscillation. The effect of this step was not apparent and not seemingly worth the effort of involving the awkward inertial mass. This follows along with the observations made during bandpass filtering, that the lower frequencies had a greater effect on signal quality and that high-frequency noise is either not present, is attenuated by the sand, or does not seem to effect measurements.

RC filtering

Several trials were conducted using an RC filter as a low and a high pass pre-filter. Unfortunately, during these measurements, the between-trial reproducibility remained poor. Thus, measurements could not be compared for a single piezoelectric receiver with and without filtering, but rather simultaneous measurements between two receivers (one with an RC filter and the other without) were made. Afterward, the filter was switched between the receivers to control for effects other than the filtering.

Following up on similar experiments previously conducted by Stephens & Gaffin (2000), a 99 kohm resistor and a 0.01 microfarad capacitor were used for the filter. For the simple setup we used, frequencies above or below the time constant, or "break point" of the RC circuit will be attenuated. The break point for this RC pair is 1010.1 Hz. Given the preferred frequency bandwidth of 300–500 Hz, this filter will likely work best as a low pass filter. This is confirmed by cursory examination of the effects seen when the filter was used as a high-pass filter; signal quality was either reduced or seemingly unaffected. However, rigorous testing using the device as a low pass filter has not been completed. It may also be desirable to adjust the resistance and capacitance values to better reflect the desired bandwidth of 300-500Hz.

Electromagnetic field effects

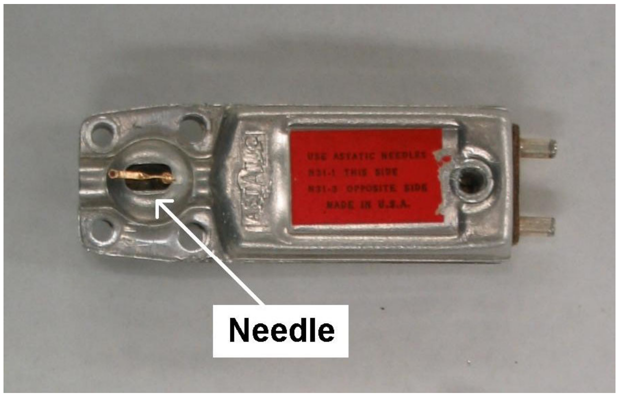
Cables and wiring not associated with the triangulation apparatus may interfere with the measurements. The signal-to-noise ratio improved when all wires near the triangulation apparatus were disconnected and removed. The use of a loosely constructed Faraday cage using window screens and aluminum foil has a yet uncertain effect.

Amplification

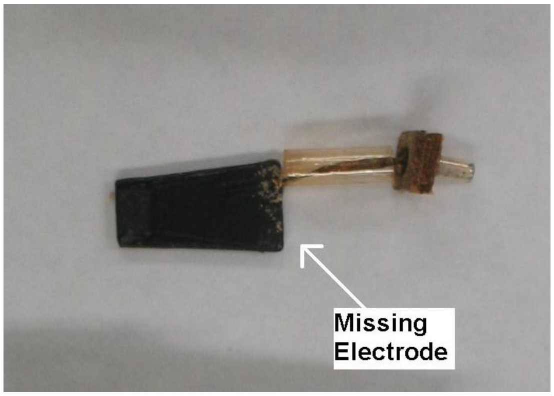
In each of the previous trials, results were often qualitative or inconclusive. This is largely the effect of the inability to reproduce a given trial. Signal intensity would often change by an order of magnitude or more on separate days, given seemingly identical circumstances and setup. More problematic was the periodic loss of signal, even in the middle of a trial, when the spikes representing the stimuli would suddenly fail to register regardless of how hard the sand was disturbed. This loss of signal could be due to saturation of the amplifier. The amplification setting was subsequently reduced from 10,000X to 1,000X or 100X. This seems to largely correct the problem.

Choice of piezoelectric material and exposed surface area of the receiver

Experimentation with the three sources of piezoelectric material used thus far indicates that highest sensitivity was achieved with the Astatic phonograph cartridge. Piezoelectric materials were also harvested from two brands of electric lighters: one purchased from the local supermarket and labeled only as a piezoelectric lighter, and the other a Scripto® brand utility lighter. These two brands of electric lighters contained transducers that were sensitive to the type of vibrations being used to a distance of approximately 20 cm. These have therefore been abandoned without further attempts to improve their sensitivity. The phonograph cartridges, as the more sensitive receivers, have been subject to several modifications to further improve their functionality. Originally, they were employed using their full casing, with the needle arm acting as the receptor and applying pressure directly to the transducer.



After testing, the cartridges were pried open and the transducer itself was used as the receptive element. This approach benefited from the increased surface area for receiving the waves, but suffered due to the fragility of pre-attached electrodes. Several electrodes were torn during handling.



Finally, the cartridge was altered by cutting away part of one of the sides, exposing the transducer but allowing it to remain within the stable casing. This seems to maximize the performance of the receivers while protecting the electrodes.

The best signals produced are sufficient to resolve a clear signal of a pencil driven into the sand at distance of more than 0.5 m. Unfortunately, they cannot, except in the very near field, resolve the footsteps of a scorpion above the baseline of background noise. For now, triangulation of a more robust signal (pencil tap) is being pursued to determine how accurately the triangulation can be performed assuming a sufficient signal. Once the technique is perfected, new sources of piezoelectrics will be sought. It may prove necessary to buy directly from a manufacturing company to achieve the necessary sensitivity.

Remaining obstacles

Having resolved a majority of the problems involved in achieving a clear signal, the greatest remaining problem is interpreting these signals. The signal is assumed to be composed of several different wave types, however, the beginnings and ends of each are difficult to precisely identify. Attempts to determine, by hand, the velocity of the respective waves based on time-of-arrival measurements failed to achieve a precision of even tens of meters per second. The principal error was the identification of the arrival of the wave front. Techniques for such identification must be well known, as seismologists routinely make such determinations (Longwell & Flint, 1955). Once we are able to better estimate the time of arrival of the waves, we will be able to begin manual triangulation. When the technique proves reliable and accurate, the system can be automated and put into practice.

Acknowledgments

We thank Greg Blass for taking care of the specimens and Dr. Mariëlle Hoefnagels for valuable editorial comments. Special thanks to Dr. Joe Bastian for supplying the Astatic brand phonographic cartridges. The experiments described here comply with the "Principles of animal care," publication No. 86-23, revised 1985 of the National Institute of Health and also with the current laws governing animal care and usage in the United States.

References

ANONYMOUS. 2004. Piezo ceramics tutorial. Morgan Electroceramics Web site. Available at: http://www.morganelectroceramics.com. Accessed April, 2004.

BACHRACH, R., J. DVORKIN, & A. NUR. 1998. *Geophysics*, 63: 1234–1240.

BROWNELL, P. H. 1977. Compressional and surface waves in sand: used by desert scorpions to locate prey. *Science*, 197: 479–481.

BROWNELL, P. H. 1984. Prey detection by the sand scorpion. *Scientific American,* 251: 86–97.

BROWNELL, P. H. 2001. Pp. 3–12 *In* P.H. Brownell & G.A. Polis (eds.). *Scorpion Biology and Research*. New York, NY: Oxford University Press.

FRANKLIN, D. & B. K. WAITS. 1990. *College Algebra: A Graphing Approach.* Addison-Wesley Publishing Company: Reading, Massachusetts. Pg. 483–492.

HOLMES, A. 1965. *Principles of Physical Geology*. Thomas Nelson and Sons LTD: New York. Pg. 913–917.

LONGWELL, C., & R. F. FLINT. 1955. *Introduction to Physical Geology.* John Wiley and Sons, Inc.: New York. Pg. 325–321.

MAHGHNANI, M. H., & R. RAMANANANTO-ANDRO. 1974. Compressional and shear wave velocities in granulite facies rocks and eclogites to 10kbar. *Journal of Geophysical Research*, 79: 5427–5432.

MASON, W. P. 1950. *Piezoelectric Crystals and their Application to Ultrasonics.* D. Van Nostrand Company, Inc. New York, 10 pp.

STEPHENS, A. V. & D. D. GAFFIN, 2000. Walking in the dark: can sand scorpions orient to objects in complete darkness? *Abstracts, Annual Meeting of the American Arachnological Association*. Lexington, Kentucky.

Euscorpius — **Occasional Publications in Scorpiology. 2004, No. 17**

Surface activity, biomass, and phenology of the striped scorpion, *Centruroides vittatus* (Buthidae) in Arkansas, USA

Tsunemi Yamashita[1]

[1]Department of Biological Sciences, Arkansas Tech University, Russellville, Arkansas 72801, USA

Summary

A population of the striped scorpion, *Centruroides vittatus* (Buthidae) was monitored for four years at an upland site in Pope County, Arkansas, USA. This surveillance was conducted to better understand the scorpion's surface activity, feeding rates, cannibalism, and biomass. The survey results indicate that scorpions are active at this site from April to November, with male and female density generally equivalent during the surveyed months. For 2000-2001, the calculated density/100 m^2 was 2.92 and the population biomass was 0.133 kg/ha. In 2003, the calculated density/100 m^2 was 2.41 and the population biomass was 0.111 kg/ha. In 2001 a Peterson mark/recapture estimate for adults was 140 individuals in the study site (SE = 85-276). A 2003 Jolly-Seber mark/recapture estimate for adults was 110 (SE=15-434). Females with young were observed in June, July, and August. The calculated feeding rate was 0.0-11.5% per survey night and the cannibalism rate (% of diet) was 9.5%. Lastly, no matings were observed during the survey period.

Introduction

Scorpions have been shown to be model research organisms for desert ecosystems (Polis, 1990, 2001). With their high density in deserts, ease of detection with ultraviolet lights, and external prey digestion, they have contributed greatly to the understanding of energy flow and other ecological factors in these environments. In spite of the large number of studies in deserts and other arid regions, scorpion biology in other terrestrial systems has not been well studied. In particular, scorpions in forested or semi-forested ecosystems of the eastern and midwestern United States are poorly understood although several species exist in these areas, e.g., *Centruroides vittatus* (Buthidae) and *Vaejovis carolinianus* (Vaejovidae) (Shelly & Sissom, 1995). Species of the genus *Centruroides* are well suited for ecological study as they can exist in a wide range of ecological habitats and may encompass a large geographic range. In this paper, I summarize surface activity patterns, density and biomass, and aspects of feeding biology for the striped scorpion, *Centruroides vittatus* (Say, 1821) in northwestern Arkansas. This scorpion encompasses a large geographic area that includes Texas, eastern New Mexico, southern Colorado, Kansas, southern Nebraska, southern Missouri, a small portion of western Illinois, western Arkansas, western Louisiana, and Oklahoma (Shelly & Sissom, 1995). In several states, *Centruroides vittatus* is the only scorpion reported: Kansas, Nebraska, Missouri, Illinois, Arkansas, and Oklahoma. Ecological studies of this scorpion were conducted in west Texas (Brown et al., 2002) and southern Texas (McReynolds, this volume), but none have investigated the biology of this species in more temperate climates.

Methods

Study site

The site selected for the study is located in Pope County, Arkansas. The study site is included within a large south facing rocky upland semi-forested area (study site = 4500m^2) with exposed sandstone substrate (37% unforested area). The forest in the study site is a typical upland habitat found in Arkansas' Interior Highlands that includes hot, dry glades with a broken Post Oak (*Quercus stellata*), Shortleaf Pine (*Pinus echinata*), and Cedar (*Juniperus ashei*) canopy and fauna characteristic of more western regions (Trauth et al., 2004). This area receives an average of 123.42 cm/year with an average July high temperature of 27.5 °C and an average January low temperature of 3.8°C (NOAA, 2002). The study site area measurements were taken with a Trimble GPS Pathfinder System and analyzed with the Trimble TSC1 Asset Surveyor software.

Scorpions were monitored at night with UV lights from the year 1999 through 2003. As the first survey years encompassed less of the active months of the scorpion, the data for the density and population biomass were taken from years 2000 and 2003 (June or April through November). Each week during the scorpion's active year, data were collected on number of each sex observed, location and activity, and feeding and prey type. Feeding rate was calculated as the proportion of individuals observed that were feeding on a given survey night (Polis, 1979). Cannibalism was calculated as the percentage of the diet that included conspecifics. Individuals were approximately categorized during the surveys as adults, juveniles, and second instars. Juveniles were those individuals that appeared markedly smaller than adults but were much larger than second instars and most likely represent third or fourth instars. These observations totaled to 69 survey dates with 2539 total scorpions (2308 adults) observed in the study.

I summarized the data as surface density/100 m^2, surface activity as a function of temperature, male versus female activity (actively moving vs. sessile), microhabitat type the scorpion was found in (on rocks, on the substrate, in grass, and in trees). In addition, the surface density was calculated from nightly survey data. This calculation was done to provide a comparable estimate to Brown et al. (2002).

The population biomass for 2001 and 2003 was calculated from a mark/recapture adult density estimate (both sexes) conducted with a Peterson method for closed populations in June 2001 and a Jolly-Seber method for open populations in August 2003. The mark/recapture surveys were conducted over four successive nights in an attempt to obtain a robust recapture rate. In 2001, I did not mark individuals for separate identification. In 2003, however, I marked each individual with unique paint marks for individual identification. To determine the number of each sex in the study site, the density estimate provided through the mark/recapture methods was adjusted with the average percentage of each sex represented in the nightly observations. The calculated number of each sex was then multiplied with average adult mass of each sex to determine total mass of each sex in the study site. After the total population mass of each sex was added together, the number was adjusted to produce total biomass (kg/ ha). Biomass estimates were also produced from nightly observation data alone to allow comparison with other studies. Lastly, the feeding regime was determined with summarizing prey type, feeding rate, and cannibalism rate (percent of diet).

Results

Surface density per 100 m^2

Scorpions were found on the surface during the UV night surveys from April to early November. The mean surface density from nightly survey data alone for 2000 was 0.818 individuals/100m^2 and for 2003 it was 0.456 individuals/100m^2. The range in surface density was 0.250 - 1.690 for 2000 and 0.044-1.093 for 2003 (Figs. 1 and 2, respectively). The estimated surface density calculated from the mark-recapture methods was 2.92 individuals/100m^2 for 2000 and 2.41 individuals/100m^2 for 2003. In both years, two peaks were seen in surface density. The first occurred in the spring (April or June) with the second peak in October. Generally, surface activity is most likely a response to ambient temperature (see below). Although no scorpions were recorded as active on the surface during December through January, rock flipping surveys did yield individuals during warm days in these months.

Juveniles and second instars showed lower average surface densities of 0.061/100m^2 (2000) and 0.064/100m^2 (2003) (Figs. 3 and 4). The ranges for these individuals were 0.021-0.376 (2000) and 0.022-0.219 (2003). In 2000, juveniles were seen from July to October with a peak in early July. Second instars were seen from late June to early October with a peak in late June. In 2003, juveniles were seen April through November with a peak in early October. Here, second instars were active during the same months as 2000 with a peak in numbers in early July.

Surface activity and air temperature

Surface activity appears to be correlated with environmental temperature (Fig. 5). Scorpion were not activity at surface temperatures below 10°C and reached the highest surface densities between 20° and 30°C. With regard to temperature, female and male surface activity do not appear to be significantly different from each other (Figs. 6 & 7).

Male and female variation in surface movement and location

When found on the surface, scorpions were categorized as actively moving on the surface or sessile. Overall, 42.97% of scorpions were observed actively moving on the surface. Males were observed more active than females with 54.40% of males (n=546) versus 34.92% of females (n=776) moving on the surface. Marked males also support the higher male surface movement observation as several males were also seen outside the study area many meters away from where

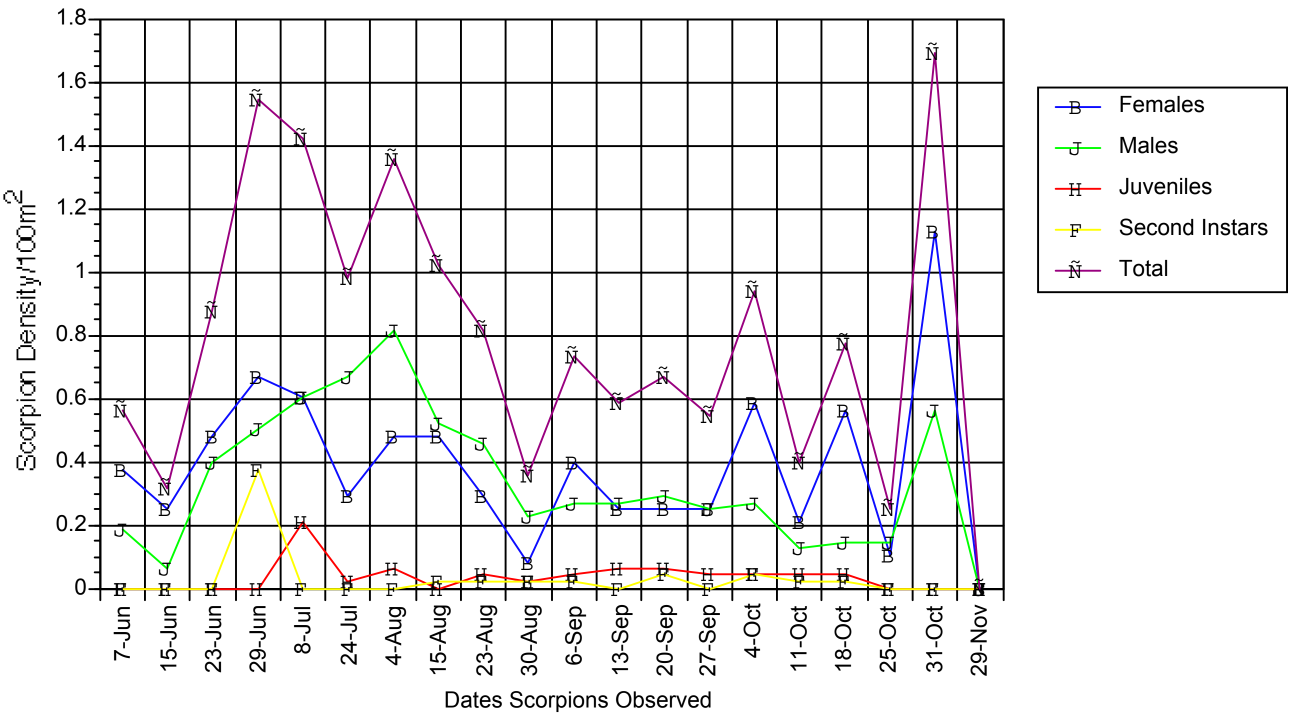


Fig. 1. Scorpion surface activity throughout the 2000 survey year.

they were marked. In contrast, several marked females were observed for a few weeks just meters from where they were marked. For example, in the weeks following the 2003 mark/recapture analysis, only one male was recaptured in the study site whereas 12 females recaptures were noted.

Adult scorpions were observed on several components of their environment. Individuals were considered above ground if they were observed greater than five centimeters above the substrate. This criteria was applied to separate individuals moving through grass and leaf litter from those further above the substrate. Although they were most prevalent on the ground on rock or leaf litter substrate (80.33%, n=961), they were also observed on top or the side of rocks (35.80%), in grass clumps or on grass blades above the ground (10.61%), and on trees (9.05%). These data represent a subset of the total observations that specifically noted where scorpions were found in a microhabitat. A greater percentage of females were observed above the ground on trees and grass than males (females: 3.22% on trees and 1.26% on grass, n=1273; males: 1.35% on trees and 0.29% on grass, n=1035). In addition, the overall percentage of adults in trees was 3.68%. Lastly, only 1.56% of all adults observed were seen on the open rock substrate away from shelter (e.g., rocks, trees, and leaf litter; n=2308).

Mark/recapture population density estimates and biomass

The 2001 Peterson mark/recapture survey resulted in a population size of 140 individuals in the study site (SE=85-276). The Jolly-Seber survey in August 2003 produced a density of 110 individuals (SE=15-434). These density numbers were adjusted with individual male and female mass (0.41g and 0.49g, respectively) to calculate a population biomass of 0.133 kg/ha for 2001 and 0.111 kg/ha for 2003. If a population biomass is estimated with nightly survey data alone, the biomass reduces to 0.0346 kg/ha for 2000 and 0.0195 kg/ha for 2003.

Feeding rate and prey type

The feeding rate for *C. vittatus* ranged from 0.0 – 11.5% with an overall average of 1.65%. Twelve different prey items were recorded with spiders as the most common prey item (Table 1). Cannibalism of smaller individuals by larger individuals was observed with a dietary of 9.30%. Cannibalism from adult males was calculated to be higher than that from females (7.14% versus 2.38%). Females, however, showed a higher percentage of prey capture, excluding cannibalism, than males (50% versus 38.1%, n for all

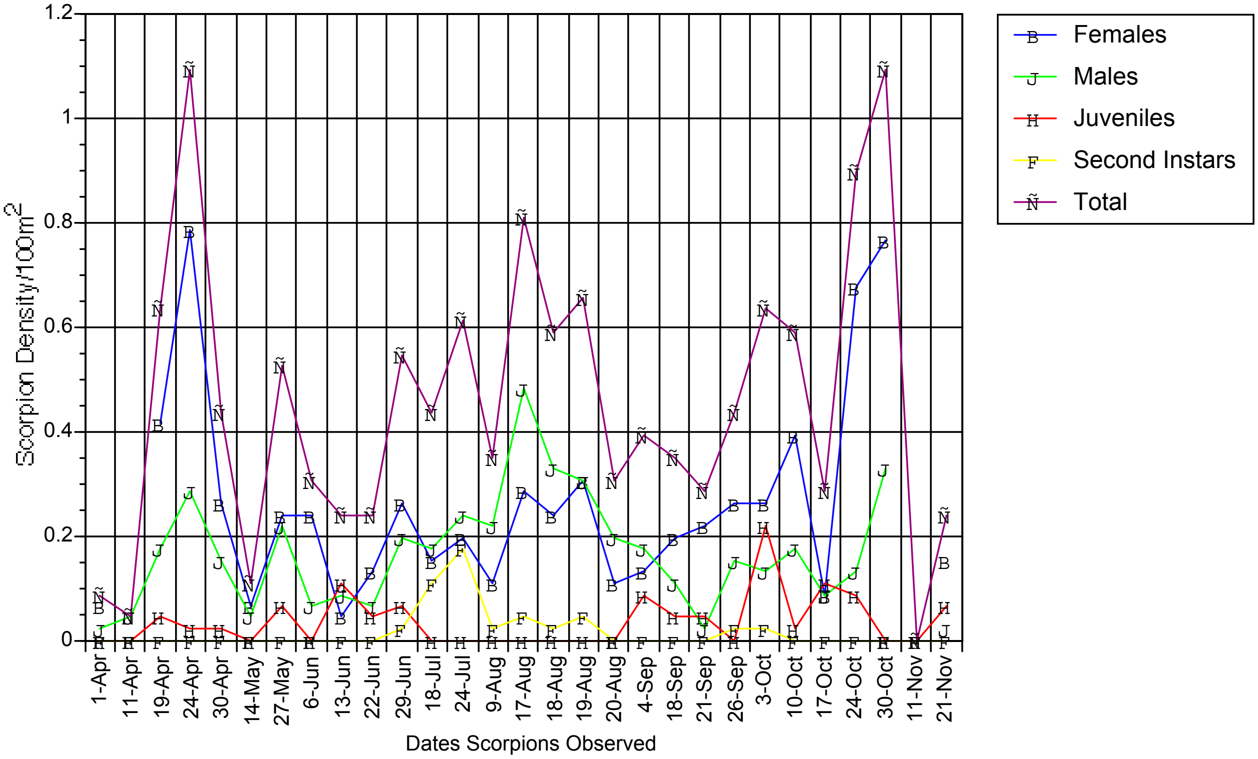


Fig. 2. Scorpion surface activity throughout the 2003 survey year.

prey taxa = 43). No second instars were recorded cannibalizing others of the same age class.

Prey Item	Prey Number	Percentage of Diet
Cannibalism	4	9.30
Caterpillar	5	11.63
Locust	7	16.23
Moth	6	13.95
Spider	12	27.91
Cricket	1	2.33
Beetle	1	2.33
Grub	1	2.33
Fly	2	4.65
Katydid	1	2.33
Crane Fly	1	2.33
Harvestmen	1	2.33
Other	1	2.33
Total	43	

Table 1: Prey items and dietary percentage in the Arkansas *C. vittatus* population.

Discussion

Surface density/100 m^2 and temperature effects

The surface activity and density was lower for the Arkansas population than other scorpion populations. In arid regions, scorpions can be active in all months (Polis, 1980). In a west Texas population of *C. vittatus*, individuals were observed in all months (Brown et al. 2002). The inactivity of the Arkansas population during the winter is most likely due to lower temperatures (Warburg and Polis, 1990). Polis (1980) observed that 4°C was the lower limit of scorpion activity in sandy deserts. The Arkansas population showed a slightly higher value of 12°C as the lowest recorded surface activity limit. The estimated surface density of 0.818 individuals/100m^2 and 0.456 individuals/100m^2 falls within recorded values from other populations (Polis, 1990; Table 6.7). However, only four of 24 recorded scorpion densities from Polis (1990) are lower than this population. Moreover, it is the lowest recorded population density for a *Centruroides* species. Brown et al. (2002) reported a population estimate of 7.36 individuals/100m^2, 2.5X higher than that of the Arkansas population. The lower density in this population may stem from a shorter activity season than that observed in more arid populations. In addition, as this scorpion

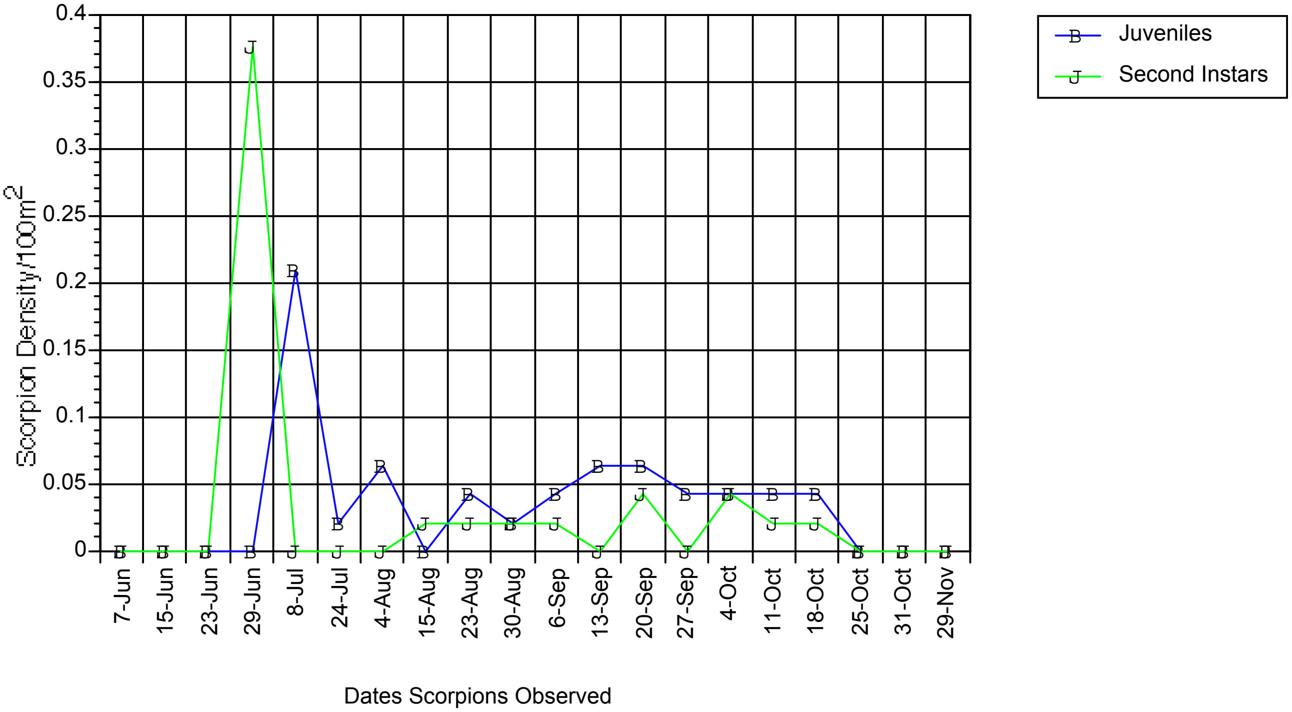


Fig. 3. Juvenile and second instar surface activity in 2000.

cannot dig deep burrows to reduce climatic effects, freezing winter temperatures and a more harsh environment most likely serves to limit population size. Scorpions in this study also reflected a summer activity decrease as noted by Polis (1980), Warburg and Polis (1990), Brown et al. (2002). In this study, the two highest peaks in surface activity occurred in the late spring/early summer and also in October.

Juveniles and second instars did not show activity patterns that differed from adults although their densities were approximately 20-30x lower than adults. Smaller, more juvenile individuals in sand scorpion populations exhibited reduction in surface activity overlap when compared to adults to reduce cannibalism from adults (Polis, 1990). The low surface activity of smaller individuals throughout the year may produce the same effect seen in sand scorpions to reduce cannibalism. In addition, as the physical environment this population occurs in is more complex than that of the sand scorpion, more opportunity for hiding in the leaf litter substrate or in trees exists and can reduce overlap with adults. The substrate complexity would reduce niche overlap with adults and may reduce the need for temporal shifts due to predation risk.

Male and female variation in surface movement and location

C. vittatus was more active on the surface than the sand scorpion (42.97% versus 1.8% recorded by Polis, 1979), which supports the more errant nature of this scorpion. As reported in the sand scorpion, male *C. vittatus* were more active than females when on the surface (Polis, 1980). This male activity is associated with reproductive behavior as males move to seek females for mating (Polis and Sissom, 1990). As mating activity was not observed in this population and seasonal spikes in male movement did not occur, I speculate prey foraging may contribute more to male movement. Females at the end of the activity season did show an activity frequency similar to males. In the last week of October in 2000 and 2003, female activity increased from the yearly average of 34.92% to 58.91% (n=129). For these four sampling dates, the male activity frequency was 60.42% (n=48). These dates may reflect increased prey foraging by both sexes or individuals seeking over wintering sites.

Although scorpions were occasionally observed on trees (9.05%), the majority of the time they were observed was on the ground or close to the ground. In the sand scorpion, 25% of prey items were carried to vegetation (Polis, 1979). In *C. vittatus*, 40.91% of

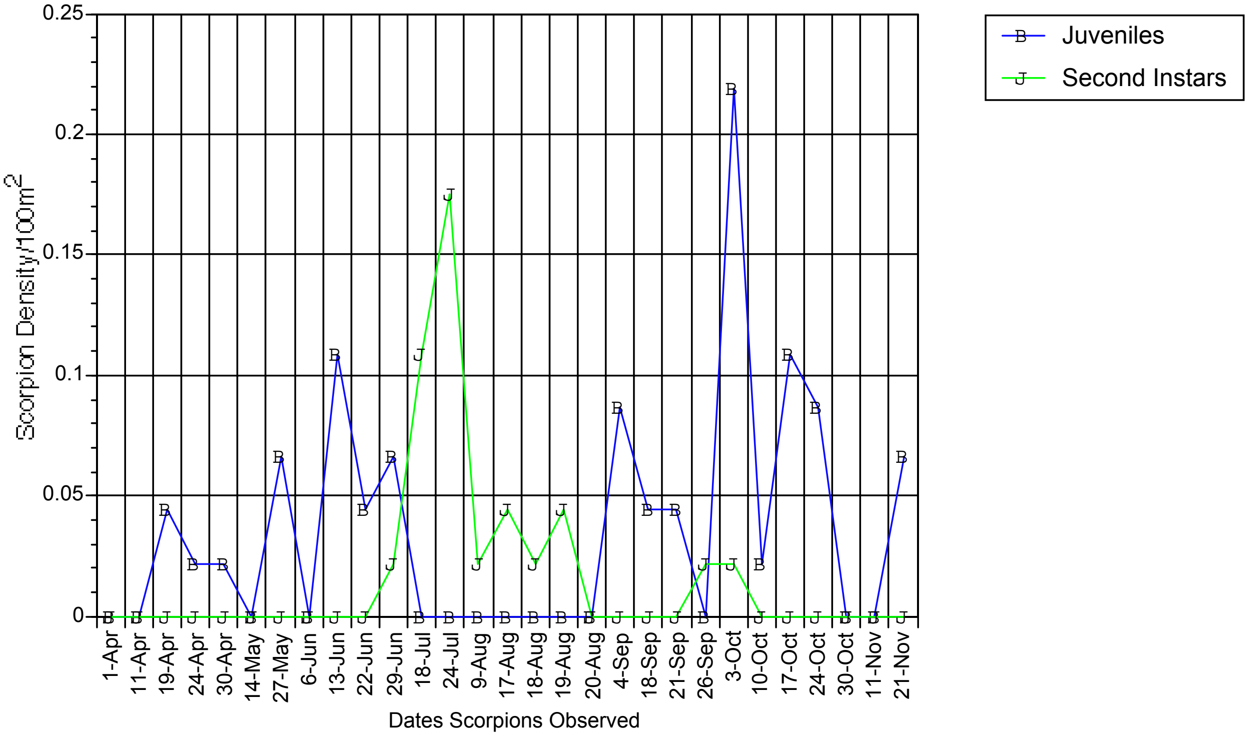


Fig. 4. Juvenile and second instar surface activity in 2003.

female feeding and 10.53% of male feeding occurred above the ground in grass or in trees (n=43); however, females were more prevalently perched above the ground (4.48% of all females observed) than males (1.64% of all observed males). These data that show that females were more likely to climb, again suggest females may occupy a homesite and remain more sedentary than males.

When compared to Brown and O'Connell's (2000) study of climbing behavior in this scorpion in west Texas, the Arkansas population shows a reduction in climbing behavior (19.3% and 25.2%, west TX; 3.68% in AR). If the data are partitioned into sexes, males show a lower percentage climbing when compared to females. Arkansas males were observed climbing 1.64%, females 4.48%. West Texas scorpions also showed similar percentages: females were observed on vegetation 14.58% and 24.32%, whereas males were observed on vegetation 8.5% and 13.89% (Brown and O'Connell, 2000).

Brown and O'Connell (2000) illuminated one potential problem in their analysis- pseudoreplication. If scorpions are measured repeatedly, the assumption of independence in the data set is violated (Hurlbert, 1984; Wise, 1993). In this study, the probability of resampling the same individual is reduced as adult recapture rates week to week were low (1/17, 5.88% to 3/20, 15% recaptures in 2003).

The predator avoidance strategy proposed in Brown and O'Connell (2000) appears as the most robust explanation for climbing behavior in Arkansas scorpions. Ground dwelling spiders (lycosids) were the most abundant prey item, suggesting that foraging on the surface was more productive than foraging above ground. Finally, the low occurrence of scorpions in open substrate away from shelter strongly suggests predator avoidance is an important adaptation in this population.

Mark/recapture population density estimates and biomass

Both density estimates conducted in this study appear similar to each other although different assumptions are inherent in each. The slightly higher density estimate for 2001 is also reflected in the number of individuals observed on the surface in that year. I speculate this population could exhibit large density fluctuations due to year-to-year climate variation during the winter.

The biomass data also reflect the reduced surface density data when compared to other scorpion populations. This population showed a biomass of 0.133 and 0.111 kg/ha (2001 and 2003 estimates, respectively). This estimate is 3X lower than the 0.31 kg/ha overall estimate reported in Brown et al. (2002). Again, the lower biomass may be representative of harsher

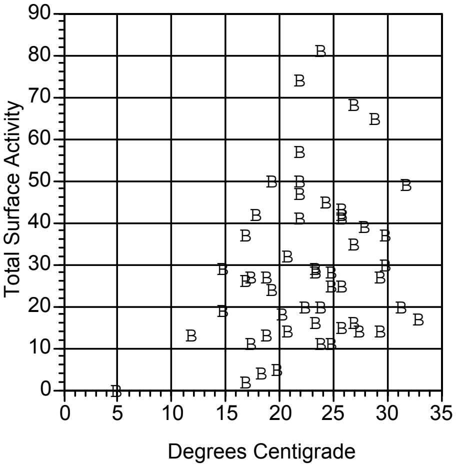


Fig. 5. Total surface activity as a function of temperature.

environmental conditions and a shorter activity season in this population. Interestingly, average adult male mass was similar in both the west Texas and Arkansas populations (0.419 g and 0.41 g, respectively), but average adult female mass was 1.5X higher in the west Texas population (0.765 g versus 0.49 g). West Texas female scorpions may undergo extra molts to achieve a larger body size (Brown, pers. comm.).

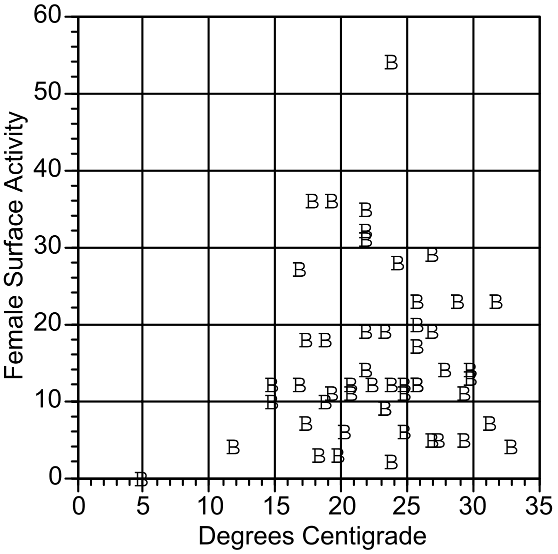


Fig. 6. Female surface activity as a function of temperature.

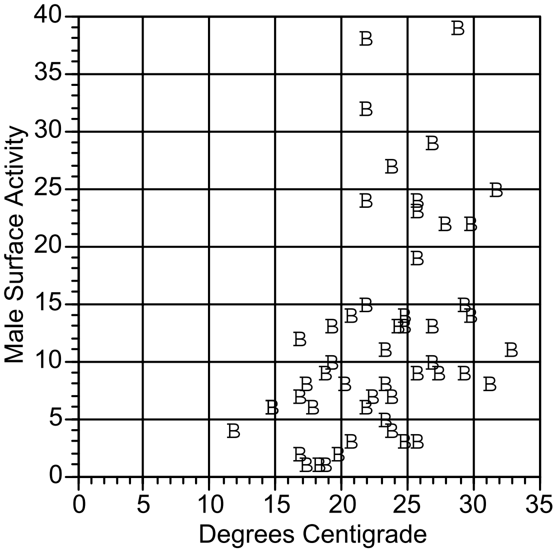


Fig. 7. Male surface activity as a function of temperature.

Feeding rate and prey type

The overall feeding rate for this scorpion was twice as low as that calculated for the sand scorpion (1.65 % versus 3.75 %) (Polis, 1979). In spite of this difference, the highest proportion of scorpions feeding was greater in this population than in the sand scorpion (11.5 % versus 8.1 %). The higher overall feeding rate in the sand scorpion may stem from larger number of days in which the sand scorpion was feeding, i.e, the striped scorpion experienced more poor days where no feeding took place. In addition, cannibalism rates were approximately the same as that reported with the sand scorpion (9.1 % versus 9.52 %, *C vittatus*). The high cannibalism rate was a surprise as buthid species are considered semi-social and regarded as representing the communal stage of sociality on the parasocial trajectory (Polis & Lourenco, 1986; Polis, 1990). This scorpion in southern populations has been found in aggregates (McAllister, 1966) and other buthids are known to overwinter together (Stahnke, 1966). Together with the lower densities, population biomass, more severe climate, and a high cannibalism rate; this population appears to exhibit evidence of food stress.

Food stress is considered to result in higher cannibalism rates than when prey are more abundant (Polis, 1988). This conclusion is somewhat paradoxical for this population as the regional ecosystem receives over 100 mm of precipitation annually and prey abundances could be high. The glade habitat, however, could exhibit lower productivity due to poor soils and the rocky substrate. The shorter activity year could result in these scorpions experiencing a smaller seasonal feeding window as well as greater metabolic demands to offset the more severe environment. In addition, food stress may be exhibited in populations that have undergone recent expansion and then experienced climate change. Ozark populations of the striped scorpion could represent those not fully adapted to environmental conditions as they may have recently expanded into this region during the warmer, drier Hypsithermal Interval approximately 8,000 to 4,000 years ago with other prairie species such as the collared lizard (*Crotaphytus collaris*) (Hutchison et al., 1999; Trauth et al., 2004). A recent phylogeographic analysis of striped scorpion populations revealed Ozark populations are difficult to separate based upon mtDNA analysis when compared to Texas populations, which supports a recent expansion hypothesis (Yamashita, unpublished data).

Conclusions

The striped scorpion (*Centruroides vittatus*) in Arkansas exhibits a lower population density, biomass, and seasonal activity compared to the west Texas population and other reported scorpion species. In addition, it shows high cannibalism rates. These factors suggest this population experiences food stress during the year. Northern populations of this scorpion may have recently expanded into their present location and may experience different environmental conditions than those present during their colonization. This climatic shift may have resulted in these populations experiencing a more metabolically stressful environment and has lead to food limitation. Food stress in this scorpion may result from a shorter feeding season and more metabolically severe overwintering conditions than those present in southern populations.

Acknowledgements

I thank the landowners who allowed access to their properties for this study. I also thank Arkansas Tech University for providing logistical support.

References

BROWN, C. A. & D. J. O'CONNELL. 2000. Plant climbing behavior in the scorpion *Centruroides vittatus*. *American Midland Naturalist*, 144: 406–418.

BROWN, C. A., J. M. DAVIS, D. J. O'CONNELL & D. R. FORMANOWITZ, Jr. 2002. Surface density and nocturnal activity in a west Texas assemblage of scorpions. *Southwestern Naturalist*, 47: 409–419.

HUTCHISON, D. W., S. T. MALCOMBER & L. S. PLETSCHER. 1999. A multidisciplinary investigation of the applicability of the Pleistocene herpetofaunal stability model to collared lizard (*Crotaphytus collaris*). *Herpetological Monographs*, 13: 81–141.

MCALISTER, W. H. 1966. The aggregating tendency of *Centruroides vittatus* Say (Arachnida: Scorpionida). *Texas Journal of Science*, 18: 80–84.

NOAA (National Oceanic and Atmospheric Administration). 2002. Climatological Data: Annual Survey, Arkansas. 107 (13).

POLIS, G. A. 1979. Prey and feeding phenology of the desert sand scorpion *Paruroctonus mesaensis* (Scorpionida: Vaejovidae). *Journal of Zoology*, London, 188: 333–346.

POLIS, G. A. 1980. Seasonal patterns and age-specific variation in the surface activity of a population of desert scorpions in relation to environmental factors. *Journal of Animal Ecology*, 49: 1–18.

POLIS, G. A. 1988. Foraging and evolutionary responses of desert scorpions to harsh environmental periods of food stress. *Journal of Arid Environments*, 14: 123–134.

POLIS, G. A. 1990. Ecology. Pp 247–293 *In*, Polis, G. A. (ed.). *The Biology of the Scorpions.* Stanford, California: Stanford University Press.

POLIS, G. A. 2001. Population and community ecology of desert scorpions. Pp 302–316 *In*, P. H. Brownell & G. A Polis (eds.). *Scorpion Biology and Research*. New York: Oxford University Press.

POLIS, G. A. & W. R. LOURENÇO. 1986. Sociality among scorpions. In, *Actas X Congreso Internacional de Aracnologia*, 1: 111–115.

POLIS, G. A. & W. D. SISSOM. 1990. Life history. Pp. 161–223 *In*, Polis, G. A. (ed.). *The Biology of the Scorpions.* Stanford, California: Stanford University Press.

SHELLEY, R.M. & W. D. SISSOM. 1995. Distributions of the scorpions *Centruroides vittatus* (Say) and *Centruroides hentzi* (Banks) in the United States and Mexico (Scorpiones, Buthidae). *Journal of Arachology*, 23: 100–110.

STAHNKE, H. L. 1966. Some aspects of scorpion behavior. *Bulletin of the Southern California Academy of Sciences*, 65: 65–80.

TRAUTH, S. E., H. W. ROBISON, & M. V. PLUMMER. 2004. *The Amphibians and Reptiles of Arkansas*. University of Arkansas Press: Fayetteville, 440 pp.

WARBURG, M. R. & G.A. POLIS. 1990. Behavioral responses, rhythms, and activity patterns. Pp 224–246 *In*, Polis, G. A. (ed.). *The Biology of the Scorpions.* Stanford, California: Stanford University Press.

Euscorpius — **Occasional Publications in Scorpiology. 2004, No. 17**

Temporal patterns in microhabitat use for the scorpion *Centruroides vittatus* (Scorpiones: Buthidae)

C. Neal McReynolds[1]

[1]Department of Biology and Chemistry, Texas A&M International University, Laredo, Texas 78041, USA

Summary

For scorpions (e.g., *Centruroides vittatus*), predation risk is often associated with the lunar cycle and prey availability with seasonal changes. When scorpions are illuminated by the moon, predation risk from nocturnal predators can increase in exposed microhabitats. Seasonal changes in precipitation and temperature can affect prey availability and thus microhabitat use by scorpions. Microhabitat use had a significant association with the lunar cycle for *C. vittatus*. Scorpions were on the ground at a significantly lower frequency during the waxing gibbous moon. During the waning gibbous moon, microhabitat use was significantly associated with moon rise. The frequency of scorpions found on the ground decreased after moon rise. However, the frequency of prey capture was not associated with the lunar cycle. Microhabitat use had a significant association with monthly classes. Ground use was higher during August and blackbrush (*Acacia rigidula*) use was higher during March and April. Scorpion height on vegetation was significantly different among monthly classes. Mean scorpion height was greater during April, March and October and less during August. Prey capture was significantly associated with monthly classes. Prey capture was low during August and high during April. Scorpion changes in microhabitat use during the lunar cycle supports a change in behavior to reduce predation risk. However, the change in microhabitat use does not appear to require a tradeoff between foraging success and predation risk. Seasonal changes in prey availability can explain differences in microhabitat use and foraging success by *C. vittatus* among monthly classes.

Introduction

Habitat selection by a predator often includes a tradeoff between higher foraging success and reducing the predator's own predation risk (Luttbeg & Schmitz, 2000; Murdoch & Sih, 1978; Werner et al., 1983; Werner & Hall, 1988). For scorpions, foraging success can be associated with seasonal changes in prey availability (Polis, 1980a, 1988; Polis & McCormick, 1986a) and predation risk from nocturnal visual predators can be associated with the lunar cycle (Hadley & Williams, 1968; Polis, 1980a; Polis et al., 1981).

Microhabitat use by scorpions can change with the lunar cycle to reduce predation risk during high illumination (see Skutelsky, 1996). Scorpions can shift nightly activity or microhabitat use to lower predation risk with high illumination. Neither Polis (1980a) nor Bradley (1988) found evidence of the lunar cycle affecting scorpion activity. However, habitat use by adult (but not juvenile) *Buthus occitanus* shifts because of the lunar cycle (Skutelsky, 1996). Seasonal changes in temperature and precipitation can affect prey availability and foraging success in scorpions (Polis, 1979, 1980a, 1988, but see Bradley, 1988).

Brown and O'Connell (2000) hypothesize that *Centruroides vittatus* (Say, 1821) (Scorpiones: Buthidae) climb into vegetation to either decrease predation risk or increase foraging success (Fig. 1). If habitat selection by the striped bark scorpion *C. vittatus* is to reduce risk of predation during high illumination from the moon, then scorpions should shift to less exposed microhabitats during the waxing gibbous phase of the lunar cycle and after moon rise during the waning gibbous phase. Scorpions can be found in more open microhabitats during waxing and waning crescent phases with low illumination from the moon. If foraging success declines as a tradeoff for lower predation risk during the lunar cycle, then foraging success of scorpions should be lower during waxing gibbous phase when predation risk is high. If habitat selection by *C. vittatus* is because of seasonal changes in weather and/or prey availability, then there should be seasonal changes in microhabitat use, scorpion height on vegetation and foraging success of scorpions. Can seasonal changes in prey availability explain these patterns?

Figure 1: *Centruroides vittatus* on Texas prickly pear cactus (*Opuntia engelmannii*) fluorescing under ultraviolet light.

Methods

Study animal

Centruroides vittatus (Say), the striped bark scorpion, has a wide distribution with Laredo, Texas in the southern portion of the species' geographic range (Shelley & Sissom, 1995). *Centruroides vittatus* is nocturnal with refuges during the day in debris, beneath vegetation, under bark and in openings in the ground. *Centruroides vittatus* and other bark scorpions rarely dig their own burrows (Polis, 1990, pers. obs.). Scorpions emerge from their refuge only occasionally to forage (Polis, 1980a; Bradley, 1988; Warburg & Polis, 1990). *Centruroides vittatus* is active on nights of emergence on the ground or in vegetation.

Habitat

This study was done on the campus of Texas A&M International University (27° 34' N 99° 25' W), Laredo, Texas. Laredo is in the Tamaulipan Biotic Province that is characterized by low precipitation and high average temperatures (Blair, 1950). The habitat of the study site can be described as thorny brush (Blair, 1950) or chaparral. Vegetation in the study site includes blackbrush (*Acacia rigidula*), guajillo (*Acacia berlandieri*), honey mesquite (*Prosopis glandulosa*), Texas prickly pear cactus (*Opuntia engelmannii*), tasajillo (*Opuntia leptocaulis*), strawberry cactus (*Echinocereus enneacanthus*), cenizo (*Leucophyllum frutescens*), guayacan (*Guaiacum angustifolium*), leather stem (*Jatropha dioica*), lotebush (*Ziziphus obtusifolia*), Spanish dagger (*Yucca treculeana*), and other species.

Data collection

Scorpions were observed at night by locating the scorpion fluorescing under ultraviolet light (see Sissom et al. 1990). The data was collected from 24 February 2000–15 April 2004. Scorpion data were collected after sunset on 211 nights between 7:30 PM CST at the earliest and 1:00 AM CST at the latest for an average of two hours per night. Data collected for each scorpion observed included date and time observed, species of scorpion, microhabitat used, the height that scorpions climbed on vegetation, position relative to sites, prey captured, prey taxa and behavior. Local temperature and

Planned Comparisons	***G***	***df***	***P***
Ground vs. Vegetation	18.319	3	$P < 0.001$
Cactus vs. Grass vs. Tree-Shrub	8.093	6	ns
Shrubs vs. Trees	5.582	3	ns
Blackbrush vs. Other Trees	1.725	3	ns
Total	33.719	15	$P < 0.01$

Table 1: Planned comparisons among microhabitat classes of the contingency table for microhabitat vs. lunar cycle classes. ns = not significant. See Fig. 2.

humidity were collected each night using a portable weather meter, Kestrel® 3000.

The microhabitat data were placed in six classes: ground, grass, cactus, shrub, blackbrush and other trees for the comparisons in this paper. The scorpion was considered on the ground if on soil, leaf litter, or rocks. Grasses were not identified to species, but all other plants were identified to species if possible. Trees included many woody species that are rarely taller than 2 meters. Shrubs included a variety of perennials such as cenizo, guayacan, leather stem, lotebush and Spanish dagger. Annuals were rare in the habitat except for ephemeral wildflowers after heavy rains and scorpions rarely climbed these wildflowers. Prey capture classes included 0 (= no prey capture) and 1 (= prey capture). Prey capture by scorpions can be observed as scorpions digest externally, thus prey items can be observed in pedipalps or chelicerae (Polis, 1979).

Lunar cycle

Microhabitat use and prey capture were compared during the lunar cycle. The lunar phase and time of moon rise or set were recorded for each collecting night from the U. S. Naval Observatory Astronomical Application internet site (http://aa.usno.navy.mil/ data/docs /RS_OneDay.html). Four lunar cycle classes were used: waxing crescent, waxing gibbous, waning gibbous and waning crescent. The waxing crescent class had 0-50% illumination of the moon disk and included the first quarter moon with 50% illumination. The moon can set during fieldwork on nights of the waxing crescent moon. The waxing gibbous class had 50-100% illumination and included the full moon with 100% illumination. The moon had already risen during fieldwork of the waxing gibbous moon. The waning gibbous class had 100-50% illumination and included the last quarter moon with 50% illumination. The moon can rise during fieldwork of the waning gibbous moon. The waning crescent class had 50-0% illumination and included the new moon with 0% illumination. The moon had already set during fieldwork of the waning crescent moon. An additional comparison of microhabitat use by scorpions before and after moon rise during the waning gibbous moon was performed to compare a period of no illumination from the moon to a period with potentially high illumination from the moon.

Seasonal

Microhabitat use, scorpion height on vegetation, and prey capture were compared during the year to determine seasonal patterns. There were ten monthly classes. Both January and February (J-F) and November and December (N-D) were pooled into a single class because of low sample sizes.

Data analyses

Comparisons of relative proportion in a contingency table of a microhabitat use or prey capture used the adjusted *G*-test for independence. A unplanned tests of homogeneity were performed on microhabitat vs. month contingency table to determine seasonal patterns of microhabitat use (Sokal & Rohlf, 1981). Orthogonal planned comparisons of microhabitat were performed on microhabitat vs. lunar cycle and microhabitat vs. month contingency tables. Orthogonal planned comparisons of monthly classes were performed on prey capture vs monthly class contingency table. The first planned comparison was based on homogeneous classes from the microhabitat vs. month contingency table. The heights of scorpions on vegetation were compared using the Kruskal-Wallis test (corrected for ties) because the class variances were heterogeneous. Dunn's multiple tests (unplanned comparison) were performed on scorpion height data with the overall $P < 0.05$.

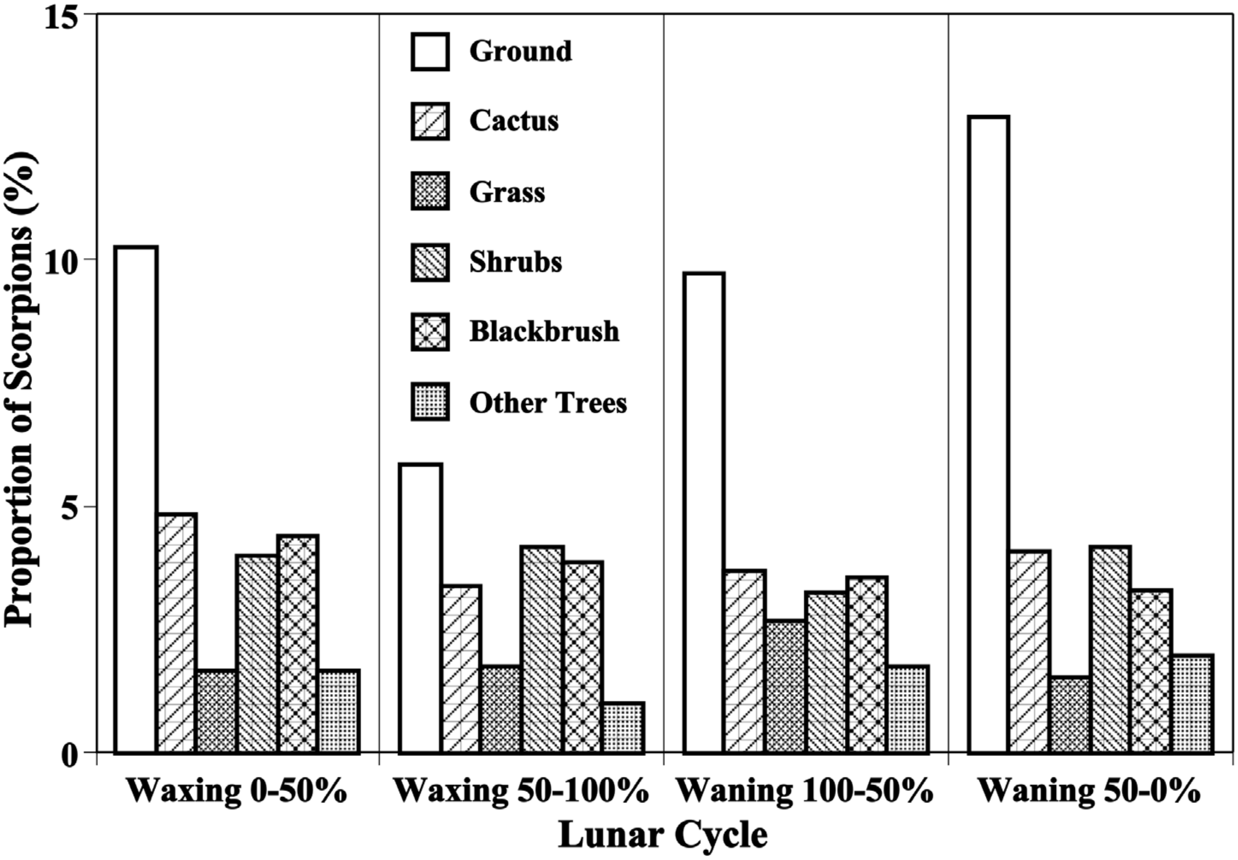


Figure 2: The proportion (%) of *Centruroides vittatus* using different microhabitats among lunar cycle classes. The frequency of microhabitat use was significantly different among lunar cycle classes ($G = 33.719$, $P < 0.01$, $df = 15$, $n = 1292$). See Table 1 for planned comparisons among microhabitat classes.

Results

Lunar cycle

Microhabitat use was significantly different among lunar cycle classes (Fig. 2). Ground class was significantly different from pooled vegetation classes in planned comparison (Table 1). The lowest frequency of scorpions on the ground was during the waxing gibbous phase. Microhabitat use was significantly different among moon rise classes during the waning gibbous phase (Fig. 3). In planned comparisons, difference in ground and pooled vegetation classes was marginally significant and grass and cactus classes were significantly different from the pooled shrub-tree classes (Table 2). The lowest frequency of scorpions on the ground and the highest frequency of scorpions on grass or cactus was after moon rise with the potential of more illumination. Frequency of prey capture was not significantly different among lunar cycle classes (Fig. 4).

Seasonal

Microhabitat use was significantly different among monthly classes (Fig. 5). The three homogenous sets (January-June, May-August and September-December) of monthly classes were determined from unplanned comparisons. Ground class was significantly different from pooled vegetation classes (Table 3). Cactus and grass classes were significantly different from pooled tree-shrub classes. The blackbrush class was significantly different from other trees. The lowest frequency of scorpions on the ground and the highest frequency in grass and cactus was during September-December. Trees were utilized at a low frequency during July and August. Blackbrush was utilized at a high frequency during March and April. Average scorpion height on vegetation was significantly different among monthly classes (Fig. 6). In unplanned comparisons of medians, scorpion height for March, April and October were significantly higher than August. Frequency of prey capture was significantly different among monthly classes (Fig. 7). In planned comparisons, January-June, July-August and

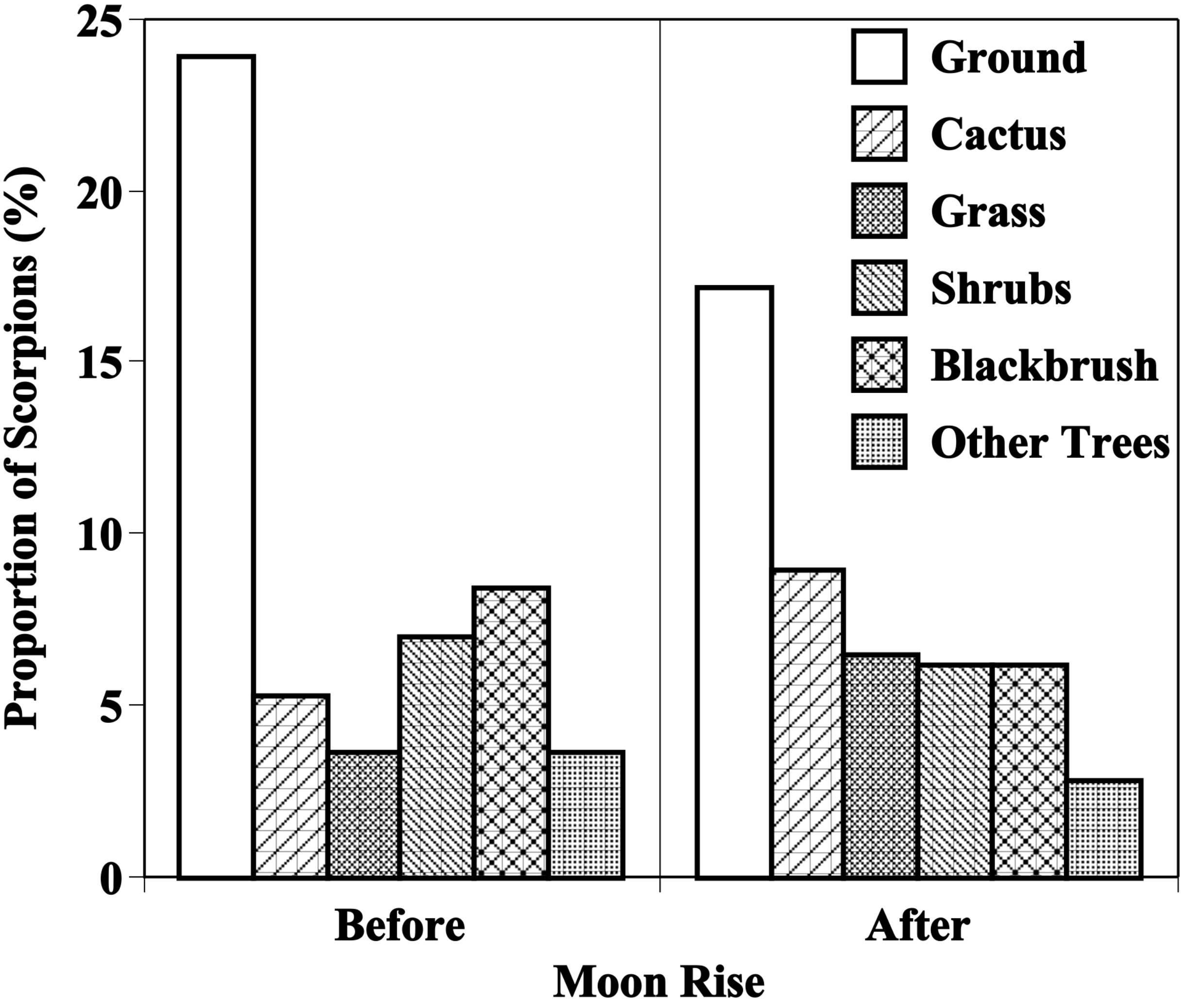


Figure 3: The proportion (%) of *Centruroides vittatus* using different microhabitats before or after moon rise during the waning gibbous phase. The frequency of microhabitat use was significantly different among moon rise classes ($G = 11.314$, $P < 0.05$, $df = 5$, $n = 335$). See Table 2 for planned comparisons among microhabitat classes.

Planned Comparisons	***G***	***df***	***P***
Ground vs. Vegetation	3.717	1	$0.05 < P < 0.1$
Cactus vs. Grass vs. Tree-Shrub	7.388	2	$P < 0.05$
Shrubs vs. Blackbrush vs. Other Trees	0.210	2	ns
Total	11.314	5	$P < 0.05$

Table 2: Planned comparisons among microhabitat classes of the contingency table for microhabitat vs. moon rise classes during the waning gibbous phase. ns = not significant. See Fig. 3.

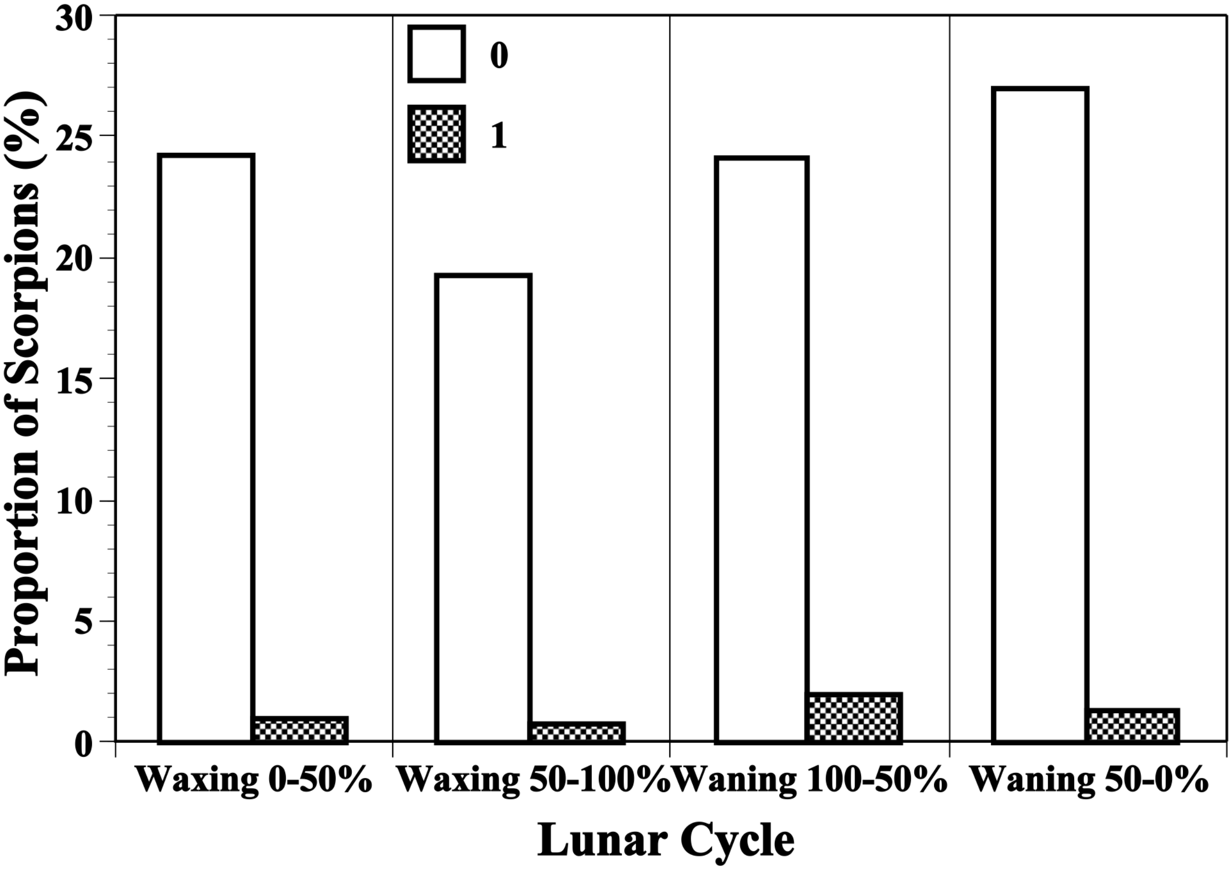


Figure 4: The proportion (%) of *Centruroides vittatus* with or without prey among lunar cycle classes (0 = no prey capture, 1 = one prey captured). The frequency of prey capture was not significantly different among lunar cycle classes ($G = 6.075$, ns, $df = 3$, $N = 1279$).

Planned Comparisons	***G***	***df***	***P***
Ground vs. Vegetation	98.894	9	$P < 0.001$
Cactus vs. Grass vs. Tree-Shrub	35.356	18	$P < 0.01$
Shrubs vs. Trees	4.801	9	ns
Blackbrush vs. Other Trees	35.796	9	$P < 0.001$
Total	174.847	45	$P < 0.001$

Table 3: Planned comparisons among microhabitat classes of the contingency table for microhabitat vs. monthly classes. ns = not significant. See Fig. 5.

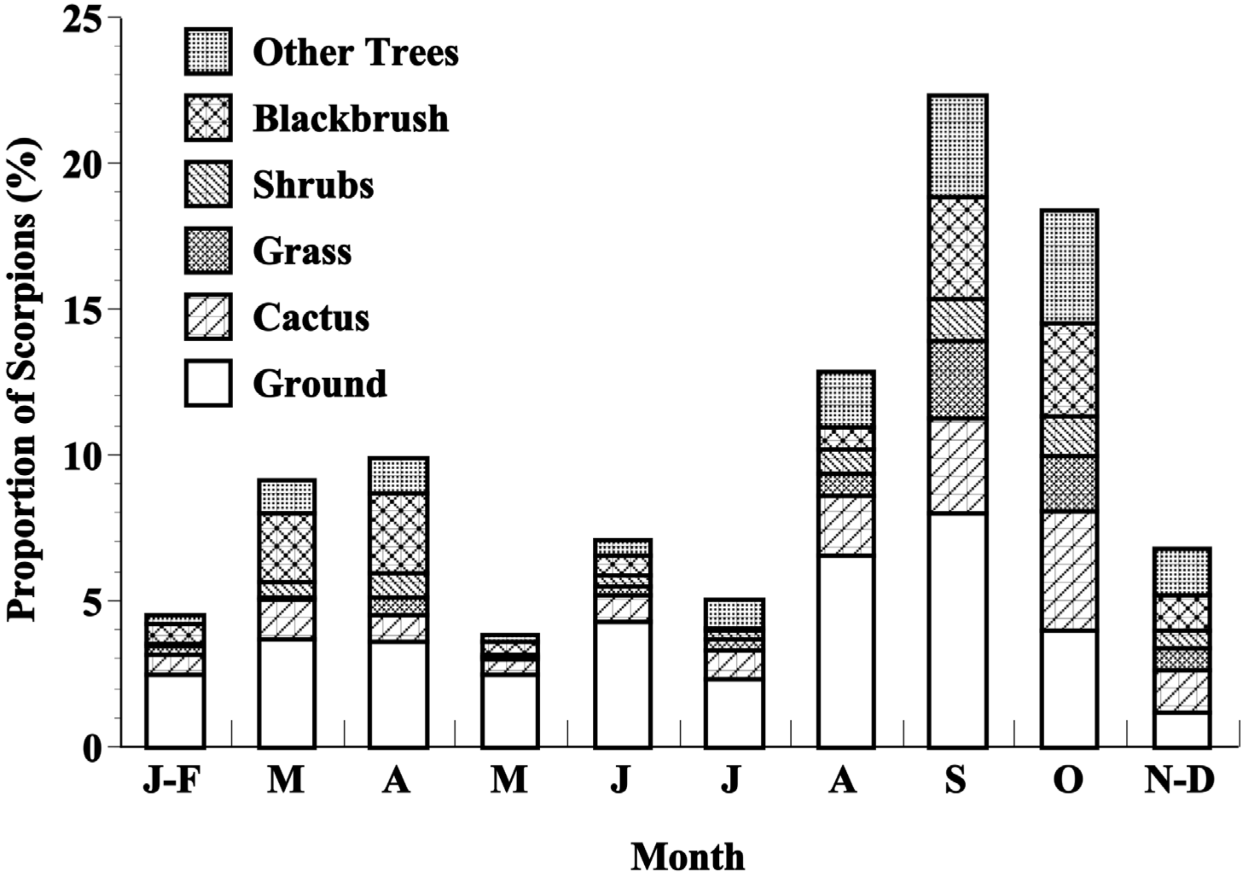


Figure 5: The proportion (%) of *Centruroides vittatus* using different microhabitats among monthly classes. The frequency of microhabitat use was significantly different among monthly classes ($G = 174.847$, $P < 0.001$, $df = 45$, $n = 1292$). Homogeneous (unplanned comparisons) sets of monthly classes included January-June (classes J-F, M, A, M and J); May-August (classes M, J, J and A); and September-December (classes S, O and N-D). See Table 3 for planned comparisons among microhabitat classes.

Planned Comparisons	***G***	***df***	***P***
J-J vs. J-A vs. S-D	10.752	2	$P < 0.01$
J-F vs. M-A vs. M-J	4.416	2	ns
March (M) vs. April (A)	0.906	1	ns
May (M) vs. June (J)	0.111	1	ns
July (J) vs. August (A)	3.885	1	$P < 0.05$
S-0 vs. N-D	0.254	1	ns
September (S) vs. October (O)	0.524	1	ns
Total	20.848	9	$P < 0.05$

Table 4: Planned comparisons among monthly classes of the contingency table for prey capture vs. monthly classes. ns = not significant. See Fig. 7.

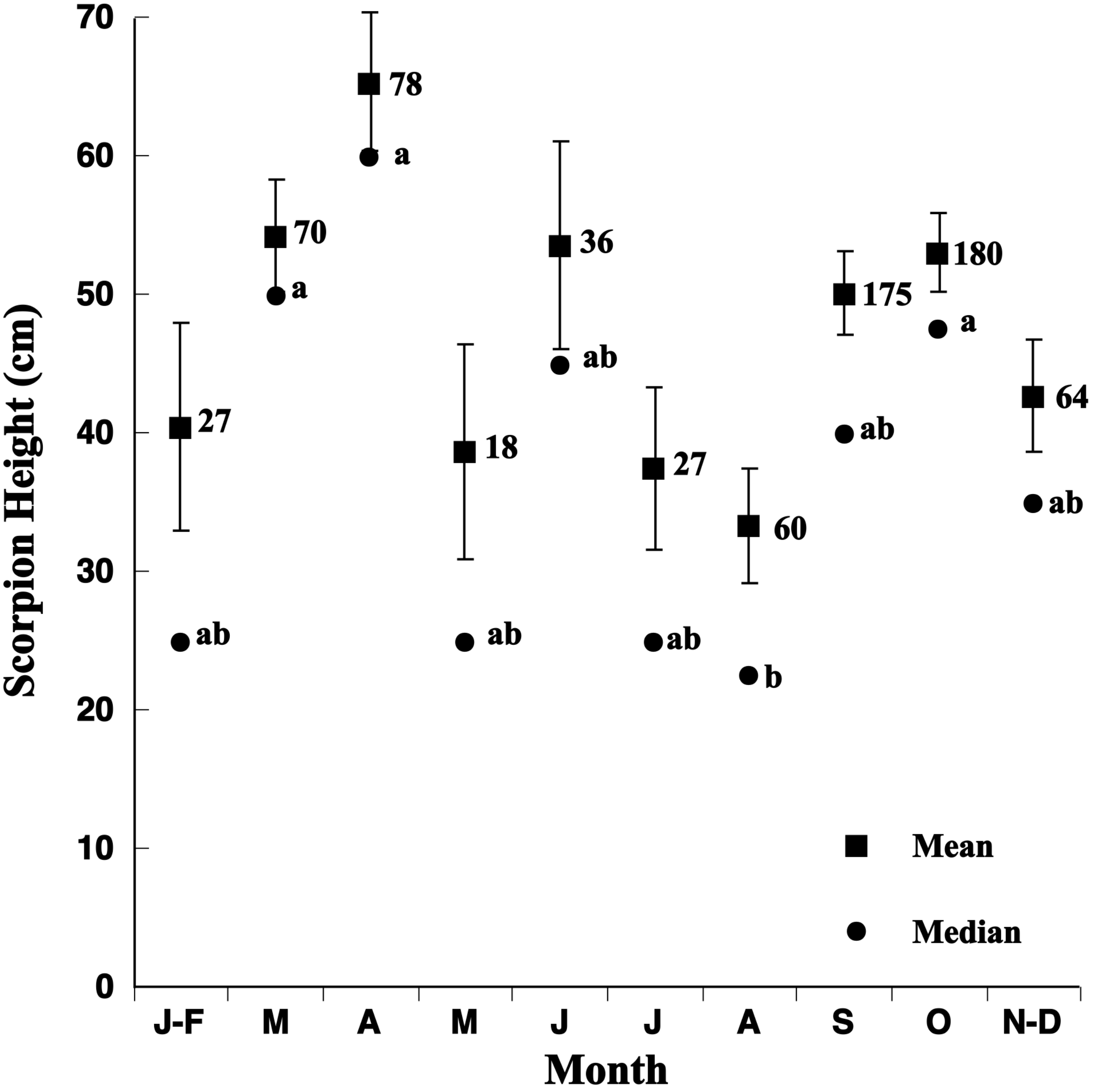


Figure 6: Both the mean and median height of *Centruroides vittatus* on vegetation among monthly classes. Scorpion height was significantly different among monthly classes (Kruskal-Wallis Statistic: *KW* = 70807 (corrected for ties), $P < 0.001$. Standard error bar (± 1 SE) and sample size (*n*) were shown for the mean of each class. Medians with the same letter were not significantly different in unplanned comparisons using Dunn's multiple tests.

September-October pooled classes were significantly different (Table 4). The planned comparison among the July and August classes was significantly different.

Discussion

Centruroides vittatus shows temporal shifts in microhabitat use. Scorpions shift to vegetation during the waxing gibbous phase and after moon rise during the waning gibbous moon. The change in microhabitat use during the lunar cycle indicates shifts in behavior to reduce predation risk when the illumination from the moon is high. Scorpions in the open (e.g., ground) could be more visible to nocturnal visual predators while climbing onto cactus, grass and other vegetation can provide shelter from predators (see Polis et al. (1981) for potential predators). Alternately, scorpions can reduce predation risk by moving beneath vegetation or remaining (or returning) to refuge during high illumination. Adult *Buthus occitanus* move under vegetation instead

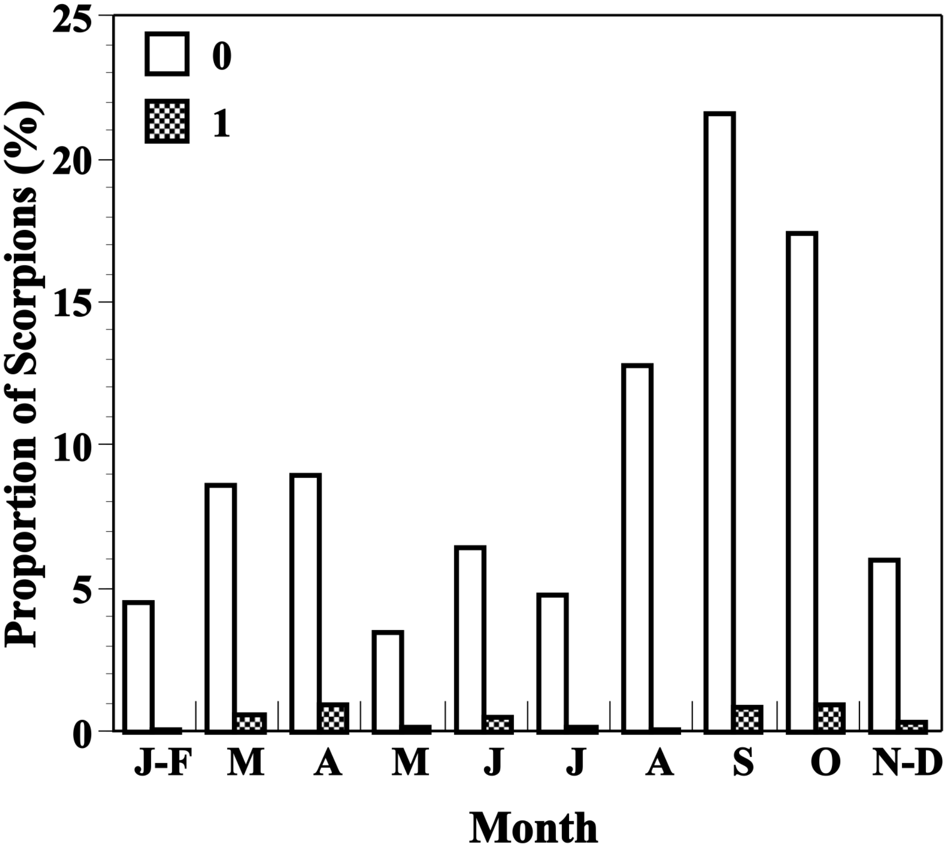


Figure 7: The proportion (%) of *Centruroides vittatus* with or without prey among monthly classes. The frequency of prey capture was significantly different among monthly classes ($G = 20.848$, $P < 0.05$, $df = 9$, $n = 1279$) See Table 4 for planned comparisons among monthly classes.

of climbing vegetation (Skutelsky, 1996). However, *Centruroides sculpturatus* activity is not affected by the lunar cycle (Hadley & Williams, 1968). Further research needs be done to determine if *C. vittatus* uses less exposed microhabitats (e.g., beneath vegetation) during high lunar illumination.

The results of prey capture during the lunar cycle do not indicate a tradeoff between predation risk and foraging success. The prey capture by *C. vittatus* did not change significantly during the periods of the lunar cycle with high illumination from the moon (waxing gibbous moon) when shifts to microhabitats to reduce predation risk are predicted. Habitat selection is not always a tradeoff between prey availability and predation risk (e.g., widow spiders (Lubin et al., 1993)). Microhabitats that have high prey availability can also provide protection from predators. Scorpions can forage in trees and shrubs with high prey availability and still have low predation risk.

Centruroides vittatus is active throughout the year except midwinter (Brown et al., 2002, unpl. data). Microhabitat use and foraging behavior of *C. vittatus* changes with seasonal change. The pattern is similar to the pattern of activity and feeding by other scorpions such as *Paruroctonus mesaensis* (Polis, 1979, 1980a). Seasonal changes in temperature and precipitation can affect prey availability and scorpion activity (Polis, 1980a but see Bradley, 1988). An important factor for changes in foraging by *P. mesaensis* is precipitation (Polis, 1988) and perhaps important in foraging by *C. vittatus* as well. Further research will be performed to determine the effect of seasonal changes (e.g., precipitation) on prey availability in blackbrush and microhabitat use by *C. vittatus*.

Seasonal changes do not just effect prey items captured but also where *C. vittatus* forages. *Centruroides vittatus* can forage and feed on the ground. Important prey items handled on the ground are ants and termites. However, scorpions feeding on ants and termites can rarely be observed because of the prey's small size, but scorpions are often observed near ant trails or nest openings and termite mud tubes (pers. obs.). *Centruroides vittatus* can forage on the ground and feed in the vegetation. Carrying captured prey into vegetation can be to reduce risk of predation (Brown & O'Connell, 2000). The risk of predation can be from intraguild predators (Polis, 1980b; Bradley & Brody, 1984; Polis & McCormick, 1986b, 1987). For *C. vittatus*, the prey captured on the ground and carried into vegetation are often intraguild prey (scorpions, spiders (Fig. 8), solpugids and centipedes) (McReynolds, in prep.). Seasonal factors can also effect the type of prey captured includ-

Figure 8: *Centruroides vittatus* with wolf spider (Lycosidae) as prey.

Figure 9: *Centruroides vittatus* with caterpillar (Lepidoptera) as prey on blackbrush (*Acacia rigidula*).

ing cannibalism (Polis, 1980b) predation on scorpions (Polis & McCormick, 1987) and predation on spiders and solpugids (Polis & McCormick, 1986b). Further research on intraguild predation on and by *C. vittatus* needs to be performed.

Centruroides vittatus can forage and feed in vegetation. An important prey item for *C. vittatus* is caterpillars (McReynolds, in prep.). Caterpillars are prey items that scorpions can encounter at a high frequency in vegetation. *Centruroides vittatus* feeding on caterpillars are often associated with blackbrush (Fig. 9) (McReynolds, in prep.). Still to be determined is how errant scorpions search microhabitats. Brown and O'Connell (2000) suggest that *C. vittatus* movement is a random walk with regard to topography (ground or vegetation) but following gradients (e.g., temperature, humidity, or prey availability) instead. Seasonal shifts in microhabitat use by *C. vittatus* can be due to seasonal changes in prey availability. Budding of flowers and foliage on blackbrush in March and April and new foliage in trees after heavy rains in the fall can increase prey availability, and scorpions can climb higher into vegetation to forage for caterpillars and other prey then. Caterpillars (Lepidoptera) are important prey items in blackbrush (McReynolds, in prep.). Do scorpions select blackbrush and other trees when prey (e.g., caterpillar) availability is high? Further research is needed to determine if scorpions change foraging behavior with seasons or prey availability and prefer certain microhabitats.

Acknowledgments

I thank my undergraduate research students from Fall 2000 to Spring 2004 for assistance in the field to collect the data for the paper. They included Elaine Botello, Ezequiel Chapa, Yareth Coutiño, Ruperto Contreras, Ricardo de Leon, Paula Flores, Nicolas Gallegos, Jose Hernandez, Mike Herrera IV, Eduardo Lopez, Ruben Mendez, Erica Morales, Metzli Ortega and Amede Rubio. I also thank Dan Mott, Julianna Quintanilla, Oscar Ramos, and an anonymous reviewer for suggestions to improve the paper immeasurably. Financial support was provided by grants from Texas A&M International University. The scorpion research at Texas A&M International University was started at the suggestion of the late Gary Polis.

References

BLAIR, W.F. 1950. The biotic provinces of Texas. *Texas Journal of Science*, 2: 93–117.

BRADLEY, R. A. 1988. The influence of weather and biotic factors on the behavior of the scorpion (*Paruroctonus utahensis*). *Journal of Animal Ecology*, 57: 533–551.

BRADLEY, R. A. & A. J. BRODY. 1984. Relative abundance of three vaejovid scorpions across a habitat gradient. *Journal of Arachnology*, 11: 437–440.

BROWN, C. A., J. M. DAVIS, D. J. O'CONNELL & D. R. FORMANOWIZ, Jr. 2002. Surface density and nocturnal activity in a west Texas assemblage of scorpions. *Southwestern Naturalist*, 47: 409–419.

BROWN, C. A. & D. J. O'CONNELL. 2000. Plant climbing behavior in the scorpion *Centruroides vittatus*. *American Midland Naturalist*, 144: 406–418.

HADLEY, N. F. & S. C. WILLIAMS. 1968. Surface activities of some North American scorpions in relation to feeding. *Ecology*, 49: 726–734.

LUBIN, Y., S. ELLNER & M. KOTZMAN. 1993. Web relocation and habitat selection in desert widow spiders. *Ecology*, 74: 1915–1928.

LUTTBEG, B. & O. J. SCHMITZ. 2000. Predator and prey models with flexible individual behavior and imperfect information. *American Naturalist*, 155: 669–683.

MURDOCH, W. W. & A. SIH. 1978. Age dependent interference in a predatory insect. *Journal of Animal Ecology*, 47: 581–592.

POLIS, G. A. 1979. Prey and feeding phenology of the desert sand scorpion *Paruroctonus mesaensis* (Scorpionidae: Vaejovidae). *Journal of Zoology* (London), 188: 333–346.

POLIS, G. A. 1980a. Seasonal patterns and age-specific variation in the surface activity of a population of desert scorpions in relation to environmental factors. *Journal of Animal Ecology*, 49: 1–18.

POLIS, G. A. 1980b. The effect of cannibalism on the demography and activity of a natural population of desert scorpions. *Behavioral Ecology and Sociobiology*, 7: 23–35.

POLIS, G. A. 1988. Foraging and evolutionary responses of desert scorpions to harsh environmental periods of food stress. *Journal of Arid Environments*, 14: 123–134.

POLIS, G. A. 1990. Ecology. Pp. 247–293 *in* Polis, G. A. (ed.). *The Biology of Scorpions*. Stanford, California: Stanford University Press.

POLIS, G. A. & S. J. MCCORMICK. 1986a. Patterns of resource use and age structure among species of desert scorpion. *Journal of Animal Ecology*, 55: 59–73.

POLIS, G. A. & S. J. MCCORMICK. 1986b. Scorpions, spiders and solpugids: predation and competition among distantly related taxa. *Oecologia*, 71: 111–116.

POLIS, G. A. & S. J. MCCORMICK. 1987. Intraguild predation and competition among desert scorpions. *Ecology*, 68: 332–343.

POLIS, G. A., W. D. SISSOM & S. J. MCCORMICK. 1981. Predators of scorpions: field data and a review. *Journal of Arid Environments*, 4: 309–326.

SHELLEY, R. M. & W. D. SISSOM. 1995. Distributions of the scorpions *Centruroides vittatus* (Say) and *Centruroides hentzi* (Banks) in the United States and Mexico (Scorpiones, Buthidae). *Journal of Arachnology*, 23: 100–110.

SISSOM, W. D., G. A. POLIS & D. D. WATT. 1990. Field and laboratory methods. Pp. 445–461 *in* Polis, G. A. (ed.). *The Biology of Scorpions*. Stanford, California: Stanford University Press.

SKUTELSKY, O. 1996. Predation risk and state-dependent foraging in scorpions: effects of moonlight on foraging in the scorpion *Buthus occitanus. Animal Behaviour*, 52: 49–57.

SOKAL, R. R. & F. J. ROHLF. 1981. *Biometry*. 2nd ed. Freeman and Company. New York.

WARBURG, M. R. & G. A. POLIS. 1990. Behavioral responses, rhythms, and activity patterns. Pp. 224–246 *in* Polis, G. A. (ed.). *The Biology of Scorpions*. Stanford, California: Stanford University Press.

WERNER, E. E., J. F. GILLIAM, D. J. HALL & G. G. MITTELBACH. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, 64: 1540–1548.

WERNER, E. E. & D. J. HALL. 1988. Ontogenetic habitat shifts in bluegill: The foraging rate-predation risk trade-off. *Ecology*, 69: 1352–1366.

Euscorpius — **Occasional Publications in Scorpiology. 2004, No. 17**

The Euroscorpion: taxonomy and systematics of the genus *Euscorpius* Thorell, 1876 (Scorpiones: Euscorpiidae)

Victor Fet [1], Michael E. Soleglad [2] and Benjamin Gantenbein[3]

[1]Department of Biological Sciences, Marshall University, Huntington, West Virginia 25755-2510, USA
[2]P. O. Box 250, Borrego Springs, California 92004, USA
[3]Department of Genetics, University of Cambridge, Downing Street, Cambridge CB2 3EH, UK

Summary

This paper provides a brief review of current literature on the systematics of one of the most intensively studied scorpion genera, *Euscorpius* Thorell, 1876 (Scorpiones: Euscorpiidae). It is a “state-of-the-genus” report for the end of 2004, when the systematics of *Euscorpius* is still far from being resolved. A number of species and “species complexes” has been recently reassessed. The molecular systematic analyses published starting in 1998 addressed a number of species and populations. The taxonomic information on *Euscorpius* in the most recent *Catalog of the Scorpions of the World* (Fet & Sissom, 2000), as of 2004, is largely obsolete. It is especially important to further address taxonomic complexes of *Euscorpius* from the Balkans and Anatolia. Currently, the genus *Euscorpius* includes 15 valid species, and this number is likely to increase due to the revisionary systematic work, based on both morphological and molecular analyses.

Introduction

This paper is intended as a succinct but exhaustive review of extensive literature on the current systematics of the genus *Euscorpius* Thorell, 1876 (Scorpiones: Euscorpiidae), one of the most intensively studied scorpion genera. Morphology of a number of species and “species complexes” of *Euscorpius* has been reassessed in recent years. The molecular analyses published starting in 1998 addressed a number of species and populations. While for some areas of the geographic range of *Euscorpius* we have a relatively good idea of the number of species present and their taxonomic identity, the situation in other areas is not clear. Multiple subspecific forms are described, but their validity is not clear. A wealth of information is scattered in the literature but a comprehensive modern revision of the entire genus has never been done. Nor is it an easy task since available material in museums is uneven: some areas, especially the Balkans and Anatolia, are severely undercollected.

Brief History of *Euscorpius*

Ecologically diverse, species of *Euscorpius* occupy a variety of habitats from xeric to mesic, from the Mediterranean shoreline to the high altitudes of the Alps, Balkans, and Taurus. A detailed taxonomic history of this genus is provided in Fet & Sissom (2000); for additional recent reviews see also: Fet, 2000, 2003; Fet & Braunwalder, 2000; Fet et al., 2002b, 2003a, 2003b; Fet & Soleglad, 2002; Gantenbein et al., 1999, 2000, 2001, 2002; Scherabon et al., 2000).

Of six species of scorpion described by Linnaeus, one was *Scorpio carpathicus* from Romania (Fet et al., 2002a, 2002b; Fet & Soleglad, 2002), which now bears the name *Euscorpius carpathicus* (L., 1767). Soon, two other distinct species were described: *Euscorpius flavicaudis* (DeGeer, 1787) and *E. italicus* (Herbst, 1800). C. L. Koch (1837a, 1837b) established a number of new species in then valid genus *Scorpius*, some of which were undeservedly “lumped” by future researchers. Thorell (1876) erected the genus *Euscorpius*, with *E. carpathicus* (L.) as its type species. Kraepelin (1899), one of the “lumpers”, recognized only four valid species in this genus: *E. carpathicus*, *E. flavicaudis, E. italicus* and *E. germanus* (C. L. Koch, 1837). This “umbrella” arrangement persisted for a long time although a number of authors started introducing subspecies, mainly in *E. carpathicus* and *E. germanus* (see Birula, 1898, 1900, 1903, 1917a, 1917b). Already Birula (1900) ironically commented that “the genus *Euscorpius* belongs to such a category of systematic groups, in which the number of species accepted by a specialist depends on how well developed this specialist’s passion was to compile long columns of synonymous species names”. He quite correctly wrote further that “…only studying the morphology of all forms as related to their geographic distribution will we possibly make some positive conclusions about the classification of this genus”.

Hadži (1929, 1930, 1931) promoted the subspecies category in *Euscorpius*, and especially Caporiacco (1950) left it with more than 40 often poorly justified subspecies. Hadži (1929) was the first who attempted to treat enormous trichobothrial variation in *Euscorpius* (albeit only total number, not patterns). The set of "*oligotrichus*", "*mesotrichus*" and "*polytrichus*" names was published by Hadži in 1929 simultaneously (in the same work) for each of three species: *E. italicus, E. carpathicus* and *E. germanus*. The geographic treatment of Hadži was not exhaustive but concentrated on Balkan populations; Hadži (1930) continued discussion of these taxa. Later (Hadži, 1956), he explained that in erecting his subspecies that were described in 1929 he did not really adhere to the taxonomic standards. He also treated his "*oligotrichus*", "*mesotrichus*" and "*polytrichus*" forms (in each of the three species he studied) as meristic classes characterizing variation, rather than Latin names. Nevertheless, these names were, and should be, treated as available Latin names according to the International Code of Zoological Nomenclature. Caporiacco (1950) as "the first reviser" according to the Code (4th Edition, 1999, Article 24.2), declared that Hadži's set of "*oligotrichus*", "*mesotrichus*" and "*polytrichus*" names are available subspecific names only for *E. italicus* and therefore are homonyms for *E. carpathicus* and *E. germanus*.

The traditional characters such as pectinal tooth number, coloration and metasomal carination (e.g. Birula, 1900, 1917a, 1917b; Caporiacco, 1950; Kinzelbach, 1975) were often inconclusive for species diagnosis, and so are total numbers of trichobothria which are variable on pedipalp manus and patella. Also, *Euscorpius* is so geographically diverse that the complete picture is often non-observable without analysis of many variable populations from many various countries—a no small task—especially in the Balkans, the center of *Euscorpius* diversity.

Trichobothrial characters, so crucial for modern understanding of *Euscorpius* systematics, have received some attention from the early authors starting from C. L. Koch (1850) who gave a survey on all the *Euscorpius* species he had described in 1837–1842, and clearly divided these species into three groups according to the number of trichobothria ("Grübchen") on the ventral aspect of pedipalp patella. Birula (1917a, 1917b) separated three subgenera based exclusively on trichobothria. However, it was Vachon (1963, 1975, 1981) who approached *Euscorpius* systematics with his unprecedented attention to this unique and extremely variable character set. An important contribution at the same time was also made by Valle (1975) who designed an independent trichobothrial character system and studied a variety of populations assigned at this time to *E. carpathicus*.

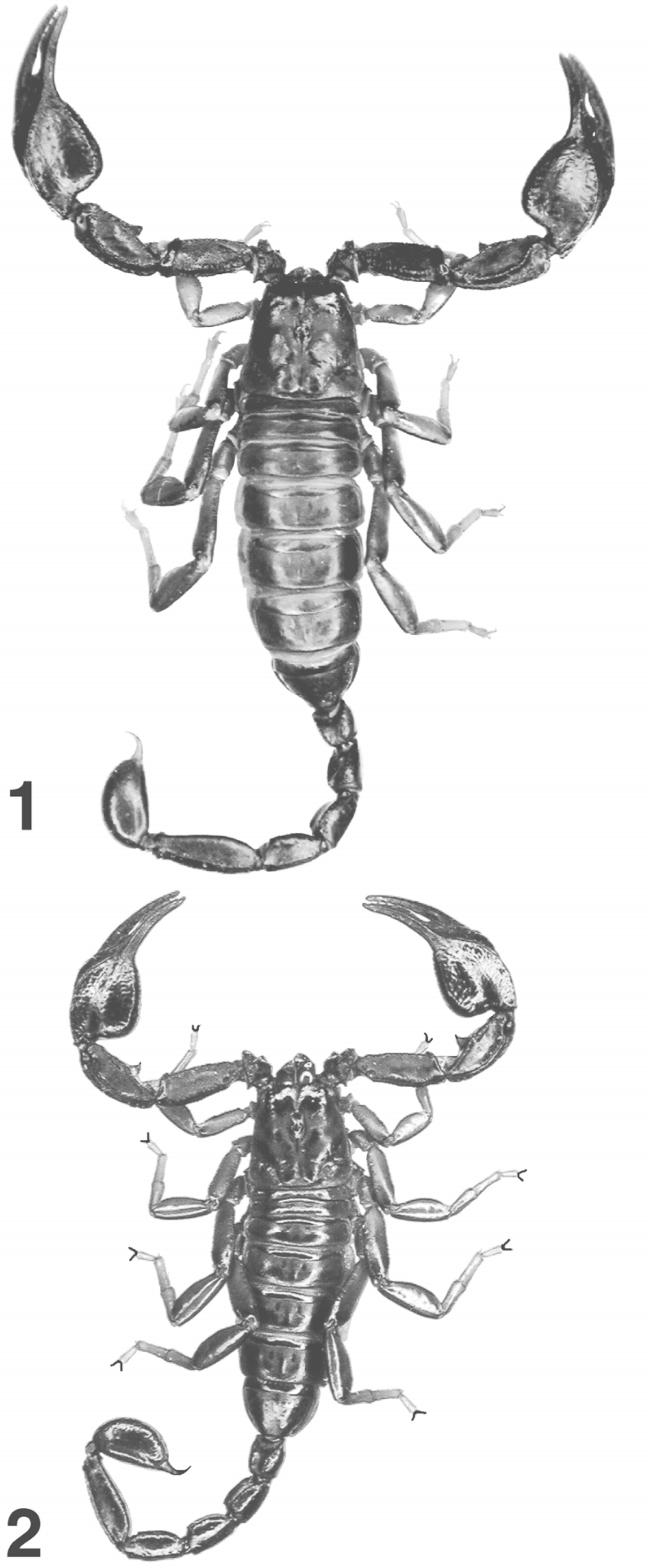
A survey of the Aegean fauna was published by Kinzelbach (1975) who was the first in many years to note that old *E. carpathicus* might include more than one species. Kinzelbach (1975) also promoted a species origin theory which advocated a hybridogenic origin for many *Euscorpius* species and populations; however, recent genetic studies using allozyme and DNA techniques did not support these assumptions. Additional observations on variation in *Euscorpius* were published by Ćurčić (1972).

Vachon & Jaques (1977) brought the issue of trichobothrial diagnosis to the center of important differences between *E. carpathicus* and *E. germanus.* Bonacina (1980), in an important morphological revision, separated and justified *E. germanus* and *E. mingrelicus*; he demonstrated that that in fact the major part of the range, formerly recognized for *E. germanus*, belongs to *E. mingrelicus*. In the decade before 1999, further regional faunistic studies were published by Fet (1986, 1989, 1993, 1997), Scherabon (1987), Lacroix (1991a, 1991b, 1995), Kritscher (1992, 1993), Crucitti (1993), Braunwalder & Tschudin (1997), and other authors who, however, rarely addressed central taxonomic issues on validity of species and subspecies. Fet & Sissom (2000) presented the exhaustive list of all taxa assigned to *Euscorpius* by 1998, i.e. species and subspecies (including nominotypic ones). However, a large portion of this information is outdated now (2004) as a result of ongoing studies.

The Recent Developments in *Euscorpius* (1999-2004)

Subgenus *Alpiscorpius* Gantenbein et al., 1999. This new subgenus was separated from *Euscorpius* s. str. as a result of the first molecular phylogenetic study (based on a fragment of 16S rRNA mitochondrial gene) of the genus *Euscorpius* (Gantenbein et al., 1999). The old subgenus *Euscorpius* s.str. was demonstrated to be polyphyletic: "*E. carpathicus"* (now *E. tergestinus*) did not form a monophyletic group with *E. germanus*. Further studies confirmed that the subgenus *Alpiscorpius* should included most forms of "*E. germanus* complex" and "*E. mingrelicus* complex", listed as subspecies of *E. germanus* and *E. mingrelicus* by Fet & Sissom (2000).

Gantenbein et al. (2000) restricted the scope of *E. germanus* (type from historical Tyrol, now Trentino-Alto Adige, Italy); see also Fet & Braunwalder (1997) for detailed taxonomic history. At the same time, Gantenbein et al. (2000) elevated *E. alpha* Caporiacco, 1950 from northern Italy (formerly a subspecies of *E. germanus*; type from Lombardy) to species level. *E. germanus* and *E. alpha* are allopatric, sibling Alpine species, which appeared as and sister groups in all further phylogenetic analyses (Scherabon et al., 2000; Fet et al., 2003a). The estimated degree of divergence between *E. germanus* and *E. alpha* clearly predates the Pleistocene glaciations,



Figures 1-2: Dorsal view. **1.** *Euscorpius italicus* (Herbst, 1800), male, Italy (after Gantenbein et al., 2002). **2.** *Euscorpius hadzii* Caporiacco, 1950, male, Albania (after Fet & Soleglad, 2002).

as it is the case for a number of other Alpine taxa. It is possible that *E. germanus* has isolated populations also in the Apennines (Guerra, 1979; Vigiani, pers. comm.) although it is not known whether they represent relict populations or are introduced by humans.

The northwestern subspecies of *E. germanus*, *E. g. beta* Caporiacco, 1950, was synonymized with *E. germanus* by Gantenbein et al. (2000). Another subspecies, *E. g. croaticus* Caporiacco, 1950, was transferred by Gantenbein et al. (2000) to "*carpathicus* complex" (see below). One more subspecies of *E. germanus*, status of which remains unclear, is *E. g. marcuzzii* from northeastern Italy and Slovenia. It was very briefly described by Valle et al. (1971); this form is a subject of our ongoing revision based on large material from Slovenia.

Euscorpius mingrelicus (Kessler, 1874; type from Georgia) as redefined by Bonacina (1980) and listed by Fet & Sissom (2000), is still under revision. It is now addressed as a "*mingrelicus* complex", which at this moment includes three valid species (*E. gamma* Caporiacco, 1950, *E. beroni* Fet, 2000, and *E. mingrelicus*). The remaining *E. mingrelicus* most likely will be split further.

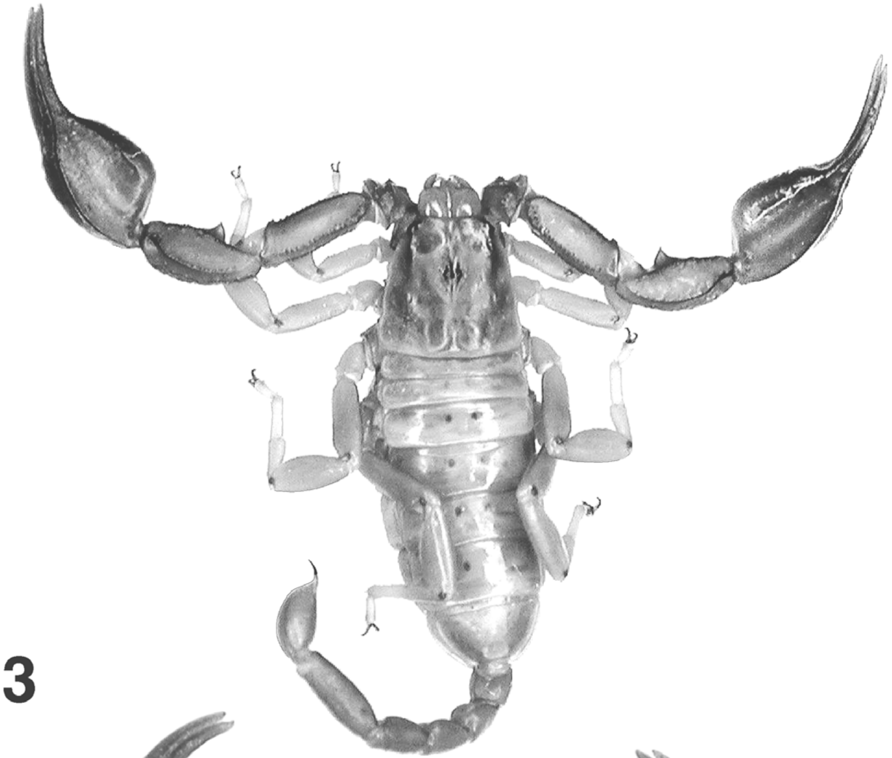
Euscorpius gamma has been separated from *E. mingrelicus* by Scherabon et al. (2000); it inhabits southern Austria, northeastern Italy, Slovenia and Croatia. Two independent systems of molecular markers (allozymes and 16S mtDNA) confirmed morphological analysis of Scherabon (1987) and revealed an identical pattern: a deep phylogenetic divergence between the Karawanken Alps population of *Euscorpius* ("K-Form" of Scherabon, 1987) as opposed to the cluster of "typical" *E. germanus* populations from western Carinthia, northern Italy and western Slovenia.

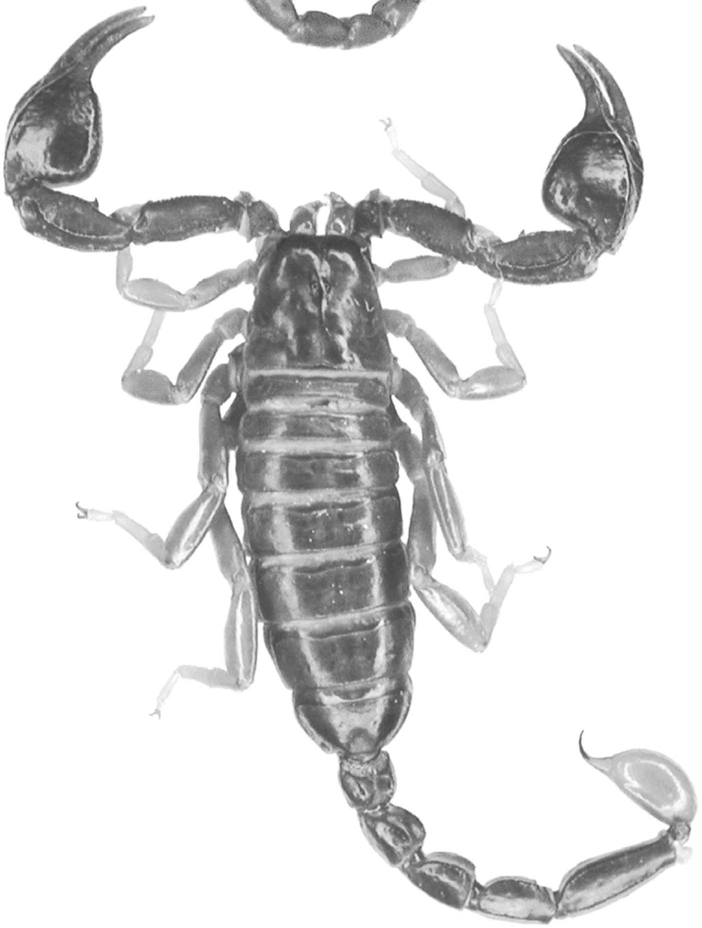
Fet (2000) described a new species *E. beroni*, from the high mountains of Albania (Prokletije Mts.), hitherto completely unknown area; this species belongs to the Balkan portion of the "*mingrelicus* complex". The rest of the Balkan "*mingrelicus* complex" includes two unclearly defined subspecies: *E. m. caporiaccoi* Bonacina, 1980 and *E. m. dinaricus* Caporiacco, 1950 (types of both from Bosnia & Herzegovina). In addition, the old name *Scorpius bosnensis* Möllendorff, 1873, could be resurrected as a senior synonym. It is unclear what name should be assigned to known populations of this complex from Montenegro and Serbia. Teruel et al. (2004) for the first time report a disjunct "*mingrelicus* complex" form from Pirin Mountains, Bulgaria. A form probably belonging to "*mingrelicus* complex" has been also recorded from the environs of Ioannina (Epiros, NW Greece) (Guerra, 1979). However, no records of "*mingrelicus* complex" exist from the eastern Balkans. Records from the Aegean islands of Tinos and Ikaria (Kinzelbach, 1975) most likely refer to a "*carpathicus* complex" form. Thus, there is a considerable disjunction in "*mingrelicus* complex" forms between the continuous Balkan and Anatolian ranges. Records from European Turkey are sparse, and the exact boundary of the range there is not clear. Fet (1989) mentioned an enigmatic record of a specimen resembling the Anatolian *E. m. phrygius* from "Moldavia" (collected by K. Jelski in 19th century), but modern Moldova and Romania have no record of "*mingrelicus* complex".

The range of "*mingrelicus* complex" in Asia embraces the entire Anatolia (Asian Turkey) as well as western Georgia (from Adzharia in the south to Abkhazia in the north), and includes also adjacent part of Russian coast of the Black Sea (north to Sochi). It is unclear whether "*mingrelicus* complex" is found south from Turkey although there are historical records labeled "Syria" (Fet & Sissom, 2000). Lacroix (1995) described three new subspecies from Anatolia (*E. m. legrandi, E. m. ollivieri,* and *E. m. uludagensis*) in addition to three already existing Anatolian-Caucasian forms (*E. m. mingrelicus, E. m. phrygius* Bonacina, 1980 and *E. m. ciliciensis* Birula, 1898; see Birula, 1898; Bonacina, 1980; Fet, 1986, 1989, 1993). It appears that the "*mingrelicus* complex" inhabits the entire Anatolian Peninsula, including high mountain ranges (Bulghar Dagh, Taurus Mts.; the highest altitude recorded for the genus *Euscorpius*, 2400 m a.s.l.). Preliminary DNA data on the Anatolian specimens of the "*mingrelicus* complex", including those from the type locality of *E. m. ciliciensis* (Fet et al. 2003a; Fet et al., in progress) reveal high genetic diversity of Anatolian populations; their sister group is *E. gamma* from the Balkans.

Subgenus *Euscorpius* s. str. (=*"carpathicus* complex"). The clear separation of the nominotypic subgenus from *Alpiscorpius* has been first discovered by Gantenbein et al. (1999) and so far has not been challenged, although "oligotrichous" trend clearly expressed in *Alpiscorpius* seems to be paralleled by certain forms in *Euscorpius* s. str. The integrity of *E. carpathicus* (L., 1758) was first challenged by Kinzelbach (1975) who introduced another species he called "*E. mesotrichus* Hadži"; this name, however, was a homonym and therefore not available; see discussion in Fet & Sissom (2000). Gantenbein et al. (2001) established the species status of the former insular subspecies *E. balearicus* Caporiacco, 1950 (Fig. 3) from the Balearic Islands (Spain). In a similar fashion, Fet (2003) elevated to species level *E. tauricus* (C. L. Koch, 1837) from Crimea, based on DNA analysis, with morphological investigation pending.

The detailed morphological study by Fet & Soleglad (2002) restricted the traditional Linnean species *E. carpathicus* (Fig. 4) only to the Romanian populations, based on analysis of numerous published data and collections, including the Linnean holotype. In addition, Fet





Figures 3-4: Dorsal view. **3.** *Euscorpius balearicus* Caporiacco, 1950, female, Balearic Islands (after Fet & Soleglad, 2002) **4.** *Euscorpius carpathicus* (Linnaeus, 1767), male, Romania (after Fet & Soleglad, 2002).

& Soleglad (2002) defined three more species in the *"carpathicus* complex", elevating them from subspecies rank: *E. hadzii* Caporiacco, 1950 (type from Albania) (Fig. 2); *E. koschewnikowi* Birula, 1903 (type from northeastern Greece) (Fig. 5), and *E. tergestinus* (C. L. Koch, 1837; type from Slovenia) (Fig. 6). Fet & Soleglad (2002) also synonymized nine former subspecies of *E. carpathicus*, namely: *E. c. apuanus* Caporiacco, 1950, *E. c. aquilejensis* Caporiacco, 1950, *E. c. concinnus* (C. L. Koch, 1837), *E. c. corsicanus* Caporiacco, 1950, *E. c. niciensis* (C. L. Koch, 1837), *E. c. oglasae* Caporiacco, 1950, and *E. c. picenus* Caporiacco, 1950, to *E. tergestinus*; *E. c. lagostae* Caporiacco, 1950, to *E. hadzii*; and *E. c. banaticus* (C. L. Koch, 1841), to *E. carpathicus*. Comparison of DNA sequences of the Romanian population with other forms of the "*carpathicus* complex" (Fet et al., 2002b) confirmed its separate status.

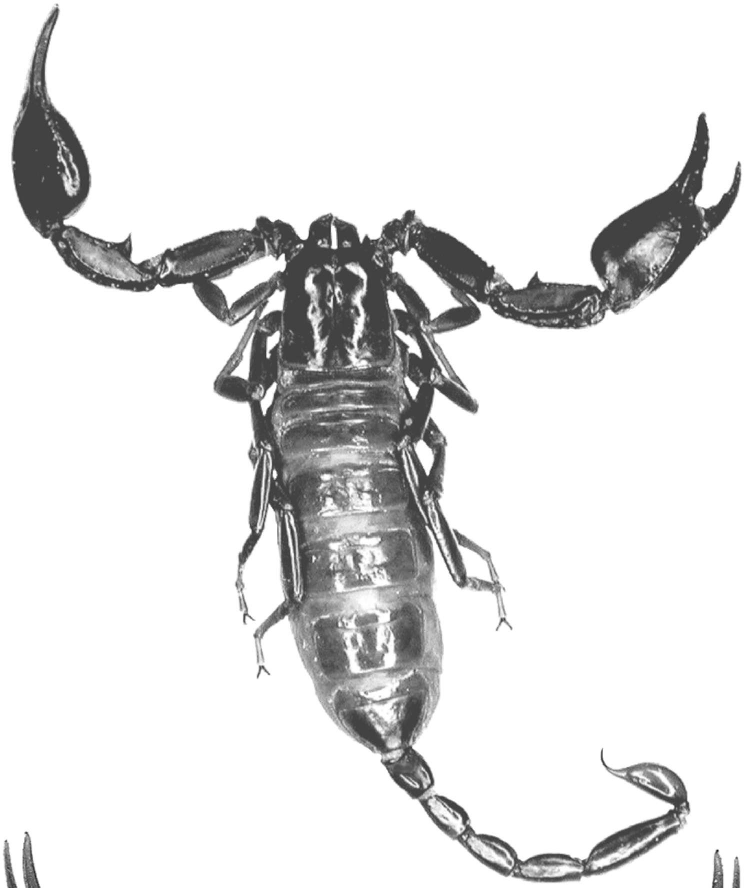
Fet et al. (2003b) continued the revisionary work on "*carpathicus* complex", based on both morphology and DNA data, and defined a diverse assemblage of populations in southern Italy, Sicily, Sardinia, Greece, and Malta (as well as some minor Mediterranean islands and North African enclaves) under the name *E. sicanus* (C. L. Koch, 1837; type from Sicily). In this study, Fet et al. (2003) synonymized with *E. sicanus* six former subspecies of *E. carpathicus*, namely: *E. c. argentarii* Caporiacco, 1950, *E. c. calabriae* Caporiacco, 1950, *E. c. canestrinii* (Fanzago, 1872), *E. c. ilvanus* Caporiacco, 1950, *E. c. linosae* Caporiacco, 1950, and *E. c. palmarolae* Caporiacco, 1950. The name *E. sicanus* applies also to those enigmatic populations from Greece, which Kinzelbach (1975) called "*E. mesotrichus* Hadži". *E. sicanus* is characterized by a unique trichobothrial pattern and number where series *eb*, and in some populations also series eb_a, have five trichobothria (as opposed to four in *E. carpathicus* or *E. tergestinus*).

While Fet & Soleglad (2002) applied the name *E. tergestinus* to most of the "western" populations of former *E. carpathicus* (France, Italy, Slovenia, Croatia), and the name *E. sicanus* to many Greek populations, at least several more forms of the "*carpathicus* complex" are present across the Balkans, on all Aegean islands, and in southern Turkey. Some of these forms are sympatric with *E. sicanus* in mainland Greece, as first demonstrated by Kinzelbach (1975) for Thessaly (Ossa, Pindos, Pilion, and Olympus). These "*carpathicus* complex" forms are currently not assigned to any species, and are under detailed investigation, including diverse populations from Bulgaria (Fet & Soleglad, in press). At the same time, some former subspecies, formerly included in *E. carpathicus*, are not currently assigned or synonymized to any species. These include four forms described from Greece: *E. "carpathicus" aegaeus* Caporiacco, 1950; *E. "c." candiota* Birula, 1903; *E. "c." ossae* Caporiacco, 1950; and *E. "c." scaber* Birula, 1903. The subspecies *E. "carpathicus" fanzagoi* Simon, 1879 was described from southwestern France but its identity is dubious. Another enigmatic subspecies, described as *E. germanus croaticus* Caporiacco, 1950 from western Croatia, was transferred by Gantenbein et al. (2000) to "*carpathicus* complex", but its validity and rank are not yet resolved. This form resembles oligotrichous populations of "*carpathicus* complex" found in southern Bulgaria (Fet & Soleglad, in press) but could represent an independent case of homoplasious trichobothrial number reduction.

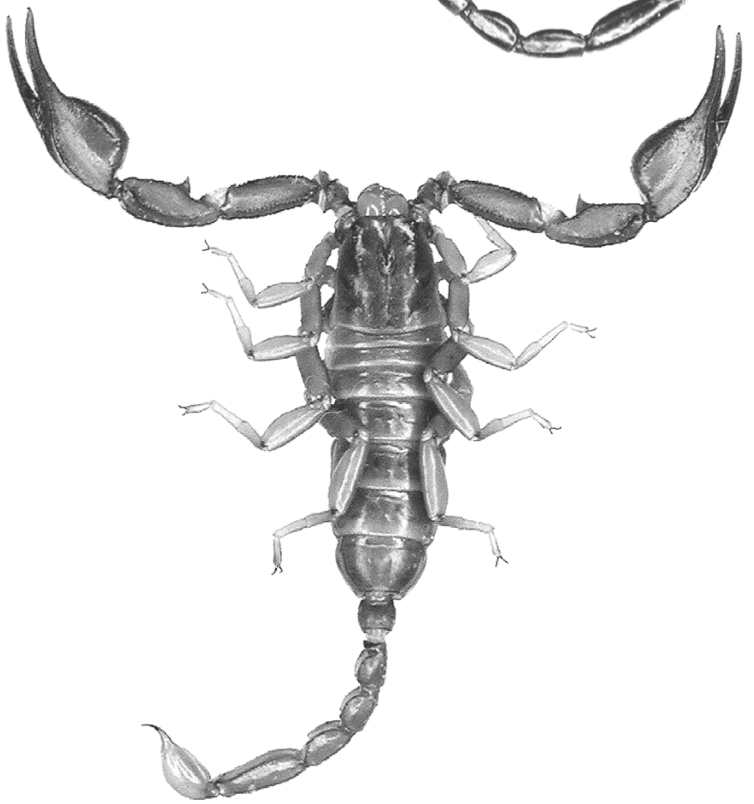
The ongoing revisionary work on this complex, in addition to the efforts of our research group, is indicated by the presentations at the 16th International Congress of Arachnology (August 2004, Gent, Belgium) by Salomone et al. (2004) and Vignoli et al. (2004) addressing Italian forms, and by Stathi et al. (2004), addressing Greek forms.

Subgenus Tetratrichobothrius Birula, 1917. This monotypic subgenus includes only *E. flavicaudis* (DeGeer, 1787) from France, Italy and Spain, and also from coastal enclaves in northern Africa. Introduced, reproducing populations exist in England and Uruguay. Fet & Sissom (2000) list five subspecies; one of these was described recently by Bonacina & Rivellini (1986). The validity of subspecies in *E. flavicaudis* has not been recently addressed. Some data on genetic diversity of *E. flavicaudis* can be found in Gantenbein et al. (2001). The within-population genetic diversity of *E. flavicaudis* was found to be close to zero; also, diversity between populations was low. These results point to a recent (postglacial) range expansion from a single refugium, accelerated through human transplantation. For ecological and behavioral study of the introduced population in England, see Benton (1991, 1992, 1993).

Subgenus Polytrichobothrius Birula, 1917. The large, conspicuous *E. italicus* (Herbst, 1800) (Fig. 1) is widespread in southern Europe and reaches eastward along the Black Sea coast to Turkey and Caucasus. Its subspecies as described by Caporiacco (1950) were annulled by Vachon (1981), as confirmed by Gantenbein et al. (2002). In fact, morphological variation within *E. italicus* is high but unstructured; preliminary genetic data (Fet et al., in press) allows suggesting recent dispersal from a glacial refugium, maybe even in historical time. This could explain absence of *E. italicus* from all Aegean islands, and from the Mediterranean islands such as Baleares, Sicily, Sardinia, Corsica, and Malta. At the same time, dispersal with humans explains preference of human habitations by this species (Birula, 1917a, 1917b; Braunwalder, 2001; Gantenbein et al., 2002) and its disjunct introductions by humans. Introduced, reproducing populations exist in Switzerland, Yemen, and Iraq, and also were historically recorded



5



6

Figures 5-6: Dorsal view. **5.** *Euscorpius koschewnikowi* Birula, 1900, female lectotype, Greece (after Fet & Soleglad, 2002) **6.** *Euscorpius tergestinus* (C.L. Koch, 1837), female, Slovenia (after Fet & Soleglad, 2002).

from Russia and Romania (Fet & Sissom, 2000; Braunwalder, 2001; Fet & Kovařík, 2003).

Gantenbein et al. (2002) demonstrated in detail that the unusual "oligotrichous" form from Peloponnese, previously assigned to *E. italicus* (Caporiacco, 1950; Vachon, 1981; Bonacina, 1982; Crucitti, 1995, 1999) deserved a species-level rank. This form was identical with subspecies *E. i. zakynthi* Caporiacco (1950) from Zakynthos Island, which, in turn, was identical with the "old species" *E. naupliensis* (C. L. Koch, 1837).

High-level phylogeny. Relationships among subgenera of *Euscorpius* are still not completely resolved. Both morphology and DNA clearly indicate that subgenus *Tetratrichobothrius* is a basal taxon, and an outgroup to all other three subgenera. DNA data also indicate a derived place for the subgenus *Polytrichobothrius* which appears to be closely related to *Euscorpius s. str.* (Gantenbein et al., 1999), while it was traditionally allied with *Tetratrichobothrius* on morphological basis (Kinzelbach, 1975). Soleglad & Fet (2003) indicated that a genus status could be justified in future for at least some of *Euscorpius* subgenera.

For decades, *Euscorpius* was placed in Chactidae (subfamily Euscorpiinae). Stockwell (1992) established family Euscorpiidae, as listed by Fet & Sissom (2000). The genus was "put into perspective" among other genera by the exhaustive cladistic revision of Euscorpiidae by Soleglad & Sissom (2001), which assigned it to a monotypic subfamily. Among other unique features, this revision emphasized the fact of enormous trichobothrial variation (neobothriotaxy) among Euscorpiidae, and particularly within *Euscorpius*——the very feature which allowed already early authors (e.g. Birula, 1917a, 1917b) to parse the genus into clusters sometimes identifiable solely by trichobothrial characters. Soleglad & Sissom (2001) clearly established a separate position of *Euscorpius* in the subfamily (Euscorpiinae) of its own.

We should comment on the position of the relict genus *Belisarius* Simon, 1879, which has been for decades placed as a sister genus of *Euscorpius* (as late as Kinzelbach, 1975), essentially from a geographic perspective (being the only other chactoid genus in Europe). Placement of this Iberian genus was unclear until recently Soleglad & Fet (2003) demonstrated its position in Chactidae (subfamily Brotheinae, tribe Belisariini). Thus, *Belisarius* is not closely related to *Euscorpius* but rather is an ancient relict with its closest relatives in South America; see Soleglad & Fet (2003) for the detailed analysis and justification.

Other studies. In addition to the studies listed above, a number of important regional faunistic and ecological surveys of *Euscorpius* species have been published in the last decade. Crucitti (1999a) and Crucitti & Cicuzza (2001) provided a review of Anatolian species; Braunwalder (2001) gave a detailed review of three Swiss species; Komposch et al. (2001), of three Austrian species; and Fet et al. (2001), of four Slovenian species. Huber et al. (2001) addressed disjunct distribution of "*E. carpathicus*" (now *E. tergestinus*) in Austria, and confirmed, using DNA data, that the Austrian populations probably are introduced by humans. Another introduced, and probably extinct, population of *E. tergestinus* from Bohemia (Czech Republic) was addressed by Kovařík & Fet (2003). Crucitti & Malori (1998), Crucitti (1999b), Fet (2000), Crucitti & Bubbico (2001) and Stathi & Mylonas (2001) published new faunistic data on a number of Balkan and Aegean populations.

In addition, Jacob et al. (2004a, 2004b) published two very important works, supplied by superb illustrations, which address the morphology of hemispermatophore in several species of *Euscorpius*. The importance of hemispermatophore characters as diagnostic has been discussed by Fet & Soleglad (2002). Studies of Jacob and coauthors confirmed what was earlier suggested by Molteni et al. (1980) about *Euscorpius* hemispermatophore variation not being diagnostic at species/subspecies level. Table 1 presents a list of all valid taxa in genus *Euscorpius*.

Further Issues and Perspectives in Taxonomy of *Euscorpius*

Study of the Alpine "*germanus* complex" of the subgenus *Alpiscorpius* will benefit from further molecular and morphological data analysis. The "*mingrelicus* complex" both in the Balkans and Anatolia is virtually untouched in either morphological or molecular aspects, and requires much more attention; however, the dearth of material especially from inland Croatia, Bosnia and Herzegovina, Serbia and Montenegro, Macedonia, and Albania at this moment may not allow definitive decisions to be presented soon. The "*carpathicus* complex" (= subgenus *Euscorpius* s.str.) in the Balkans presents the same challenge; much more research has to be done on the material from the above listed Balkan countries as well as Greece and Bulgaria. Western populations of "*carpathicus* complex" (mainly from Italy) are better understood but still far from revisionary level. Marginal and isolated forms from regions such as Crimea and Romania have to be addressed in-depth. Relationships of species (or possibly species complexes) *E. hadzii* and *E. sicanus* have to be addressed further. The subgenera *Tetratrichobothrius* and *Polytrichobothrius* will probably need less attention since the former is clearly monotypic, and two species of the latter are now rather well understood.

Subgenus *Alpiscorpius* Gantenbein et al., 1999

"*germanus* complex":

- *Euscorpius alpha* Caporiacco, 1950: Italy, Switzerland
- *Euscorpius germanus* (C. L. Koch, 1837):
    - *E. g. germanus* (C. L. Koch, 1837): Austria, Italy, Slovenia, Switzerland
    - *E. g. marcuzzii* Valle et al., 1975: Italy, Slovenia

"*mingrelicus* complex":

- *Euscorpius beroni* Fet, 2000: Albania
- *Euscorpius gamma* Caporiacco, 1950: Austria, Croatia, Italy, ?Montenegro, ?Serbia (eastern boundary unclear).
- *Euscorpius mingrelicus* (Kessler, 1874):
    - *E. m. mingrelicus* (Kessler, 1874): Georgia, Russia, Turkey
    - *E. m. caporiaccoi* Bonacina, 1980: Bosnia & Herzegovina, ?Montenegro, ?Serbia.
    - *E. m. ciliciensis* Birula, 1898: Turkey
    - *E. m. dinaricus* Caporiacco, 1950: Bosnia & Herzegovina, ?Montenegro, ?Serbia.
    - *E. m. legrandi* Lacroix, 1995: Turkey
    - *E. m. ollivieri* Lacroix, 1995: Turkey
    - *E. m. phrygius* Bonacina, 1980: Turkey
    - *E. m. uludagensis* Lacroix, 1995: Turkey

Subgenus *Euscorpius* Thorell, 1876 (= "*carpathicus* complex"):

- *Euscorpius balearicus* Caporiacco, 1950: Spain (Balearic Islands).
- *Euscorpius carpathicus* (Linnaeus, 1758): Romania.
- *Euscorpius hadzii* Caporiacco, 1950: Albania, Bosnia & Herzegovina, Bulgaria, Croatia, Greece, Macedonia, Montenegro, Serbia.
- *Euscorpius koschewnikowi* Birula, 1903: Greece.
- *Euscorpius sicanus* (C. L. Koch, 1837): Greece, Italy (with Sicily and Sardinia), Madeira, Malta, northern Africa (Egypt, Libya, Tunisia).
- *Euscorpius tauricus* (C. L. Koch, 1837): Ukraine (Crimea).
- *Euscorpius tergestinus* (C. L. Koch, 1837): Albania, Croatia, Greece, France (with Corsica), Italy, Monaco, San Marino, Slovenia; introduced to Czech Republic (now extinct), Austria; eastern boundary unclear.

Formally valid subspecific forms not assigned to a certain species:

- *E. "carpathicus" aegaeus* Caporiacco, 1950: Greece.
- *E. "carpathicus" candiota* Birula, 1903: Greece (Crete).
- *E. "carpathicus" croaticus* Caporiacco, 1950: Croatia.
- *E. "carpathicus" fanzagoi* Simon, 1879: France, ?Spain.
- *E. "carpathicus" ossae* Caporiacco, 1950: Greece.
- *E. "carpathicus" scaber* Birula, 1903: Greece.

Subgenus *Polytrichobothrius* Birula, 1917

- *Euscorpius italicus* (Herbst, 1800): Albania, Croatia, France, Georgia, Greece, Italy, Macedonia, Monaco, Montenegro, Russia, San Marino, Slovenia, Switzerland, Turkey; northern Africa (Algeria, Morocco, Tunisia); introduced to Iraq, Yemen, ?Romania.
- *Euscorpius naupliensis* (C.L. Koch, 1837): Greece (Peloponnese).

Subgenus *Tetratrichobothrius* Birula, 1917

- *Euscorpius flavicaudis* (DeGeer, 1787)
    - *E. f. flavicaudis* (DeGeer, 1787): France (with Corsica), Italy (with Sardinia), Spain (with Balearic Islands); northern Africa (?Algeria, ?Tunisia); introduced to England and Uruguay.
    - *E. f. algeriacus* (C.L. Koch, 1838): Algeria.
    - *E. f. cereris* Bonacina & Rivellini, 1986: Italy
    - *E. f. galitae* Caporiacco, 1950: Algeria, Tunisia
    - *E. f. massiliensis* (C.L. Koch, 1837): France.

Table 1: List of all valid taxa in genus *Euscorpius*.

Acknowledgements

B.G. was supported by the SNF-IHP grant (83-EU-065528). We thank Janet Beccaloni, Marco Bellini, Petar Beron, Alberto Bonacina, Matt Braunwalder, Philip Brownell, Marco Colombo, Pierangelo Crucitti, Božidar Ćurčić, Hieronymus Dastych, Christo Deltschev, Jason Dunlop, Gérard Dupré, Galina Fet, Iris Gantenbein, Matt Graham, Jürgen Gruber, Paul Hillyard, Dietmar Huber, Ayşegül Karataş, Ahmet Karataş, Ragnar Kinzelbach, Christian Komposch, František Kovařík, Viktor Krivochatsky, Jean-Bernard Lacroix, Mario Langourov, Scott Larcher, Carlo Largiadèr, Kirill Mikhailov, Plamen Mitov, Moises Mylonas, Kevan Palmer, Guillem Pons, Valentin Popa, Dimitar Raichev, Gordon Ramel, Hubert Rausch, Jan Ove Rein, Nicola Salomone, Patrick Schembri, Bernhard Scherabon, Adolf Scholl, Paul Selden, Boris Sket, Iasmi Stathi, Roland Stockmann, Konrad Thaler, Marco Valle, Valentina Vigiani, Valerio Vignoli, Mark Volkovich, Sarah Whitman, Alexander Winkler, Eric Ythier, and Thomas Ziegler for the gifts and loans of *Euscorpius* material over many years, and for their advice and help. Mark Barker, Elizabeth Fet, Iris Gantenbein, Matt Graham, Joshua Greenwood, Erica Price, and W. Ian Towler provided their skilled help in DNA lab procedures. All information in this paper is presented in good faith according to our current knowledge, and we apologize if we inadvertently left our anybody's contribution to the understanding of that multifaceted, diverse and unique Euroscorpion, the genus *Euscorpius* Thorell, 1876.

References

BENTON, T. G. 1991. The life history of *Euscorpius flavicaudis* (Scorpiones, Chactidae). *Journal of Arachnology*, 19 (2): 105–110.

BENTON, T. G. 1992. The ecology of the scorpion *Euscorpius flavicaudis* in England. *Journal of Zooogy, London,* 226 (3): 351–368.

BENTON, T. G. 1993. The reproductive ecology of *Euscorpius flavicaudis* in England. *Memoirs of Queensland Museum*, 33 (2): 455–460.

BIRULA, A. A. 1898. Ein Beitrag zur Kenntnis der Skorpionenfauna Kleinasiens. *Horae Societatis Entomologicae Rossicae*, 33: 132–140.

BIRULA, A. A. 1900. Scorpiones mediterranei Musei Zoologici mosquensis. *Izvestiya Imperatorskogo Obshchestva Lyubitelei Prirody, Istorii, Antropologii i Etnografii* (*Societas Caesarea Amicorum Rerum Naturalium, Anthropologiae Ethnographiae Universitatis Moscoviensis*), 98, 3(1): 8–20 (in Russian).

BIRULA, A. A. 1903. Miscellanea scorpiologica. V. Ein Beitrag zur Kenntnis der Skorpionenfauna der Insel Kreta. *Annuaire du Musée Zoologique de l'Académie Impériale des Sciences de St.-Pétersbourg* 8: 295–299.

(BIRULA, A. A.) BYALYNITSKII-BIRULYA, A. A. 1917a. *Arachnoidea Arthrogastra Caucasica. Pars I.* Scorpiones. Mémoires du Musée du Caucase, Tiflis: Imprimerie de la Chancellerie du Comité pour la Transcaucasie, A(5), 253 pp. (in Russian). English translation: 1964. Arthrogastric Arachnids of Caucasia. 1. Scorpions. Jerusalem: Israel Program for Scientific Translations, 170 pp.

(BIRULA, A. A.) BYALYNITSKII-BIRULYA, A. A. 1917b. *Faune de la Russie et des pays limitrophes fondee principalement sur les collections du Musée Zoologique de l'Académie des Sciences de Russie. Arachnides (Arachnoidea)*. Petrograd, 1(1): xx, 227 pp. (in Russian). English translation: 1965. *Fauna of Russia and Adjacent Countries. Arachnoidea. Vol. I. Scorpions.* Jerusalem: Israel Program for Scientific Translations, xix, 154 pp.

BONACINA, A. 1980. Sistematica specifica e sottospecifica del complesso "*Euscorpius germanus*" (Scorpiones, Chactidae). *Rivista del Museo Civico di Scienze Naturali "Enrico Caffi"* (Bergamo), 2: 47–100.

BONACINA, A. 1982. Note preliminari sulla sistematica sottospecifica di *Euscorpius italicus* (Herbst) (Scorpiones, Chactidae). *Rivista del Museo Civico di Scienze Naturali "Enrico Caffi"* (Bergamo), 4: 3–16.

BONACINA, A. & G. RIVELLINI. 1986. *Euscorpius flavicaudus cereris*: nuova sottospecie dell'Italia meridionale (Scorpiones, Chactidae). *Rivista del Museo Civico di Scienze Naturali "Enrico Caffi"* (Bergamo), 10: 73-78.

BRAUNWALDER, M. E. 2001. Scorpions of Switzerland: summary of a faunistic survey. Pp. 279–286 *In*: Fet, V. & P. A. Selden (eds). *Scorpions 2001. In memoriam Gary A. Polis*. British Arachnological Society, Burnham Beeches, Bucks.

BRAUNWALDER, M. E. & M. TSCHUDIN. 1997. *Skorpione. Eine Einführung mit besonderem Augenmerk auf beide Schweizer Arten.* (Biologie einheimischer Wildtiere, 1/47). Zürich: Infodienst Wildbiologie & Oekologie, 16 pp.

CAPORIACCO, L. di. 1950. Le specie e sottospecie del genre "*Euscorpius*" viventi in Italia ed in alcune zone confinanti. *Memorie/Accademia nazionale dei Lincei*, (ser. 8) 2: 159–230.

CRUCITTI, P. 1993. Distribution and diversity of Italian scorpions. *Redia*, 76(2): 281–300.

CRUCITTI, P. 1995. *Iurus dufoureius* (Brullé) nel Peloponneso occidentale e considerazioni sulla scorpiofauna dei Minthi Óros (Grecia). *Bolletino della Società Entomologica Italiana*, 127(2): 91–98.

CRUCITTI, P. 1999a. The scorpions of Anatolia: biogeographical patterns. *Biogeographia*, 20: 81–94.

CRUCITTI, P. 1999b. Scorpion species diversity in southwestern Peloponnese, Greece (Scorpiones). *Contributions to Zoogeography and Ecology of the Eastern Mediterranean Region*, 1: 251–256.

CRUCITTI, P. & F. BUBBICO. 2001. Contributo alla conoscenza del genere *Euscorpius* Thorell, 1876 nel Peloponneso sud-occidentale (Scorpiones, Euscorpiidae). *Bolletino del museo civico di storia naturale di Venezia,* 52: 41–57.

CRUCITTI, P. & D. CICUZZA. 2001. Scorpions of Anatolia: ecological patterns. Pp. 225–234 *In*: Fet, V. & Selden, P.A. (eds). *Scorpions 2001. In memoriam Gary A. Polis*. British Arachnological Society, Burnham Beeches, Bucks.

CRUCITTI, P. & M. MALORI. 1998. Scorpioni (Scorpiones) del Pindo (Grecia). *Giornale italiano di Entomologia*, 9: 127–130.

ĆURČIĆ, B. P. M. 1972. Considerations upon the geographic distribution and origin of some populations in the genus *Euscorpius* Thorell (Chactidae, Scorpiones). *Rapport de la Commission International de la Mer Méditerranée*, Monaco, 21(3): 83–88.

FET, V. 1986. Notes on some *Euscorpius* (Scorpiones: Chactidae) from Greece and Turkey. *Rivista del Museo Civico di Scienze Naturali "Enrico Caffi"* (Bergamo), 9(1985): 3–11.

FET, V. 1989. A catalogue of scorpions (Chelicerata: Scorpiones) of the USSR. *Rivista del Museo Civico di Scienze Naturali "Enrico Caffi"* (Bergamo), 13(1988): 73–171.

FET, V. 1993. Notes on *Euscorpius mingrelicus* (Kessler, 1874) from the Caucasus. *Rivista del Museo Civico di Scienze Naturali "Enrico Caffi"* (Bergamo), 16(1993): 1–8.

FET, V. 1997. A note on *Euscorpius carpathicus* (Scorpiones: Chactidae) from the Crimea. *Journal of Arachnology*, 25(1): 106–108.

FET, V. 2000. Scorpions (Arachnida, Scorpiones) from the Balkan Peninsula in the collections of the National Museum of Natural History, Sofia. *Historia Naturalis Bulgarica*, 11: 47–60.

FET, V. 2003. The Crimean scorpion, *Euscorpius tauricus* (C.L. Koch, 1837) (Scorpiones: Euscorpiidae): an endemic species supported by mitochondrial DNA evidence. *Arthropoda Selecta* (Moscow), 11(4): 271–276.

FET, V. & M. E. BRAUNWALDER. 1997. On the true authorship and taxonomic history of *Euscorpius germanus* (C. L. Koch, 1837) (*nec* C. L. Koch, 1836; *nec* Schaeffer, 1766) (Scorpiones: Chactidae). *Bulletin of the British Arachnological Society*, 10(8): 308–310.

FET, V. & M. E. BRAUNWALDER. 2000. The scorpions (Arachnida, Scorpiones) of the Aegean area: current problems in taxonomy and biogeography. *Belgian Journal of Zoology*, 130 (Suppl. 1): 17–22.

FET, V., M. E. BRAUNWALDER & H. D. CAMERON. 2002a. Scorpions (Arachnida, Scorpiones) described by Linnaeus. *Bulletin of the British Arachnological Society*, 12(4): 176–182.

FET, V., B. GANTENBEIN, E. V. FET & V. POPA. 2002b. *Euscorpius carpathicus* (Linnaeus, 1767) from Romania (Scorpiones: Euscorpiidae): mitochondrial DNA data. *Biogeographica* (Paris), 78(4): 141–147.

FET, V., B. GANTENBEIN, AY. KARATAŞ & A. KARATAŞ (in press). An extremely low genetic divergence across the range of *Euscorpius italicus* (Scorpiones: Euscorpiidae). *Journal of Arachnology*.

FET, V., AY. KARATAŞ, E. V. FET & A. KARATAŞ. 2003a. [First data on the molecular phylogeny of *Euscorpius* (Scorpiones: Euscorpiidae) from Turkey]. *Zoologicheskii Zhurnal,* 82 (12): 1518–1521 (in Russian).

FET, V. & F. KOVAŘÍK. 2003. A record of *Euscorpius* (*Polytrichobothrius*) *italicus* (Herbst, 1800) (Scorpiones: Euscorpiidae) from Iraq. *Acta Societatis Zoologicae Bohemicae*, 67: 179–181.

FET, V., M. KUNTNER & B. SKET. 2001. Scorpions of Slovenia: a faunistic and biogeographical survey. Pp. 255–266 *In*: Fet, V. & P. A. Selden (eds.). *Scorpions 2001. In memoriam Gary A. Polis.* Burnham Beeches, Bucks: British Arachnological Society.

FET, V. & W. D. SISSOM. 2000. Family Euscorpiidae Laurie, 1896. Pp. 355–380 *in* Fet, V., W. D. Sissom, G. Lowe & M. E. Braunwalder. *Catalog of the Scorpions of the World* (1758–1998). New York, NY: New York Entomological Society, 690 pp.

FET, V. & M. E. SOLEGLAD. 2002. Morphology analysis supports presence of more than one species in the "*Euscorpius carpathicus*" complex (Scorpiones: Euscorpiidae). *Euscorpius*, 3: 1–55.

FET, V. & M. E. SOLEGLAD. (in press). Fauna and zoogeography of scorpions (Arachnida: Scorpiones) in Bulgaria. In, Fet, V. & A. Popov (eds). *Biogeography and Ecology of Bulgaria.* Dordrecht–Boston: Kluwer Academic Publishers.

FET, V., M. E. SOLEGLAD, B. GANTENBEIN, V. VIGNOLI, N. SALOMONE, E. V. FET & P. J. SCHEMBRI. 2003b. New molecular and morphological data on the "*Euscorpius carpathicus*" species complex (Scorpiones: Euscorpiidae) from Italy, Malta, and Greece justify the elevation of *E. c. sicanus* (C. L. Koch, 1837) to the species level. *Revue Suisse de Zoologie*, 110(2): 355–379.

GANTENBEIN, B., L. BÜCHI, M. E. BRAUNWALDER & A. SCHOLL. 1998. The genetic population structure of *Euscorpius germanus* (C. L. Koch) (Scorpiones: Chactidae) in Switzerland. Pp. 33–40. In: Selden, P. A. (ed.), Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997, 14–18 July, 1997.

GANTENBEIN, B., V. FET, M. BARKER & A. SCHOLL. 2000. Nuclear and mitochondrial markers reveal the existence of two parapatric scorpion species in the Alps: *Euscorpius germanus* (C. L. Koch, 1837) and *E. alpha* Caporiacco, 1950, stat. nov. (Scorpiones, Euscorpiidae). *Revue Suisse de Zoologie,* 107(4): 843–869.

GANTENBEIN, B., V. FET, C. R. LARGIADÈR & A. SCHOLL. 1999. First DNA phylogeny of *Euscorpius* Thorell, 1876 (Scorpiones: Euscorpiidae) and its bearing on taxonomy and biogeography of this genus. *Biogeographica* (Paris), 75(2): 49–65.

GANTENBEIN B., M. E. SOLEGLAD & V. FET. 2001. *Euscorpius balearicus* Caporiacco, 1950, stat. nov. (Scorpiones: Euscorpiidae): molecular (allozymes and mtDNA) and morphological evidence for an endemic Balearic Islands species. *Organisms, Diversity, and Evolution*, 1(4): 301–320.

GANTENBEIN, B., M. E. SOLEGLAD, V. FET, P. CRUCITTI & E. V. FET. 2002. *Euscorpius naupliensis* (C.L. Koch, 1837) (Scorpiones: Euscorpiidae): elevation to the species level justified by molecular and morphology data. *Revista Ibérica de Aracnologia*, 6: 13–43.

GUERRA, M. 1979. Catalogo degli scorpioni del genere *Euscorpius* conservati nella raccolta del Museo civico di scienze naturali di Bergamo. *Rivista del Museo Civico di Scienze Naturali "Enrico Caffi"* (Bergamo), Supplemento, 294 pp.

HADŽI, J. 1929. Skorpije Schmidtove zbirke. *Euscorpius italicus polytrichus* n. ssp. i ostale nove rase (Die Skorpione der Schmidt'schen Sammlung: *Euscorpius italicus polytrichus* n. ssp und andere neue Rassen). *Glasnik Muzejskega Drustva za Slovenijo*, (B), 10(1–4): 30–41 (in Serbo-Croatian).

HADŽI, J. 1930. Die europäischen Skorpione des Polnischen Zoologischen Staatsmuseums in Warszawa. *Annales Musei Zoologici Polonici*, 9(4): 29–38.

HADŽI, J. 1931. Der Artbildungsprozess in der Gattung *Euscorpius* Thor. *Archivio Zoologico Italiano*, 16(1–2): 356–362 (IX Congrès international de zoologie).

HADŽI, J. 1956. Justification for the introduction of subspecies into the genus *Euscorpius* Thor. *Bulletin Scientifique, Conseil des Académies de la R. F. P. Yugoslavie*, 1955, 2(2): 50–51.

HUBER, D., B. GANTENBEIN, V. FET & B. SCHERABON. 2001. *Euscorpius carpathicus* (L.) from Austria (Scorpiones: Euscorpiidae): phylogenetic position clarified by mitochondrial DNA analysis. Pp. 273–278 in: Fet, V. & P. A. Selden (eds.). *Scorpions 2001. In memoriam Gary A. Polis.* Burnham Beeches, Bucks: British Arachnological Society.

JACOB, A., B. GANTENBEIN, M. E. BRAUNWALDER, W. NENTWIG & C. KROPF. 2004a. Complex male genitalia (hemispermatophores) are not diagnostic for cryptic species in the genus *Euscorpius* (Scorpiones: Euscorpiidae). *Organisms, Diversity & Evolution*, 4(1–2): 59–72.

JACOB, A., I. GANTENBEIN, M. E. BRAUNWALDER, W. NENTWIG & C. KROPF. 2004b. Morphology and function of male genitalia (spermatophores) in *Euscorpius italicus* (Euscorpiidae, Scorpiones): Complex spermatophore structures enable safe sperm transfer. *Journal of Morphology*, 260(1): 72–84.

KINZELBACH, R. 1975. Die Skorpione der Agäis. Beiträge zur Systematik, Phylogenie und Biogeographie. *Zoologische Jahrbücher, Abteilung für Systematik*, 102(1): 12–50.

KOCH, C. L. 1837a. Die Arachniden. Nürnberg: C. H. Zeh'sche Buchhandlung, 3(6): 105–115.

KOCH, C. L. 1837b. Die Arachniden. Nürnberg: C. H. Zeh'sche Buchhandlung, 4(1-5): 1–108.

KOCH, C. L. 1850. Scorpionen. *In* Uebersicht des Arachnidensystems. Nürnberg: C. H. Zeh'sche Buchhandlung, 5: 86–92.

KOMPOSCH, C., B. SCHERABON & V. FET. 2001. Scorpions of Austria. Pp. 267–272 *in*: Fet, V. & P. A. Selden (eds.). *Scorpions 2001. In Memoriam Gary A. Polis.* Burnham Beeches, Bucks: British Arachnological Society.

KOVAŘÍK F. & V. FET. 2003. Scorpion *Euscorpius (Euscorpius) tergestinus* (C. L. Koch, 1837) (Scorpiones: Euscorpiidae) in central Bohemia. *Acta Societatis Zoologicae Bohemicae,* 67: 189–192.

KRAEPELIN, K. 1899. Scorpiones und Pedipalpi. *In* F. Dahl (ed.), *Das Tierreich*. Herausgegeben von der Deutschen Zoologischen Gesellschaft. Berlin: R. Friedländer und Sohn Verlag, 8 (Arachnoidea): 1–265.

KRITSCHER, E. 1992. Erstnachweis von Skorpionen auf den Maltesischen Inseln. *Euscorpius carpathicus candiota* (Birula, 1903) (Arachn.: Scorp.: Chactidae) auf Malta und Gozo. *Annalen des Naturhistorischen Museums in Wien*, (B), 93: 185–188.

KRITSCHER, E. 1993. Ein Beitrag zur Verbreitung der Skorpione im östlichen Mittelmeerraum. *Annalen des Naturhistorischen Museums in Wien*, (B), 94/95: 377–391.

LACROIX, J.-B. 1991a. Faune de France; Arachnida: Scorpionida. 5e note. Sub-genus (*Euscorpius*) Thorell, 1876. *Arachnides*, 8: 17–36.

LACROIX, J.-B. 1991b. Faune de France (Arachnida: Scorpionida). 6e note. 2A. Sub-genus (*Polythrichobothrius*) Birula, 1917. *Arachnides*, 10: 14–25.

LACROIX, J.-B. 1995. *Euscorpius (E.) mingrelicus* Kessler, 1876 en Turquie anatolienne (Arachnida: Scorpionida). *Arachnides*, 26: 4–6.

MOLTENI, M. G., BONACINA, A., C. ROSELLA. & G. VAILATI. 1983. Aspetti anatomici ed istologici dell' organo parassiale di *Euscorpius germanus* (C. L. Koch) (Scorpiones). *Rivista del Museo Civico di Scienze Naturali "Enrico Caffi"* (Bergamo), 6: 125–154.

SALOMONE, N., V. VIGNOLI, F. FRATI. & F. BERNINI. 2004. Phylogenetic relationships between the sibling species *Euscorpius tergestinus* and *E. sicanus* (Scorpiones, Euscorpiidae) as inferred from mitochondrial and nuclear sequence data. *Abstracts, 16th International Congress of Arachnology. 2–7 August 2004, Gent, Belgium.*

SCHERABON, B. 1987. Die Skorpione Österreichs in vergleichender Sicht unter besonderer Berücksichtigung Kärntens. *Carinthia II. / Naturwiss. Beiträge zur Heimatkunde Kärntens / Mitteilungen des Naturwissenschaftlichen Vereins für Kärnten. Klagenfurt, Verlag des Naturwissenschaftlichen Vereins für Kärnten* 45: 78–158.

SCHERABON, B., B. GANTENBEIN, V. FET, M. BARKER, M. KUNTNER, C. KROPF & D. HUBER. 2000. A new species of scorpion from Austria, Italy, Slovenia and Croatia: *Euscorpius gamma* Caporiacco, 1950, stat. nov. (Scorpiones: Euscorpiidae). Pp. 253–262 *in* Gajdoš, P. & S. Pekár (eds.). *Proceedings of the 18th European Colloquium of Arachnology, Stará Lesná, 1999. Ekológia (Bratislava),* 19, Suppl. 3.

SOLEGLAD, M. E. & V. FET. 2003. High-level systematics and phylogeny of the extant scorpions (Scorpiones: Orthosterni). *Euscorpius*, 11: 1–175

SOLEGLAD, M. E. & W. D. SISSOM. 2001. Phylogeny of the family Euscorpiidae Laurie, 1896: a major revision. Pp. 25–111 *in* V. Fet & P. A. Selden (eds.). *Scorpions 2001. In Memoriam Gary A. Polis.* Burnham Beeches, Bucks: British Arachnological Society.

STATHI, I. & MYLONAS, M. 2001. New records of scorpions from the central and eastern Mediterranean area: biogeographical comments, with special reference to the Greek species. Pp. 287–296 *In*: Fet,

V. & P. A. Selden (eds). *Scorpions 2001. In memoriam Gary A. Polis.* British Arachnological Society, Burnham Beeches, Bucks.

STATHI, I., A. PARMAKELIS & M. MYLONAS. 2004. The evolutionary footsteps of scorpions in the Aegean. *Abstracts, 16th International Congress of Arachnology. 2–7 August 2004, Gent, Belgium.*

STOCKWELL, S. A. 1992. Systematic observations on North American Scorpionida with a key and checklist of the families and genera. *Journal of Medical Entomology*, 29(3): 407–422.

TERUEL, R., V. FET, V. & L. F. DE ARMAS. 2004. A note on the scorpions from the Pirin Mountains, southwestern Bulgaria (Scorpiones: Buthidae, Euscorpiidae). *Euscorpius*, 14: 1–11.

THORELL, T. 1876. On the classification of scorpions. *Annals and Magazine of Natural History*, 4(17): 1–15.

VACHON, M. 1963. Remarques sur l'utilisation, en systématique, des soies sensorielles (trichobothries) chez les Scorpions du genre *Euscorpius* Thorell (Chactidae). *Bulletin du Muséum National d'Histoire Naturelle, Paris,* (2), 34: 347–354 (Date on the cover 1962; published February 22, 1963).

VACHON, M. 1975. Recherches sur les Scorpions appartenant ou déposés au Muséum d'Histoire naturalle de Genève. I. Contribution à une meilleure connaissance des espèces et des sous-espèces de Scorpions du genre "*Euscorpius*" Thorell, 1876 (Fam. des Chactidae). *Revue Suisse de Zoologie*, 82(3): 629–645.

VACHON, M. 1981. Remarques sur la classification sous-spécifique des espèces appartenant au genre *Euscorpius* Thorell, 1876 (Scorpionida, Chactidae). *Atti della Società Toscana di Scienze Naturali, Memorie, (B),* 88 (suppl.): 193–203. (Comptes-rendus 6ème Colloque d'arachnologie d'expression Française (Colloque International Européen), 1981 Modena-Pisa).

VACHON, M. & M. JAQUES. 1977. Recherches sur les Scorpions appartenant ou déposés au Muséum d'Histoire naturelle de Genève. 2. Contribution à la connaissance de l'ancienne espèce *Scorpius banaticus* C. L. Koch 1841, actuellement considérée comme synonyme de *Euscorpius carpathicus* (Linné 1767) (Fa. des Chactidae). *Revue Suisse de Zoologie*, 84(2): 409–436.

VALLE, A. 1975. Considerazioni intorno alle sottospecie di *Euscorpius carpathicus* (L.) (Scorpiones, Chactidae). *L'Ateneo Parmense, Acta Naturalia*, 11(1): 209–234.

VALLE, A., M. T. BERIZZI, M. BONINO, R. GORIO, E. GIMMILLARO-NEGRI & A. PERCASSI. 1971. Le popolazioni italiane di *Euscorpius germanus* (C. L. Koch) (Scorpiones, Chactidae). *Atti dell'VIII Congresso Nazionale Italiano di Entomologia* (Firenze, 4-7 Settembre 1969): 93–96.

VIGNOLI V., N. SALOMONE, T. CARUSO & F. BERNINI. 2004. The *Euscorpius tergestinus* (C. L. Koch, 1837) (Scorpiones: Euscorpiidae) complex in Italy: biometrics on sympatric cryptic species. *Abstracts, 16th International Congress of Arachnology. 2–7 August 2004, Gent, Belgium.*

Euscorpius — **Occasional Publications in Scorpiology. 2004, No. 17**

The platypus of a scorpion: the genus *Pseudochactas* Gromov, 1998 (Scorpiones: Pseudochactidae)

Victor Fet [1], Michael E. Soleglad [2] and Alexander V. Gromov [3]

[1]Department of Biological Sciences, Marshall University, Huntington, West Virginia 25755-2510, USA
[2]P. O. Box 250, Borrego Springs, California 92004, USA
[3] Institute of Zoology, Akademgorodok, Almaty, 480060, Republic of Kazakhstan

---

Summary

Soleglad & Fet (2001, 2003a, 2003b) demonstrated that *Pseudochactas* Gromov, 1998 is the most basal member of Recent scorpions (infraorder Orthosterni), which also shares some characters with the Carboniferous fossil scorpion family Palaeopisthacanthidae. This genus belongs to a separate family, superfamily, and parvorder of extant scorpions. Major phylogenetic features of the lineage are discussed, as well as biogeography of this unique relict. This veritable "platypus of a scorpion" deserves further study in all aspects.

Introduction

The monotypic genus *Pseudochactas* was described by Gromov (1998) from Uzbekistan and Tajikistan based on the type species, *Pseudochactas ovchinnikovi* (Fig. 1) as the sole representative of the monotypic family Pseudochactidae. Soleglad & Fet (2001) established a separate orthobothriotaxic "Type D" for *Pseudochactas*, indicating its exclusive and basal position among all extant scorpions.

Systematics and Phylogeny

Gromov (1998: 1003) observed that "It is possible that the representative of this new family (Pseudochactidae) stands close to the common ancestor of all these families [the Recent scorpions]". As Soleglad & Fet (2001) demonstrated based on trichobothrial patterns, *Pseudochactas* is certainly a basal member of Recent scorpions, and also shows significant affinity in some characters with the Carboniferous fossil scorpion family Palaeopisthacanthidae. Soleglad & Fet (2001) established a special trichobothrial Type D for *Pseudochactas* in addition to Types A, B, and C proposed by Vachon (1974).

Lourenço (2000) placed Pseudochactidae in his superfamily Chaeriloidea, without any justification. Soleglad & Fet (2001, 2003a, 2003b) demonstrated that *Pseudochactas* is the most basal member of Recent scorpions (infraorder Orthosterni) (Fig. 2), and also shares some characters with the Carboniferous fossil scorpion family Palaeopisthacanthidae. Soleglad & Fet (2003b) created four parvorders (taxonomic category between infraorder and superfamily) for extant scorpions (all included in infraorder Orthosterni). The monotypic parvorder Pseudochactida, established by Soleglad & Fet (2003b), includes the monotypic superfamily Pseudochactoidea, also established by these authors. The diagnosis applicable to this parvorder and superfamily, as well as to the family Pseudochactidae, is as follows:

Synapomorphies. Orthobothriotaxy type D; dorsal edge of cheliceral movable finger without basal denticle; ventral surface of leg tarsus with two sub-median rows of spinules; transverse anterior carinae developed on metasomal segments I–III; stigma small and oval in shape. Important Symplesiomorphies. Two ventral median carinae of metasomal segment V; sternum of type 1, lacking horizontal compression; median denticle row (MD) of pedipalp chelal finger arranged in oblique groups; pedipalp chela exhibits "8-carinae" configuration; pedipalp patella exhibits "7-carinae" configuration; ventral edge of cheliceral movable finger crenulated; dorsal edge of cheliceral movable finger with single subdistal denticle; ventral surface of cheliceral fixed finger with denticles.

Biogeography and Ecology

The genus *Pseudochactas* was found only in two restricted localities in the mountains of Central Asia (Figs. 3–4): it was first collected by Sergei Ovchinnikov

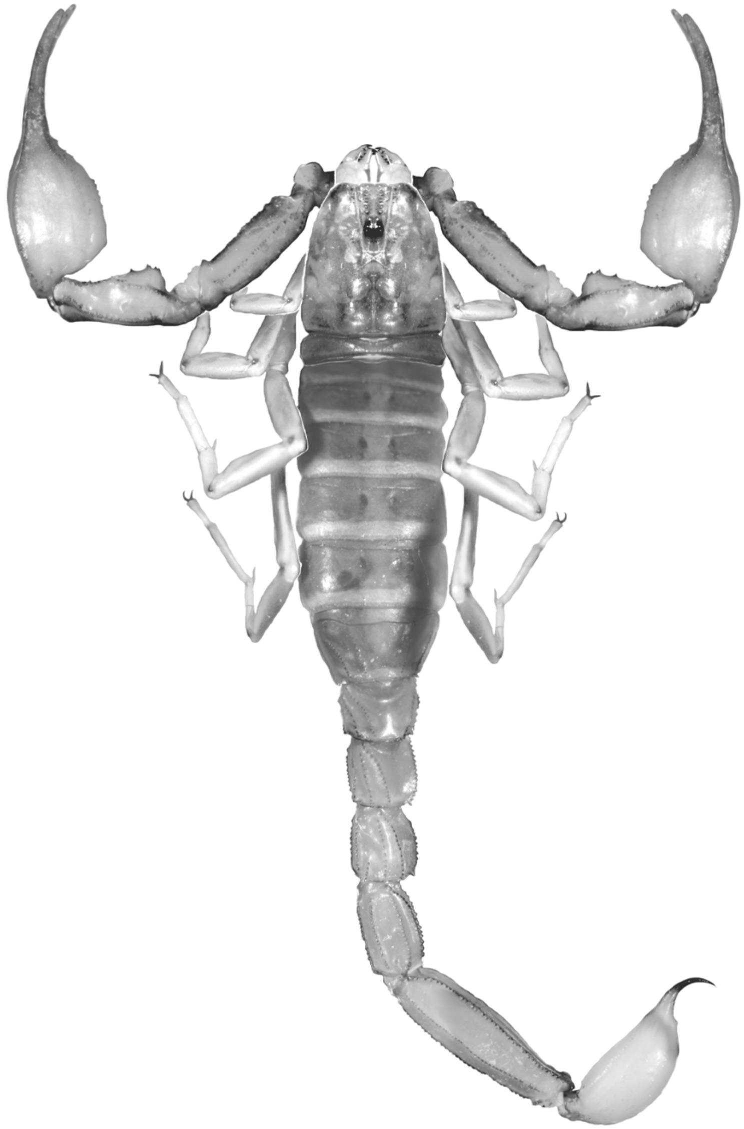


Figure 1: *Pseudochactus ovchinnikovi* Gromov, 1998, female (after Soleglad & Fet, 2003)

(Fig. 5) and Oleg Lyakhov in the Surkhandarya Region of southern Uzbekistan (Babatag Mountains), and by Sergei Zonstein in Gandzhino, eastern Tajikistan. The relict character of *Pseudochactas* distribution could be due to its preservation in mild-climate, low-mountain depressions of Babatag and Gandzhino ranges, with desert surroundings at lower altitudes (Figs. 6–8).

Ecologically, this is not a desert scorpion; it actively forages on wet mud along the temporary waterways, and likely spends most of dry season in hibernation (V. Fet & A. Gromov, pers. observation, Dukhone, Babatag Mountains, Surkhandarya Region, Uzbekistan, May 1–4, 2002).

Judging from their ancestral position in scorpion phylogeny, the parvorder and superfamily could have been established in Permian/Triassic, We cannot speculate on whether this lineage was localized or widespread since there are no fossils belonging to Pseudochactida, and the parvorder is represented by a single monotypic genus.

Although fossil Pseudochactida are absent, inference from other orthostern fossils Soleglad & Fet (2003b) discussed the possible Pangaean origin (Permian to Triassic time) of four extant scorpion parvorders. Two of these partvorders (Buthida and Iurida) still enjoy the world domination, albeit in Iurida with significant disjunctions possibly due to extinctions (superfamilies Iuroidea, Chactoidea). At the same time, two other parvorders (Pseudochactida and Chaerilida) currently survive only in Asia, each with a single relict genus, *Pseudochactas* and *Chaerilus*. Through Cretaceous, many animal taxa persisted as relicts while

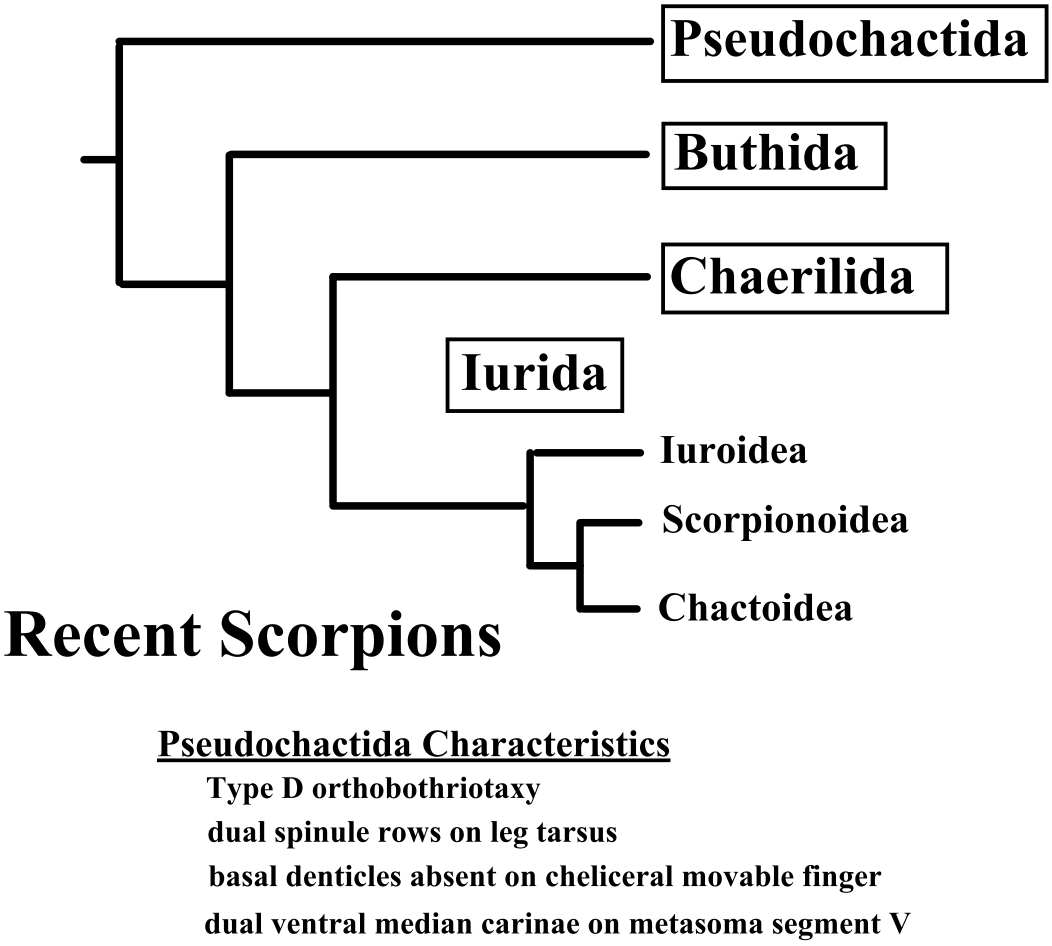


Figure 2: Phylogenetic position of parvorder Pseudochactida (after Soleglad & Fet, 2003b).

other perished during the global restructuring of ecosystems (Zherikhin, 1978). The parvorder Pseudochactida—the most primitive extant group of scorpions—appears to have survived in such a relict condition.

Landmasses on which scorpions could have evolved were available in the vicinity of modern Tajik Depression for over 200 Ma. The core of Asia was assembled during the late Paleozoic; already in the Early Carboniferous, the Tajik depression was part of a geographically continuous east-west elongate territory extended from north China westward to the Scythian-Turanian platform (Heubeck, 2001). In Jurassic, most of Central Asia was a dry land, with increasingly more arid climate. In Cretaceous, modern Kizylkum desert was covered by sea transgression while the southwestern part of the Tajik Depression was dominated by the coastal landscapes with lagoons and river deltas (Kryzhanovsky, 1965). Seasonality was much less expressed, mountains were low and arid, with major tectonic unheaval that created Pamiro-Alai starting only in the Neogene (late Eocene); at the same time real deserts emerged (Sinitsyn, 1962; Atamuradov, 1994; Kazenas & Baishashov, 1999). Therefore, taxa such as *Pseudo-chactas* could be relicts who survived extensive restructuring of ecosystmes in the end of Cretaceous (Zherikhin, 1978) on the islands of Tethys.

With the discovery of *Pseudochactas*, we now know that four rather than three scorpion lineages survived the K-T extinctions. Modern superfamilies of scorpions are known from the Upper Cretaceous of Burma (Chaeriloidea; Santiago-Blay et al., 2004) and Brazil (Scorpionoidea; Soleglad & Fet, 2003b; and possibly Chactoidea; F. Menon & P. Selden, pers. comm).

The Cenozoic aridization and mountain buildup provided ample opportunities for further isolation of relict taxa. *Pseudochactas* could represent a remnant of littoral fauna of the receded Tethys Ocean, captured in mountain depression by Tertiary uplift. Many important floral elements of littoral origin are found in low

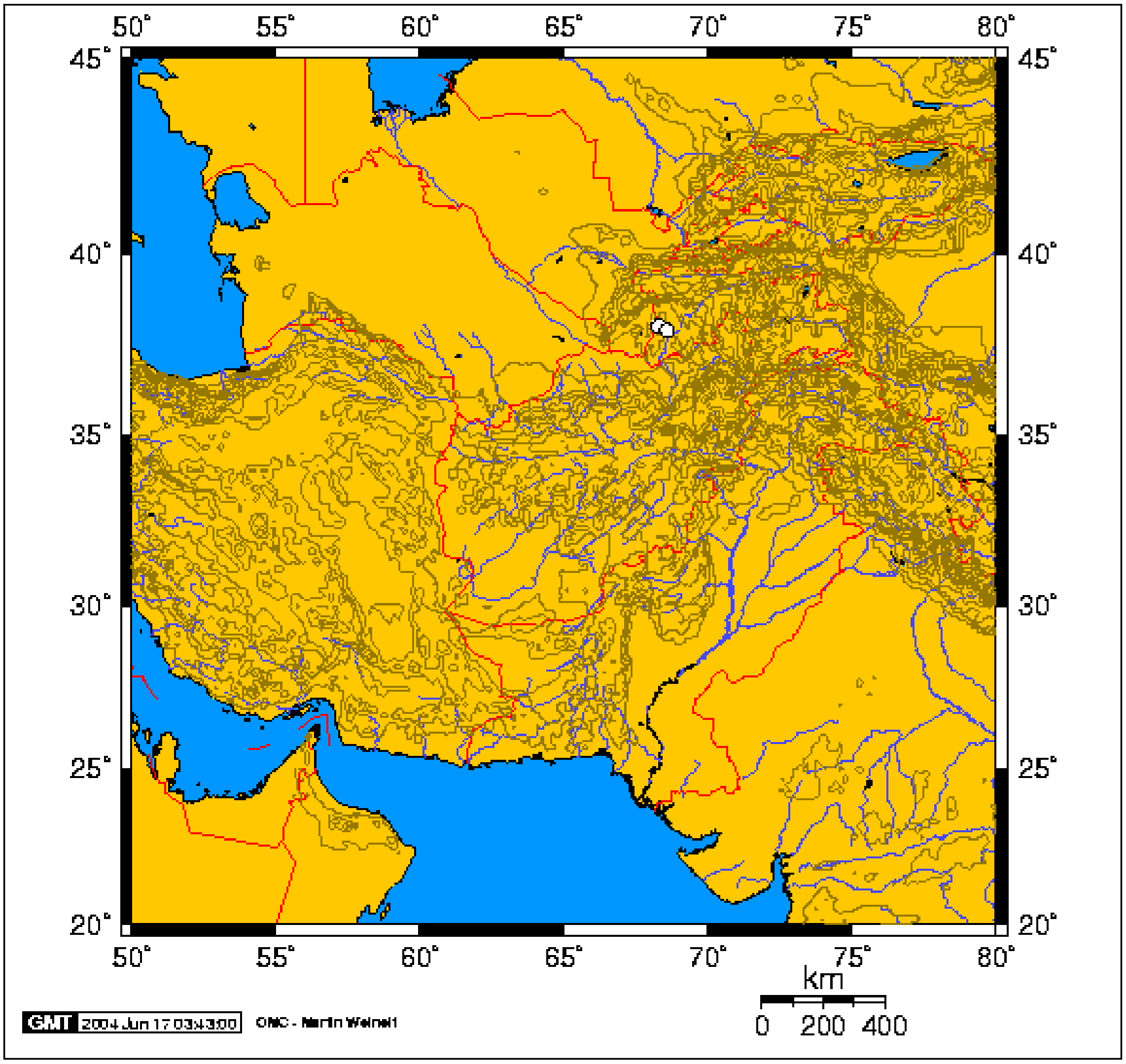


Figure 3: Geographic localities of *Pseudochactas* in southern Central Asia.

mountains of Uzbekistan and Tajikistan (Kamelin, 1979). Although not so ancient as *Pseudochactas* is assumed to be, other relict taxa are known in southern Central Asia and are hypothesized to have evolved on the islands of the eastern Tethys during Upper Cretaceous or Lower Tertiary, e. g. a monotypic darkling beetle genus *Allotadzhikistania* (Coleoptera: Tenebrionidae) or many endemic species of *Dorcadion* (Coleoptera: Cerambycidae) (Kryzhanovsky, 1965).

Modern climate in Tajik Depression is one of the mildest in Southern Central Asia, with the longest frostless period (Korzhenevsky, 1960; Bogdanova et al., 1968). This feature, along with availability of shelters in cracks and under tree roots, could have contributed to survival of this unique, relict scorpion lineage.

This veritable "platypus of a scorpion" deserves further study in all aspecs. In fact, comparison with the bizarre, relict platypus does not do any justice to *Pseudochactas* since the first known fossil Monotremata are Cretaceous (Rich et al., 2001) while Pseudochactida should have split from all other scorpion parvorders well before Triassic (Soleglad & Fet, 2003b).

Acknowledgements

David Neff was instrumental in performing high quality SEM micrography of *Pseudochactas* published in Soleglad & Fet (2003b). We thank Sergei Ovchinnikov and Yuri Marusik for sending the current photograph of Sergei Ovchinnikov. V.F.'s and A.G.'s travel to Uzbekistan in search of the *Pseudochactas* in 2002 was supported by the National Geographic Society Research and Exploration Fund grant 7001-01, and was facilitated by the enthusiastic hospitality and help of Alex and Elena Kreuzberg.

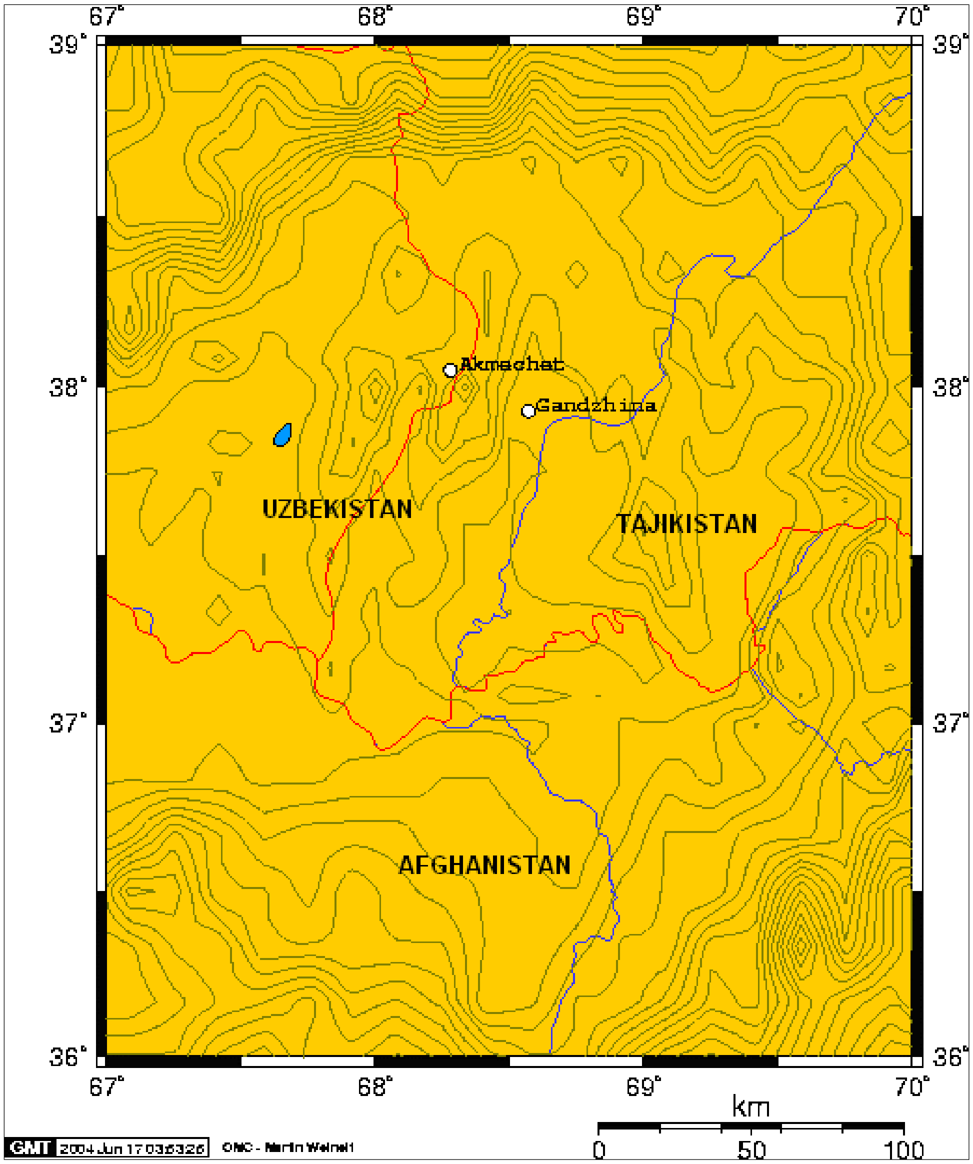


Figure 4: Geographic localities of *Pseudochactas* in southern Central Asia (close-up).

References

ATAMURADOV, KH. I. 1994. Paleogeography of Turkmenistan. Pp. 49–64 *In*, Fet, V. & Kh. I. Atamuradov (eds.). *Biogeography and Ecology of Turkmenistan.* Kluwer Academic Publishers, Dordrecht.

BOGDANOVA, N.M., E.M. MURZAEV & V.M. CHUPAKHIN. 1968. [Central Asian mountains and plateaus]. Pp. 368-392 In: *Srednyaya Aziya* [*The Central Asia*]. Moscow: Nauka, 484 pp.

FET, V. 2000f. Family Pseudochactidae Gromov, 1998. P. 426 *in* Fet, V., W. D. Sissom, G. Lowe & M. E. Braunwalder. *Catalog of the Scorpions of the World (1758–1998).* New York, NY: New York Entomological Society.

GROMOV, A.V. 1998. A new family, genus and species of scorpions (Arachnida, Scorpiones) from southern Central Asia. *Zoologichesky Zhurnal*, 77(9): 1003–1008 (in Russian, English summary). English translation: *Russian Journal of Zoology*, 1998, 2(3): 409–413.

HEUBECK, C. 2001. Assembly of central Asia during the Middle and Late Paleozoic. *Memoir 194: Paleozoic and Mesozoic Tectonic Evolution of Central and Eastern Asia: From Continental

Figure 5: The arachnologist Sergei Ovchinnikov (Bishkek, Kyrgyzstan), the namesake and one of the first collectors of *Pseudochactas ovchinnikovi* (photo by Yuri Marusik, 2004).

Assembly to Intracontinental Deformation. The Geological Society of America, pp. 1–22.

KAMELIN, R.V. 1979. *Kukhistaskii raion gornoi Srednei Azii. Botaniko-geograficheskii analiz* [*The Kuhistan District of Montane Central Asia, A Botanical Geographical Analysis*]. Komarov Readings, No. 31. Leningrad: Nauka, 116 pp. (in Russian).

KAZENAS, V.L. & B.U. BAYSHASHOV. 1999. [Geological history and genesis of fauna of Kazakhstan and adjacent territories in epochs of development of mammals and anthophilous insects]. In: YASHCHENKO, R.V. (ed.), *Tethys Entomological Research*, 1: 5-46 (in Russian).

KORZHENEVSKY, N.L. 1960. *Priroda Srednei Azii* [*The Nature of Central Asia*]. Tashkent: Izdatelstvo SAMGU, 211 pp. (in Russian).

KRYZHANOVSKY, O.L. 1965. *Sostav i proiskhozhdeniye nazemnoi fauny Srednei* Azii [*The Composition and Origin of the Terrestrial Fauna of Middle Asia (Based Primarily on Coleopteran Material)*]. Moscow & Leningrad: Nauka, 420 pp. (in Russian). English translation, 1980. New Delhi, India (Smithsonian Institution Translation Program).

LOURENÇO, W.R. 2000. Panbiogeographie, les familles des scorpions et leur repartition geographique. *Biogeographica* (Paris), 76(1): 21–39.

RICH, T.H., P. VICKERS-RICH, P. TRUSLER, T.F.FLANNERY, R. CIFELLI, A. CONSTANTINE, L. KOOL, & N. VAN KLAVEREN. 2001. Monotreme nature of the Australian Early Cretaceous mammal *Teinolophos*. *Acta Palaeontologica Polonica*, 46(1): 113–118.

SANTIAGO-BLAY, J.A., V. FET, M.E. SOLEGLAD & S. ANDERSON. 2004. A new genus and subfamily of scorpions from Cretaceous Burmese amber

Figure 6: Habitat of *Pseudochactas* in Uzbekistan: Babatag Mountains, view of Surkhandarya Valley separating Uzbekistan and Tajikistan.

Figure 7: Habitat of *Pseudochactas* in Uzbekistan: Babatag Mountains, Dukhone sai (ravine), Chagam uchastok (area) of Shurchi leskhoz (Forest Management District).

Figure 8: Habitat of *Pseudochactas* in Uzbekistan (Dukhone).

(Scorpiones: Chaerilidae). *Revista Ibérica de Aracnología*, 9: 3–14.

SINITSYN, V.M. 1962. *Paleogeografiya Azii* [*Paleogeography of Asia*] . Izd. AN SSSR, Moscow–Leningrad, 268 pp. (in Russian).

SOLEGLAD, M.E. & V. FET. 2001. Evolution of scorpion orthobothriotaxy: a cladistic approach. *Euscorpius*, 1: 1–38.

SOLEGLAD, M.E. & V. FET. 2003a. The scorpion sternum: structure and phylogeny (Scorpiones: Orthosterni). *Euscorpius*, 4: 1–34.

SOLEGLAD, M.E. & V. FET. 2003b. High-level systematics and phylogeny of the extant scorpions (Scorpiones: Orthosterni). *Euscorpius*, 11: 1–175.

VACHON, M. 1974. Étude des caractères utilisés pour classer les familles et les genres de Scorpions (Arachnides). 1. La trichobothriotaxie en Arachnologie, Sigles trichobothriaux et types de trichobothriotaxie chez les Scorpions. *Bulletin du Muséum National d'Histoire Naturelle, Paris,* (3), 140 (Zool. 104), mai-juin 1973: 857–958.

ZHERIKHIN, V.V. 1978. *Razvitie i smena melovykh i kainozoiskikh faunisticheskikh kompleksov (trakheinye i khelitserovye)* [*Development and Succession of the Cretaceous and Cenozoic Faunistic Complexes (Tracheata and Chelicerata)*]. Nauka: Moscow, 200 pp. (in Russian).